



## SYMPOSIUM

# A Solution Strategy to Include the Opening of the Opercular Slits in Moving-Mesh CFD Models of Suction Feeding

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**Synopsis** The gill cover of fish and pre-metamorphic salamanders has a key role in suction feeding by acting as a one-way valve. It initially closes and avoids an inflow of water through the gill slits, after which it opens to allow outflow of the water that was sucked through the mouth into the expanded buccopharyngeal cavity. However, due to the inability of analytical models (relying on the continuity principle) to calculate the flow of fluid through a cavity with two openings and that was changing in shape and size, stringent boundary conditions had to be used in previously developed mathematical models after the moment of the valve’s opening. By solving additionally for the conservation of momentum, computational fluid dynamics (CFD) has the capacity to dynamically simulate these flows, but this technique also faces complications in modeling a transition from closed to open valves. Here, I present a relatively simple solution strategy to incorporate the opening of the valves, exemplified in an axisymmetrical model of a suction-feeding sunfish in ANSYS Fluent software. By controlling viscosity of a separately defined fluid entity in the region of the opercular cavity, early inflow can be blocked (high viscosity assigned) and later outflow can be allowed (changing viscosity to that of water). Finally, by analyzing the CFD solution obtained for the sunfish model, a few new insights into the biomechanics of suction feeding are gained.

## Introduction

### Unidirectional suction feeding: the importance of opening of the caudal valves

The motion of water can carry along suspended food items considerably better than less viscous and less dense fluids such as air (Rubenstein and Koehl 1977). Nearly all aquatic feeders exploit these physical properties of water when capturing prey (Herrel et al. 2012). Many of these are suction feeders: they generate a flow of water into a rapidly expanding oral cavity. This feeding mechanism overcomes the tendency of prey to be pushed away by the bow wave of the approaching predator (Dullemeijer 1994; Van Wassenbergh et al. 2010). It is therefore not surprising that suction is used to capture prey, often even highly evasive ones, by many aquatic vertebrates (e.g., Lauder 1983) as well as by some predatory plants (Singh et al. 2011; Llorens et al. 2012).

Inside the head of aquatic anamniotes, distinct intra-oral entities of volume are often defined. The buccal volume starts posterior of the mouth’s aperture, continues medial of the gill arches, and ends at the entrance of the esophagus. Sometimes this cavity is referred to as the buccopharyngeal or oropharyngeal cavity (e.g., Liem 1984), where “buccal” or “oral” only refers to the portion lying anterior to the gill arches, and “pharyngeal” refers to the portion medial of the gill arches (Lauder 1983). In fish and gill-bearing salamanders, the intra-oral volume further consists of the left and right opercular cavities (parabranchial cavities in elasmobranchs) that form the space between the gills and their external covers. In ray-finned fishes, these external covers are formed by the opercular series of bones (opercula and subopercula) and more ventrally by the branchiostegal membranes (consisting mainly of skin

supported by long slender bones: the branchiostegal rays, attached to the hyoid).

It is generally accepted that it is sufficient to consider only a single functional unit as the expanding cavity during powerful suction feeding (e.g., van Leeuwen 1984; Muller and Osse 1984; Sanford and Wainwright 2002; Van Wassenbergh et al. 2005) as the gill filaments then separate so that relatively large openings form through which water can pass with (probably) minimal resistance from the buccal cavity to the opercular cavities (Osse 1969; Alexander 1974; Muller et al 1982). Note, however, that not all of the sucked water will exit via one of the two opercular cavities, as often a large opening is formed between the hyoid arch and the first gill arch, the so-called hyoid shunt (van Leeuwen 1984).

This exit of water through the operculo-branchiostegal slits (from this point onward referred to as the opercular slits) is of central importance to suction-feeding performance (van Leeuwen 1984). It allows fish to engulf a volume of water much greater than the summed expansion of their buccal and opercular cavities (van Leeuwen, 1984; Higham et al. 2006; Kane and Higham 2014). Depending on the speed of swimming during suction feeding, the opening of the opercular slits generally occurs shortly before (e.g., a fast swimmer *Salmo gairdneri*; van Leeuwen 1984) or shortly after (e.g., a stationary suction feeder *Clarias gariepinus*; Van Wassenbergh et al. 2005) reaching maximal oral gape. As this instant of peak gape generally coincides with the instant at which the prey passes the aperture of the mouth (Muller and Osse 1984), an important part of the process of capturing prey (namely the intra-oral transport of the prey while closing the mouth) takes place with opened caudal valves. Based on *in-vivo* flow visualization of two species of centrarchid fishes (largemouth bass and bluegill sunfish), Day et al. (2005) estimated that a volume of water of about twice the expanded volume enters the mouth during the capture of prey. Furthermore, the estimated volume of water sucked in by *Salmo gairdneri* before the opening of the opercular slits was estimated to be only about 18% of the total volume of water flowing through the mouth (van Leeuwen 1984). In addition, suction-feeding fish are able to maintain an inflow of water until the mouth is almost closed (Day et al. 2005; Higham et al. 2005), which likely decreases the prey's chances of escaping. This distinguishes fishes as unidirectional suction feeders from bidirectional suction feeders (e.g., snake-necked turtles: Aerts et al. 2001; pipid frogs: Carreño and Nishikawa 2010; post-metamorphic salamanders: Deban et al. 2001; seals: Marshall et al. 2014) that

need to gently expel the sucked water through the narrowly opened mouth afterward, during the phase when the buccopharyngeal cavity slowly compresses to its initial volume.

