

## No trade-off between biting and suction feeding performance in clariid catfishes

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Accepted 26 October 2006

### Summary

It is generally assumed that biting performance trades off with suction performance in fish because both feeding types may place conflicting demands on the cranial musculo-skeletal system. However, the functional consequences of morphological adaptations enhancing biting on the mechanics and performance of suction feeding in fish remain obscure. In this study, suction feeding performance was compared between three clariid catfish species differing considerably in their biting capacity, by measuring the velocity of a standardized prey being sucked into the buccal cavity using high-speed cineradiography. In addition, buccal volume changes during prey capture were quantified by ellipse modelling. As all species were able to accelerate the prey to similar peak velocities, our results demonstrate the possibility for catfishes to increase bite performance considerably

without compromising suction performance. The amount of buccal expansion in the ventral direction is approximately equal for all species. Consequently, the system generating expansion through ventral rotation of the lower jaw, hyoid and pectoral girdle is apparently not constrained (mechanically or architectonically) by the hypertrophy of the jaw adductors. As the effect of a reduced magnitude of lateral expansion (suspensorium abduction) on suction performance in Clariidae appears to be negligible (for example in *Gymnallabes typus*), these data demonstrate the dominant role of ventral expansion for producing suction in these fish.

Key words: prey capture, X-ray video, kinematics, catfish, buccal volume.

### Introduction

Evolution towards optimal performance is prevented whenever two ecologically relevant functions require opposing biomechanical or physiological adaptations (Stearns, 1992). Such evolutionary trade-offs are often observed in case certain components of the musculo-skeletal system have to participate in different functions: a certain change in one aspect of the system increases the performance of a given function, but at the same time may reduce the organism's efficiency in performing an other, morphologically coupled function (e.g. Vanhooydonck and Van Damme, 2001; Van Damme et al., 2002; Pasi and Carrier, 2003; Schondube and Del Rio, 2003). Identifying such conflicts in the performance of ecologically relevant functions is basic to our understanding of the evolutionary processes associated with species radiations. Furthermore, analyses of the constraints on the compatibility of functions may provide insight into the ecological potential (potential niche width) of animals (Barel, 1983).

One of the most striking examples of a complex and integrated system that has to fulfil a large number of crucial biological functions is probably the cranial musculo-skeletal

system of fishes (Liem, 1980). It has to cope with capturing, processing and transporting prey, breathing water or air, participating in sensory perceptions, providing protection for the major sense organs and brains, and serving as a streamlined bow in locomotion. Logically, each of these functions calls for specific, structural and dynamical requirements to the animal's cranial system. As a result, the morphological diversity in a certain trait exhibited in taxa will be evolutionary constrained due to the disparate functional demands on this trait. This was demonstrated recently in the oral jaw system of Labrid fishes (Alfaro et al., 2005).

Different functional aspects can also be distinguished within the process of prey capture: prey can either be caught by suction feeding (generating a flow of water that drags the prey towards and into the mouth) and/or by biting (e.g. scraping algae or picking molluscs off the substrate with the oral jaws). It is hypothesised that biting a prey or sucking it directly into the mouth are two functionally conflicting ways of getting food into the buccal cavity (Barel, 1983; Bouton et al., 1999; Sibbing and Nagelkerke, 2001). It is therefore assumed that suction feeding and biting can be combined only to a certain extent,

and at certain costs. This hypothesis appears to be supported by the observation that specialized biters usually possess other anatomical, functional, dietary and behavioural features that distinguish them from species that rely primarily upon suction feeding to capture prey (Alfaro et al., 2001).

However, many fish species still seem to combine biting and suction seemingly efficiently (Turingan and Wainwright, 1993; Bouton et al., 1998; Van Wassenbergh et al., 2004; Janovetz, 2005), and to our knowledge, no experimental study has yet directly demonstrated the proposed inverse relationship between biting and suction performance (see Bouton et al., 1998). Consequently, the underlying biomechanical basis responsible for the proposed conflicting demands on the oral jaw apparatus (for biting) and the buccal expansion apparatus (for suction feeding) remains to be demonstrated.

In this paper, suction performance is quantified and compared between species of air-breathing catfish (Clariidae) that differ in bite performance. In this group of fishes, hypertrophy of the jaw adductors (Fig. 1) is a derived feature that has evolved at least four times independently (Jansen et al., 2006) and is associated with a drastic increase in maximal bite force (Herrel et al., 2002) and a larger proportion of hard prey (mainly coleopterans) in the diet (Huysentruyt et al., 2004). Nevertheless, our observations have shown that even the species with the most extreme jaw adductor hypertrophy still apply considerable buccal expansion before impacting the jaws onto the prey, and manage to drag relatively large prey into the mouth by suction. Furthermore, as Clariidae appear to generate suction predominantly by expanding their buccal cavity in the ventral direction (Van Wassenbergh et al., 2004), the fact that the jaw adductors are bulging dorso-laterally from the head (see Fig. 1) may indicate the avoidance of spatial interference with the buccal expansion system in course of the evolution. In this way, it is possible that the trade-off between biting and suction feeding performance, as suggested for other groups of fishes (Barel, 1983; De Visser and Barel, 1996), does not apply to Clariidae.

As suction feeding behaviour is thus maintained despite the considerable increase in bite performance in several clariid



Fig. 1. Side view of the head of *Gymnallabes typus* that clearly shows the bulging, hypertrophied jaw adductor muscles.

species, this group of fishes provides a unique opportunity to test the proposed trade-off between suction and biting performance in a number of evolutionary lineages. It also allows us to examine the biomechanical consequences of the morphological variation associated with increasing bite performance on the kinematics of buccal cavity expansion.

## Materials and methods

### *Species, morphology, phylogeny and bite performance*

According to a recent molecular phylogenetic study (Jansen et al., 2006), species with eel-like bodies, hypertrophied jaw adductors and a narrow skull roof have arisen at least four times independently within the Clariidae. Each time, a sister group relation with a non-specialized *Clarias*-like ancestor is observed. In this study, we focus on two lineages from which three clariid species were selected (Fig. 2): *Clarias gariepinus* (Burchell 1822), *Gymnallabes typus* (Günther 1867) and *Channallabes apus* (Günther 1873).

