

Suction power output and the inertial cost of rotating the neurocranium to generate suction in fish

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1 **Highlights**

- 2 • Neurocranial rotation dynamics of fish is described by an inverse dynamic model.
- 3 • The inertial cost of accelerating the neurocranium is small in largemouth bass.
- 4 • Kinetic energy of the neurocranium is probably converted into suction work.
- 5 • Suction performance is not limited by cranial mass in generalized percomorph fish.

6 **Abstract**

7 To expand the buccal cavity, many suction-feeding fishes rely on a considerable contribution
8 from dorsal rotation of the dorsal part of the head including the brains, eyes, and several
9 bones forming the braincase and skull roof (jointly referred to as the neurocranium). As the
10 neurocranium takes up a large part of the total mass of the head, this rotation may incur a
11 considerable inertial cost. If so, this would suggest a significant selective pressure on the
12 kinematics and mass distribution of the neurocranium of suction feeders. Here, an inverse
13 dynamic model is formulated to calculate the instantaneous power required to rotate the
14 neurocranium, approximated by a quarter ellipsoid volume of homogeneous density, as well
15 as to calculate the instantaneous suction power based on intra-oral pressure and head volume
16 quantifications. We applied this model to largemouth bass (*Micropterus salmoides*) and
17 found that the power required to rotate the neurocranium accounts for only about 4% of the
18 power required to suck water into the mouth. Furthermore, recovery of kinetic energy from
19 the rotating neurocranium converted into suction work may be possible during the phase of
20 neurocranial deceleration. Thus, we suggest that only a negligible proportion of the power
21 output of the feeding muscles is lost as inertial costs in the largemouth bass. Consequently,
22 the feeding performance of piscivorous suction feeders with generalised morphology,
23 comparable to our model species, is not limited by neurocranial motion during head

1 expansion. This suggests that it is thus not likely to be a factor of importance in the evolution
2 of cranial shape and size.

3 **Key Words:** biomechanics, inverse dynamics, prey capture, cranium

4 **1. Introduction**

5 Many aquatic vertebrates rely on generating a flow of water from the external environment
6 into the mouth to capture prey (e.g., Lauder and Schaffan, 1993). Conservation of mass and
7 the incompressibility of water dictate that any expansion of the buccopharyngeal cavity will
8 generate a flow of water. During this process, which is typically referred to as suction
9 feeding, prey items situated in the flow field in front of the mouth will experience
10 hydrodynamic forces (Holzman et al., 2007; Skorczewski et al., 2010; Wainwright and Day,
11 2006). These forces are associated with highly unsteady water flows: adult suction feeders
12 generally manage to accelerate water and prey from standstill to over 1 m s^{-1} in less than 0.05
13 s (Higham et al., 2006a; van Leeuwen, 1984; Van Wassenbergh et al., 2007a). In order to
14 maximize suction feeding success on prey adhering to the substrate or trying to escape, the
15 sudden increase in flow velocity in front of the mouth must be maximized. In other words,
16 suction feeders must transfer as much kinetic energy to the water in the shortest possible
17 amount of time. Consequently, to maximise prey capture performance, suction feeders must
18 maximise instantaneous power.

19 To generate this power, fish mainly rely on contraction of the voluminous post-cranial
20 musculature (Aerts, 1991; Camp and Brainerd, 2014; Carroll and Wainwright, 2006;
21 Coughlin and Carroll, 2006; Muller, 1987; Thys, 1997; Van Wassenbergh et al., 2007b).
22 This musculature consists of hypaxial (ventral to the vertebral column) and epaxial (dorsal to
23 the vertebral column) components (Fig. 1A). Contraction of the hypaxial muscles rotates the
24 pectoral girdle posteriorly, while contraction of the epaxial muscles induce a dorsal rotation

1 of the neurocranium (Fig. 1B). Despite rotating different skeletal elements, the role of
2 hypaxial and epaxial muscle contractions in suction generation is identical: they both increase
3 the angle between the pectoral girdle and the neurocranium, which in turn causes a
4 displacement of the “roof” and the “floor” of the mouth cavity away from each other. This
5 separation increases the buccopharyngeal volume. The increased angle between pectoral
6 girdle and neurocranium results in an additional complex sequence of coupled motions of the
7 hyoid arch and lower jaw which push on the ventral side of the mouth cavity tissues, and
8 which via the hyoid also enforce widening of the head by suspensorium abduction (Aerts,
9 1991; De Visser and Barel, 1996; Muller, 1989). Although relatively small cranial muscles
10 such as the *sternohyoideus*, *protractor hyoideus*, *levator arcus palatini*, and *levator operculi*
11 probably assist in powering suction (e.g., Osse, 1968), their cumulative mass, and thus
12 potential contribution to power generation, is small compared to the hypaxials and/or epaxials
13 (Carroll and Wainwright, 2009).

14 Not all power produced by the feeding musculature will result in water acceleration: an
15 unknown amount of the muscle’s power output will be lost due to the musculoskeletal
16 mechanics underlying suction generation. Examples are joint friction, stretching of skin,
17 resistive stress in the adductor muscles (e.g. *adductor mandibulae* during mouth opening),
18 hydrodynamic resistance at the external head surfaces, and the inertia of the elements
19 involved in expanding the buccopharyngeal cavity. A study on suction feeding of the catfish
20 *Clarias gariepinus* estimated that inertial force (integral over the entire buccopharyngeal
21 cavity of acceleration multiplied by mass of the displaced tissues) is about 10% of the
22 pressure force on the buccopharyngeal cavity surfaces (Van Wassenbergh et al., 2005).
23 However, as *C. gariepinus* relies almost entirely on ventral depressions of the floor of the
24 mouth cavity to generate suction, *C. gariepinus* is atypical compared to many other suction

1 feeders (Gibb and Ferry-Graham, 2005) in showing (on average) no rotation of the
2 neurocranium.

