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



Sam Van Wassenbergh^{a,b,*}, Steven W. Day^c, L. Patricia Hernández^d,
Timothy E. Higham^e, Tyler Skorczewski^{f,g}

^a Department of Biology, Ghent University, K. L. Ledeganckstraat 35, B-9000 Gent, Belgium

^b Department of Biology, University of Antwerp, Universiteitsplein 1, B-2610 Antwerpen, Belgium

^c Department of Mechanical Engineering, Rochester Institute of Technology, 76 Lomb Memorial Dr., Rochester, NY 14623, USA

^d Department of Biological Sciences, Lisner Hall Rm 340, The George Washington University, 2023 G St NW, Washington, DC 20052, USA

^e Department of Biology, University of California, 900 University Avenue, Riverside, CA 92521, USA

^f Department of Mathematics, University of Utah, 155 S 1400 E, Salt Lake City, UT, USA

^g Department of Mathematics and Statistics, Cornell College, 600 First Street SW, Mount Vernon, IA, USA

HIGHLIGHTS

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

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ABSTRACT

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

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1. Introduction

Many aquatic vertebrates rely on generating a flow of water from the external environment into the mouth to capture prey (e.g., [Lauder and Schaffan, 1993](#)). Conservation of mass and the incompressibility of water dictate that any expansion of the buccopharyngeal cavity will generate a flow of water. During this process,

* Corresponding author at: Department of Biology, Ghent University, K. L. Ledeganckstraat 35, B-9000 Gent, Belgium. Tel.: +32 9 264 52 33; fax: +32 9 264 53 44.

E-mail address: sam.vanwassenbergh@ugent.be (S. Van Wassenbergh).

which is typically referred to as suction feeding, prey items situated in the flow field in front of the mouth will experience hydrodynamic forces (Holzman et al., 2007; Skorczewski et al., 2010; Wainwright and Day, 2007). These forces are associated with highly unsteady water flows: adult suction feeders generally manage to accelerate water and prey from standstill to over 1 m s^{-1} in less than 0.05 s (Higham et al., 2006a; van Leeuwen, 1984; Van Wassenbergh et al., 2007a). In order to maximize suction feeding success on prey adhering to the substrate or trying to escape, the sudden increase in flow velocity in front of the mouth must be maximized. In other words, suction feeders must transfer as much kinetic energy to the water in the shortest possible amount of time. Consequently, to maximise prey capture performance, suction feeders must maximise instantaneous power.

To generate this power, fish mainly rely on contraction of the voluminous post-cranial musculature (Aerts, 1991; Camp and Brainerd, 2014; Carroll and Wainwright, 2006; Coughlin and Carroll, 2006; Muller, 1987; Thys, 1997; Van Wassenbergh et al., 2007b). This musculature consists of hypaxial (ventral to the vertebral column) and epaxial (dorsal to the vertebral column) components (Fig. 1A). Contraction of the hypaxial muscles rotates the pectoral girdle posteriorly, while contraction of the epaxial muscles induce a dorsal rotation of the neurocranium (Fig. 1B). Despite rotating different skeletal elements, the role of hypaxial and epaxial muscle contractions in suction generation is identical:

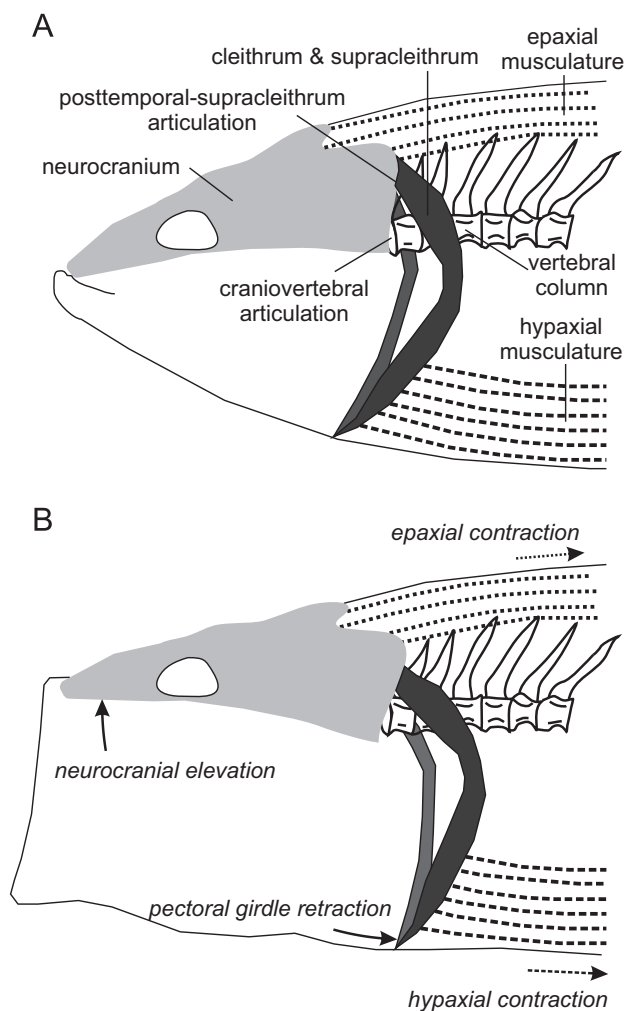


Fig. 1. Components and motions responsible for the main power input for suction feeding. Schematic illustrations at the start (A) and at maximum head expansion (B) are given. Drawings are based on video images (Svanbäck et al., 2002) and skeletal drawings (Gregory, 2002).

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

Not all power produced by the feeding musculature will result in water acceleration: an unknown amount of the muscle's power output will be lost due to the musculoskeletal mechanics underlying suction generation. Examples are joint friction, stretching of skin, resistive stress in the adductor muscles (e.g. *adductor mandibulae* during mouth opening), hydrodynamic resistance at the external head surfaces, and the inertia of the elements involved in expanding the buccopharyngeal cavity. A study on suction feeding of the catfish *Clarias gariepinus* estimated that inertial force (integral over the entire buccopharyngeal cavity of acceleration multiplied by mass of the displaced tissues) is about 10% of the pressure force on the buccopharyngeal cavity surfaces (Van Wassenbergh et al., 2005). However, as *C. gariepinus* relies almost entirely on ventral depressions of the floor of the mouth cavity to generate suction, *C. gariepinus* is atypical compared to many other suction feeders (Gibb and Ferry-Graham, 2005) in showing (on average) no rotation of the neurocranium.

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

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

To determine to what extent inertial costs of rotating the neurocranium affect suction performance, we address the following aims: (1) formulate an inverse dynamic model for estimating the instantaneous power requirement for rotating the neurocranium as observed on lateral-view high-speed videos, (2) establish a theoretical framework and mathematical models for calculating

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