The neurocranium of *C. gariepinus* forms a broad, closed roof that partly covers the relatively small jaw adductor muscles (Cabuy et al., 1999). Its overall cranial morphology resembles that of *Heteropneustes fossilis*, which can be considered as a sister species of Clariidae (Agnese and Teugels, 2005; Diogo, 2005; Jansen et al., 2006). Biomechanical modelling has shown that the maximal bite forces that can be exerted by *C. gariepinus* are considerably less than species with jaw adductor hypertrophy (Herrel et al., 2002) (Fig. 2). Yet, *C. gariepinus* has a broad diet, which not only includes relatively soft prey such as insect nymphs, fish and shrimps, but also harder prey such as crabs, beetles and snails (Bruton, 1979). Although this species shows different kinds of foraging behaviours, including bottom feeding, surface feeding or group hunting, prey are generally captured by a combination of suction feeding and biting (Bruton, 1979; Van Wassenbergh et al., 2004). The individuals used in the experiments (see further) were either aquarium-raised specimens obtained from the Laboratory for Ecology and Aquaculture (Catholic University of Leuven, Belgium) or specimens obtained from aquacultural facilities (Fleuren and Nooijen BV, Someren, The Netherlands).

In contrast to *C. gariepinus*, *G. typus* and *C. apus* have bulging, hypertrophied, jaw adductors and a narrow skull roof (Fig. 1) (Cabuy et al., 1999; Devaere et al., 2001; Devaere et al., 2005). This increase in jaw muscle size, the reduction of the bony skull roof, and the development of the more anguilliform body is the result of independent, convergent evolution in these two species (Agnese and Teugels, 2005; Jansen et al., 2006) (Fig. 2). Additionally, bite performance in *G. typus* and *C. apus* is much better than in *C. gariepinus* (Fig. 2). This appears to be reflected in the diet, with the species with jaw adductor hypertrophy exhibiting a special preference for coleopterans (Huysentruyt et al., 2004). *G. typus* individuals were commercially imported from the west of Tropical Africa (exact location unknown), and *C. apus* were wild-caught in Northern Gabon.

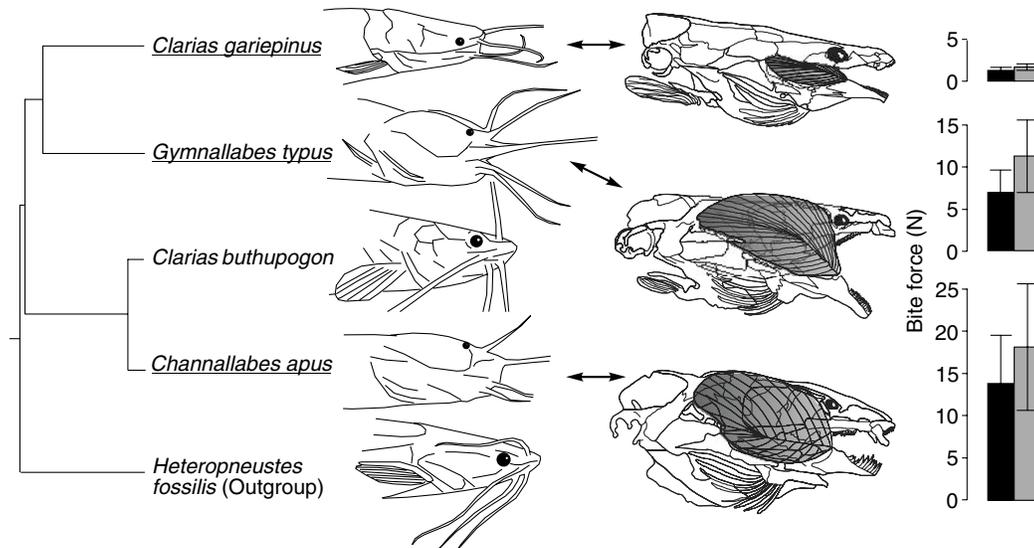


Fig. 2. Partial phylogeny of Clariidae based on the consensus tree of several analyses on ribosomal DNA sequences presented elsewhere (Jansen et al., 2006) indicating the species studied (*Clarias gariepinus*, *Gymnallabes typus* and *Channallabes apus*). Illustrations of the external head morphology (left drawings) showing the closed skull roofs of *C. gariepinus*, *Clarias buthupogon* and the outgroup sister species of Clariidae *Heteropneustes fossilis*, as opposed to the hypertrophied jaw adductors in *G. typus* and *C. apus* that fill a large part of the head behind the eyes. This jaw adductor hypertrophy has evolved four times independently in Clariidae, of which only two lineages are illustrated here. The jaw adductors imposed on osteological drawings of the head (right drawings) for the three species studied clearly illustrate the jaw muscle hypertrophy in *G. typus* and *C. apus* compared to the relatively slender jaw muscles of *C. gariepinus*, which are partly covered by neurocranial bones. The graphs give the maximal bite force (perpendicular to the lower jaw) at the anteriormost teeth (black bars) and posteriormost teeth (grey bars) of animals with a cranial length scaled to 39 mm and at a gape angle of  $10^\circ$  as calculated by Herrel et al. (Herrel et al., 2002).

#### Quantifying suction performance

The velocity and travel distance of a standardised prey that is sucked into the buccal cavity was measured using high-speed X-ray videos (Fig. 3). In order to minimise the chance of prey escaping during a suction feeding attempt, the prey has to be displaced into the buccal cavity as fast as possible (importance of prey velocity). It is also advantageous for a predator to transport the prey over a large distance, starting to draw the prey toward its mouth from as far as possible away (minimising approaching distance) to as far as possible inside the mouth cavity (reducing the chance of prey escape before the mouth is closed). Therefore, prey velocity as well as travel distance of the prey are crucial aspects of suction performance.