3 Dorsorotation of a large neurocranial mass for generating buccopharyngeal expansion may
4 require an important fraction of the power budget of suction feeding. Of the potential sources
5 of power loss identified above, it is the most conspicuous candidate as it is both massive and
6 experiences large accelerations. In adult fishes, the functional unit referred to here as
7 “neurocranium” typically includes a strongly ossified protective braincase and the brain, the
8 eyes surrounded by the circumorbital bones, and anterior bony elements such as the rostrum,
9 ethmoid, and vomer. During suction feeding, the neurocranium is rotated along with the
10 suspensoria, upper oral and pharyngeal jaws attached to it. Measurements of *Micropterus*
11 *salmoides* (*largemouth bass*), for example, show that the mass of this functional unit equals
12 approximately 60% of the total cranium (including sternohyoideus and cleithrum).

13 Given the importance of feeding success for survival, a considerable inertial cost to rotate the
14 neurocranium would imply a significant selective pressure on the shape and size of the
15 neurocranium (or more specifically on the pitching moment of inertia about the instantaneous
16 center of neurocranial rotation). Alternatively, recruitment of only the relatively light-weight,
17 ventro-lateral series of skeletal elements by the hypaxial muscles for generating suction
18 power would probably be favoured in case evolution has resulted in a neurocranium that is
19 too heavy to retain a reasonable power efficiency (e.g. inertial losses divided by
20 hydrodynamic power output). Unfortunately, the relative importance of the inertial cost of
21 neurocranial elevation is currently unknown. Yet, this mechanical insight seems essential to
22 better understand the functional morphology and kinematics of suction feeding fish.

23 To determine to what extent inertial costs of rotating the neurocranium affect suction
24 performance, we address the following aims: (1) formulate an inverse dynamic model for

1 estimating the instantaneous power requirement for rotating the neurocranium as observed on
2 lateral-view high-speed videos, (2) establish a theoretical framework and mathematical
3 models for calculating the total hydrodynamic power of suction feeding from different
4 sources of experimental data and model simulations, (3) evaluate the results of these models
5 for suction feeding in a species with a generalized percomorph trophic habit (*Micropterus*
6 *salmoides*).

7 **2. Methods**

8 *2.1 Inverse dynamic model of neurocranial rotation*

9 To calculate the inertial power required to rotate the neurocranium, the following
10 mathematical model is used. The shape of the neurocranium is modeled as a quarter of an
11 ellipsoid. This shape is chosen since elliptical cross-sections have proven to fit the external
12 contours of fish relatively accurately (Drost and van den Boogaart, 1986), and ellipsoids can
13 capture the anterior narrowing of a streamlined head. By setting l (length), h (height) and w
14 (width) as the dimensions of the neurocranium (Fig. 2), the volume (V) of the quarter
15 ellipsoid model of the neurocranium is

$$16 \quad V = \frac{1}{4} \frac{4}{3} \pi l h \frac{w}{2} = \frac{1}{6} \pi l h w \quad (1).$$

17 Assuming a uniform density (ρ) of the tissues filling this quarter ellipsoid, its mass (m) equals

$$18 \quad m = \frac{1}{6} \pi l h w \rho \quad (2).$$

19 Assigning the origin of an orthogonal coordinate frame to the center of the full ellipsoid (x -
20 axis = posterior-anterior; y -axis = ventral-dorsal; z -axis = left-right; Fig. 2) results in a
21 location of the center of mass (COM) of the quarter ellipsoid at point $(3l/8, 3h/8, 0)$. The

1 moment of inertia for rotation about the z -axis through the origin of this coordinate frame
 2 (i.e., pitching about the base corner of the quarter ellipsoid) can be derived (e.g. Landau and
 3 Lifshitz, 1976):

$$4 \quad I_{origin} = \frac{\rho l h w \pi}{30} (l^2 + h^2) \quad (3).$$

5 Using the parallel axis theorem we have the following result:

$$6 \quad I_{COM} = I_{origin} - m d_{origin}^2 \quad (4)$$

$$7 \quad I_{cr} = I_{COM} + m d_{cr}^2 \quad (5)$$

8 , where d is defined as the distance from the center of mass to the specified point, cr refers to
 9 center of rotation and $origin$ is the initial position of the corner of the quarter ellipsoid (z -axis,
 10 Fig. 2). Combining equations 2-5 results in

$$11 \quad I_{cr} = m \left(\frac{l^2 + h^2}{5} + d_{cr}^2 - d_{origin}^2 \right) \quad (6)$$

12 , where I_{cr} corresponds to the modeled moment of inertia for the observed pitch rotation of
 13 the neurocranium. Although the position of the center of rotation can shift during head
 14 rotation in fish (e.g. de Lussanet and Muller, 2007), we are forced to use the average center of
 15 rotation of the entire phase of head rotation because the spatial resolution of the lateral-view
 16 image does not allow a reliable determination of cr for smaller time steps. In our case, point
 17 cr is determined from two video images: one just before, and one just after completion of
 18 head rotation. The positions before and after rotation of two anatomical landmarks (e.g.
 19 dorsal tip of the snout, eye or opercular) are connected by lines. Next, lines are drawn
 20 perpendicular to the midpoint of each of these lines, and their intersection defines cr (Fig

1 2B). Since the latter procedure is only valid if translation is zero, in case of significant
2 forward locomotion it is necessary to align the trunk of the fish (e.g. pelvic and dorsal fins)
3 on the two analyzed images.

4 According to Newton's second law for rotation, the instantaneous moment required to
5 overcome the effects of inertia $M_{nc(t)}$ is given by

$$6 \quad M_{nc(t)} = -I_{cr} \ddot{\alpha}_{(t)} + M_{am(t)} \quad (7)$$

7 , where $\ddot{\alpha}_{(t)}$ is the instantaneous angular acceleration of neurocranial rotation, and $M_{am(t)}$ the
8 added mass moment (i.e. the moment needed to accelerate the volume of water immediately
9 surrounding the neurocranium). Moments resisting the dorsal rotation (= a positive angular
10 velocity according to right-hand rule with the coordinate system of Fig. 2A) are defined as
11 negative.