### From analytical to computational models of suction feeding

Despite the importance of the water sucked into the mouth after the opercular valves have opened, the final phase of suction feeding cannot be easily incorporated into the existing mathematical models of the hydrodynamics of suction feeding. Analytical models, such as the expanding cone model (Muller et al. 1982; Muller and Osse 1984), multi-cone models (Van Wassenbergh et al. 2006; Bishop et al. 2008), multi-elliptical-cylinder models (e.g., Drost and van den Boogaart 1986; Aerts et al. 2001; Van Wassenbergh et al. 2005; Roos et al. 2009), calculate the velocities of flow based on the principle of continuity (i.e., the incompressibility of water) applied to expanding volumes with a single opening: the aperture of the mouth. As soon as the opercular slits open, the equations of continuity alone are insufficient to determine in what direction and how fast the water is flowing. To surpass this limitation, Muller et al. (1982) fixed the velocity of the water entering the mouth's aperture (as a new boundary condition) from the moment the opercular slits open. Ideally, however, the outflow dynamics could be simulated also if the equations of conservation of momentum of the water (Euler equations for inviscid flow or the Navier–Stokes equations for viscous flow) are solved. This type of simulation can be performed using the method of computational fluid dynamics (CFD). However, with the help of modern, versatile, commercial CFD-simulation software it remains particularly challenging to tackle the dynamic transition from a closed to an open valve (e.g., Ramajo and Nigro 2008; Song et al. 2010; Annerel et al. 2011). One of the reasons for this is that the appearance of a new connection between fluid zones (in this case between the opercular cavity and the water outside of the fish) requires a change in boundary conditions, and hence the set-up of a new simulation. To model the full cycle of combustion in a car engine, for example, Ramajo and Nigro (2008) solved the flow inside the cylinders and the exhaust ducts as two separate domains using commercial CFD software, while their custom-written FORTRAN functions fed solution of one domain as initial conditions in the other domain at the appropriate time. However, most industrial or biomedical engineering applications focus either on the opening

or closing process, thereby leaving a tiny opening in the valve at the beginning or end of the simulation (e.g., Srikanth and Bhasker 2009; Song et al. 2010; Wang et al. 2010; Dawy et al. 2013). A second factor of complexity is that action of the valve typically takes place in complex geometries with highly compliant walls involving strong fluid-structure interactions (Yoganathan et al. 2004; Annerel et al. 2011).

Moving-mesh CFD models (i.e., simulations with moving or shape-changing components in the domain) are of great promise for the analysis of suction-feeding biomechanics (Van Wassenbergh and Aerts 2009) and already have proved very useful for testing fundamental principles in the biomechanics of suction feeding, such as the effect of the relative increase in viscous forces in the suction flows generated by suction feeders of small size (Drost et al. 1988; Roos et al. 2011; Yaniv et al. 2014). These studies used models with symmetry about the long axis of the fish, but fully 3D morphologies also can be used to dynamically simulate suction caused by programmatically prescribed head-surface deformations in CFD software (e.g., ANSYS Fluent) as shown in a recent study on suction feeding by a giant salamander (Heiss et al. 2013). The latter study demonstrated that recent advances in 3D-surface reconstruction of animals based on laser scanning or X-ray micro-computed tomography can be integrated with this type of biomechanical analysis.

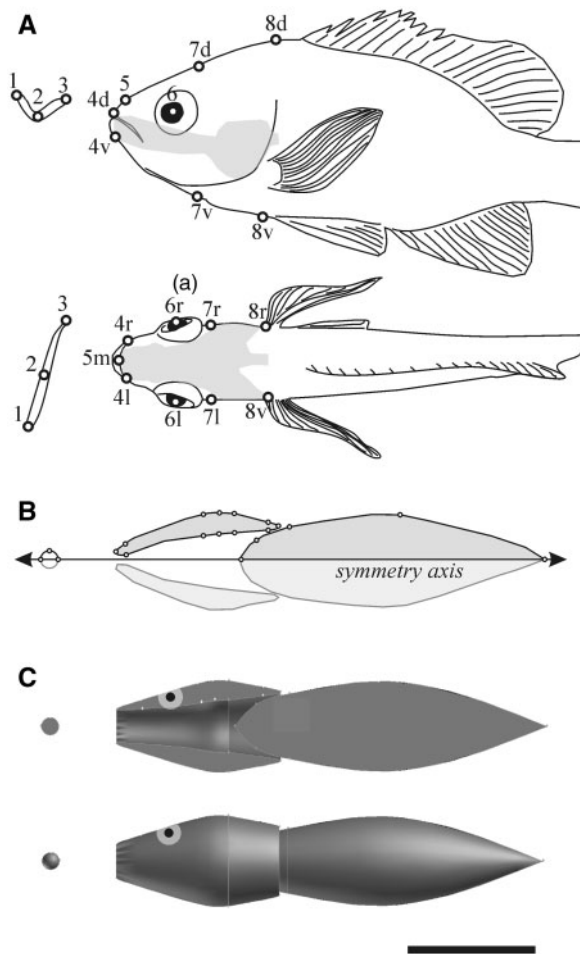
## Methods

In this article, I present a strategy to incorporate opercular valve outflow in moving-mesh CFD models of suction feeding. Doing so, my objective is not to aim for the most accurate possible model for the hydrodynamics of the opening of the opercular valves using state-of-the-art approaches in fluid-structure interaction modeling (e.g., Annerel et al. 2011), but rather to provide a means to allow the basic dynamics of a full expansion-compression cycle in a unidirectional suction feeder to be analyzed with the smallest possible adjustments compared to the existing moving-mesh CFD models mentioned above. The model will build upon an earlier version of an axially symmetric model in ANSYS Fluent of a suction-feeding sequence by the sunfish *Lepomis gibbosus* (total length = 75.7 mm) capturing a freely suspended bloodworm (Van Wassenbergh and Aerts 2009) (see Supplementary Video 1).