These prey were spherical, 6 mm diameter pieces of meat from boiled North Sea shrimp. In order to visualise the position of the centre of the prey, a small, steel marker was inserted into the middle of each prey. These prey were attached loosely on the tip of a blunt-tipped needle so that very little force was needed to release the prey from the needle. The prey-loaded needles were placed horizontally at the end of a narrow, projecting corridor (25 cm long, 8 cm wide, 15 cm high) in the 201 test aquaria in which the catfish were trained to capture food. The thin Plexiglas walls (2 mm) of the corridor minimised the amount of X-ray absorption. X-ray videos ( $250 \text{ frames s}^{-1}$ ) were recorded using a Philips Optimus M200 X-ray generator (Philips, Eindhoven, The Netherlands) coupled

to a 14-inch image intensifier and a Redlake MotionPro camera (Redlake, Tucson, AZ, USA).

Although the standardised prey were relatively small, results from a previous study on prey capture kinematics using X-ray videos (Van Wassenbergh et al., 2005) indicated that *C. gariepinus* does not reduce its suction effort while capturing this type of prey compared to, for example, firmly attached shrimps (Fig. 4). Note that our catfish often had to perform several attempts to detach a single piece of shrimp by suction. Also for *G. typus* and *C. apus*, no modulation of prey capture kinematics as a function of size, shape or attachment strength could be discerned (Van Wassenbergh et al., 2006a). Consequently, although a certain amount of strike-to-strike variability will inevitably occur (Van Wassenbergh et al., 2006a), there is no reason to assume that our experimental prey may have elicited submaximal suction performance. In addition, we are convinced that the X-ray video recording process (in particular the vibration that is suddenly produced by switching on the X-ray generator) provides further motivation to the anxious catfish to capture the prey as fast and efficient as possible, in order to return quickly to their preferred hiding places in the aquarium.

Prey captures were recorded for six individuals (three *C. gariepinus* with cranial lengths of 70.2, 74.5 and 94.1 mm; one *G. typus* of 22.0 mm and two *C. apus* of 24.5 and 26.0 mm cranial length; cranial length is defined as the distance between the rostral tip of the premaxilla and the caudal tip of the

occipital process) in lateral view (10 sequences per fish were analysed) and dorsoventral view (five sequences per fish were analysed). Only prey capture sequences that were approximately perpendicular to the camera lens were used. The

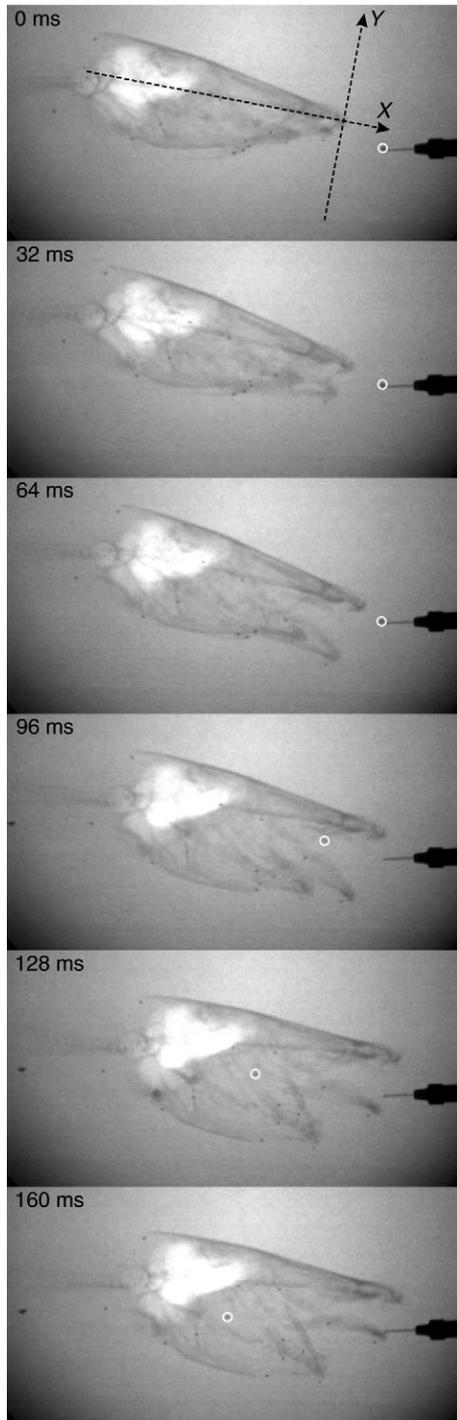


Fig. 3. Selected X-ray video frames for *Clarias gariepinus* (cranial length 70.2 mm) capturing a spherical piece of shrimp meat (into which a radio-opaque marker was inserted) presented loosely on the top of a needle. White circles highlight the prey. The fish-bound frame of reference is shown in the top frame.

prey marker, the rostral tip of the upper jaw and three additional points equally distributed along the roof of the buccal cavity (for lateral view X-ray videos) or along the medial axis of the head (for ventral view X-ray videos) were digitised frame-by-frame using Didge (version 2.2.0; Alistair Cullum, Creighton University, Omaha, USA). The position of the origin (upper jaw tip) and the inclination of an orthogonal frame of reference moving with the neurocranium were calculated. Least-squares linear regression of the four landmarks on the line of reference (buccal cavity roof or medial line) determined the slope of the X-axis. Next, prey positions were recalculated in the fish-bound frame of reference. In order to reduce digitisation noise, a fourth-order, zero phase-shift Butterworth low-pass filter was applied to the data, with cut-off frequencies adjusted according to the duration of the prey transport. Finally, three-point floating averages divided by the time between two consecutive frames (0.004 s) yielded velocities in the direction of the X and Y axes.