12 The moment required to overcome drag force on the quarter-ellipsoid neurocranium, $M_{drag(t)}$,
13 will also be calculated. This drag force results from the flow that moves over the dorsally
14 rotating neurocranium. A certain fraction of this moment is contributing to repositioning of
15 water at the mouth entrance, for example at the snout tip, which can be regarded as part of the
16 generated flow used to capture the prey. However, the other fraction will move water in a
17 direction (e.g. deflecting laterally) that is not useful for prey capture, and could be regarded
18 as a cost in addition to the inertial costs of eq. 7. Because of this ambiguity to classify drag
19 force either as a hydrodynamic cost or benefit to suction feeding, we will discuss $M_{drag(t)}$ as a
20 separate factor. Note, in this respect, that this moment is probably very small (Van
21 Wassenbergh et al. 2005).

1 Since power equals the scalar product of the moment and angular velocity vectors, the power
2 required to overcome neurocranial rotation inertia $P_{nc(t)}$ and external hydrodynamic resistance
3 is

$$4 \quad P_{nc(t)} = \mathbf{M}_{nc(t)} \cdot \dot{\boldsymbol{\alpha}}_{(t)} \quad (8)$$

5 , where $\dot{\boldsymbol{\alpha}}_{(t)}$ is the instantaneous angular velocity of neurocranial rotation. Negative values of
6 power from this equation denote a cost of power that needs to be delivered by the muscles.

7 *2.2 CFD estimates of quarter ellipsoid drag and added mass moment coefficients*

8 The moment required to overcome drag forces and acceleration reaction forces (i.e. added
9 mass) exerted on an elevated quarter of a full ellipsoid that rotates about a principal axis are
10 calculated using computational fluid dynamics (CFD) software. To do so, ellipsoids
11 consisting of four quarters of non-uniform rational B-splines (NURBS) surfaces are
12 constructed using VRMesh 5.0 Studio (VirtualGrid, Bellevue City, USA). The length radius
13 of the ellipsoids is always 50 mm, and 49 combinations of the width and height (as defined in
14 Fig. 2A) of 5, 10, 20, 40, 80, 160 and 320 mm were used. NURBS ellipsoids are imported
15 into ANSYS DesignModeler 14.5.7 (Ansys Inc., Canonsburg, USA) to be surrounded by a
16 spherical flow domain of 300 mm for the smaller ellipsoids, and 1000 mm for the ellipsoids
17 with radii of 160 mm or 320 mm. The flow domain was meshed using Ansys Meshing
18 14.5.7. In the absence of a formal convergence study, a comparison of moment output from a
19 low density (0.17 million cells) and high density mesh (1.1 million cells) with comparable
20 time step scaling showed an underestimation by 7 ± 5 % (mean \pm s.d.), indicating that the
21 level of accuracy of the low-density mesh is sufficient considering the explorative nature of
22 this study. In Ansys Fluent 14.5.7, the ellipsoids are subjected to three constant
23 accelerations, representing a situation with slow, medium and high head acceleration for

1 feeding fish: (1) $5000 \text{ }^\circ \text{ s}^{-2}$ (time step size = 0.002 s; number of time steps = 120; final
2 velocity = $1200 \text{ }^\circ \text{ s}^{-1}$; angle rotated = 144 °), (2) $25000 \text{ }^\circ \text{ s}^{-2}$ (time step size = 0.0004 s;
3 number of time steps = 120; final velocity = $1200 \text{ }^\circ \text{ s}^{-1}$; angle rotated = 28.8 °), and (3)
4 $100000 \text{ }^\circ \text{ s}^{-2}$ (time step size = 0.0001 s; number of time steps = 120; final velocity = $1200 \text{ }^\circ \text{ s}^{-1}$;
5 angle rotated = 7.2 °). Simulations are unsteady, viscous (i.e. full Navier-Stokes equations
6 solved) laminar flow models, where the mesh of the entire flow domain is rotated at constant
7 acceleration with respect to the fixed reference frame. The outer boundary of the sphere is
8 defined as a pressure outlet. The ellipsoid surfaces have no-slip boundary conditions.

9 The relative contribution of drag (a velocity dependent factor) and added mass (an
10 acceleration dependent factor) are derived from the slope and intercept of least-squares
11 regression fitted to the calculated hydrodynamic moment at a quarter spheroid surface (more
12 specifically the average of the two representative quarters) divided by water density ($\rho =$
13 1000 kg m^{-3}) and head length to the fifth power *versus* the square of instantaneous velocity
14 (Fig. 3). We use the average slope of the three accelerations as an estimate of the moment
15 per squared radian s^{-1} (= dimensionless drag moment coefficient C_{M_drag}) and the average of
16 the three y-axis intercepts divided by their respective acceleration as the moment per radian s^{-2}
17 (= dimensionless added mass moment coefficient C_{M_am}). This allows us to calculate the
18 instantaneous external moment on the quarter ellipsoid due to drag by

$$19 \quad \mathbf{M}_{drag(t)} = -C_{M_drag} l^5 \rho \dot{\alpha}_{(t)} \left| \dot{\alpha}_{(t)} \right| \quad (9)$$

20 , and the moment due to acceleration of the added mass by

$$21 \quad \mathbf{M}_{am(t)} = -C_{M_am} l^5 \rho \ddot{\alpha}_{(t)} \quad (10)$$

22 , where l is the head length of the specimen. The scaling relationships proportional to l^5 are
23 validated by isometrically doubling the size of one of the CFD models. Note that, in contrast

1 to the inertial term in eq. (7) which can be calculated for any given left-right axis, eq. (9) as
2 well as eq. (10) imply the rotation occurs about an axis through the corner of the quarter
3 ellipsoid (origin in Fig. 2B) for calculating the external hydrodynamic resistance. We are
4 forced to make this assumption to avoid excessive complication of the model. Note also that
5 the flow regime (i.e., the importance of viscous *versus* inertial effects as captured in the
6 Reynolds number) of the presented drag (Table 1) and added mass moment coefficients
7 (Table 2) corresponds to typical speed and sizes ranges of adult fish, and may therefore not
8 be applicable to individuals with a head length considerably smaller or larger than 50 mm.