The first step in defining the model is to construct the model's initial geometry. The geometry of the sunfish model is based on the external and internal

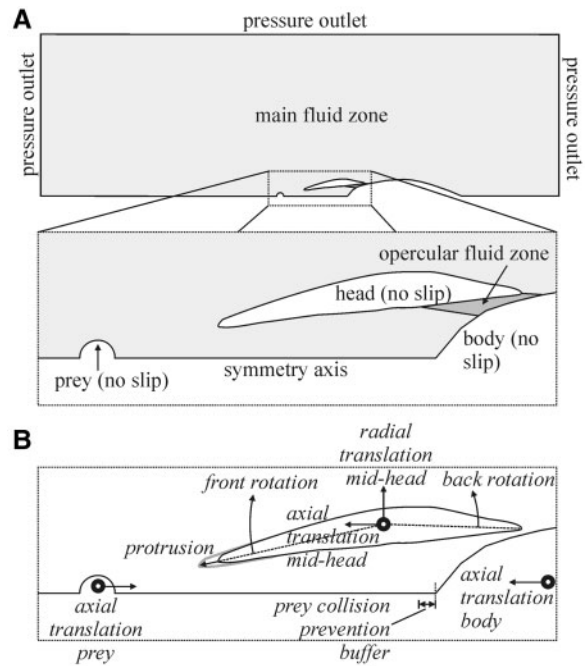
dimensions of the head at three positions along its length (Fig. 1A): at the front (aperture of the mouth), middle (just posterior of the eyes), and back (at the level of the dorsal part of the opercular slits) of the head. Spline curves fitted to control points at the external and internal contours at these three cross-sections formed the head of the model (Fig. 1B). The initial, internal dimensions of the jointed buccopharyngeal and opercular cavities were determined, based on dorsoventral and lateral X-ray images of a specimen of which the cavity of the mouth was filled with a radio-opaque, barium sulfate solution (see also Figure 9 of Roos et al. 2009). The body of the fish was modeled as a spindle of which the shape and size is controlled by five landmarks (Fig. 1B). A small gap of about 0.3 mm separated the surfaces of the head from those of the body at the level of the opercular slits. The prey was modeled as a sphere of 1-mm radius of which the distance to the center of the mouth matches that of the bloodworm at the onset of expansion of the head (Fig. 1). This geometrical set-up was performed in Gambit 2.4.6 (Ansys Inc., Lebanon, PA, USA).

A second step is to define the geometry of the fluid domain, to mesh this domain, and to assign boundary conditions. The key of the present solution strategy lies in this section. Two lines were constructed between control nodes on the head and the body at the opercular gap (Fig. 2). This allows defining two fluid zones: (1) the main fluid zone surrounding head and body, and filling the buccopharyngeal cavity, and (2) the opercular fluid zone filling the narrow margin at the opercular opening (Fig. 2). The physical properties assigned to the main fluid zone were that of normal water at 20°C (density 998.2 kg/m<sup>3</sup>, viscosity 1.003 mPa s). To prevent flow through the opercular slits into the buccopharyngeal cavity at the instants when the opercular valves are closed in reality, the initial viscosity of the fluid in the opercular zone was set at a value 200 times higher (roughly the viscosity between that of water and that of honey). At the instant at which the valves are supposed to open, this initially much more viscous liquid changed its viscosity to that of water through a user-defined function (DEFINE\_PROPERTY) as soon as the average pressure in the cells of the opercular fluid zone became positive in the previous time step. This opercular pressure was one of the output variables calculated after each time step (DEFINE\_EXECUTE\_AT\_END). Declaring this variable as a global, static variable in the C-language user-defined function script allows it to be called for by the DEFINE\_PROPERTY macro assigned to control the viscosity of the opercular



**Fig. 1** Geometry of the axially symmetric model of suction feeding in the sunfish *Lepomis gibbosus*. Outlines of the sunfish and prey (bloodworm) in (A) show the position of the numbered anatomical landmarks from which position coordinates were determined for each high-speed video frame. The basic geometry of the model parameterized by the positions of 20 control points is shown in (B). Graphical 3D-reconstructions of the model after rotation about the symmetry axis are illustrated both mid-sagittally (C, top) and in external view (C, bottom). Scale bar, 20 mm.