Prey velocities were determined in the fish-bound frame of reference, primarily because of simplicity: this enabled us, for example, to display prey trajectories and plots of prey velocity *versus* prey position with respect to the fish (see further). Note, however, that differences in the swimming velocity of the fish towards the prey during suction feeding can complicate the interpretation of the fish-bound frame velocity data: forward translation of the head with open mouth and closed branchiostegal and opercular valves causes a positive pressure component inside the mouth cavity (Muller et al., 1982), which reduces the effort needed to expand the head. In other words, a certain amount of compensatory suction (needed to keep the

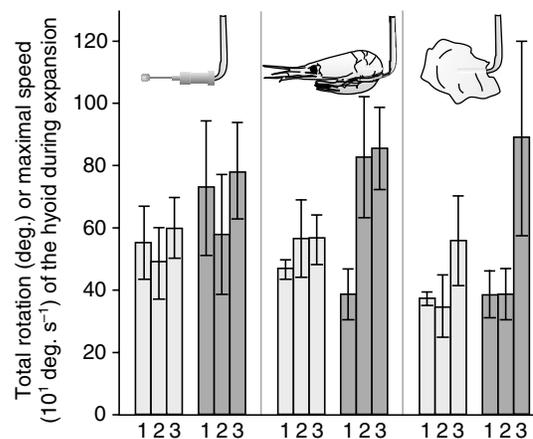


Fig. 4. Comparison of the average magnitude of rotation (light grey) and average peak velocity of hyoid depression (dark grey) for three *C. gariepinus* individuals (1–3) capturing three different prey (illustrated above) during X-ray video recording [kinematic data from Van Wassenbergh et al. (Van Wassenbergh et al., 2005)]. The graph shows that suction effort on the relatively small, spherical prey attached on the tip of a needle (left) is not reduced compared to suction feeding sequences on firmly attached prey (shrimp; middle) or large, voluminous prey pieces (fish; right). Values are means  $\pm$  s.d.;  $N=10$ , 5 and 5 for the three prey, respectively (for each individual).

water and prey motionless in the earth-bound frame) is indirectly powered by the fish's swimming musculature, which facilitates buccal expansion. For the present study on clariid catfishes, however, the animals' velocity in the direction of the prey is always relatively low compared to the measured velocity of the prey in the earth-bound frame (average 7.9% for the three sequences with the fastest prey movement for each individual). Consequently, although minor interspecific differences in approaching speed are observed (mean  $\pm$  standard deviation of  $0.085 \pm 0.011 \text{ m s}^{-1}$  for *C. gariepinus*,  $0.052 \pm 0.015 \text{ m s}^{-1}$  for *G. typus* and  $0.040 \pm 0.011 \text{ m s}^{-1}$  for *C. apus*), these differences will probably have little effect on the results of our study. On the other hand, if this small difference in velocity is due to the fish sucking themselves forward (due to momentum conservation), comparing fish-bound frame velocities of the prey is the most appropriate approach. Given that the head-to-body mass ratio follows the same trend as the approaching speed (highest in *C. gariepinus* and lowest in *C. apus*), the latter situation is a distinct possibility.

The small difference between the density of the prey (average density of  $1029 \text{ kg m}^{-3}$ ) and the density of the water ( $1000 \text{ kg m}^{-3}$ ) implies that the force due to gravitation after the prey is released from the needle is relatively low and may be neglected, given that the velocity of the prey sinking in motionless water after 0.1 s (the approximate maximum duration of prey transport in our catfish) is only  $0.024 \pm 0.002 \text{ m s}^{-1}$  (mean  $\pm$  s.d.;  $N=20$ ). Consequently, the velocity of the prey is almost entirely induced by suction and the prey's velocity profile will adequately reflect the amount of suction generated by the catfish. Furthermore, this gravitational factor is equal for all species and will thus not influence the results of our comparative study.

The species included in the analysis differ in absolute head size: the anguilliform species *G. typus* and *C. apus* have smaller

heads than the more fusiform *C. gariepinus*. If suction performance is subject to scaling effects, then this may influence the results. Scaling data on suction flow velocities in *C. gariepinus* (Van Wassenbergh et al., 2006b) allows us to evaluate the importance of differences in head size on the output of the suction performance experiments described above. Although the results of this study generally did not show significant differences in maximal flow velocities in relation to head size, the average (and thus most likely) scaling relationship shortly posterior to the mouth aperture is a decrease in peak flow velocity with increasing size proportional to (cranial length) $^{-0.24}$ . To account for this, we additionally compared the prey velocity data as a function of cranial length with respect to the scaling relationship of flow velocity for *C. gariepinus* (Van Wassenbergh et al., 2006b).

#### Buccal expansion kinematics

The increase in the volume of the buccal cavity is responsible for the flow of water (and prey) into the mouth. In order to evaluate potential interspecific differences in buccal expansion, the buccal volume increase during suction is modelled using a method similar to the one outlined by Drost and Van den Boogaart (Drost and Van den Boogaart, 1986). The expanding buccal volume is approximated by a series of elliptical cylinders, in which the major and minor axis of each ellipse corresponds to the width and height of the buccal cavity at a certain position along the head's mediosagittal axis. The following data is needed for this: (1) the dimensions of the buccal cavity (i.e. the width and height at specific points along the midsagittal axis), for example from the head in compressed state; and (2) measurements of the changes of these ellipse axes in time during suction feeding.