9 2.3 Inverse dynamic calculation of suction power

10 Suction power output can be assessed using the hydrodynamic resistance experienced by the
11 intra-oral mouth-cavity surfaces moving outward while generating the suction flow (Aerts,
12 1991; Carroll et al., 2006; de Jong et al., 1987; Van Wassenbergh et al., 2005). Consider a
13 given cross-section of the buccal cavity (Fig. 4). The intra-oral curve of this cross-section
14 that borders the buccal cavity can be divided into chord segments of infinitesimal length dc
15 (Fig. 4). This cross-sectional chord dc will form a surface segment parallel with the x -axis by
16 multiplying it with dx , a vector running parallel with the x -axis. The surface area of this
17 segment is $dc dx$, while the direction of this surface will be given by the surface normal unit
18 vector \hat{s} which we arbitrarily point away from the buccal cavity center. To generate suction,
19 this surface element will move outward (i.e. away from the buccal cavity center) in the cross-
20 sectional plane by a translation of $d\mathbf{r}$ (Fig. 4).

21 Two types of hydrodynamic forces will be exerted on this surface element: pressure forces
22 and shear forces. Pressure forces act normal to the surface, while shear forces are parallel
23 with the surface. As a given movement causing expansion $d\mathbf{r}$ per definition will be
24 perpendicular to the surface (e.g. as in a radial expansion of a cylinder, but the same

1 relationships would also apply to axially expanding surfaces such as the retracting piston
 2 crown in a cylinder), only pressure forces need to be accounted for in our inverse dynamic
 3 calculation to resolve power (since only force components parallel with the displacement
 4 require power). In our model, we assume that the no pressure force is exerted at the non-
 5 wetted side of our intra-oral surface element. In this way, only the intra-oral gauge pressure
 6 p_g (i.e. measured pressure – hydrostatic pressure) needs to be considered. Previous
 7 computational studies have shown that p_g is uniform along a single cross-section (Van
 8 Wassenbergh and Aerts, 2009). Although a limited amount of variation along the length of
 9 the buccopharyngeal cavity is possible (Lauder, 1983; Van Wassenbergh and Aerts, 2009),
 10 we assume that the average pressure, as measured in-vivo somewhere central in the mouth
 11 cavity, is applying uniformly over the entire cavity. Pressure force \mathbf{F}_p on the surface segment
 12 is given by

$$13 \quad \mathbf{F}_{p(t)} = p_{g(t)} dc_{(t)} dx \hat{\mathbf{s}} \quad (11)$$

14 , so that the instantaneous suction power $P_{s(t)}$ required to generate the opposite force ($-\mathbf{F}_{p(t)}$)
 15 and thereby achieving a dynamic equilibrium is calculated as

$$16 \quad P_{s(t)} = -p_{g(t)} \hat{\mathbf{s}} \cdot \frac{d\mathbf{r}_{(t)}}{dt} dc_{(t)} dx \quad (12).$$

17 Since the expansive motions are perpendicular to the intra-oral surface, $\hat{\mathbf{s}} \cdot d\mathbf{r}_{(t)}$ equals the
 18 scalar $dr_{(t)}$. Integrated over the entire buccopharyngeal surface area, total instantaneous
 19 suction power $P_{s(t)}$ is

$$20 \quad P_{s(t)} = -p_{g(t)} \int_{\text{anterior}}^{\text{posterior}} \oint \frac{dr_{(t)}}{dt} dc_{(t)} dx \quad (13)$$

21

1 The total instantaneous expansion volume of the buccal cavity $dV_{buccal(t)}$ equals

2

$$3 \quad dV_{buccal(t)} = \int_{\text{anterior}}^{\text{posterior}} \oint dr_{(t)} dc_{(t)} dx$$

4 (14).

5 Thus, equation 13 can be rewritten as

$$6 \quad P_{s(t)} = -p_{g(t)} \frac{dV_{buccal(t)}}{dt} \quad (15)$$

7 This implies that instantaneous suction power can be calculated if the temporal profiles of
8 intra-oral pressure and increase in head volume are known. Note that eq. (15) assumes
9 pressure to be distributed uniformly over the entire buccal cavity surface. Positive numbers
10 of $P_{s(t)}$ require power input from the musculature causing buccal expansion, negative values
11 of $P_{s(t)}$ mean that the buccal surface motion is driven by energy of the water flow relative to
12 the fish.

13 2.4 Morphology

14 Three *Micropterus salmoides* specimens (standard lengths 127, 140, and 190 mm) are used to
15 determine the geometry of the model. Neurocranium length (l) is measured as the distance
16 along the centerline of the body from the rostral tip of the premaxilla up to the level of the
17 anteriormost point on the pectoral fin base. The latter point also serve as the location where
18 neurocranium width (w) is measured. Next, dissecting along the frontal plane through the tip
19 of the premaxilla, the neurocranium (*sensu lato*; also including dorsal parts of the suspensoria
20 and opercula) is removed and weighed. Assuming a tissue density of 1000 kg m^{-3} , the
21 neurocranium height (h) is determined so that the calculated mass of the quarter ellipsoid

1 formed by l , w and h (Fig. 2) matches the measured mass. The data from the three specimens
2 are then averaged and normalized to neurocranium length (l). The best-fitting height position
3 of the quarter ellipsoid is determined by overlaying this model with lateral-view photographs
4 of one of the specimens. These morphological input variables are scaled isometrically to the
5 size of the individuals from which the kinematic data were collected.

6 2.5 Kinematics

7 Kinematics of four *Micropterus salmoides* individuals feeding on small goldfish suspended
8 by a small wire are analyzed (one strike per individual). The *M. salmoides* individuals are
9 filmed in 200 liter tanks using a high-speed NAC Memrecam Ci digital system (Tokyo,
10 Japan) operating at 500 images s^{-1} . Lateral and ventral views of the feeding events are
11 obtained via a mirror underneath the prey oriented at 45° . Two floodlights (600 W) on either
12 side of the camera illuminate the experimental tank.

