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Morphology, Kinematics, and Dynamics: The Mechanics of Suction Feeding in Fishes

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Synopsis Suction feeding is pervasive among aquatic vertebrates, and our understanding of the functional morphology and biomechanics of suction feeding has recently been advanced by combining experimental and modeling approaches. Key advances include the visualization of the patterns of flow in front of the mouth of a feeding fish, the measurement of pressure inside their mouth cavity, and the employment of analytical and computational models. Here, we review the key components of the morphology and kinematics of the suction-feeding system of anatomically generalized, adult ray-finned fishes, followed by an overview of the hydrodynamics involved. In the suction-feeding apparatus, a strong mechanistic link among morphology, kinematics, and the capture of prey is manifested through the hydrodynamic interactions between the suction flows and solid surfaces (the mouth cavity and the prey). It is therefore a powerful experimental system in which the ecology and evolution of the capture of prey can be studied based on first principals.

Introduction

Suction feeding is the process of capturing prey by generating a flow of water into a rapidly expanding mouth cavity. This expansion of the mouth cavity (i.e., the buccal and opercular cavities in fishes) coincides with a sub-ambient pressure inside the mouth. If the prey fails to react in time to escape, forces that the flowing water exerts onto the prey cause the prey to be carried through the gaping mouth. Without this feeding mechanism, the prey would be pushed away by the approaching predator by a bow wave of water moving along with the predator. The purpose of this review is to give an overview of the key aspects of the morphology and mechanics of the process of capturing prey by suction in adult Actinopterygian fishes. We start by illustrating the key morphological components of the musculoskeletal system of suction feeders and

how these components move during buccal expansion. We then explain how this system functions to generate suction, and then describe what is currently known about the resulting dynamics of flowing water. We further discuss how suction flows translate into the capture of prey, and conclude with a discussion of the limits to our current understanding of suction feeding.

Morphology

Skeletal elements

Expansion of the head is driven by complex musculoskeletal linkage systems (e.g., Anker 1978, 1987; Fig. 1). Providing a detailed description of the anatomy of the cranial musculoskeletal system is beyond the scope of this review article. For a clear and detailed illustration of the cranial morphology of a percomorph suction feeder (a cichlid), we

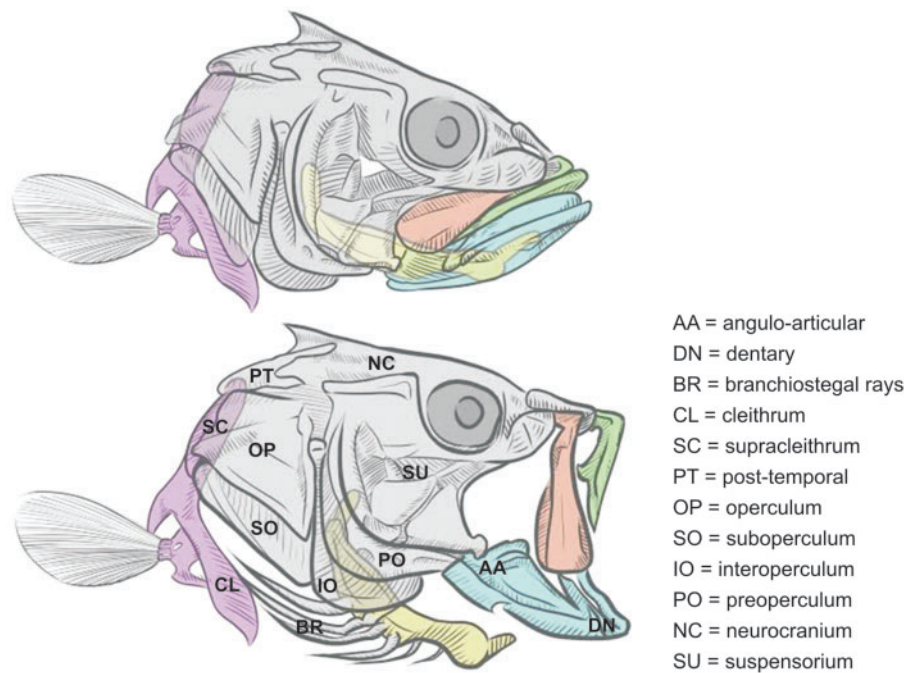


Fig. 1 Cranial morphology highlighting the principle skeletal components contributing to expansion of the head during suction feeding. Mouth closed (top) and open (bottom) are shown for an adult largemouth bass (*Micropterus salmoides*; Perciformes, Centrarchidae). The following are highlighted by colored shading: (1) The oral jaws, including the premaxilla (green), maxilla (orange), lower jaw (blue), (2) the composite hyoid (yellow), and (3) the pectoral girdle (purple).

recommend the series of papers by (Anker 1978, 1986, 1987, 1989). We restrict ourselves to the following skeletal units, which all have a crucial role during the suction-feeding process: (1) the oral jaws, (2) the hyoid, (3) the suspensorium, (4) the opercular series and branchiostegal membrane, (5) the neurocranium, and (6) the pectoral girdle. The anatomy is illustrated in Fig. 1 for one of the most commonly used species in studies of feeding mechanics, the largemouth bass (*Micropterus salmoides*; Perciformes, Centrarchidae). There is certainly tremendous diversity in the skeletal morphology and resulting kinematics of suction-feeding fishes. In the context of suction feeding, however, this morphological and biomechanical diversity serves a similar function: to rapidly expand the mouth cavity and open the mouth. Therefore, rather than explore this diversity, we present this single species as an example of a typical high-performance suction feeder.