The first type of data is obtained from lateral and ventral view radiographs of an unexpanded head of each of the species

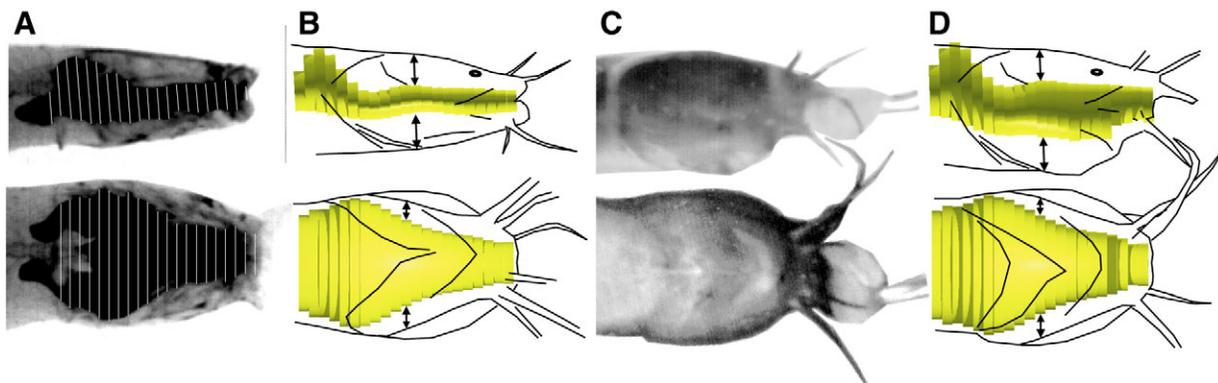


Fig. 5. Illustration of the steps carried out in modelling the buccal volume increase, as a series of 21 elliptical cylinders in *C. apus*. (A) The height and width of the buccal cavity were measured at several positions using X-ray images of the (compressed) catfish head filled with radio-opaque fluid. (B) These measurements were used to construct the elliptical cylinder model for buccal volume, which is assumed to occur inside the catfish's head prior to the start of suction feeding. (C) Next, simultaneous lateral and ventral high-speed videos were recorded of catfish capturing pieces of fish. (D) Finally, by assuming that the thickness of the head tissues bordering the buccal cavity does not change in time (see arrows), the increases in the radii of each elliptical cylinder during suction could be calculated. Note that the part of the hypertrophied jaw adductors extending laterally at the level of the eyes is not included in the external head boundaries as seen from a ventral view (see lower drawings in B and D).

in which the bucco-pharyngeal cavity is filled with a radio-opaque (Barium) fluid (Fig. 5A). The line connecting the upper jaw tip to a point equidistant between the base of the right and left pectoral fin served as the mediosagittal axis. Height and width of the buccal cavity were measured at 21 points equally distributed along this axis. For *C. apus*, which lacks pectoral fins, a fixed point at the approximate position of the pectoral girdle joint was used instead. It was assumed that this situation (i.e. the buccal volume distribution for the preserved specimen at rest) reflects the moment prior to start of the suction event (Fig. 5B).

To obtain the second type of data, high-speed videos were recorded for *C. gariepinus* (two individuals; cranial lengths of 28.4 and 29.5 mm), *G. typus* (one individual; 22.0 mm cranial length) and *C. apus* (two individuals; cranial lengths of 24.5 and 26.0 mm) capturing pieces of cod (*Gadus morhua*) that were pinned onto a plastic coated steel wire (Fig. 4, third type of prey). The recordings were made using a Redlake Imaging Motionscope digital high-speed video camera at 250 frames per second simultaneously in lateral and ventral view on the feeding catfish, using a mirror placed at 45° (Fig. 5C). Two floodlights (600 W) provided the necessary illumination. Three feeding sequences that were approximately perpendicular to the camera lens were selected for each individual. Next, the upper and lower contours of the catfish's head were digitised frame by frame (50 points each) in the lateral and ventral view. At the same time, the coordinates of the mediosagittal axis, described above, were also digitised. The contour coordinates were recalculated in a new frame of reference moving with the fish, with the upper jaw tip as origin and mediosagittal axis as the x-axis. Next, the distance between the corresponding coordinates of the upper and lower contours, and between the left and right contours were extracted at 21 equally spaced intervals along the mediosagittal axis. Digitisation noise was reduced after applying a fourth order, zero phase-shift Butterworth low-pass filter (cut-off frequency of 30 Hz) to the profiles of length and width *versus* time. Finally, buccal volume models were calculated for each video frame by assuming that the thickness of the tissue layer between the internal (buccal cavity) and external (head contours) boundaries of the head

remains constant (Fig. 5B,D). To allow comparison between individuals of different size, all models were isometrically scaled to a length of 25 mm.

### Statistics

In order to test whether the species differ in the maximal suction velocity of the standardised prey, the total distance travelled by the prey, and a variable combining these two aspects of suction performance (peak prey velocity  $\times$  total distance of travel), two-way analyses of variance (ANOVAs) were performed. Unless stated otherwise, the independent variables in these analyses are species (fixed) and individual (nested within species: random).

However, as *G. typus* is represented only by a single data point (i.e. maximum for one individual), a comparison of the maximum prey velocities between the three species studied was not possible. Therefore, two alternative statistical approaches were used. First, only the two species with the most extreme difference in bite performance, *C. gariepinus* and *C. apus*, were compared by ANOVA. In that case, differences between these two species could be analysed if variation between individuals (random effect) is accounted for without the nested design. We also performed a second approach by pooling the individuals from the species with jaw adductor hypertrophy (Figs 1, 2). In this way, maximal suction performance of the powerfully biting catfish (*G. typus* and *C. apus*) was compared to the species with the weakest bite (*C. gariepinus*) using the mixed-model, nested ANOVA-design described above. The significance level of  $P=0.05$  is used. All statistical analyses were performed with SPSS 13.0 (SPSS Inc., Chicago, USA).