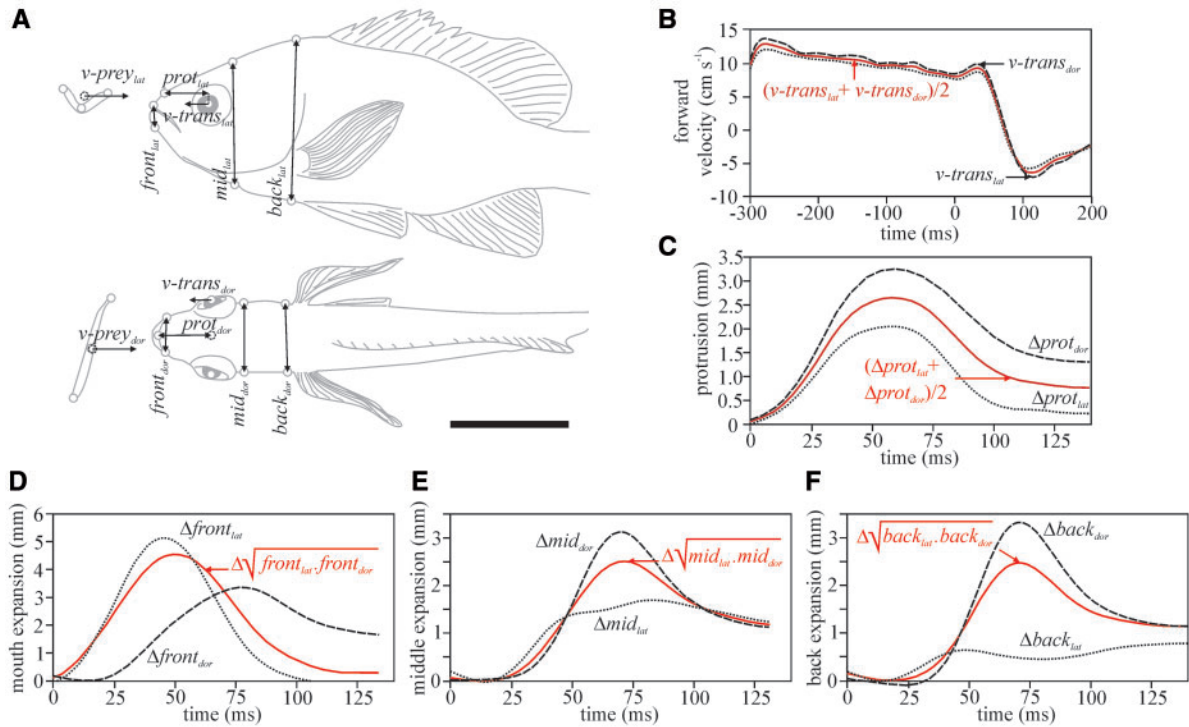
cell zone. The reasoning behind the choice of the criterion of opening the opercular slits when pressure inside the buccal cavity becomes positive is that the opening of the valve is considered a predominantly passive, flow-driven phenomenon (Hughes and Shelton 1958). The remaining boundary conditions were the same as in previous moving-mesh suction models (Van Wassenbergh and Aerts 2009; Heiss et al. 2013; Yaniv et al. 2014): pressure outlets at the outer boundaries, and the no-slip condition enforced at the solid boundaries (head, body, and prey). The model was meshed with 100,060 triangles (node spacing of 60  $\mu\text{m}$  in the mouth cavity) using Gambit. Further information on user-defined function in ANSYS Fluent can be found in the ANSYS



**Fig. 2** CFD domain indicating the boundary conditions (A) and kinematic input variables included in the grid deformation functions (B). Note that the fluid zone is subdivided into two parts in order to assign different physical properties to the fluid adjacent to the gill cover. The internal boundary of the opercular fluid zone (by approximation) transects the branchial arches, but this choice was arbitrary.

Fluent UDF Manual (e.g., version 14.5 published in 2012).

A third step is to prescribe the motion of the model to match the high-speed video as closely as possible. The kinematics of capturing prey were determined on the basis of 23 anatomical landmarks (11 in lateral view, 12 in dorsal view; Fig. 1A) from which 2D-coordinates were measured frame-by-frame on the high-speed video images. Landmarks numbered 4, 7, and 8 (Fig. 1A) allowed the calculation of the instantaneous height and width at the front, middle, and back of the head (Fig. 3A). The anterior–posterior displacement of the eye (landmark 6 in Fig. 1A) was used to calculate the axial translational velocity of the fish (Fig. 3B). The anterior–posterior displacement of the average of the coordinates of three landmarks on the bloodworm (two tips and the approximate center; numbered 1, 2, and 3 in Fig. 1A) was used to calculate the instantaneous velocity of the prey. Collision of the prey with the body was avoided by defining a minimal distance from prey to body, and overwriting the calculated velocity of the prey with the axial velocity of the fish as soon as this threshold was exceeded (see prey-collision-prevention buffer



**Fig. 3** Kinematics of the modeled prey-capture event. The meaning of the kinematic variables derived from the anatomical landmarks (Fig. 1A) is illustrated in (A). Smoothed kinematic profiles from corresponding lateral-view (dotted lines) and dorsal-view variables (dashed lines) are given in each graph, together with either the arithmetic (B, C) or geometric mean (D–F) (thin full line; online in red). The expansion variables shown in graphs (C–F) are indicated by  $\Delta$ , meaning that these are instantaneous distances minus the distance at rest. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

in Fig. 2B). Protrusion of the jaw was calculated as the distance between the tip of the premaxilla (landmark 5 in Fig. 1A) and the eye (or the central point between the eyes in dorsal view). To reduce manual coordinate-digitization noise, raw data were subjected to a fourth-order Butterworth filter (low-pass cut-off frequency of 20 Hz) designed to cause no phase shift (Winter 2004). First-order central differences in time were used to calculate velocities from displacements. To allow parameterization of the model's kinematic input, sinusoidal functions were used to fit each profile with separate parameters (offset, amplitude, and wavelength) defining the expansive and compressive parts of the profiles. Despite the differences between the kinematic profiles of width and height (Fig. 3D–F), only a single radial expansion profile can be used as model input per cross-section due to axial symmetry of the model. The best approximation of the instantaneous cross-sectional area is to take the geometric mean (i.e., square root of the product) of instantaneous width and height and use it as the instantaneous radius of the model (Fig. 3D–F). Due to the camera's perspective and scaling imperfections, slight differences were also observed in the kinematic profiles

of variables that could be measured both in lateral and dorsal view: velocity of the prey, velocity of the fish (Fig. 3B), and protrusion (Fig. 3C). The parametric input profiles were therefore fit to the arithmetic means of the lateral-view and dorsal-view variables (Fig. 3B, C).

Now that the kinematics of expansion, protrusion, and swimming are known (Fig. 3), they can be implemented in ANSYS Fluent to move the mesh. There are 6 degrees of freedom in the model (Fig. 2B): (1) axial translation of the head and body, (2) radial translation of the mid-point of the head, (3) rotation of the anterior part of the head about the head's mid-point, (4) rotation of the posterior part of the head about the mid-point of the head, (5) protrusion of the mouth, and (6) axial translation of the prey. Using relative rotation of the parts of the head allows a more natural flapping of the opercular valve. The independent radial expansions at the tip of the jaw and the tip of the opercular region (Fig. 3D,F) were converted into rotations relative to the mid-point of the head. All of these motions are controlled within the CFD-solver software by a user-defined function (DEFINE\_GRID\_MOTION) that was compiled, loaded, and assigned to the

appropriate zones in the dynamic mesh panel of ANSYS Fluent.