The oral jaws border the mouth's aperture, and consist of the upper jaw and the lower jaw. The functional upper jaw of the largemouth bass consists of a tooth-bearing premaxilla and a toothless maxilla (Fig. 1). When the lower jaw (mandible) is lowered, the posterior end of the maxillaries swing down and their anterior end pushes forward the lateral portions of the premaxillaries (e.g., Van Dobben 1935; Gosline 1971; Alexander 1974; Motta 1984). The

bilateral premaxilla structure slides forward and this motion is called jaw protrusion. The lower jaw consists of the left and right mandibles connected by connective tissue at their symphysis. The bony mandible is composed of a posterior part, the retro-articular and angulo-articular (forming the joint with the quadrate of the suspensorium), and anteriorly a tooth-bearing dentary. The connection between the anterior and posterior parts (which includes the remnant of Meckel's cartilage and connective tissue) can allow torsion along the long axis of the mandible (Aerts 1985; Gosline 1987), and in some fishes even bending in the sagittal plane (Konow and Bellwood 2005; Ferry-Graham and Konow 2010).

The hyoid arch is a well-developed structure that is of central importance to suction feeding (Osse 1969; Muller 1989; Aerts 1991; Van Wassenbergh et al. 2012). The main left and right elements of the hyoid (rigid unit formed by the hypohyal, the anterior ceratohyal, and the posterior ceratohyal) consist of two "bars" converging anterior-medially to form a joint at their symphysis. They are suspended from the suspensorium just distal to the margin of the hyomandibula by a small bone, the interhyal (Adriaens and Verraes 1994).

The suspensoria (left and right) form large parts of the sides of the head, and suspend the lower jaw and hyoid. Each suspensorium is made up by several

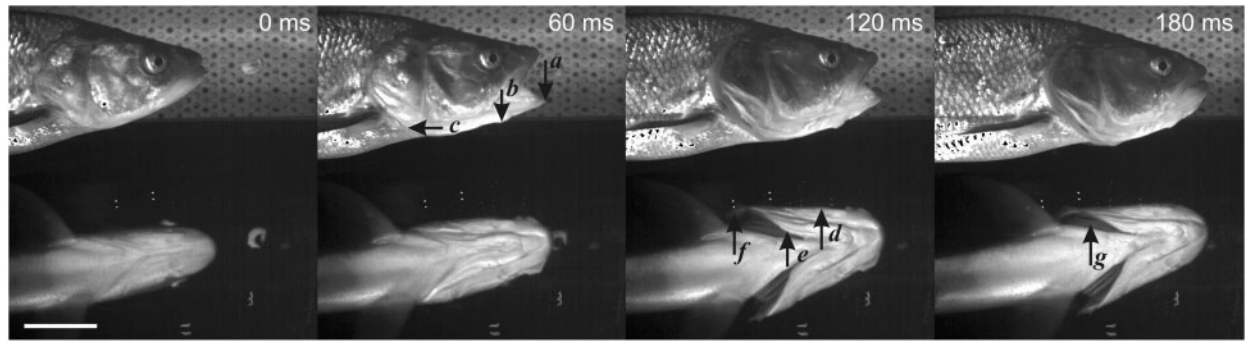


Fig. 2 Time-sequence of suction feeding by a cyprinid fish (*Aspius aspius*) from simultaneous lateral view (top) and ventral view (bottom), illustrating the typical rostro-caudal sequence expansion and compression of the mouth cavity: mouth-opening (arrow a) is followed by a depression of the floor of the mouth-cavity by the hyoid (arrow b), sideways abduction of the left and right cheekbones (suspensorium, arrow d) and retraction of the pectoral girdle (cleithrum, arrow c). Generally, shortly after the mouth has reached its maximal opening, the valves at the back of the head (gill cover, arrow f, and the branchiostegal membrane, arrow e) open to allow the outflow of water that was sucked into the mouth cavity. At this time, the mouth cavity starts to compress again to its initial volume. During opercular outflow, the space between the gill filaments increases (arrow g), which probably allows for a low-resistance flow in-between the branchial arches. Scale bar, 50 mm.

bones, including an anterior part, the palatoquadrate (originating ontogenetically from the mandibular arch), and a posterior part, the hyomandibular and symplectic (originating ontogenetically from the hyoid arch). However, as both parts are firmly connected to each other, the suspensorium can be regarded as a single functional unit. At the ventral side, the suspensorium incorporates joints that suspend the lower jaw as well as the attachment site for the interhyals that suspend the hyoid bars. Dorsally, each suspensorium articulates with the neurocranium at two locations, one anterior approximately at the level of the maxilla, and one posterior behind the eye. Together, these two articulations form a hinge allowing the suspensorium to swing laterally (abduction) and back medially (adduction) (Fig. 2) (de Visser and Barel 1996).

The opercular bones and the branchiostegal membrane cover the gills. Posteriorly, these elements can create the opening that allows water to exit the opercular cavity. These elements can function as a one-way valve, as inflow into the opercular cavities can be prevented by branchiostegal and opercular adduction; yet, some inflow through the opercular slit just after opening has been observed for *Salmo* by van Leeuwen (1984). The opercular bones of the largemouth bass consist of an operculum, a suboperculum (ventral of the operculum), an interoperculum (between the suboperculum and the posterior side of the lower jaw, connected to the latter via the interoperculo-mandibular ligament), and a preoperculum (close to the suspensorium). By rotating the operculum–suboperculum–interoperculum postero-dorsally around the joint between the

operculum and the hyomandibula (suspensorium) the interoperculo-mandibular ligament is pulled posteriorly, which in turn contributes to the depression of the mandible (so-called opercular mouth-opening mechanism) (Gosline 1971; Aerts and Verraes 1984).

The functional unit referred to as “neurocranium” typically includes a strongly ossified protective braincase, the eyes surrounded by the circumorbital bones, and anterior bony elements such as the rostrum and vomer. The ventral surface of the neurocranium forms the roof of the buccal cavity. During suction feeding, the neurocranium typically is rotated postero-dorsally along with the upper oral jaws, the pharyngeal jaws, and the suspensorium attached to it. The neurocranium articulates with the pectoral girdle at a joint between the post-temporal (which attaches to the posterior region of the neurocranium) and the supracleithrum. The left and right supracleithra and cleithra form a strongly ossified arch running ventrally to form an interdigitating connection fused where the cleithra meet. Dorsal rotation of the neurocranium involves rotation about the joint between the post-temporal and supracleithrum, and this joint is a key feature of the suction-feeding mechanism throughout ray-finned fishes (Actinopterygii) (Van Wassenbergh et al. 2015).

