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Hydrodynamic modelling of aquatic suction performance and intra-oral pressures: limitations for comparative studies

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The magnitude of sub-ambient pressure inside the bucco-pharyngeal cavity of aquatic animals is generally considered a valuable metric of suction feeding performance. However, these pressures do not provide a direct indication of the effect of the suction act on the movement of the prey item. Especially when comparing suction performance of animals with differences in the shape of the expanding bucco-pharyngeal cavity, the link between speed of expansion, water velocity, force exerted on the prey and intra-oral pressure remains obscure. By using mathematical models of the heads of catfishes, a morphologically diverse group of aquatic suction feeders, these relationships were tested. The kinematics of these models were fine-tuned to transport a given prey towards the mouth in the same way. Next, the calculated pressures inside these models were compared. The results show that no simple relationship exists between the amount of generated sub-ambient pressure and the force exerted on the prey during suction feeding, unless animals of the same species are compared. Therefore, for evaluating suction performance in aquatic animals in future studies, the focus should be on the flow velocities in front of the mouth, for which a direct relationship exists with the hydrodynamic force exerted on prey.

Keywords: prey-capture; feeding; buccal pressure; dynamical modelling; catfish

1. INTRODUCTION

To generate suction, animals rapidly expand their bucco-pharyngeal cavity, resulting in a flow of water into the mouth (Muller *et al.* 1982; Muller & Osse 1984; Aerts *et al.* 2001; Ferry-Graham *et al.* 2003). In this way, prey suspended in the water in front of the mouth can be accelerated towards the mouth, caught between the oral jaws or even completely engulfed and transported through the mouth cavity. A rapid drop of pressure inside the bucco-pharyngeal cavity accompanies this process (e.g. Alexander 1970; Van Leeuwen & Muller 1983; Wainwright & Turingan 1996; Nemeth 1997; Sanford & Wainwright 2002; Svanbäck *et al.* 2002).

In fishes, the amount of pressure generated inside the buccal (mouth) cavity is often used as a measure of prey-capture performance. However, it is well-known that this is an *indirect* measure of performance, as it does not provide any direct indication of the effect of the suction act on the prey item (Ferry-Graham & Wainwright 2002). Prey are drawn towards the mouths of suction feeders together with the flow of water surrounding the prey. As the forces exerted on the prey are proportional to the speed of the flow near the prey, inducing sufficiently high flow velocities has a clear ecological importance. Consequently, intra-oral pressure can only be related to suction performance if pressure also correlates with the flow velocity during the suction process.

This will indeed be the case if the speed of expansion of a given bucco-pharyngeal system is increased; the flow velocities and sub-ambient pressure magnitudes will increase as well (Muller *et al.* 1982). Experimental studies also demonstrated that the magnitude of buccal pressure increases with increasing speed of expansion of the cranial system (Sanford & Wainwright 2002; Svanbäck *et al.* 2002) or in situations where increased cranial expansion speed would be expected, such as increased predator motivation (Lauder 1980) or increased prey elusivity (Nemeth 1997). For these reasons, buccal pressure magnitude is generally considered a valuable metric of suction feeding performance (Lauder 1983; Lauder *et al.* 1986; Grubich & Wainwright 1997; Carroll *et al.* 2004).

However, the link between speed of expansion of the buccal cavity and buccal pressures (Sanford & Wainwright 2002; Svanbäck *et al.* 2002) has only been demonstrated within a single species, with individuals showing a similar size, morphology and kinematics of the expanding feeding system. Nevertheless, buccal

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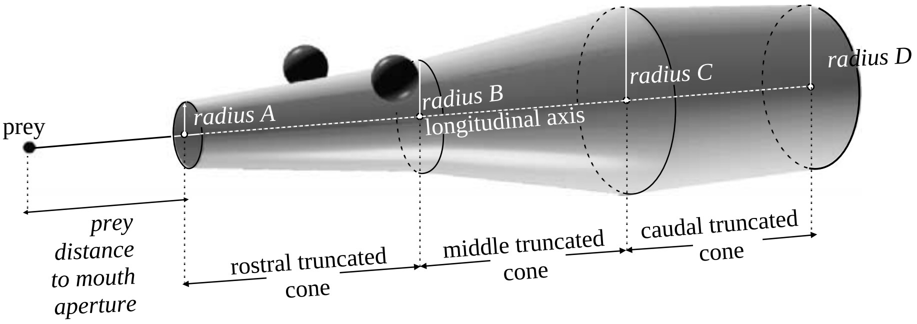