Some of the simulated motions were not prescribed *a priori*, but are caused by the suction flows that were generated. Flow solutions were used to move the prey by the above-mentioned user-defined function that summed the forces exerted at the surface of the prey (pressure forces and shear forces in the axial direction), and solved for acceleration using Newton's second law of motion (assuming a density equal to that of the surrounding water). Also the forward acceleration of the fish was solved in this function by summing the hydrodynamic forces exerted at the surfaces of the head and body (and assuming a mass of 5 g for the measured sunfish). This forward acceleration during suction can be regarded as a fulfilment of the laws of the conservation of momentum when a volume of water is accelerated posteriorly (see Muller and Osse 1984; Aerts et al. 2001). To do so, the fish was first accelerated to its observed velocity of swimming (0.1 m/s; Fig. 3B) during the first 30 ms of the simulation, was moved at constant velocity for another 5 ms, after which the axial acceleration of the fish was calculated from Newton's second law of motion.

The model was solved for 2400 time steps of 0.1 ms with the buccal expansion starting at time 0 (time step 400). The pressure-based solver (chosen to obtain fast-converging solutions) was used with a node-based Green-Gauss gradient treatment. The latter achieves a higher accuracy in unstructured triangular grids compared to the other options in ANSYS Fluent. The first-order implicit unsteady formulation option was used in the simulation because moving-mesh simulations (see above) currently only work 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 momentum equations. The pressure-velocity coupling was solved using the robust, default SIMPLE scheme. The latter is a discretization method that uses a relationship between velocity and pressure corrections to enforce conservation of mass and to obtain the pressure field. Using a larger time step of 0.4 ms did not substantially influence the solution (e.g., only 1% difference in peak sub-ambient pressure in the opercular fluid zone, and 0.1% difference in peak speed of flow at the mouth), indicating that 0.1 ms was more than sufficiently small. The software was set to move mesh nodes (spring-based smoothing algorithm; spring constant factor = 0.5; Laplace node relaxation = 1) and re-mesh (make new mesh for triangles smaller than  $2 \times 10^{-7}$  m and larger than  $2 \times 10^{-4}$  m)

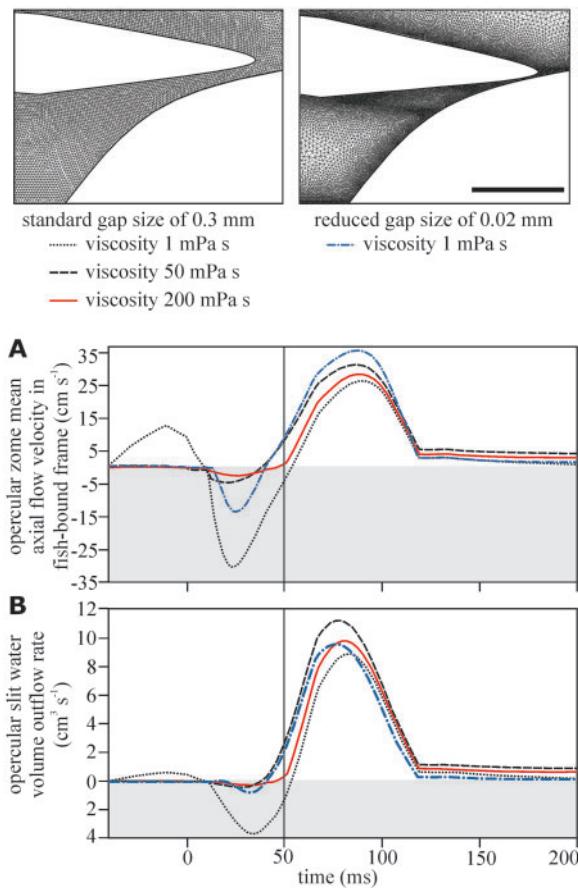
after every time step to adjust the internal nodes in response to the motion of the boundaries prescribed in the mesh-motion user-defined function. A mesh-convergence analysis was performed by comparing the solution with that of a much coarser mesh (9509 triangles, node spacing in the mouth cavity 2.66 times larger), which showed a 9% lower peak amplitude of opercular pressure, and a 0.4% higher peak of flow velocity at the mouth's aperture (both peaking at the same time). This suggests that the used mesh was sufficiently fine.

A large set of output variables were calculated at the end of each time step by a user-defined function (DEFINE\_EXECUTE\_AT\_END) hooked to Fluent. This set includes the peak and mean instantaneous velocities of flow (axial and radial), the volumetric rate of inflow or outflow, and mean pressure at the level of the mouth's aperture and the opercular opening, and instantaneous requirements of the expansion for power and work.

## Results and discussion

### Output and validation of the model

The controlled modification of the viscosity in the opercular zone was successful in avoiding almost all of the flow that would otherwise enter the opercular cavity through the small gap at the gill slits of the sunfish model. In Fig. 4, the model's output of flow in the opercular cell zone is compared with a case in which there was no increased viscosity during the sub-ambient pressure stage of suction feeding. The difference is drastic: for example, peak speed of inflow decreases from 0.30 m/s, resulting in a back-flow volume of 12% of the peak buccal volume, to 0.025 m/s with only about 1% of peak buccal volume sucked through the gill slits due to the 200-fold increase in viscosity (Fig. 4). In theory, this small amount of inflow could be eliminated by further increasing the viscosity. However, this caused the CFD solver to iterate to a diverging instead of a converging solution at the time of switching from the increased to the normal viscosity of water, probably due to the excessively abrupt change in the physical properties of the system. The same problem also appeared when another, at first sight logical, modeling strategy was tried to cancel out opercular inflow: fixing the flow velocity in the opercular fluid zone (set to take the axial velocity of the fish), followed by a switch to a normally resolved velocity also failed to be solved by Fluent. Yet, if necessary, the remaining small amount of opercular inflow can be eliminated by narrowing the gap.