Muscles

The most important muscles that contribute to buccal expansion in ray-finned fishes are described below. Although these muscles can vary somewhat in their contractile properties, they are all comprised of fast glycolytic muscle fibers that permit quick and powerful expansion during suction feeding

(Aerts et al. 1987; Carroll et al. 2004, 2009; Van Wassenbergh et al. 2007a). The most voluminous muscles to contribute to suction are the post-cranial muscles: the epaxial and hypaxial muscles (Muller 1987; Thys 1997; Carroll and Wainwright 2009; Camp and Brainerd 2014). The epaxials insert on the posterior region of the neurocranium dorsal to the joint between the post-temporal and supracleithrum, and thus generate a dorsal rotation of the neurocranium about this joint. The hypaxials, in contrast, insert on the cleithra. Contraction of the hypaxial muscles will cause a posterior rotation (or retraction) of the pectoral girdle (Camp and Brainerd 2014).

Other important muscles for suction feeding are the sternohyoideus, the protractor hyoidei, and the levator opercula (Lauder 1983). The sternohyoideus connects the cleithrum to the symphysis of the hyoid (via a tendon and a sesamoid bone, the urohyal) (Wainwright et al. 2006). Although the sternohyoideus is crucial in transmitting the force from the retraction of the cleithrum to the hyoid, its capacity to actively shorten (and produce power) while being retracted by the cleithrum is variable (Carroll and Wainwright 2006, 2009, 2011; Van Wassenbergh et al. 2007b; Camp and Brainerd 2014). The protractor hyoidei originates on the ceratohyals and inserts on the lower jaw. It helps to open the mouth by depressing the lower jaw (Gosline 1971; Adriaens et al. 2001; Van Wassenbergh et al. 2005). The levator operculi can cause opening of the mouth through the opercular mouth-opening mechanism (see above), and is hypothesized to be mainly important during the initial stages of opening the mouth during suction feeding (Van Wassenbergh et al. 2005). Additional details of muscle function in this species are included in Camp and Brainerd (2015).

Skeletal kinematics and dynamics

Ray-finned suction-feeding fishes vary in their hunting strategy, and so does the speed at which they approach their prey. There are a number of factors that dictate this strategy, including size of the mouth, size of the body, and type of prey (Wainwright et al. 2001; Higham 2007; Higham et al. 2007; Kane and Higham, this volume). Although there are general metrics to quantify the use of ram and suction (Norton and Brainerd 1993), it is becoming increasingly apparent that the strategies used in approaching prey are complex, and that movements that occur during a strike vary considerably between species and may also be modulated by an individual fish

to vary from one strike to another. Fishes that exhibit fast starts during the capture of prey, such as cottids and esocid pikes, are often ambush predators that rely more on accelerating toward the prey (Kane and Higham 2011). In contrast, fishes relying more on suction might approach the prey slowly. Regardless of the strategy, all fishes must deal with the fact that suction is only effective over a very limited distance from the predator's mouth (Day et al. 2005). This constraint makes it important for fishes to accurately position their mouth relative to the prey, whether they are approaching slowly or quickly. For those species that exhibit high swimming speeds capturing prey, a larger mouth might offset the limitations imposed by the relatively small volume of water ingested (Higham et al. 2007). Regardless, fishes that swim while attacking prey must integrate these complex systems in order to accurately capture the item.

Apart from approaching the prey, the first action to take place is the start of mouth-opening. As mentioned above, the mechanisms used in opening the mouth during suction feeding are complex, as they involve different mechanical pathways in different fishes lineages (Gosline 1971). Mouth-opening can be caused by opercular rotation via the interoperculo-mandibular ligament (Durie and Turingan 2004), by hyoid retraction via the mandibulohyoid ligament, or by contraction of the protractor hyoidei muscles (the latter can be assisted by posterior movement of the hyoid where this muscle originates). How these different mouth-opening mechanisms are recruited during suction feeding is still unclear (Otten 1982; Hunt Von Herbing et al. 1996; Diogo and Chardon 2000; Adriaens et al. 2001; Van Wassenbergh et al. 2005). The initial period of a feeding typically involves a slow rotation of the lower jaw, which speeds up significantly during the phase when more suction is being produced (Sanford and Wainwright 2002).

The buccal cavity is expanded dorsoventrally as well as laterally to generate suction (Fig. 2) (Lauder 1980). The dorsoventral expansion involves sagittal-plane rotations of the lower jaw, hyoid, pectoral girdle, and neurocranium. After the onset of depressing the lower jaw, the epaxial and hypaxial muscles contract, causing the neurocranium to be rotated dorsally about the joint between the post-temporal and supracleithrum (often referred to as neurocranial elevation) and the pectoral girdle to be retracted (Camp and Brainerd 2014). The increased angle between neurocranium and pectoral girdle causes the hyoid to be depressed (i.e., the tip rotates ventrally) as it is pulled back by the sternohyoideus muscle

(Muller 1987). Contraction of the sternohyoideus, if such occurs, will further increase the depression of the hyoid. The combined effect of these movements is that the floor of the buccal cavity is pulled ventrally and the roof of the buccal cavity moves dorsally.

Lateral expansion (Fig. 2) involves the abduction of the suspensoria and opercula. Each suspensorium hinges with the neurocranium, thereby effecting lateral swinging (Gosline 1971; de Visser and Barel 1996). The forces responsible for pushing the suspensoria laterally come from the retraction of the hyoid (by the sternohyoideus, and indirectly also resulting from hypaxial and epaxial activity). Depression of the hyoid is accompanied by a laterally directed movement and force on the medial surface of the suspensoria (at the interhyal's joint) (Muller 1989; Aerts 1991; de Visser and Barel 1996). As abduction of the suspensoria inevitably causes the left-to-right distance between the lower jaw and hyoid articulations with the suspensorium to widen, the location of the joint between the mandible and the quadrate also will move laterally. The levator arcus palatini, a muscle that can directly abduct the suspensorium, is assumed to be of minor importance during suction feeding due to its relatively small size and unfavorable moment arm (Aerts 1991; de Visser and Barel 1996; Leysen et al. 2011).