Figure 1. The geometry of the model. Four independent radii (radius A, B, C and D) constitute three hollow, truncated cones (rostral, middle and caudal cone) of equal length along the longitudinal axis.

pressure magnitudes have also been used as a synonym for suction feeding performance when comparing multiple species, each having a different morphology of the feeding system (Wainwright & Shaw 1999; Carroll *et al.* 2004). In this situation, however, the above-mentioned relationships with suction performance have not yet been demonstrated, neither theoretically nor experimentally. Yet, it might be possible that some species will require larger buccal pressures to induce, for example, a similar displacement of the prey towards the mouth.

In this paper, theoretical modelling is applied in order to test whether intra-oral pressure can be used as a metric for suction performance in aquatic animals that show differences in morphology or kinematics of their bucco-pharyngeal expansion. The advantage of suction models is that calculations of pressure (Muller *et al.* 1982) can be combined with more direct quantifications of suction performance, such as calculating movement of prey with respect to the suction-feeding animal (Van Wassenbergh *et al.* 2006).

2. MATERIAL AND METHODS

2.1. Model of suction feeding

As a model for aquatic suction feeding, the expanding cone model of Muller *et al.* (1982) was used (see also Muller & Osse (1984)). This hydrodynamic model allows the calculation of pressure and flow velocity inside and in front of expanding cones, which are open at the mouth aperture and closed at the other end. The shape of a fish's head can often be approximated fairly well by such conical profiles (Muller & Osse 1984). When compared with *in vivo* monitoring of water flow patterns during prey-capture in fishes (Day *et al.* 2005) and pressure measurements (Van Leeuwen & Muller 1983) the output of this model appears to be accurate. Therefore, it has been used frequently to gain insight in the dynamics of the suction feeding process (Van Leeuwen & Muller 1984; Drost & van den Boogaart 1987; Aerts *et al.* 1987; Viladiu *et al.* 1999; Van Wassenbergh *et al.* 2005).

The model of Muller *et al.* (1982) calculates flow velocities inside and in front of a hollow, expanding cone (with a circular opening at the front and closed at the back) for which the expansion kinematics are prescribed. Inside the cone, velocity calculations are based on the principle of continuity, meaning that any increase in volume must be filled instantaneously with water and thus generate a flow relative to the fishes' head. In front of the cones' opening, the flow is assumed to describe a circular vortex filament, of which the strength and shape depends on the size of the mouth opening, the magnitude of the flow velocity inside the mouth aperture and the swimming speed of the fish. For positions along the axis of rotational symmetry of the model, Muller *et al.* (1982) have derived analytical solutions for flow velocities in front of the model's mouth, as well as formulae for pressure inside the expanding cone. For a more detailed theoretical background on this model, its assumptions and the mathematical formulae for calculating flow velocities and pressures, we refer to the original publications (Muller *et al.* 1982; Muller & Osse 1984).

An adapted version of the model by Muller *et al.* (1982) was programmed using Microsoft Visual Basic for applications within Excel 2000. In contrast to the original model (Muller *et al.* 1982), our model now consists of three interconnected, truncated cones (figure 1). In this way, the kinematics of the mid-region (hyoid region) of the expanding structure can be set independently of the radial expansion of the front (mouth aperture) and more posterior region (opercular region) of the hollow, triple, truncated cones (figure 1). As argued in Muller & Osse (1984), models like these allow a more accurate modelling in case of significant depressions of the hyoid apparatus (the well ossified, V-shaped structure located caudal to the lower jaw that has a crucial role in generating suction), which occurs in many fishes (Ferry-Graham & Lauder 2001). Consequently, the rostro-caudal expansion-wave observed in most suction feeding aquatic vertebrates, can be simulated more precisely.

The following data is needed as input for the model: the four radii of the triple, truncated cone at time zero (start of mouth opening), the maximal radii at these positions, the time at which these maxima are reached, and a 'delay time' for the start of expansion at the middle and back of the expanding profile (figure 1). This delay time is the time after the start of mouth opening (time zero) for which radii remain constant. The shape of the kinematic profiles of the radii, from start to maximum, is fitted to the rising part of a sine function. This simple function approximates the real displacement pattern of feeding structures, for example the lower jaw, hyoid or operculum during abduction (e.g. Aerts *et al.* 1987; Gillis & Lauder 1995; Sanford & Wainwright 2002; Van Wassenbergh *et al.* 2004).