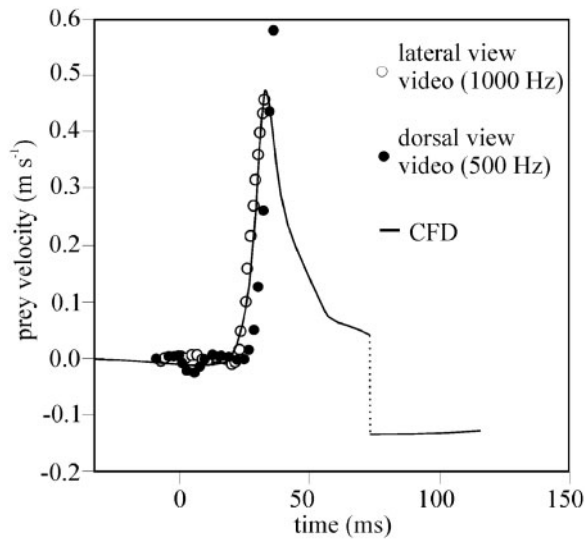
**Fig. 4** Performance of different settings for initial viscosity of the opercular fluid in the CFD model in preventing inflow during suction (shaded area), and comparison with a model using only a strongly decreased size of the opercular gap (mesh zoomed in on the opercular gap shown at the top). The dotted line represents the models' output without modified viscosity ( $\mu = 1.003 \times 10^{-3} \text{ Pa s}$ ), the dashed line with the initial viscosity increased 50 times ( $\mu = 50 \times 10^{-3} \text{ Pa s}$ ), the full line (online in red) with the velocity increased 200 times ( $\mu = 200 \times 10^{-3} \text{ Pa s}$ ), and the dash-dot line (online in blue) with the narrowed opercular gap without modified viscosity. Scale bar; 2.5 mm. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

The strength of combining a moderately narrow gap with locally controlled fluid viscosity to prevent opercular inflow over the more traditional type of CFD-simulation of the functioning of the valve by keeping a very tiny gap is further illustrated by a simulation performed with the opercular gap decreased from 0.3 mm to 0.02 mm (Fig. 4). Models with the original, larger gap, combined with the locally increased viscosity, outperformed the narrow-gap model with unmodified viscosity in preventing this inflow. The presented modeling strategy does not necessitate the local refinement of the mesh (and hence increase in computational time) required for such a narrow gap. Furthermore, control over the

closed-to-open transition is simpler and also more versatile since it is independent of the expansion kinematics at the back of the head. If, for example, skin flaps at the edges of the opercular bones are still closing the opercular slits while the gill covers have started to abduct (a situation common during respiration in fishes; Schmidt-Nielsen 1997), this situation can be modeled without including the actual motion of these laps of skin.

The accuracy of the model in predicting suction-feeding performance of the sunfish was assessed in two ways: First, the velocity of the bloodworm measured from the high-speed video (average of landmarks 1–3 of Fig. 1A) was compared with the calculated velocity of the prey in the CFD-simulation. The model performed well, as shown by the comparison displayed in Fig. 5. Second, the timing of opening of the opercular slit predicted by the model (time of transition from negative to positive pressure at the opercular region) was compared with that observed on the video images. The latter showed opening to occur approximately at the frame of a simulation flow time of 48 ms, while the model predicted opening to occur at 50.9 ms (Fig. 6). Consequently, these two tests show that the hydrodynamics of capturing prey are simulated with an accuracy that can be considered as high, given the model's geometrical and kinematical simplifications.

Primary model output for flow patterns and pressure (Fig. 1A–B) generally corresponded well with the experimental data from the literature (see also Supplementary Videos 2 and 3). Two-dimensional velocities of flow in the earth-bound frame in front of the mouth of 0.1 m/s have been calculated from visualization of flow for *L. gibbosus* (Lauder and Clark 1984). More recent particle image velocimetry studies on a closely related and morphologically similar species, *Lepomis macrochirus*, showed velocities reaching 0.5 m/s (Fig. 2 in Day et al. 2005). Pressures (down to  $-300 \text{ Pa}$ ) were relatively low in magnitude compared to measured values for sunfish (generally below  $-1000 \text{ Pa}$ ; Lauder 1980), but the small, unattached, dead prey used for the video may not have elicited the most powerful suction. However, the model can still be improved in several ways: First, there is still a reasonably large amount of water blown out of the mouth during the phase of buccal compression (Fig. 7A, frames 80 and 100 ms; Fig. 7F, negative velocities at the mouth between  $t = 0.05$  and  $0.10 \text{ s}$ ), which probably does not occur in reality (Lauder and Clark 1984). This may either be caused by an overestimated velocity of buccal compression, not having just the tips of the upper

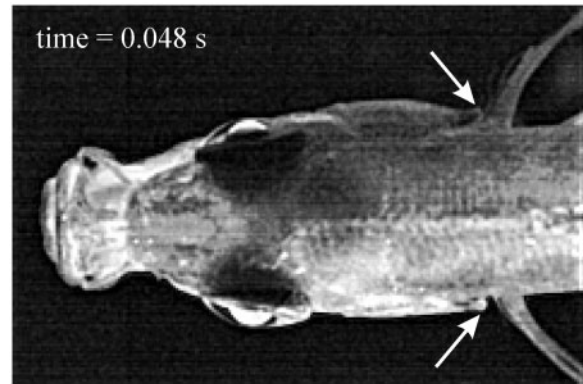


**Fig. 5** Comparison of the predicted velocity of the prey from CFD and the observed velocity of the bloodworm (using the average position of landmarks 1, 2, and 3 of Fig. 1A).