There are three ways in which the opercular cavities may be expanded. First, the operculum and suboperculum form a unit that articulates anteriorly with the hyomandibula; when the lower ends of the suspensoria are spread, these articulations are carried outward (Gosline 1971). Second, the branchiostegal rays articulate basally with the hyoid bars. The lateral expansion of the hyoid bars will thus spread the branchiostegal rays laterally. Finally, the momentum of the water sucked into the forward-moving buccal cavity will help the gill cover and branchiostegal membrane to be pushed open as these water-masses move toward the branchiostegal and opercular slits (Osse 1969).

The multiple mechanisms contributing to cranial rotation, depression of the lower jaw, or lateral expansion of the mouth cavity all function in coordination during a single feeding event. Together, these expanding elements form a wave of expansion of the buccal cavity that progresses from the aperture of the mouth to the opercular slits. This rostral-caudal (or anterior to posterior) wave of expansion, and the associated timing of the functional components supporting the expansion wave, is repeatedly observed in a wide range of vertebrate suction feeders (e.g., Muller and Osse 1984; Schwenk 2000; Aerts et al.

2001; Dean and Lannoo 2003; Bishop et al. 2008): opening of the mouth is followed by depression of the hyoid and abduction of the suspensoria, which in turn is followed by abduction of the opercular and branchiostegal membranes. This wave-like progression of the kinematics of buccal and opercular expansion allows peak velocity of the flow of water into the mouth to occur near the onset of peak opening of the mouth (Bishop et al. 2008) and may minimize the success of prey attempting escape (Muller et al. 1982).

Fluid mechanics of suction feeding

Buccal expansion drives the flow of fluid

The hydrodynamics of suction feeding in fishes can be summarized as generating strong unidirectional flow of water into the expanding mouth and out through the opercular and branchiostegal slits. When a mouth cavity with closed opercular and branchiostegal slits starts to increase in volume, the pressure within it drops rapidly (Lauder 1980a, 1980b), and water flows through the mouth's orifice to fill the extra volume (Alexander 1969, 1970; Lauder 1980b; Muller et al. 1982). This gradient of pressure (lower within the mouth than outside the mouth) acts to accelerate the fluid, working against inertia and viscosity of the fluid. Expansion of the opercular cavity and compression of the mouth cavity, as well as the momentum of the water itself, act to continue the flow of water through the mouth and out the gills.

As long as the opercular and branchiostegal slits are closed, the principle of continuity dictates that any increase in buccal volume must be filled instantaneously with water flowing into the mouth. Alexander was the first to use this principle to calculate the volume of water sucked into the mouth, in order to estimate the distance fishes can suck food into the mouth (Alexander 1967). Since the instantaneous speed of the flow passing the mouth's opening can be calculated by dividing the instantaneous rate of buccal expansion by the instantaneous cross-sectional area of the aperture of the opened mouth, more recent studies relied on the continuity principle to calculate time-varying profiles of the velocity of suction flow. Through the years, such models have refined their estimates of the change in buccal volume by mimicking the intra-oral shape as truncated cones (Aerts 1991; Muller et al. 1982; Van Leeuwen 1984; Viladiu et al. 1999), double-truncated or triple-truncated cones (Bishop et al. 2008; Van Wassenbergh et al. 2006b), or a longer series of small elliptical cylinders (Drost and Van Den

Boogaart 1986; Roos et al. 2009b; Van Wassenbergh et al. 2006a). These models used high-speed cinematography to deduce the patterns of expansion of the buccal cavity from external landmarks. This approach not only allows estimates of the velocity of flow at the mouth's aperture, but also along any local cross-section of the buccal cavity (Muller et al. 1982; Van Wassenbergh et al. 2006a; Roos et al. 2009b).

The expanding truncated-cone models by Muller and co-workers provided the fundamentals for understanding the fluid dynamics of suction feeding (Muller et al. 1982). They used a set of analytical equations to describe the links among forward swimming, buccal expansion, buccal pressure, and suction flows inside and outside the mouth (Muller et al. 1982). Unfortunately, this type of mathematical modeling cannot be used reliably for the entire strike, since the system becomes mathematically indeterminate as soon as there is more than one opening (i.e., from the instant of the opening of the opercular and branchiostegal slits). Consequently, except for the article included in this volume that presents a computational fluid dynamics model of a sunfish, including the opening of its opercular slits (Van Wassenbergh 2015), our current insight into suction-feeding dynamics of fish during this later period of their strike relies entirely on experimental measurements of buccal pressure and on visualization of flow in front of the mouth by tracking particles (Lauder and Clark 1984; Muller and Van Leeuwen 1985) or by particle-image velocimetry (PIV) (Ferry-Graham et al. 2003; Day et al. 2005; Higham et al. 2006b; Holzman et al. 2008a; Staab et al. 2012).

Mechanistic relation of skeletal and fluid mechanics

There is a clear coupling between the flow of fluid and the musculoskeletal system. As typically explained, the mouth's expansion (kinematics) drives the flow of fluid (hydrodynamics). A faster rate of mouth-opening, for an individual, corresponds to higher velocities and accelerations of flow, and therefore greater suction pressures within the mouth (Muller and Osse 1984; Lauder et al. 1986; Sanford and Wainwright 2002; Higham et al. 2006b). One attempt to relate the fluid mechanics of suction feeding to skeletal mechanics models the cranial morphology as a single lever that transmits muscle force that acts to expand the buccal cavity (Carroll et al. 2004; Wainwright et al. 2007; Holzman et al. 2008a). Morphological measurements are used to estimate the muscle force (based on the physiological cross-sectional area of the epaxial muscles) that is

transmitted through a simple lever mechanism to lift the head and expand the buccal cavity and allow calculation of a "suction index". The morphological measurements yield estimated force that acts over the buccal area, which have units that are equivalent to pressure. This approach has several simplifying assumptions. It treats the expansion of the mouth as primarily dorsoventral, and is aimed at modeling maximal performance. In addition, the suction index provides no information on the timing of peak pressure. Nevertheless, suction index was strongly correlated with the measured buccal pressure across species of centrarchids (Carroll et al. 2004), and was strongly correlated with peak speeds of flow experimentally measured at the mouths of suction-feeding bluegill sunfish ranging in size from 60 to 190 mm SL (Holzman et al. 2008a).