Unless specific boundary conditions are used, the model becomes undetermined if any of the posterior valves (the opercula and branchiostegal membranes, which initially seal the gill chamber and prevent backflow of water) open (Muller *et al.* 1982). Therefore, it was chosen not to perform model simulations for the entire expansion–compression cycle, but limit all simulations to the expansive phase. More specifically, the calculations are ended at the time at which maximal mouth opening is reached. In general, the sub-ambient pressure peaks are observed before maximal mouth opening (Van Leeuwen & Muller 1983; Sanford & Wainwright 2002). This instant of maximal mouth opening is generally around the time the prey enters the mouth, which is usually followed by opening of the posterior valves (Van Leeuwen & Muller 1984). Consequently, given the purpose of the present study, it is not essential to continue calculations after the time of valve opening, which would require additional assumptions to the model.

2.2. Calculation of prey displacement

The displacement of a hypothetical prey that is subjected to the calculated spatio-temporal flow velocity patterns is determined. It was assumed that the prey has the same density as the water. In that case, gravitational force and hydrostatical lift will cancel each other out. If the prey is presented in the flow field before it is disturbed by suction, and if the suction-induced flow (as calculated in absence of the prey) is spatially uniform for the volume taken by the prey, such neutrally buoyant prey will theoretically be displaced in the same way as the water at the prey's position in absence of the prey (Landau & Lifshitz 1982; Mordant & Pinton 2000). Consequently, the instantaneous velocity of this prey equals the instantaneous flow velocity at the position of the prey, and its displacement until the next time step can easily be calculated. Note that the assumption of spatially uniform flow at the position of the prey will only hold for prey that are small relative to the size of the mouth opening to which the suction vortex converges.

2.3. Head shape diversity in catfishes

The variability in head morphology exhibited by a large and morphologically diverse group of teleost fishes, the catfishes (Siluriformes), was used as a starting point for the model simulations. This diversity in external head dimensions was explored by measuring the height of the head at three positions on images of the primary type specimens of 63 species (10 families). We excluded all specialized algae-scrapers (Loricariidae). Except for Clariidae, which were measured from Devaere (2005), all pictures were provided by the California Academy of Sciences, San Francisco (http://www.calacademy.org/research/ichthyology).

To exclude differences in absolute size of the specimens, the head length (distance between the tip of the jaws and the back of the operculum) was always scaled to 72 mm. The head height was measured at 2, 37 and 72 mm caudal of the tip of the jaws. Next, the catfishes were plotted in a three-dimensional morphospace (figure 2). From this morphospace, three species were selected for further analyses: (i) *Clarias gariepinus*, a species with narrow head size at all three positions (front, middle and back of the head), (ii) *Channallabes apus*, a species closely related to *C. gariepinus* that shows relatively minor differences in external head shape compared to the latter species and (iii) *Corydoras agassizii*, a species from the genus that is most distant from *C. gariepinus* on the head-shape morphospace because of its steeply increasing head height towards