## Results

### Suction performance

The clariid species with increased bite capacity (*G. typus* and *C. apus*) do not show a significant decrease in maximal peak velocities or mean peak velocities of standardised prey sucked into the buccal cavity (Fig. 6, Table 1). For example, the highest prey velocity ( $1.15 \text{ m s}^{-1}$ ) along the mediosagittal axis of the catfish's head was observed for *C. apus*, the species also

Table 1. Interspecific comparison of individual means and maxima of peak prey velocities and the total distance travelled by a standardised prey due to suction

	Peak velocity ( $\text{m s}^{-1}$ )		Travel distance (cranial lengths)		Peak velocity $\times$ travel distance ( $\text{m s}^{-1} \times$ cranial lengths)		<i>N</i>
	Mean	Maximum	Mean	Maximum	Mean	Maximum	
<i>C. gariepinus</i>	0.76 $\pm$ 0.04	1.01 $\pm$ 0.07	0.59 $\pm$ 0.02	0.71 $\pm$ 0.03	0.46 $\pm$ 0.01	0.70 $\pm$ 0.05	3
<i>G. typus</i>	0.58	0.97	0.66	0.98	0.40	0.74	1
<i>C. apus</i>	0.70 $\pm$ 0.06	1.04 $\pm$ 0.11	0.63 $\pm$ 0.02	0.80 $\pm$ 0.08	0.44 $\pm$ 0.02	0.74 $\pm$ 0.01	2
<i>P</i> (ANOVA)	0.46* 0.21 <sup>†</sup>	0.82* 0.93 <sup>†</sup>	0.40* 0.20 <sup>†</sup>	0.27* 0.13 <sup>†</sup>	0.54* 0.26 <sup>†</sup>	0.61* 0.50 <sup>†</sup>	

Values are mean  $\pm$  s.e.m.

\*Results from ANOVAs comparing *C. gariepinus* to *C. apus*.

<sup>†</sup>Individuals from the species with high bite performance (*G. typus* and *C. apus*) are pooled and compared by ANOVAs to *C. gariepinus*, the species with the lowest bite force.

capable of producing the highest bite forces (Fig. 2). Even the species for which the lowest maximal prey velocities were measured, *G. typus* ( $0.97 \text{ m s}^{-1}$ ; Fig. 6), still performed better on this aspect of suction performance compared with two out of the three individuals from the least specialised biter *C. gariepinus* (each  $0.94 \text{ m s}^{-1}$ ). Also after correcting for potential scaling effects, maximal peak velocities still do not differ significantly between the species (see Fig. 7).

No significant differences were found between the species in the maximum relative distance (expressed in numbers of cranial lengths) travelled by the prey from the moment of its release from the needle until the end of prey displacement (ANOVA,  $P$  always  $>0.13$ ). Also relative travel distance multiplied by peak prey velocity did not differ significantly between the species (Table 1). This variable can be considered as a combination of the prey velocity magnitude and the

distance (relative to head length) over which a certain prey velocity level is maintained.

#### Buccal expansion

Increases in the volume of the buccal cavity were calculated for a number of suction feeding sequences by modelling (Fig. 8). The largest buccal volume increases were observed for *C. gariepinus* ( $0.76 \pm 0.10 \text{ cm}^3$ ; mean  $\pm$  standard error), the smallest for *G. typus* ( $0.53 \pm 0.07 \text{ cm}^3$ ), and *C. apus* was intermediate ( $0.68 \pm 0.10 \text{ cm}^3$ ). However, if expansion in the lateral direction is removed (by keeping the horizontal radii constant in time), the interspecific differences are considerably reduced ( $0.50 \pm 0.04$ ,  $0.43 \pm 0.08$  and  $0.50 \pm 0.07 \text{ cm}^3$ , respectively). Consequently, a substantial difference is noted in the average amount of volume increase due to lateral expansion ( $0.26 \pm 0.07$ ,  $0.10 \pm 0.08$  and  $0.18 \pm 0.05 \text{ cm}^3$ , respectively).