13 Anatomical landmark positions are determined frame-by-frame to calculate gape distance and
14 neurocranium angle. Gape distance is defined as the distance between the tip of the
15 premaxilla and the tip of the dentary. Four landmarks that are approximately evenly
16 distributed along the dorsal contour of the neurocranium on the lateral-view images are used
17 to calculate the angle of the neurocranium with respect to the earth-bound frame of reference.
18 Digitization noise is reduced by applying a low-pass fourth-order zero phase-shift
19 Butterworth filter (cut-off frequency of 40 Hz) to the raw data. Time-derivatives for
20 calculating angular velocities and accelerations of the neurocranium use the difference
21 between one frame before and one frame after a given instant. A center of head rotation is
22 estimated as described earlier (see Fig. 2B) for each of the four feeding sequences. However,
23 we choose to use the centroid of these four coordinates as the rotation center (cr) in our
24 model to reduce random uncertainty in the estimation of the individual rotation centers.

1 The instantaneous volume of the head is determined using the ellipse method (Drost and van
2 den Boogaart, 1986) in which the expanding head volume is approximated by a series of
3 elliptical cylinders, in which the major and minor axis of each ellipse corresponds to the
4 width and height of the head at a certain position along the head's mediosagittal axis. The
5 upper and lower contours of the head of the largemouth bass are digitized frame-by-frame (20
6 points each) in lateral and ventral view. At the same time, the coordinates of the
7 mediosagittal axis are also digitized. The contour coordinates are recalculated to a new frame
8 of reference moving with the fish. Next, the distance between the left and right contours are
9 extracted at 21 equally spaced intervals along the mediosagittal line between upper jaw tip
10 and a point in between the tips of the opercula. Similar to the procedure outlined for the
11 standard kinematical analysis, digitization noise is reduced using a Butterworth filter
12 algorithm applied to the profiles of length and width versus time. As the volume of head
13 tissues will not change during suction generation, the instantaneous change in external head
14 volume will equal the instantaneous change in the volume of the buccal cavity ($dV_{buccal(t)}$).

15 *2.6 Pressure*

16 As synchronized recordings of buccal pressure and dual-view high-speed videos are not
17 available to us, pressure profiles of *M. salmoides* are derived from the literature. This is
18 possible since previous studies showed that both the timing and magnitude of pressure can be
19 predicted (within a certain range of uncertainty) based on the kinematic profile of mouth
20 opening (i.e. gape). The time at which the peak negative pressure in *M. salmoides* is reached
21 typically occurs midway between the times the gape reaches 20% and 95% of the maximum
22 gape observed during a strike (Day et al., 2007; Higham et al., 2006b). The pressure
23 magnitude then drops to approach zero (i.e. ambient hydrostatic pressure) within 20 ms after
24 the time of peak gape (Day et al., 2007; Higham et al., 2006b). These relationships of buccal

1 pressure timing with the gape profile of *M. salmoides* are taken into account in the simulated
2 pressure profiles that are used in our model. The magnitude of the pressure peak is derived
3 from the relationship of this pressure (p_g in kPa) with the time to reach peak gape ($TTPG$ in
4 ms) published by Higham and co-workers (Higham et al., 2006b):

$$5 \quad \log p_g = -0.75 \log TTPG + 1.6 \quad (16).$$

6 To cover the 95% prediction interval of this observed relationship, additional model
7 simulations are performed with the intercept (constant 1.6) increased by 0.47 to obtain the
8 upper 95% prediction limit for p_g and decreased by 0.47 to obtain the lower 95% prediction
9 limit.

10 **3. Results**

11 *3.1 Model geometry*

12 The measurements of three *M. salmoides* individuals (head length (l) = 48 ± 10 mm; mean \pm
13 s.d.) show a mean head width of $0.53 \pm 0.07 l$. The calculated height to achieve a balance
14 between the measured neurocranium mass and that of the quarter ellipsoid model is $0.34 \pm$
15 $0.07 l$ (Fig. 4). Using cubic spline interpolation with the data in Tables 1 and 2 reveals a drag
16 moment coefficient of -0.0018 and an added mass coefficient of 0.0081, respectively. The
17 selected alignment of the quarter ellipsoid with respect to the head is shown in Figure 4. A
18 mean center of rotation (white cross in Fig. 5) is obtained from the positions of the center of
19 rotation determined separately on each of the four prey-capture videos (white spheres in Fig.
20 5). The head length of the individuals (numbered 1 to 4) from these four videos is
21 respectively 5.61, 5.88, 6.09, and 7.12 cm. These head lengths result into neurocranium
22 quarter ellipsoid model masses of, respectively, 16.3, 18.8, 20.9, and 33.4 g (i.e., identical to
23 the measured masses), and pitching moments of inertia about the mean center of rotation of,

1 respectively, 0.95, 1.20, 1.43, and $3.11 \times 10^{-5} \text{ kg m}^2$ (83% of the moments of inertia about the
2 corner of the quarter ellipsoid).

3 *3.2 Kinematic input and simulated pressures*

4 Time zero is set as the start of mouth opening. Dorsal rotation of the neurocranium lasts up
5 to $48 \pm 12 \text{ ms}$, of which it accelerates during the first $31 \pm 10 \text{ ms}$ (Fig. 6A,B). The time of
6 peak neurocranium acceleration ($20 \pm 9 \text{ ms}$) precedes the estimated time of peak suction
7 pressure by $6 \pm 3 \text{ ms}$ (Fig. 6B,D). The relatively low correlation coefficient of pressure
8 magnitude in function of time to peak gape for *M. salmoides* (Higham et al., 2006b; $r^2 =$
9 0.29), results in a relatively large 95% prediction interval for peak pressure (between -12 ± 2
10 kPa and $-1.4 \pm 0.2 \text{ kPa}$; Fig. 6D). The rate of volume increase calculated by the ellipse
11 modelling procedure shows a very consistent pattern, with a negligible speed during the
12 approximate initial $13 \pm 6 \text{ ms}$, followed by a rapid increase in speed up to a maximum at $40 \pm$
13 10 ms .