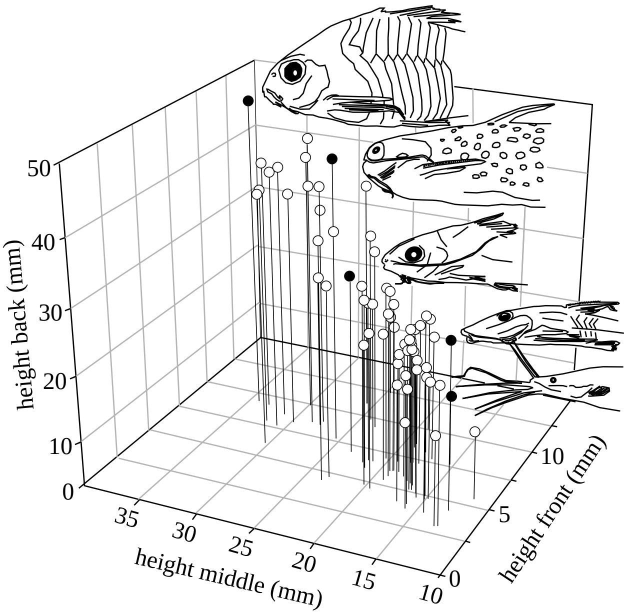

Figure 2. Morphospace showing the measured head heights at three positions along the head (front, middle and back) for 63 species of catfishes. This graph was used to explore the variability in head shapes in this group of fishes. The five species indicated (black circles) are (from bottom to top) *Clarias gariepinus* (Clariidae), *Hemidoras morrisi* (Diplomystidae), *Brachyrhamdia imitator* (Pimelodidae), *Tatia galaxies* (Auchenipteridae) and *Corydoras latus* (Callichthyidae). The other species included in the analysis are: *Channallabes alvarezi*, *Dolichallabes microphthalmus*, *Gymnallabes nops*, *Platyclarias machadoi* (Clariidae), *Diplomystes nahuelbutaensis*, *Doras nebulosus*, *Hassar praelongus*, *Hypodoras forficulatus*, *Opsodoras hemipeltis*, *O. ternetzi*, *Orinocodoras eigenmanni*, *Trachydoras atripes* (Diplomystidae), *Istlarius balsanus* (Ictaluridae), *Chasmocranus peruanus*, *Duopalatinus peruanus*, *Leptorhamdia marmorata*, *Megalonema pauciradiatum*, *Nannoglanis bifasciatus*, *Platypogon caerulorostris*, *Rhamdella rusbyi*, *Rhamdia duquei* (Pimelodidae), *Ceratoglanis pachynema*, *Silurus goae* (Siluridae), *Tympanopleura alta*, *T. nigricollis* (Ageneiosidae), *Paramphilius goodi*, *Galeichthys azureus*, *G. eigenmanni*, *G. xenauchen*, *Hexanematichthys henni*, *Netuma mazatlana*, *Tachysurus emmelane*, *T. evermanni*, *T. liropus*, *T. steindachneri* (Amphiliidae), *Trachycorystes coracoideus*, *Centromochlus gyrinus*, *Pseudepapterus cucuhyensis*, *Tocantinsia depressa* (Auchenipteridae), *Aoria henryi*, *Liocassus hirsutus*, *Mystus multiradiatus*, *M. mysticetus*, *M. pahangensis* (Bagridae), *Aspidoras eurycephalus*, *Callichthys barbatus*, *Corydoras acutus*, *C.australe*, *C. bond*, *C. cochui*, *C. episcopi*, *C. fowleri*, *C. juquiaae*, *C. metae*, *C. potaroensis*, *C. semiaquilus*, *C. stenocephalus* and *C. sychri* (Callichthyidae).