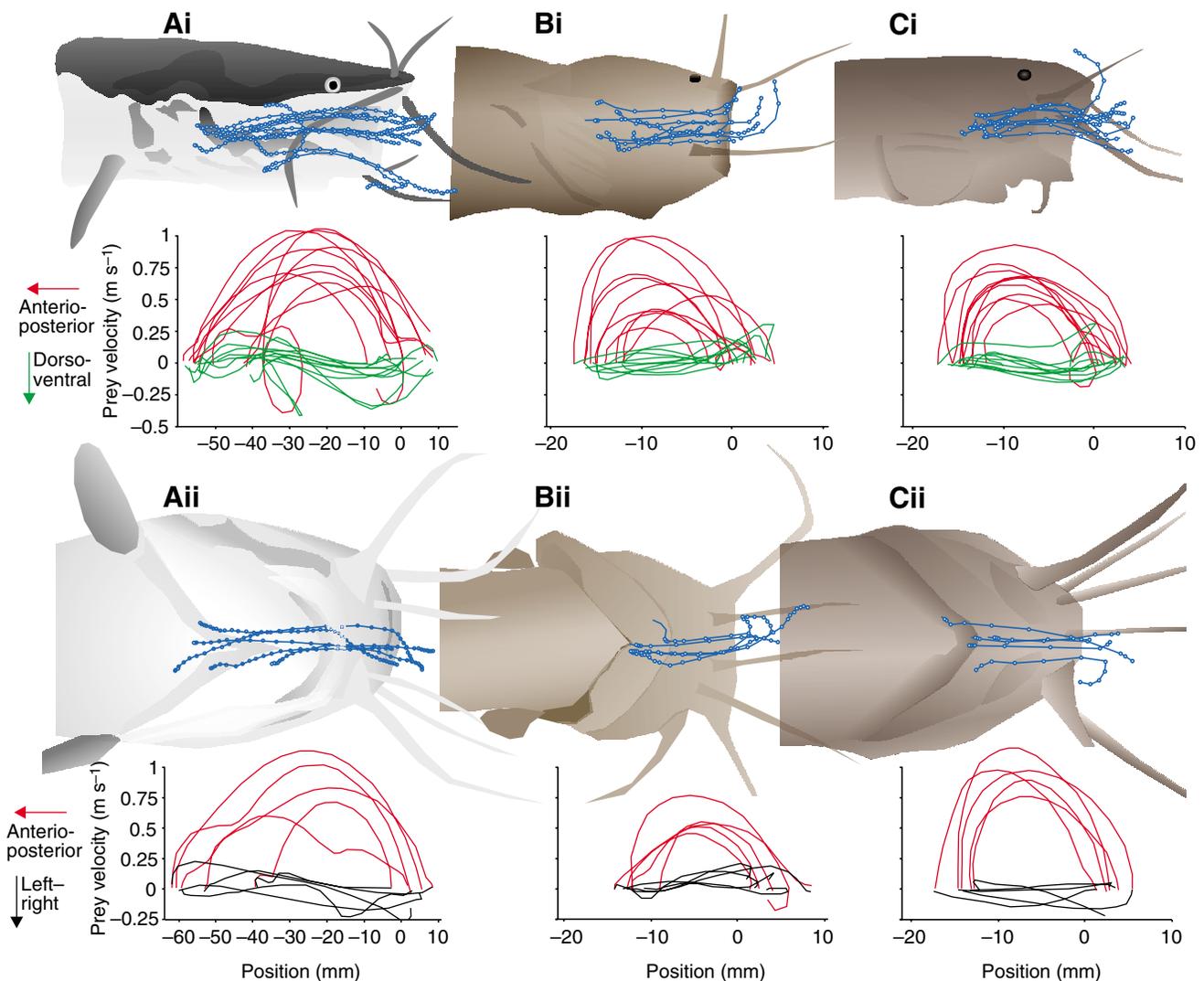


Fig. 6. Lateral (Ai–Ci) and ventral view (Aii–Cii) prey trajectories (blue curves and circles) and the corresponding plots of prey velocities versus prey position (graphs) for an individual of each species with the highest suction performance (A: *C. gariepinus*, B: *G. typus* and C: *C. apus*). Prey velocities and positions are in the fish-bound frame of reference. Colour codes and positive directions of the velocities are explained on the left side of the graphs.

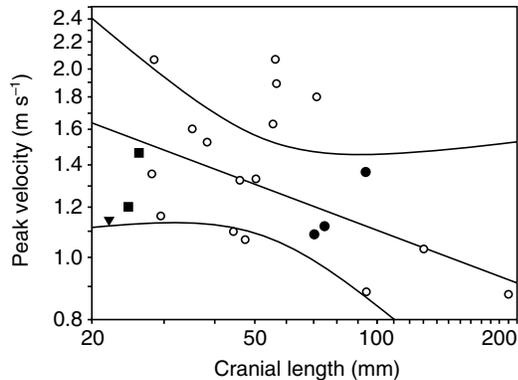


Fig. 7. Logarithmic plot of peak prey velocities as a function of cranial length (individual maxima of unfiltered data; filled black symbols) and the scaling relationship (least-squares regression with 95% confidence limits) of peak flow velocities (white circles) (from Van Wassenbergh et al., 2006b). *C. gariepinus* is represented by circles, *G. typus* by the triangle and *C. apus* by squares. No significant interspecific differences between *C. gariepinus* and *C. apus* were found for the residuals of peak prey velocities with respect to the scaling relationship (ANOVA,  $P=0.41$ ).

### Discussion

Suction feeding and biting generally require conflicting morphological adaptations to the cranial system in fishes (Barel, 1983). The short and robust oral jaws of specialized biters (e.g. Turingan and Wainwright, 1993; Friel and Wainwright, 1999; Albertson et al., 2003) as opposed to long, highly protrusible jaws of some specialized suction feeders (e.g. Motta, 1984; Westneat, 1989; Ferry-Graham et al., 2002) are a well-studied example of this. Given the diversity in food characteristics, it is therefore not surprising that the mode of feeding (suction or biting) is usually reflected in the fishes' diet, which in turn can often be predicted fairly well from morphology (Sibbing and Nagelkerke, 2001).

However, developing a certain morphological or behavioural

modification to increase bite performance (e.g. enabling the fish to crush hard prey) does not necessarily imply a reduced performance in capturing other, maybe less available or less preferred prey types by suction. This will only be the case if every possible option to increase this bite performance (e.g. increasing jaw adductor cross-sectional area, increasing the moment arms of the lower jaw closing leverage or increasing the strength of the oral jawbones) reduces suction feeding performance. Consequently, although it is obvious that the optimal design for a biter and a suction feeder are different (illustrated by the extreme morphologies of specialists), it may still be possible that some adaptations for biting do not compromise suction performance. Unfortunately, very little is known about potential interferences between the system causing buccal expansion and the system producing bite forces. Therefore, an important goal is to identify evolutionary pathways of specialisation towards biting or suction feeding and their respective functional consequences. We may learn from this to what extent biting and suction feeding can be combined efficiently.

The result of the present study on clariid catfishes exemplifies the possibility of increasing bite performance considerably (Fig. 2) without substantially compromising suction performance (Figs 6, 7; Table 1). The anguilliform species with hypertrophied jaw adductors, *G. typus* and *C. apus*, are able to produce bite forces that are, respectively, more than five and 11 times larger than *C. gariepinus* (Fig. 2) (Herrel et al., 2002). However, these species still manage to accelerate a standardised prey to similar velocities during suction feeding. A logical question following these observations is: 'why doesn't biting performance trade-off with suction performance in these Clariidae?'

A functionally important characteristic of Clariidae is their dorsoventrally flattened heads (Figs 1, 5). Alexander (Alexander, 1970) recognised that fishes with this type of head shape predominantly rely on ventral expansion (i.e. depression) of the buccal cavity for suction feeding, and less on lateral