and lower jaws moving straight to each other to close the mouth, or having an outflow opening that was too narrow. The axial symmetry of the current model makes it unusable for answering certain functional-morphological questions. For example, the shape of the mouth is known to have an important effect on the external flow field (e.g., Skorczewski et al. 2012) and this shape generally differs from being perfectly planar and circular, at least during some stage of suction feeding. Also biomechanical analyses of other aspects, such as the lifting of the rostrum from the substrate to draw water under the body to assist benthic feeding in rays (Dean and Motta 2004; Wilga et al. 2012), the ventral deviation of the flow behind the aperture of the mouth toward the depressing hyoid apparatus as observed in catfish (Van Wassenbergh et al. 2007), or the dominating ventral outflow of water anterior of the first gill arch as noted for rainbow trout (van Leeuwen 1984) call for full 3D models. Yet, the present approach to modeling the opening of the opercular valve by using a programmatically controlled change in viscosity for separate fluid entities near the valves, is by no means restricted in application to axisymmetric models.

### Insights into the mechanics of suction-feeding

The strength of moving-mesh CFD models in biomechanical analyses is that virtually all aspects of the dynamics of the hydrodynamic action can be extracted from the solution during post-processing (e.g., Young et al. 2009; Zheng et al. 2013). This allows analysis of aspects of suction mechanics that



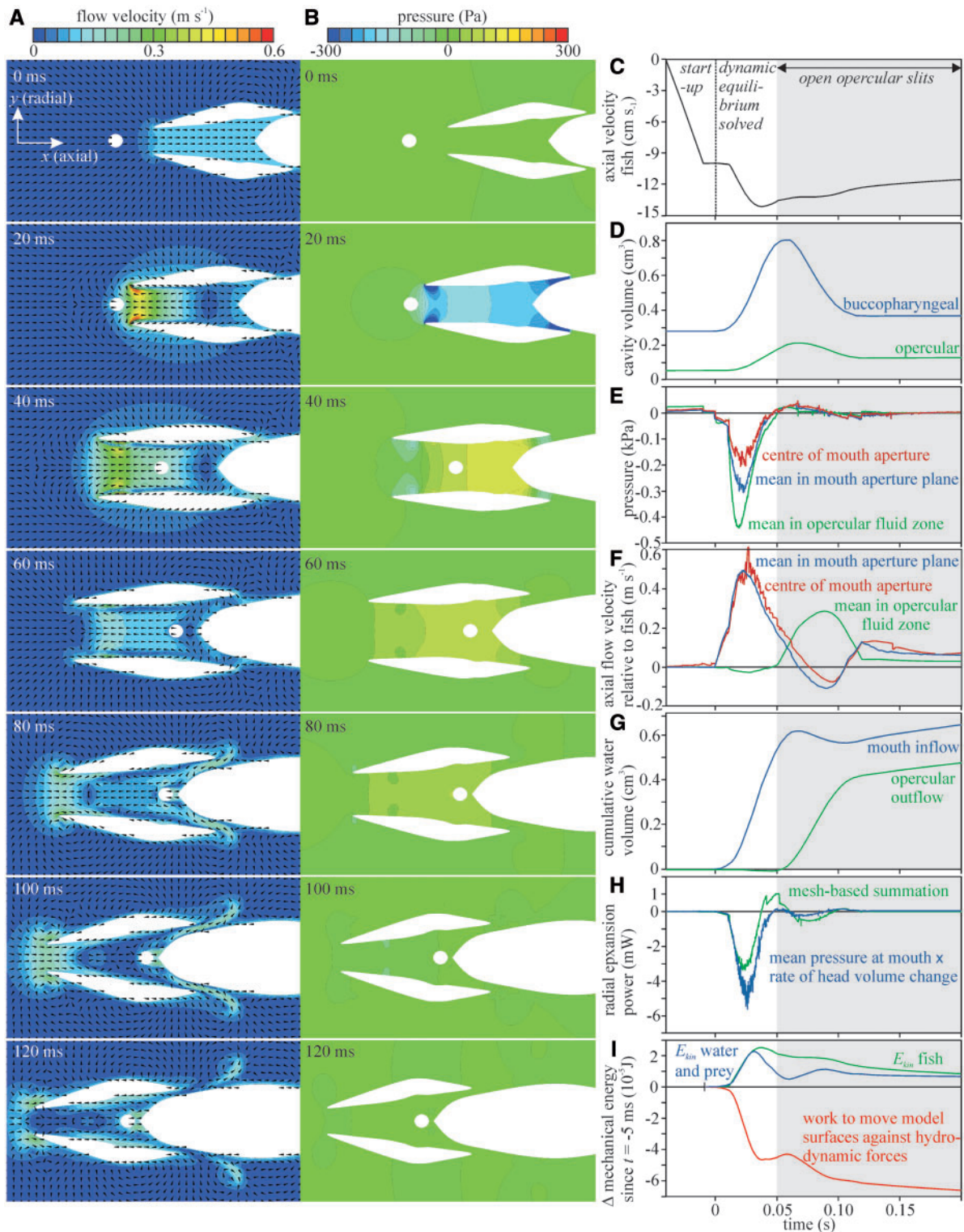
**Fig. 6** First video frame from the modeled prey-capture sequence that shows opening of the gill slits (flow time = 48 ms). The timing of this event is predicted reasonably well by the model; the calculated time at which the opercular pressure becomes positive was 50.9 ms).

are not possible, or are too complex to solve analytically. Below, I discuss two of these aspects that can help to better understand the behavior and functional morphology of suction feeders.