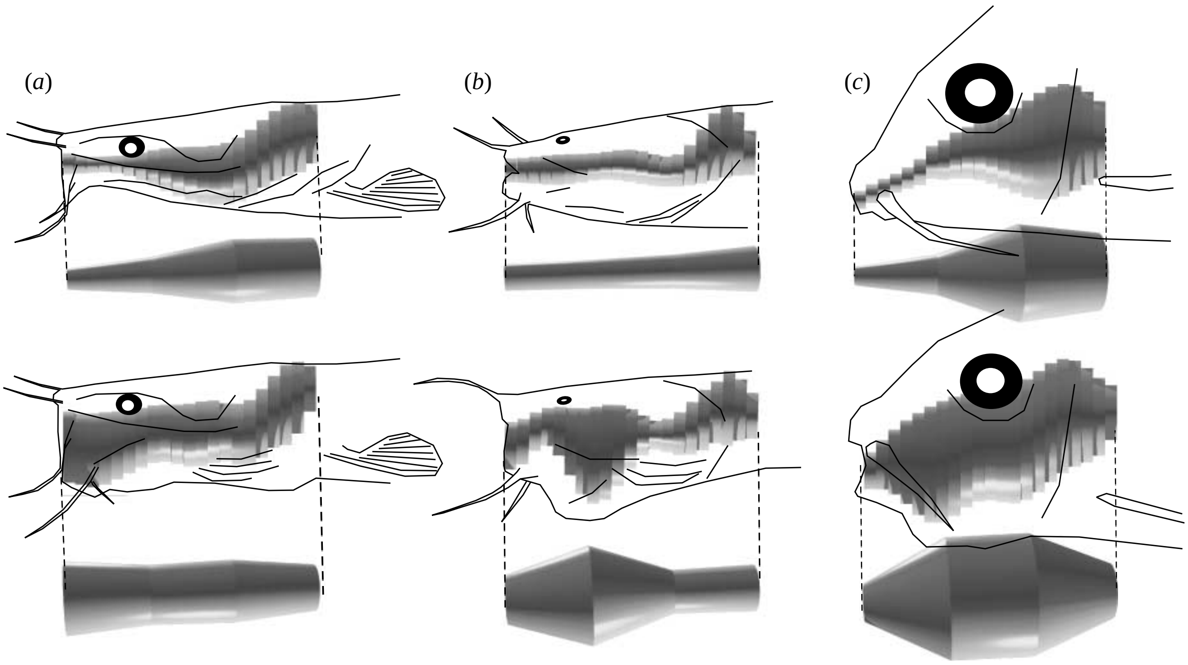

Figure 3. Bucco-pharyngeal cavities of (*a*) *C. gariepinus*, (*b*) *C. apus* and (*c*) *C. agassizii* reconstructed as a series of 21 elliptical cylinders in compressed state (top drawings) and expanded state (bottom drawings) based on X-ray images. The rotational symmetric, triple cone models used for the simulations of suction feeding are illustrated below each ellipse reconstruction.

the back of the skull (figure 2). In this way, it is possible to use an ecologically relevant degree of diversity in morphology in the simulations with models of different shapes (see further).

For one specimen of each of these three species (*C. gariepinus*, *C. apus* and *C. agassizii*), the dimensions of the bucco-pharyngeal cavity were measured (figure 2). This was done based on digital X-ray photographs (Philips Optimus X-ray generator coupled to a 14 in. image intensifier and a Redlake Motion Pro camera) made in lateral and dorsoventral view after filling the mouth with radio-opaque (barium) fluid. The contours of the bucco-pharyngeal cavity were digitized (using Didge, v. 2.2.0, A. Collum). Next, this data was used to reconstruct the volume of the bucco-pharyngeal cavity, from the mouth aperture to the base of the pectoral fin, as a series of 21 elliptical cylinders (see also Van Wassenbergh *et al.* (2006)). These bucco-pharyngeal volume reconstructions were performed for heads in compressed and expanded state (figure 3). Head expansion by manipulation of the preserved specimens was obtained by opening the jaws and pushing the hyoid tip caudo-ventrally. Note that the gills are inevitably included in this bucco-pharyngeal volume.

2.4. Model simulations

During simulations of suction, three independent radii of the models (radii A to C on figure 1) were increased. The most caudal radius at the level of the pectoral fin (radius D on figure 1) lies beyond the expandable region of the catfishes' heads and was therefore kept constant in time. The initial volume before expansion always corresponded to the triple-cone that approximated best the measured volume of the bucco-pharyngeal cavity in compressed state of the species under consideration (figure 3). The medio-sagittal length of the triple-truncated cones was always 70 mm, corresponding to the cranial size of the individuals from which the most complete kinematic data is available. All models move forward with a constant velocity of 0.1 m s^{-1}. The expansion and translation of the models caused a small, spherical, neutrally buoyant prey to move from a distance of 20.7 mm in front of the model's mouth, to reach the centre of the mouth opening after 80 ms (which is the time at which maximal mouth opening is reached). This prey was presented on the extension of the longitudinal axis of the model (i.e. the axis of rotational symmetry; figure 1). When entering the mouth, the prey always had a velocity of 1.3 m s^{-1} in an earth bound frame of reference. Consequently, all prey will have an equal, caudally directed momentum at the moment of prey uptake (the time our model simulations are ended). Therefore, prey will theoretically have the same chance of escaping after this moment if they start moving in the opposite direction of the flow.

The kinematics of head expansion are well known for one of the selected species, *C. gariepinus* (Van Wassenbergh *et al.* 2005). In a first simulation (referred to as simulation A), the magnitudes of expansion and the kinematic timings of expansion closely resemble experimental observations for this species (Van Wassenbergh *et al.* 2005). In a second simulation (simulation B), the delay time for the expansion of radius C (see figure 1) was increased by 10 ms. Next, in order to preserve the performance of simulation A (i.e. prey entering the mouth at 1.3 m s^{-1} after 80 ms), the time was adjusted after which maximal expansion of the mid-region of the model (radii B and C; figure 1) is reached. In this way, only the relative timings of the expansion were altered, without changing the shape of the cones prior to expansion, as well as the cones' maximal radii.