Spatio-temporal patterns of flow

During a feeding event, water is drawn from outside the mouth, creating a flow field external to the mouth. The flow generated in front of the fish is fundamental to feeding because it is this flow that draws prey into the mouth. Theory, modeling, and empiricism have been applied to understand this flow field. For the sake of simplicity, we will first discuss the case of a fish that does not move during the suction event, and then add forward swimming to the discussion. Suction flows are characteristic of those observed when fluid is drawn into an orifice by a pressure gradient. However, because the suction is brief, steep accelerations occur and the flow is considered "unsteady". Typically, expansion of the mouth is rapid, with time to peak opening ranging 4–40 ms, and the entire duration of the cycle approximately 10–100 ms for smaller (SL < 50 cm) fish (Gibb and Ferry-Graham 2005). Correspondingly, flow speed can peak to more than 3 m s^{-1} within 4–6 ms and generate steep temporal accelerations of more than 40 m s^{-2} (Day et al. 2005; Higham et al. 2006a; Holzman et al. 2008a; Staab et al. 2012).

Suction flows follow a stereotypical temporal pattern that is related to the dynamics of mouth-expansion. Detectable flows are visualized when the mouth starts opening, and water flows into the mouth through the entire cycle of the gape, until the mouth closes (Day et al. 2005; Higham et al. 2006a; Holzman et al. 2008a; Staab et al. 2012). The ability to maintain a flow into the mouth after maximal buccal expansion is due to the anterior-to-posterior wave of cranial expansion and inertia driving water

through the mouth and exiting the opercles (Bishop et al. 2008). In centrarchids, the peak speed of flow occurs very close to the time of maximum gape, immediately following the period of rapid mouth-opening (Day et al. 2005; Higham et al. 2006a; Holzman et al. 2008a). In goldfish the mouth is held open for extended periods, and peak flow is variable and delayed in comparison to centrarchids (Staab et al. 2012). In both cases, peak flow consistently occurs when the mouth is fully opened (Fig. 3). The duration of time over which the flow continues into the mouth varies from species to species, but some show a period of sustained flow while the mouth is held open (e.g., Aerts 1990). Bishop et al. (2008) examined the role of the aforementioned anterior-to-posterior wave of mouth-expansion in determining the timing of peak velocity of flow (Fig. 4, top row). They determined that the wave of expansion is critical in generating peak flows that correspond to the time of peak mouth-opening.

Direct visualization of suction flows using PIV reveals great variation in maximal speed of flow both between individuals and within individuals. Using this technique, the speed of flow in the earth-bound frame is measured at a distance of half mouth-diameter from the mouth's center, and those values are reported below. Flow-speed measured for adult bluegill (SL ~ 15 cm) ranged from 0.15 to 0.8 m s^{-1} . Based on the law of continuity, it is expected that, faster expansion will result in more rapid speeds of flow for any given buccal geometry. Indeed, within individuals, peak flow is generally correlated with the speed of mouth-opening (Day et al. 2005; Higham et al. 2006a; Holzman et al. 2008a; Staab et al. 2012). The same principle implies that greater expansion of the mouth's cavity will result in faster flows if size of the aperture scales with negative allometry to buccal volume. In bluegill, flow-speed increased with size of the fish, from a mean of 0.2 m s^{-1} for a fish approximately 50 mm long to a mean of approximately 0.7 m s^{-1} for a fish approximately 200 mm long (Holzman et al. 2008a). PIV data on the diversity of suction performance is limited to a few species, with an observed range of $0.15\text{--}0.8 \text{ m s}^{-1}$ of 2D magnitudes of velocity in the midsagittal plane when measured half mouth-diameter away from the mouth's center.

Suction flows are also characterized by steep spatial gradients of the speed and pressure of flows, decaying rapidly as a function of the distance from the mouth's aperture (Day et al. 2005; Higham et al. 2006a; Holzman et al. 2008a; Staab et al. 2012). In the earth-bound frame of reference, flow speed at the