14 *3.3 Model output*

15 The peak moment to overcome the effects of inertia when rotating the neurocranium (M_{nc} , eq.
16 (7)) is $-0.018 \pm 0.017 \text{ N m}$, and is reached at $19 \pm 8 \text{ ms}$ (Fig.6E). The acceleration of the
17 neurocranial mass is the dominant factor in this variable, being responsible for about 68% of
18 this moment. The moment due to added mass (about 32% of M_{nc}) is significantly smaller.
19 The overall moment M_{nc} contributed to a peak power cost (P_{nc}) of $-0.15 \pm 0.16 \text{ W}$ (Fig. 6F)
20 reached at $22 \pm 9 \text{ ms}$. The mean work in the interval of negative P_{nc} is $-0.0019 \pm 0.0023 \text{ J}$,
21 which equals the kinetic energy of the rotating neurocranium (and added mass) at the peak
22 observed velocity. Because of the negative drag moment coefficient for the leading quartile
23 of the rotating ellipsoid matching the shape of *M. salmoides* neurocranium (due to dominant
24 negative pressures at its lateral sides), a moment to overcome steady-state drag on the roof of

1 the neurocranium was not required: this flow resulted in a negligibly small moment (median
2 0.03% of M_{nc}) assisting dorsal rotation of the neurocranium.

3 Peak suction power is generated at a later instant than peak P_{nc} , namely at 31 ± 16 ms (Fig.
4 6G). Peak suction power magnitude, on average 6 ± 4 W (upper 95% pressure limit = $19 \pm$
5 13 W, lower 95% pressure limit = 2.2 ± 1.5 W) is consistently higher than peak P_{nc} , on
6 average 0.15 ± 0.16 W. The ratio of peak P_{nc} over peak P_s is 0.019 ± 0.009 (upper 95%
7 pressure limit = 0.007 ± 0.003 , lower 95% pressure limit = 0.057 ± 0.026). At the time of
8 peak P_{nc} , the ratio of P_{nc} over P_s is 0.040 ± 0.019 (upper 95% pressure limit = 0.014 ± 0.006 ,
9 lower 95% pressure limit = 0.11 ± 0.05). The total work of generating suction is 0.11 ± 0.08
10 J (upper 95% pressure limit = 0.3 ± 0.2 J, lower 95% pressure limit = 0.04 ± 0.03 J). The
11 ratio of the mechanical energy cost of neurocranial rotation during the interval of negative P_{nc}
12 over the total suction work is 0.015 ± 0.009 (upper 95% pressure limit = 0.005 ± 0.003 , lower
13 95% pressure limit = 0.045 ± 0.027)

14 **4. Discussion and conclusion**

15 We found that the inertial costs of rotating the neurocranium have a negligible impact on
16 suction performance in largemouth bass, a generalized percomorph suction feeder. We
17 estimated the loss not to exceed 4.0% of the generated suction power throughout the feeding
18 sequence. In the worst case scenario for the bass, when focussing on the time at which this
19 cost was maximal and performing the simulations with the lowest possible pressure
20 magnitudes, the loss in power was 11% of the generated suction power. Yet, even in this
21 worst case scenario, the energetic cost in neurocranial acceleration was only about 4.5% of
22 the delivered suction work. However, an equally plausible scenario, using actual pressures
23 approaching the upper limit observed in previous studies (Higham et al., 2006b; Svanbäck et

1 al., 2002), predicted power and work for cranial rotation are less than 1.5% of suction power
2 and work.

3 Independent of which scenario was followed, we can conclude that the head expansion
4 system involving neurocranial dorsorotation efficiently transfers muscle power to drawing
5 water into the mouth in our model species. Given the considerably smaller mass of the
6 anatomical elements bordering the lateral and ventral side of the buccal cavity compared to
7 the neurocranium, it can be expected that the total inertial cost of head expansion will be less
8 than twice the calculated values presented here for the neurocranial rotation. A previous
9 study on the catfish *Clarias gariepinus* estimated this total inertial cost to be about 10% (Van
10 Wassenbergh et al., 2005). However, a later computational study showed that the equations
11 used in that study are likely to underestimate intra-oral pressure by a factor of 2 (Van
12 Wassenbergh and Aerts, 2009), which would imply a total inertial cost of about 5% for *C.*
13 *gariepinus*. Because of the (on-average) absence of neurocranial rotation in *C. gariepinus*,
14 we *a priori* expected the inertial costs to be higher for the largemouth bass due to its
15 considerable neurocranial rotation. Our data showed that this is not the case, as the total
16 inertial costs in *M. salmoides* are likely to be of similar or even lower magnitude than this 5%
17 estimate for *C. gariepinus*.

18 The kinetic energy put into rotational acceleration of the neurocranium may be converted to
19 suction work when the neurocranium decelerates. The timing of the calculated profiles of
20 suction feeding dynamics show neurocranial deceleration (movement energy being
21 attenuated) overlapping the phase when suction is still being generated (Fig. 6B,G). As the
22 dorsal rotation of the roof of the buccal cavity contributes to buccal expansion, the
23 deceleration of this dorsal rotation of the neurocranium may thus contribute to powering
24 suction. This can similarly be viewed as the neurocranium being decelerated by the negative

1 buccal pressures, to which its own movement contribute, exerted at its ventral surface. Work
2 invested by the feeding musculature into acceleration of musculoskeletal elements involved
3 in buccal expansion early in the suction act may thus contribute to suction at a later instant
4 when these elements decelerate. The idea of conversion of kinematic energy of cranial
5 rotation to suction has been proposed previously for syngnathid fishes (de Lussanet and
6 Muller, 2007). Although the mechanism and timing of suction generation relative to cranial
7 rotation is highly modified in syngnathids (Van Wassenbergh et al., 2013, 2014), the same
8 energy conversion principle may thus apply during suction feeding by *M. salmoides*. This
9 could further reduce or even erase the already very low energetic cost to suction performance
10 due to neurocranial acceleration.