For the models in which the initial configuration corresponds to the head dimensions of the two species other than *C. gariepinus* (figure 3; simulations C and D), the following procedure was followed to preserve an equal suction performance. First, a simulation was run for the models increasing in volume from the compressed to the expanded situation as illustrated in figure 3 using the timings of expansion of *C. gariepinus* (simulation A). Next, the timings of expansion of radius B and C of the model (see figure 1) were adjusted, so that the prey now enters the mouth after 80 ms. This adjustment mimics differences in the speed of the abduction of the hyoid and suspensorium (respectively, pushing the ventral and lateral sides of the bucco-pharyngeal cavity outwards), by which we can tune the strength of the vortex filament in front of the mouth, given a previously defined size and expansion of the mouth aperture. Finally, as the latter adjustment not necessarily results in prey entering the mouth at 1.3 m s^{-1}, the model was further fine-tuned by adjusting the maximal value for radius B (see figure 1).

For the model of *C. agassizii*, however, unrealistic flow velocities (greater than 20 m s^{-1}) were obtained if the expansion times observed for *C. gariepinus* were used in the simulations. To correct this, the maximal expanded radius of the mouth aperture, as measured from the X-ray images (figure 3) was increased by 20%, while the maximal radius at the level of the hyoid (radius B in figure 1) was reduced by 20% before the adjustments (described above) to obtain equal suction performance.

Note that in order to simulate the prey displacement described above, more than one kinematic solution is possible for a given initial model configuration. However, we did not explore all different expansions inducing similar prey displacement for each model. Yet, the presented solutions (table 1; figure 4) are examples for which the following criteria are fulfilled: first, the rostro-caudal wave of expansion is preserved. Secondly, the kinematics of expansion are relatively close to the experimentally observed prey-capture kinematics for one of the modelled catfishes. Thirdly, the initial configuration and maximal expansion of the mouth cavity correspond closely to the measurements of compressed and expanded mouth cavities of manipulated specimens.

3. RESULTS

3.1. Kinematic differences and pressure output

The presented suction model enabled us to perform simulations in which the kinematics and/or the shape of the expanding, truncated cones were altered, without changing the travel time until the moment of capture of a hypothetical prey and the speed of this prey at the moment it passes through the mouth opening (table 1; figure 4). In two of these simulations (simulations A and B; figure 4*a*,*b*), only the relative timings of the expansions differ, with no changes to the shape of the cones prior to expansion, as well as to the maximal radii (table 1). Therefore, these models are representative for a small change in relative timing of prey-capture kinematics.

Table 1. Numerical characteristics of four model simulation (A–D) of equal suction performance.

	A	B	C	D
start radius A[a] (mm)	2.97	2.97	3.70	2.62
maximal radius A[a] (mm)	5.97	5.97	5.70	6.70
start radius B[a] (mm)	5.11	5.11	4.03	5.83
maximal radius B[a] (mm)	12.11	12.11	13.80	13.50
start radius C[a] (mm)	9.12	9.12	4.76	14.16
maximal radius C[a] (mm)	11.92	11.92	6.20	17.58
radius D[a] (mm)	8.48	8.48	6.51	11.30
max. expansion time A[a] (ms)	80	80	80	80
max. expansion time B[a] (ms)	100	99	100	135
max. expansion time C[a] (ms)	100	102	100	145
delay time B[a] (ms)	5	5	5	5
delay time C[a] (ms)	10	20	10	5

[a] See figure 1 for an illustration of the different radii (A–D) used in the model.

Despite these small kinematic differences between models A and B (see figure 4*a*,*b*), the magnitude of the calculated pressure inside these models during suction differs (figure 5): peak negative pressure at the mouth aperture in simulation A (−4.25 kPa) is 6.7% lower than the value calculated for B (−3.99 kPa). At the back of the expanding models, negative pressure peaks reach −2.16 and −1.97 kPa, respectively, for simulations A and B (figure 5). This corresponds to pressures that are 9.5% lower in A with respect to B.

3.2. Head shape differences and pressure output

The results from the equal-performance simulations with the models mimicking morphological differences in catfishes show considerable differences in the generated sub-ambient pressures inside the expanding models (figure 5). For example, peak sub-ambient pressure at the level of the mouth aperture in simulations A, C and D are, respectively, −4.25, −1.65, −2.90 kPa (figure 5). The standard deviation of these results is 1.30 kPa, which almost half the average peak sub-ambient pressure magnitude in these three simulations (−2.93 kPa). The same pattern is observed for peak pressures magnitudes at other positions inside the expanding models, and also for pressures averaged over time.