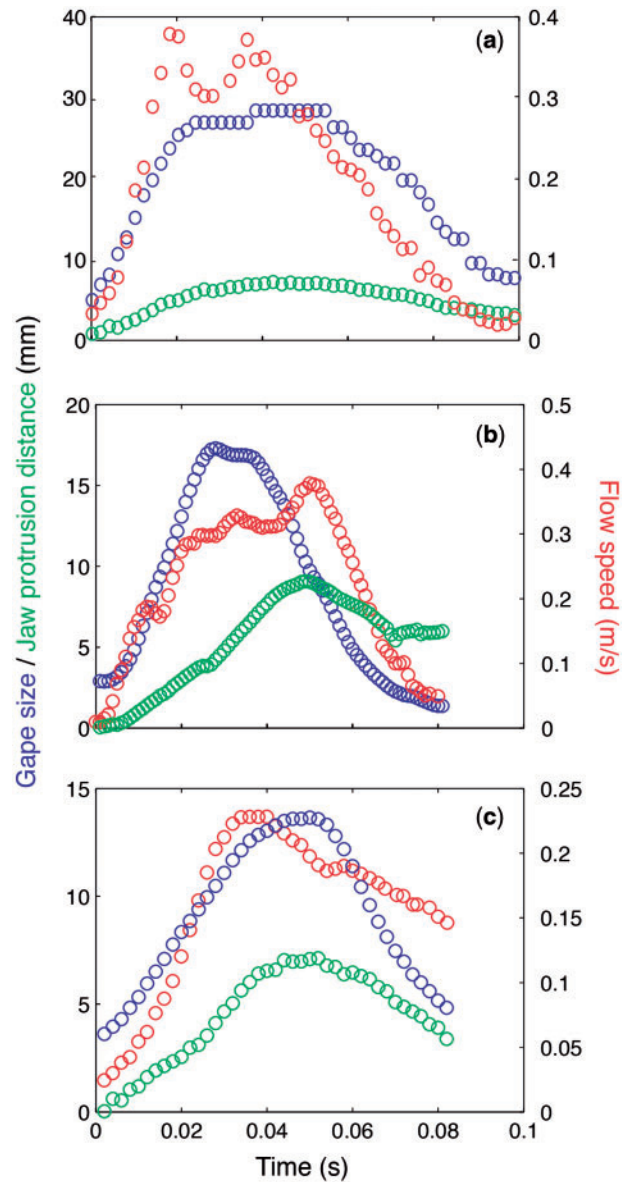


Fig. 3 Characteristic temporal pattern of suction feeding showing the profile of the fluid's speed (red) in relation to gape (blue) and the distance the jaw protrudes (green) for three species: (a) largemouth bass, (b) bluegill, and (c) goldfish. Data from Day et al. (2007) and Staab et al. (2012). Fluid's speed shown at a distance $1/2$ peak gape in front of the fish, as was done in these studies.

time of peak gape can accelerate from near stagnation at a distance of one gape diameter to more than 3 m s^{-1} at the mouth's center, producing water-strain rates of more than 100 s^{-1} (Holzman and Wainwright 2009). When the mouth is circular and planar (like the aperture of a garden hose) the flow field is highly stereotypical and radially symmetric around the mouth (Skorczewski et al. 2010, 2012). This is because water is drawn from all directions toward the aperture, generating a “mushroom-like”

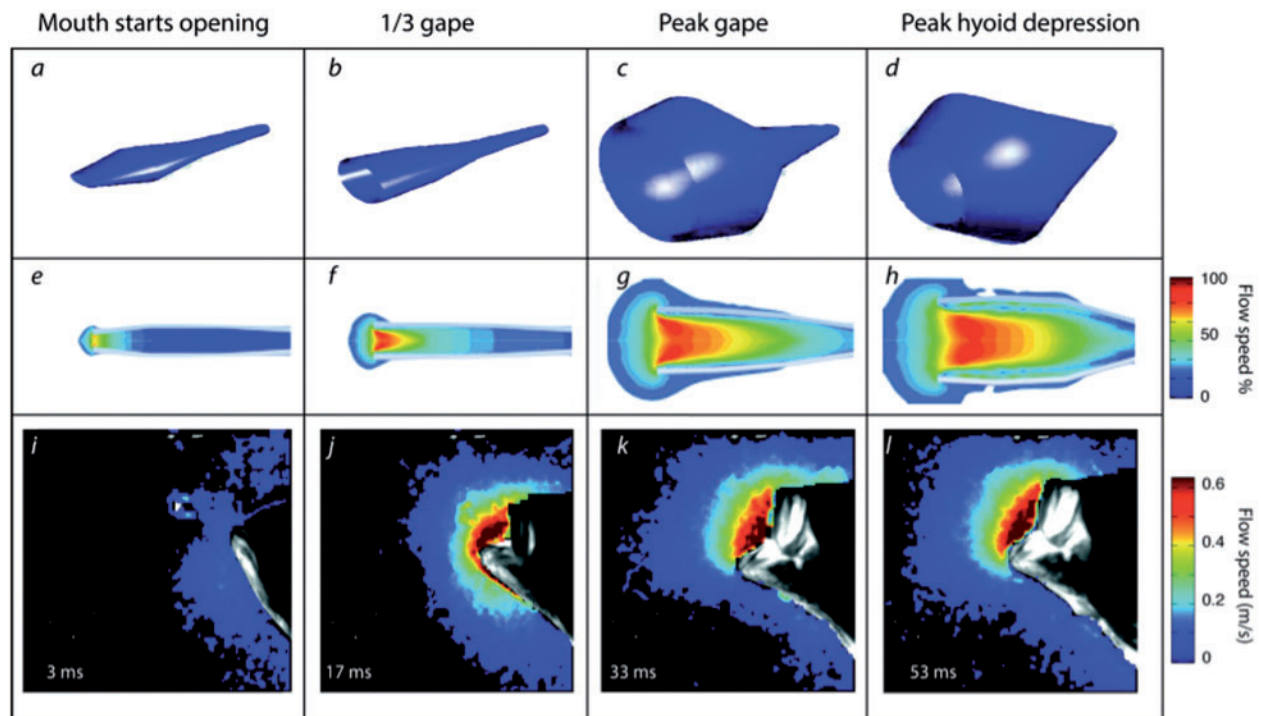


Fig. 4 Buccal volume and suction-flows during expansion of the mouth. (a–d) Scaled diagram of buccal volume based on a triple-cone model (Bishop et al. 2008). (e–h) CFD model of flows inside and outside the mouth (R. Holzman, unpublished data). Colors represent the flow speed as a fraction of the maximum instantaneous flow speed. (i–l) PIV visualization of suction flows of *Astronotus ocellatus* (R. Holzman, unpublished data). Each columns correspond to a stage of the mouth's opening. Note that kinematics are different for each of the three models. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

shape of ingested water (see Fig. 4, lower row). This pattern of flow implies that water nearest the aperture moves fast (because water is collected from a small volume), and water further from the aperture moves more slowly (because water is collected from a large volume) (Alexander 1969). The decay in speed of flow is abrupt; at a distance of half mouth-diameter it is approximately 28% of the speed at the center of the mouth, and approximately 5% at a distance equivalent to one mouth-diameter (Day et al. 2005; Higham et al. 2006a; Holzman et al. 2008a; Staab et al. 2012), as illustrated in Fig. 5. This pattern of decay is consistent throughout the mouth's opening and closing cycle over a range of mouth sizes of approximately 3–30 mm and along transects extending at various angles relative to the fish's mouth (Day et al. 2007). It is interesting to note that one strategy a suction feeder can use to enhance the speed of water flowing around the prey is to feed close to a firm substrate, such as a rock. This will restrict the region from which water can flow into the mouth, and result in higher flow speeds of flow in front of the mouth than when the fish is feeding in mid-water (Nauwelaerts et al. 2007; Van Wassenbergh and Aerts 2009; Wilga et al. 2012).