11 Our results support one of the assumptions of several recent publications that link the size of
12 the epaxial muscles to suction performance (so-called suction index) in species showing
13 variation in head size and shape (Carroll et al., 2004; Collar and Wainwright, 2006; Holzman
14 et al., 2012a, 2012b). This assumption was that the proportion of muscle power that goes into
15 acceleration of cranial elements is overall negligible or similar between species, so that the
16 inertial properties of the head have no influence on the suction index. Our results suggest
17 that this is a valid assumption for species that do not differ too drastically from the
18 largemouth bass in cranial morphology or behaviour.

19 It can be concluded that the relatively low cost of neurocranial rotation explains why this
20 motion is not avoided in many suction-feeding species (Gibb and Ferry-Graham, 2005;
21 Muller, 1987). It also allows the post-cranial muscles inserting dorsally of the cranio-
22 vertebral articulation to be recruited in a mechanically efficient way to power suction (Camp
23 and Brainerd, 2014). This result also indirectly implies that size, shape and mass distribution
24 of the neurocranium is not likely to be evolutionary constrained by suction performance (but

1 see pipefish and seahorses for exceptions; de Lussanet and Muller, 2007; Roos et al., 2010),
2 which perhaps contributed to the extensive diversity of suction feeding fishes.

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1 **Tables**

2 **Table 1:** Drag moment coefficients of a quarter of an ellipsoid in function of width and

3 height to be used with eq. (9).

C_{M_drag}	width aspect ratio (w/l)							
		0.1	0.2	0.4	0.8	1.6	3.2	6.4
height aspect ratio (h/l)	0.1	0.0002	-0.0015	-0.0037	-0.0007	0.0191	0.0449	0.0739
	0.2	0.0002	-0.0006	-0.0025	-0.0073	-0.0128	-0.0210	-0.0666
	0.4	0.0007	0.0004	-0.0003	-0.0017	-0.0055	-0.0132	-0.0290
	0.8	0.0018	0.0014	0.0013	0.0019	0.0016	0.0032	0.0070
	1.6	0.0082	0.0072	0.0078	0.0155	0.0467	0.1346	0.3468
	3.2	0.0696	0.0832	0.1779	0.5880	2.1855	6.6637	18.026
	6.4	0.8385	1.4974	4.3943	14.304	56.911	183.01	612.14

4 See Fig. 2A for definitions of head length (l), width (w) and height (h)

5

6 **Table 2:** Added mass moment coefficients of a quarter of an ellipsoid in function of width

7 and height to be used with eq. (10).

C_{M_am}	width aspect ratio (w/l)							
		0.1	0.2	0.4	0.8	1.6	3.2	6.4
height aspect ratio (h/l)	0.1	0.0006	0.0020	0.0068	0.0215	0.0604	0.1519	0.3420
	0.2	0.0006	0.0019	0.0061	0.0195	0.0525	0.1245	0.2736
	0.4	0.0006	0.0014	0.0044	0.0142	0.0410	0.0996	0.2161
	0.8	0.0010	0.0008	0.0013	0.0027	0.0074	0.0184	0.0411
	1.6	0.0043	0.0051	0.0109	0.0325	0.1037	0.2928	0.7083
	3.2	0.0347	0.0650	0.1961	0.6991	2.4320	7.7295	20.467
	6.4	0.3143	0.5929	1.9016	7.1212	25.039	83.511	210.56

8 See Fig. 2A for definitions of head length (l), width (w) and height (h)

1 **Figure legends**

2

3 **Fig. 1** Components and motions responsible for the main power input for suction feeding.

4 Schematic illustrations at the start (A) and at maximum head expansion (B) are given.

5 Drawings are based on video images (Svanbäck et al., 2002) and skeletal drawings (Gregory,
6 2002).

7 **Fig. 2** Geometry of the quarter ellipsoid model used for inverse dynamics calculation of the

8 power required to accelerate the neurocranium. The oblique frontal view (A) shows the

9 neurocranium dimensions used in the model (l = length, w = width, h = height), while the

10 lateral view (B) shows the coordinate system's origin at the *origin* point, the centre of mass

11 (COM) position, and illustrates the procedure used to determine the centre of rotation (cr)

12 through the intersection of the midperpendiculars of lines $p1-p1'$ and $p2-p2'$ (the accent

13 denotes the position after neurocranial rotation).

14 **Fig. 3** CFD model geometry and example of hydrodynamic moments of a rotating ellipsoid.

15 Data is shown for an ellipsoid with radii of 50 mm long, 80 high and 40 mm wide at three

16 constant accelerations. CFD data was sampled once every 10 time steps for ellipsoid quarters

17 1 and 3 ($q1, q3$). Regressions used to derive the coefficients of drag moment and added mass

18 moment, and the final single equation model is illustrated. See 2.2 for further information.

19 **Fig. 4** Outline of the model input for deriving the equations to calculate suction power output.

20 Input variables are the pressure forces (gauge pressure p_g) and expansive motion of the

21 buccopharyngeal cavity surfaces (dr). Cross-sectional curve segments dc and anterior-

22 posterior increments dx form the surface increment which has the unit normal vector \hat{s} .

23 **Fig. 5** Geometry of the largemouth bass model. The height (h) and width (w) of the relative

24 to head length (l) and position of the quarter ellipsoid model of the neurocranium as well as

1 the measured centers of head rotation (open spheres) and their centroid (white cross) are
2 illustrated. Scale bar, 20 mm.

3 **Fig. 6** Kinematic input and model output of four prey-capture events by largemouth bass.
4 Panels show the kinematic input of neurocranial rotation (A-B; positive = snout moving
5 dorsally) and rate of head volume change (C; positive = expansion), simulated pressure
6 profiles (with 95% prediction interval range as grey curves) (D; eq. (14)), the calculated
7 neurocranium moment (E; eq. (7); negative = resisting the dorsal rotation) and power (F, eq.
8 (8); negative = power required from action of muscles and tendons) to overcome effects of
9 head mass inertia and hydrodynamic forces exerted at the external surface, suction power
10 output (G, eq. (13)).