4. DISCUSSION

Pressure measurements are the most traditional method of quantifying suction performance in aquatic vertebrates (Ferry-Graham & Wainwright 2002). However, when it comes to comparing suction performance of animals that show a different morphology and kinematics of the feeding system, the present theoretical analysis suggests strong potential limitations to

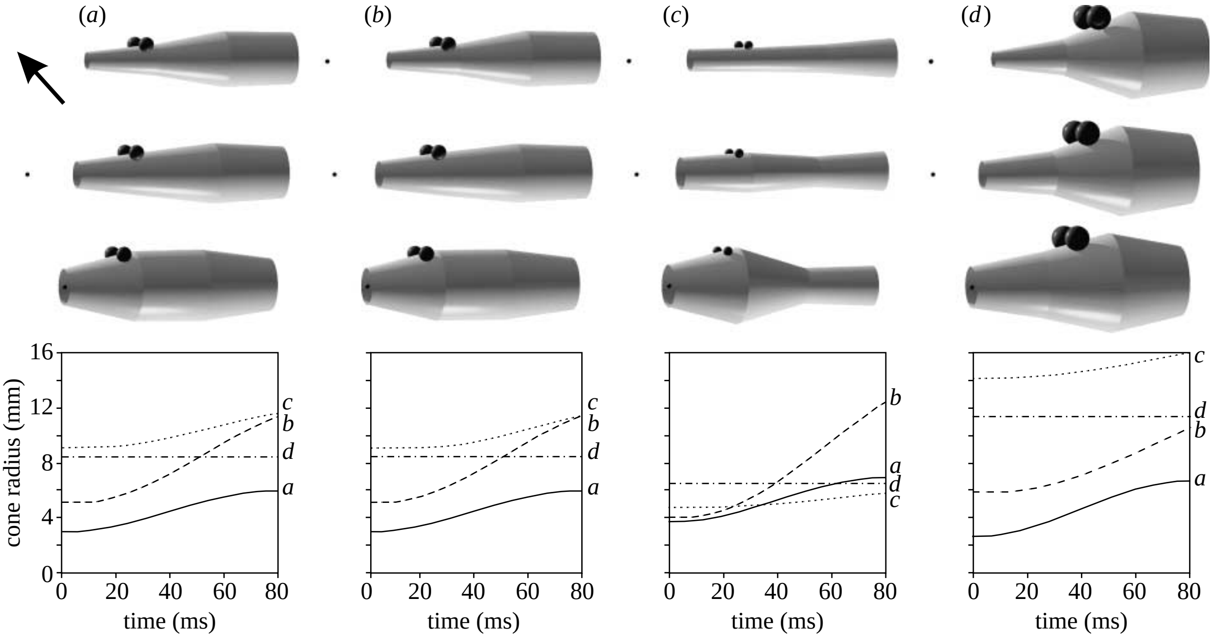

Figure 4. Three-dimensional representation of the suction models used in this study (top drawings; time 0, 40 and 80 min are shown) and their respective expansion kinematics (graphs below). The legend of the different radii (see figure 1) are given at the right-hand side of each graph. (*a*) and (*b*) are both models for the buccopharyngeal expansion in *C. gariepinus*, differing only in kinematic timing of expansion. (*c*) and (*d*) are models for *C. apus* (figure 3*c*) and *C. agassizii* (figure 3*c*). Note that all models are able to transport the small prey (arrow) in front of the mouth towards the mouth in the same way.

this approach. Our results indicate that similar prey displacement, and hence capture success, does not necessary occur when different animals generate similar intra-oral pressures. In other words, equal pressures do not automatically have the same effect on the prey in animals with differently shaped bucco-pharyngeal cavities.

Yet, in case similar-sized individuals of the same species are compared that only show subtle differences in kinematic timings of head expansion (figure 4*a versus b*), the modelling results show that equal performance occurs at relatively similar pressure inside the mouth: all pressure differences are still lower than 10% if the same prey displacement and velocity are simulated with slightly altered kinematics. These results are in accordance with experimental results showing a relationship between suction performance and the amount of intra-oral, sub-ambient pressure within conspecific suction feeders of similar size (Lauder 1980; Nemeth 1997).

However, even when comparing suction generated by two catfish heads that are morphologically relatively similar compared to the total diversity in head shapes in this group of teleost fishes (figure 2), pressure is not an ecologically relevant indicator of suction performance. For example, equal suction performance was simulated with sub-ambient pressure peaks reduced by 61% near the mouth aperture in the model for *C. apus* (figures 3*c*, 4*c*) compared to the simulation for a species from the same family (Clariidae), *C. gariepinus* (figures 3*a* and 4*a*). If we increase the speed and magnitude of the expansion in the mid-region of the *C. apus* model until the same peak sub-ambient pressure is obtained as in the *C. gariepinus* model, then the neutrally buoyant prey placed at 20.7 mm in front of the mouth will now enter the mouth after 70 ms (instead of 80 ms), or the prey will still reach the mouth in 80 ms from a distance of 22.7 mm (instead of 20.7 mm).