How suction flows translate into the capture of prey

The ultimate goal of the suction-feeding fish is to get the prey into its mouth and contain it there. To close the distance between the mouth and the prey, the fish can employ forward swimming (ram) and/or protrude its upper jaw, which (in the earth-bound frame of reference) moves the predator's mouth toward the prey (Van Leeuwen 1984). The other means of closing that distance is to exert force on the prey, which (in the earth-bound frame of reference) moves the prey toward the predator's mouth. These means are not mutually exclusive, but they produce interesting hydrodynamic interactions.

In general, three hydrodynamic forces act on the prey to drag it into the mouth: drag force, the pressure-gradient across the prey, and the acceleration reaction force (Wainwright and Day 2007). The prey can respond by exerting a force to swim away (or at an angle) from the suction forces, or by clinging to a holdfast. Drag force is the result of a differential in speed between the prey and the flow around it, and it scales with the cube of that differential, the prey's area, and how poorly streamlined the prey is (captured by its drag coefficient). Pressure-gradient

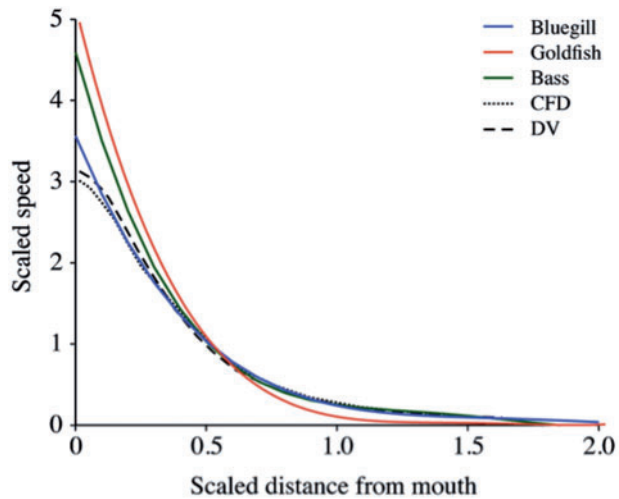


Fig. 5 Ubiquity of spatial gradients in the velocities of fluid in front of the mouth of suction-feeding fishes. Data based on PIV visualization of bluegill, goldfish, and bass (full lines), as well as a CFD model of pumpkinseed sunfish (dotted line), and the double vortex model (dashed line). Distances are scaled by mouth-diameter. Speed of flow is scaled such that at a distance of half gape it equals unity. (This figure is available in black and white in print and in color at *Integrative and Comparative Biology* online.)

force results from spatial and temporal gradients in speed of flow (acceleration) in the direction of the flow. It scales with the magnitude of those accelerations, and with volume of the prey (but is largely independent of the prey's shape). Acceleration reaction force (added-mass force) acts on the prey when water is accelerated around the prey. It scales with the magnitude of the relative acceleration of the prey and water, the prey's volume, and how poorly streamlined the prey is (captured by its added-mass coefficient).

The relative contributions of these hydrodynamic forces depend on characteristics of the prey and of the predator (Holzman et al. 2007, 2008b, 2008c, 2012; Wainwright et al. 2007; Wainwright and Day 2007). Generally, drag forces contribute relatively little to moving the prey toward the mouth, with acceleration-based forces dominating in most scenarios. Thus, the ability of fish to exert strong forces on their prey depends on the fish's ability to generate gradients in the speed of the suction flows. Such gradients are produced by rapid expansion of the mouth, and are generally stronger when the mouth's aperture is small (Holzman et al. 2007, 2008b, 2012; Wainwright et al. 2007). Prey of any shape, even extremely well-streamlined ones, will be accelerated by the pressure gradient. Additionally, utilizing these gradients strongly depend on the ability of the fish to time its strike and maximize the accelerations that the prey experiences (Holzman

et al. 2007, 2008b). Many prey can certainly generate force through an escape response. This is beyond the scope of this review, but is addressed by Fields and Yen (1997), Kjørboe and Visser (1999), and MacKenzie and Kjørboe (1995). By calculating the force exerted on the prey during the strike, it is also possible to treat the aquatic encounter of predator and prey as a hydrodynamic interaction between a solid particle (representing the prey) and the unsteady suction flows around it. Thus, it is possible to integrate the effects of morphology, physiology, skull kinematics, ram, and fluid mechanics on suction-feeding performance, defined as the ability of the fish to exert sufficient force on the prey to draw it into the mouth. This approach yielded insights into the functional mechanisms used to capture different types of prey (Holzman et al. 2012) and the performance trade-offs that result from modifications to the morphology and kinematics of the skull (Holzman and Wainwright 2009; Gemmill et al. 2013, 2014).

The forward motion of the fish has several hydrodynamic consequences. Before the mouth opens, the moving body of the predator pushes water in front of it which could alert the prey of its approach (Holzman and Wainwright 2009). The forward movement of the mouth also changes the shape of the ingested parcel of water from a symmetric round "mushroom" in a low-ram case to an elongated sphere in a high-ram scenario (Weihs 1980; Higham et al. 2005). Finally, the forward motion of the mouth (through ram, jaw-protrusion, and fast cranial elevation) rapidly moves the center of the mouth toward the prey. Because flow speeds are greater near the mouth's orifice, the forward motion of the mouth can generate an independent source of temporal acceleration, adding to the forces that drag the prey toward the mouth (Holzman et al. 2008b, 2008c, 2012). This means that protrusion of the jaw, when timed strategically, enhances the hydrodynamic forces that suction feeders exert on their prey.