Figure 1

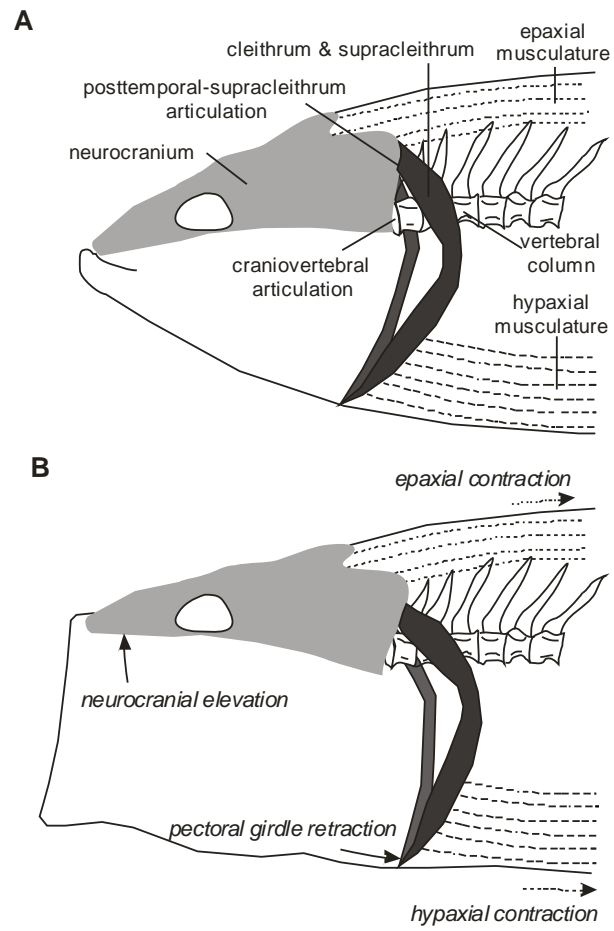


Figure 2

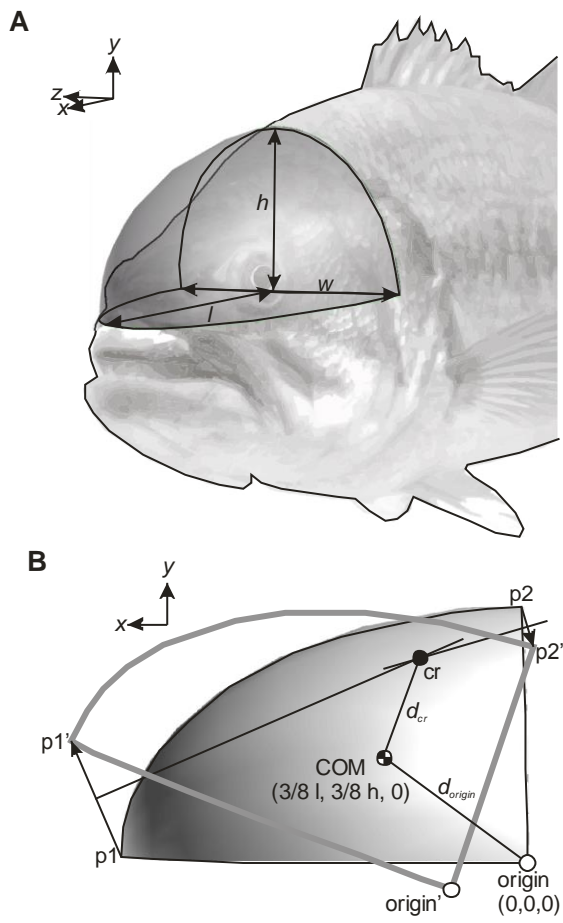


Figure 3

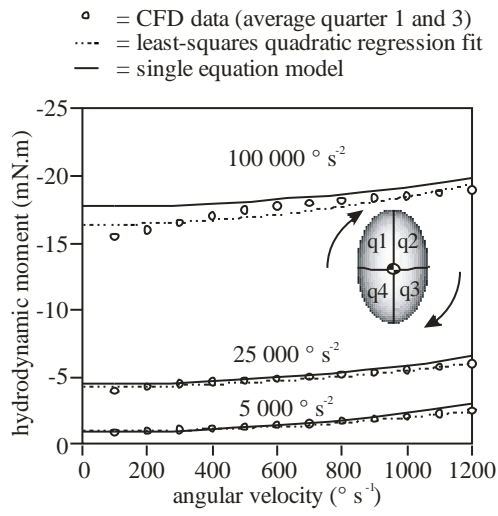


Figure 4

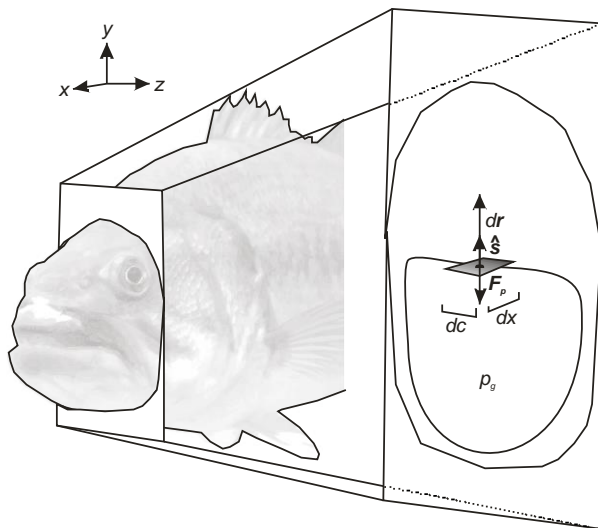


Figure 5

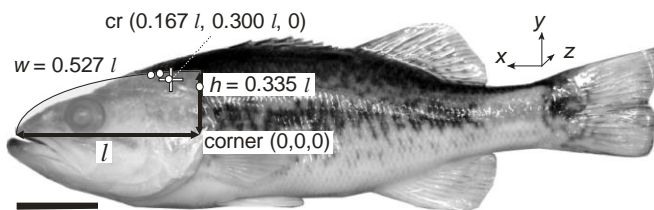


Figure 6