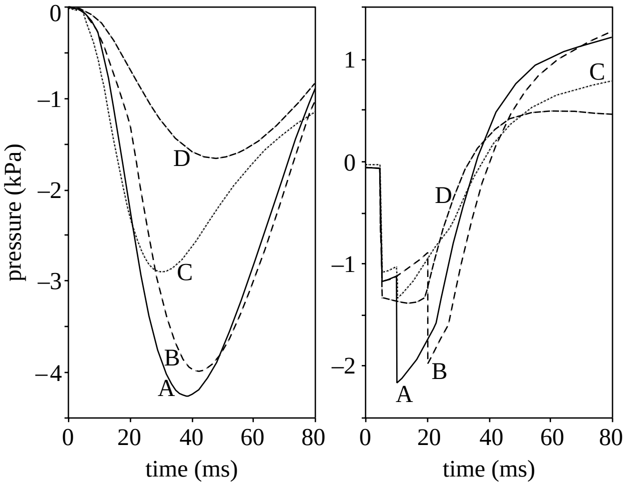

Figure 5. Calculated pressure profiles at the level of the mouth aperture (left graph) and at the back of the model (right graph) for the six equal-performance simulations (A to D corresponding to table 1 and figure 4).

Although it could be expected that this difference in pressure for suction feeders generating the same prey displacement will even be more pronounced when comparing more diverging head shapes, this relationship is not observed. If we compare the results for two distantly related catfishes that show a considerable difference in the shape of the bucco-pharyngeal cavity (*C. gariepinus* and *C. agassizii*; figure 3*a*,*c*), the calculated difference in pressure for the equal-performance simulations is still considerable (more than 30% difference; figure 5) but less than the difference between the models of the two more similar species (figure 3*a*,*b*). This illustrates the unpredictability of the relationship between intra-oral pressure and prey transport.

So far, all model simulations used expanding profiles of the same mid-sagittal length. What if not only the shape of the expanding profile, but also its total length differs? A previous study has shown that the relations between body size, speed of cranial expansion, flow velocities and prey-capture performance are complex (Van Wassenbergh *et al.* 2006). It appeared, for example, that larger African catfish (*C. gariepinus*) were able to pick up prey by suction from larger distances compared to smaller individuals of this species (Van Wassenbergh *et al.* 2006). Yet, the corresponding buccal pressures did not change significantly (Van Wassenbergh *et al.* 2005). Consequently, also the relation between pressure and performance is far from obvious in a context of differently sized animals, even if all head dimensions remain exactly proportional to total head length.

In conclusion, the relation between the amount of generated sub-ambient pressure and the force exerted on the prey during suction feeding is theoretically unpredictable, unless similar sized animals of the same species are compared that also show similar kinematic timings of bucco-pharyngeal expansion. Therefore, the results of the present study indicate that future comparative studies on suction feeding performance in an ecological context should preferably use more direct quantifications of suction performance rather than pressure measurements. A better alternative is to use water flow velocity measurements by using the digital particle image velocimetry technique (Ferry-Graham *et al.* 2003; Day *et al.* 2005; Higham *et al.* 2005), or flow velocity calculations by combining prey-capture kinematics recorded with high-speed cameras and ellipse models (Drost & van den Boogaart 1987; Aerts *et al.* 2001; Van Wassenbergh *et al.* 2006). The force dragging the prey toward the mouth is proportional to the velocity and acceleration of the water. Therefore, in contrast to data on the pressure inside the mouth cavity, suction performance can easily be extracted from data on flow velocities in front of the mouth.

Still, intra-oral pressure is a very important metric from a biomechanical and physiological point of view as the magnitude of sub-ambient pressure, and the consequent force resisting head expansion due to the pressure gradient between inside and outside of the mouth cavity, is the dominant factor in constraining an individual's prey-capture performance (Aerts *et al.* 1987; Carroll *et al.* 2004; Van Wassenbergh *et al.* 2005). Yet, our data shows that the capacity of generating such low intra-oral pressures can only be viewed in terms of *physiological* performance, and do not predict the animal's suction feeding success during a predator–prey encounter.

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