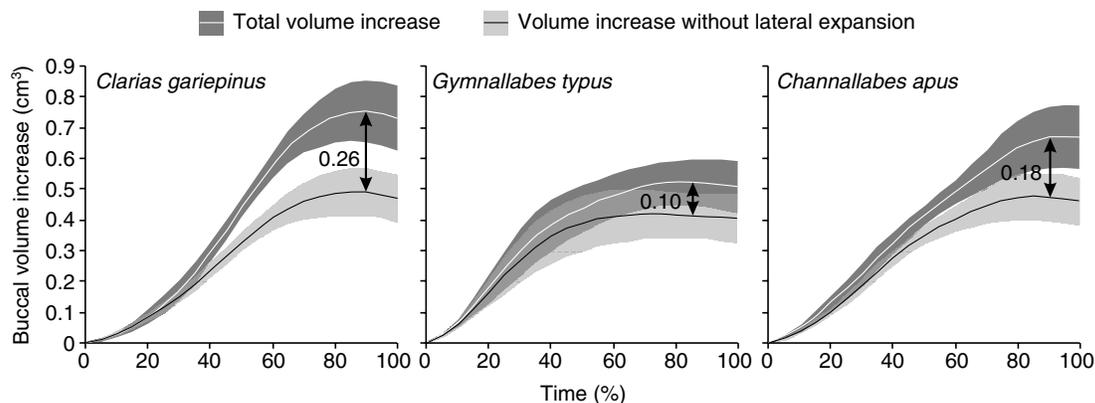


Fig. 8. Increase in the volume of the bucco-pharyngeal cavity during suction feeding calculated using ellipse models (see also Fig. 5). The 100% relative time ( $x$ -axis) corresponds to one frame after maximal volume. All models are scaled to a length of 25 mm. In addition to the total volume increase (ventral and lateral expansion), also the volume increase due to only ventral expansion is shown (legend above graphs). Shaded areas indicate standard errors. The arrows indicate the volume increase due to lateral expansion.

expansion (i.e. suspensorium abduction). Our modelling of the volume increase of the buccal cavity during expansion in Clariidae supports this: if only ventral expansion occurred (on average) 74% of the total observed volume increase would still have been reached, whereas lateral expansion only would result in 20% of the total expansion (the remaining 6% is due to the interaction between both directions of expansion). Clariidae differ in this aspect from the more laterally flattened cichlid fishes, the group for which the trade-off between biting and suction has been studied most intensively (Barel, 1983; De Visser and Barel, 1996; De Visser and Barel, 1998; Bouton et al., 1998; Bouton et al., 1999). It has been proposed for cichlid fishes that in order to accommodate thicker jaw adductor muscles (increasing bite force) the cichlid's head has to widen, which implies a lateral displacement of the touching point between the hyoid and the suspensorium. This displacement increases the angle between the hyoid bars, which in turn would reduce the optimality of the starting position of the hyoid (De Visser and Barel, 1996). However, the morphological modification causing this trade-off for cichlid fishes, i.e. widening of the head as a result of jaw adductor hypertrophy, does not occur in Clariidae [for illustrations see Herrel et al. (Herrel et al., 2002)]. In these catfishes, the neurocranial roof has been reduced to a small, medial ridge of bones, which makes room available for the jaw adductor muscles to 'bulge' dorsolaterally from the head without the need for adjusting the spatial configuration of the hyoid-suspensorium apparatus. In addition, the suprapreopercle and the fourth infraorbital bones, positioned respectively at the posterior and anterior margins of the jaw adductors, have reduced considerably (Cabuy et al., 1999; Devaere et al., 2001).

As no factors of potential interference between the systems for hyoid depression (i.e. caudoventral rotation of the hyoid bars and the pectoral girdle, coupled by the sternohyoideus muscle) and the adaptations for increasing bite force can be identified in Clariidae, it is not surprising that no interspecific differences in the volume increase due to ventral expansion are observed in these catfishes (Fig. 8). However, especially in *G. typus*, but also in *C. apus*, the contribution to the total volume increase by lateral expansion (i.e. suspensorium abduction) does seem to be restricted with respect to the species without the hypertrophied jaw muscles, *C. gariepinus* (Fig. 8). Consequently, the increase in bite performance may interfere with the capacity of abduction (lateral swing) of the suspensoria. This was also concluded previously from a study comparing the prey capture kinematics of *C. gariepinus* with a species with a moderate degree of jaw adductor hypertrophy, *Clariallabes longicauda* (Van Wassenbergh et al., 2004). Two reasons have been suggested to explain this reduced lateral expansion. Firstly, a considerable increase of the visco-elastic jaw adductor mass inserting both on the suspensorium and the neurocranium may passively constrain the lateral swing of the suspensorium. Secondly, a stronger and increasingly interdigitated connection of the suspensorium with the neurocranium may be needed in order to resist the large reaction forces and moments caused by the large bite forces

exerted onto prey. This more firmly 'locking' of the suspensorium associated with adductor mandibulae hypertrophy has been observed in all Clariidae (Cabuy et al., 1999; Devaere et al., 2001; Herrel et al., 2002) and could therefore restrict the suspensorium in rotating laterally. However, despite this reduction in lateral expansion capacity (Fig. 8), the overall effect of this on maximal suction feeding performance is apparently negligible (Figs 6, 7, Table 1).

In conclusion, the results of our study comparing species from two evolutionary lineages of Clariidae demonstrates that convergent morphological evolution toward increasing bite performance does not necessarily lead to a reduced suction feeding performance. This is in contrast to what has been proposed for other groups of fishes (Barel, 1983). Clariid catfishes have dorsoventrally flattened heads and predominantly rely on ventral expansion of the buccal cavity to produce suction. We hypothesise that potential spatial constraints by increasing the jaw adductor size on the buccal expansion system is avoided by the narrowing of the roof of the neurocranium, enabling the jaw adductors to develop freely in the dorsolateral region of the head without interfering with the depression of the hyoid. Although a reduced capacity of lateral expansion (suspensorium abduction) is observed in the powerfully biting species (presumably due to passive resistance of the jaw adductor mass spanning the suspensorium and/or the strengthened articulation of the suspensorium with the neurocranium) the contribution of this lateral expansion to the total buccal expansion is relatively limited and, probably for this reason, does not result in a reduced suction capacity.

The authors gratefully acknowledge support of the Special Research Fund of the University of Antwerp. The research was further supported by a FWO grant 6.0388.00. A.H. and S.V.W. are postdoctoral fellows of the fund for scientific research – Flanders (FWO-VI).

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