Suction feeders suck themselves forward during the generation of suction (Muller et al. 1982; Aerts et al. 2001). Despite the fact that the approaching motion of the suction feeder is a very important factor in determining prey-capture performance (e.g., van Leeuwen and Muller 1984; Holzman et al. 2008; Kane and Higham 2011; Tran et al. 2010), this aspect of suction-feeding mechanics has rarely been quantified (but see Aerts et al. 2001). The cause of this acceleration is (negative) pressure force pointing to the outside (i.e., into the water) of the forward-facing surfaces at the posterior end of the mouth's cavity (corresponding to the anterior part of "body" in the present model; Fig. 2). This causation can also be viewed in terms of the conservation of momentum (Aerts et al. 2001): the total momentum (mass  $\times$  velocity) cannot change in a closed system in which no external forces and/or moments apply. The suction-induced backward momentum of the water will therefore be countered by forward momentum of the fish.

The present CFD model showed that a relatively low-effort suction act (relatively low peak pressure of  $-0.3$  kPa) by a sunfish accelerates the fish from  $0.1$  to over  $0.14$  m/s during the course of the time when suction pressure was generated. As noted by Muller and Osse (1984), this effect will be larger in fish with a small body mass relative to suction power. The extreme example of animals making use of this effect are snake-necked turtles (Chelodina) in which only the extendible neck and head are taking





**Fig. 7** Results from the CFD model. The magnitudes of flow velocity (colors, see legend on top) and directions (arrowheads), and gauge pressures (colors, see legend on top) are given in respectively (A) and (B) for 20 ms intervals of the simulation (see also Supplementary Videos 2 and 3). Temporal profiles of several important variables are given in the right column of graphs (C-I). The gray background indicates the phase of the opened opercular slits in these graphs. Note that the opercular fluid zone refers to the region as defined in Fig. 2A. Mean values from the plane of the mouth's aperture are taken from cell data for the anteriormost 5% of the head. In (I) the work required from the feeding musculature is defined as negative, while outputs of work (kinetic energy increases) are defined as positive.

all the forward momentum and shoot forward to overtake agile prey. Relatively large-headed, ambush-hunting fishes such as stonefish (Synanceiidae) or anglerfishes (*Antennarius*; Grobecker and Pietsch 1979) also make special use of this rapid forward acceleration due to suction, probably assisted by their locomotor system. The present modeling strategy provides unique opportunities to study this aspect of mechanics of suction feeding in these fishes.

One of the consequences of this momentum-conservation effect is that the generated power by the suction-feeder's musculature during the capture of prey is converted into a change in kinetic energy of the sucked water, as well as a change in kinetic energy of the fish. In other words, as shown here for the sunfish model (Fig. 7I), only approximately half of the work done during suction was converted into suction flows as observed from the earth-bound frame of reference. A question that comes to mind is then: why many suction feeders do not bypass this effect, for example, by holding onto the substrate with their fins. In this way, there is no closed system (consisting of the water and the suction feeder) where the conservation of momentum applies because external, ground-reaction forces are in play, with the consequence that a larger fraction of muscle power results in acceleration of water (and of prey). There are two disadvantages to suction from a fixed position: First, performing the same expansion without forward movement is energetically more costly, so that expansion of the head inevitably will be performed at lower speed from a fixed, standstill position. This comes down to the difference between the extremes of "compensatory suction" (i.e., wrapping the oral cavity volume around a parcel of water that remains motionless in the earth-bound frame of reference) and "inertial suction" (i.e., accelerating the water in the earth-bound frame of reference) as defined by Van Damme and Aerts (1997), or, similarly, to the effect of "translation pressure" that reduces the expansion load as described by Muller et al. (1982). Second, by involving higher velocities and accelerations of flow (relative to the earth-bound frame) the prey will be alerted earlier by the generated disturbances to flow in the case of fixed-position suction feeding (Holzman and Wainwright 2009; Gemmell et al. 2013).

Second, CFD can help validate assumptions used in calculations based on empirical measurements. An important variable is suction power, which is typically defined as the power needed to expand the head against the hydrodynamic resistance (Van Wassenbergh et al. 2005). This variable can be

linked back to the morphology and contractile mechanics of the muscles that generate suction, as muscle power is considered the main factor limiting the speed of head expansion (Aerts et al. 1987; Van Wassenbergh et al. 2005; Carroll and Wainwright 2009). The requirement for instantaneous suction power can be estimated by multiplying instantaneous sub-ambient pressure inside the mouth's cavity and the instantaneous rate of change in the volume of the head (Carroll and Wainwright 2009). However, this estimate relies on several assumptions, as discussed in more detail by Van Wassenbergh et al. (2015). Ideally, local pressures and rates of expansion at infinitesimally narrow, cross-sectional subdivisions of volume in the mouth cavity should be used for this calculation, but usually (for practical reasons) only pressure at a single point is measured in the experiment. The comparison of a calculation of the power of radial expansion power based on the finite volume mesh from the present model (pressure and viscous force in the radial direction  $\times$  radial velocity, then summing this for each element of surface mesh element in the head) with a single pressure point, for example, mean pressure in the region of the mouth (Fig. 7E, blue curve) multiplied by the time derivative of the change in head volume (based on Fig. 7D, sum of both curves) is shown in Fig. 7H. There is definitely a general resemblance between the two curves, but it should be taken into account that both the timing (0.024 ms vs. 0.028 ms) and the magnitude (3 mW vs. 4.5 mW) of the peak can vary substantially because of the assumptions of the calculations based on experimental data.

In conclusion, incorporating the opening of the opercular slit and dynamically solving the motion of prey and fish due to suction add significantly to the prospective of CFD as a tool for studying the functional morphology and biomechanics of suction feeders. The option to change the kinematic or morphological input parameters of the present model has not been explored in this article, but potentially can be used to explore the mechanical consequences of the wide variety of morphology and feeding kinematics observed in nature.

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## Supplementary data

Supplementary Data available at *ICB* online.

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