Limitations of understanding

Some limitations of understanding of the mechanics of suction feeding are related to the limited number of species studied, effects of size on the hydrodynamics of suction feeding, the flow within the mouth, and how precisely the generated flow relates to morphology and kinematics.

Ability to generalize

Although much is known about the kinematics and morphology of suction feeding in fishes, studies on hydrodynamics are based on investigation of a small

number of species. There is substantial unexplored diversity among fishes, which will be critical for understanding the evolution of phenotypic diversity. The general pattern of suction-feeding kinematics seems highly conserved, and the hydrodynamic basis of suction feeding is reasonably well understood. Taken together, these facts argue that the described patterns of flow probably are highly conserved across fishes. However, most of the information on the temporal and spatial patterns of suction flows have been obtained from visualization of flows and from numerical modeling. Both techniques are “low-throughput”, requiring high technical and computational skills, and our interpretation is based on high-quality data generated for a few selected species. Thus, caution in making broad generalization is warranted before more data on the diversity of suction feeding is available.

Suction feeding by large fishes

Much like very small fishes, large fishes will experience a number of constraints on their ability to feed by suction. One of these constraints is that the duration of a suction act inevitably increases with the size of the suction feeder (e.g., Richard and Wainwright 1995; Van Wassenbergh *et al.* 2005; Lowry and Motta 2008). This calls for ontogenetic “tuning” both of the lever systems (Wainwright and Shaw 1999; Herrel *et al.* 2005) and of the contractile properties of the muscles involved in expansion of the head (Van Wassenbergh *et al.* 2007a; Carroll and Wainwright 2011). However, most of what we know is from small or medium-sized fishes in the laboratory. Some of the largest species of fishes examined in the laboratory include sturgeon 70 cm long (Carroll and Wainwright 2003), bowfin 37 cm long (Muller and Osse 1984), Atlantic cod 38 cm long (Muller and Osse 1984), asp 47 cm long (Van Wassenbergh and De Rechter 2011), snook up to 31 cm long (Wainwright *et al.* 2006), air-breathing catfish 92 cm long (Van Wassenbergh *et al.* 2005), and a variety of sharks (e.g., nurse sharks up to 110 cm long) (Matott *et al.* 2005). However, researchers are limited by laboratory space, and studies of larger species tend to use circular (or semicircular) tanks. Two options exist for future work attempting to detail the dynamics of suction feeding in very large predatory fishes. First, one can utilize extremely large aquaria, some of which can reach 12 m long with a volume of 45,000 liters (Seamone *et al.* 2014). These often are housed at field stations, and this provides the ability to examine predator–prey interactions under controlled conditions.

Alternatively, one can utilize portable high-speed cameras in order to capture events in the wild. This is a growing area of research, and it is extremely promising in terms of understanding how, why, and when big fishes attack prey. Filming in nature provides the added benefit of incorporating ecologically relevant variables.

Effects of viscosity on smaller fish

Due to viscosity, water that flows over a solid surface will experience a shearing force, similar to friction, that will act to slow down the particles nearest the stagnant surface (Vogel 1994). In the context of suction feeding in typical adult-sized fish, viscosity only affects a very thin layer of fluid and it is valid to treat the flow as inviscid, particularly for large sizes of mouths (Van Wassenbergh and Aerts 2009). However, larval fish swim and feed at low Reynolds numbers, well below 100 (Re based on the mouth’s peak gape and on maximum velocity of fluid) (Drost *et al.* 1988; Muller and Videler 1996; Hernández 2000; China and Holzman 2014; Yaniv *et al.* 2014). In this low Re regime, viscous effects should have considerable effects on the dynamics of flow and, consequently, on suction performance. A thorough review of the effect of viscosity on suction-feeding performance in the viscous regime of larval fish is addressed by Holzman *et al.* (2015).

Flow internal to the mouth

The pressure of the fluid inside the buccal cavity has direct implications for skeletal and buccal kinematics. This pressure exerts a substantial force onto the inner tissues of the mouth, in turn effecting skeletal and muscle loads. This is a true fluid–structure interaction as skeletal kinematics affect the flow and the flow affects skeletal kinematics. While this principle is clear, the ability to predict hydrodynamic flows or suction-feeding performance based on morphology and kinematics has been confounded by the two previous limitations of our understanding, namely the knowledge of the flow within the mouth and quantitative models of the musculoskeletal system. We have only a conceptual idea of the flow inside the mouth during suction feeding, especially for its later stages when the opercular and branchiostegal valves open. This is particularly important for understanding the transport of prey and directly relates to the musculoskeletal forces required to expand the mouth. Existing measurements of the internal flow are limited to single-point measurements of pressure and a single dataset of X-ray

visualization of the motion of prey within the mouth (Van Wassenbergh et al. 2005) and single-point anemometer measurements within one species (Muller and Osse 1984). There have been a limited number of computer models aimed at simulating suction-flow internal to the mouth (Fig. 4, middle row), but these are currently complex and unvalidated simulations due to the complex and transient geometry (Van Wassenbergh and Aerts 2009).

Expansion and relaxation of the mouth have another understudied role in intra-oral transport. Even after the prey has crossed the mouth's orifice, it still must reach the esophagus, at the posterior end of the mouth cavity. In suspension-feeding fish, gill-arch structures function as a sieve (Hoogenboezem et al. 1991) or a cross-flow filter that concentrates particles toward the esophagus (Sanderson et al. 1991, 2001). There is no doubt that the flow inside the mouth helps transport the prey through the buccal cavity in suction-feeding fishes as well. It is also generally assumed that the gill rakers or the pharyngeal jaws help to maintain the prey in the mouth during the evacuation of water. However, due to the difficulties inherent in directly measuring and visualizing flows inside the mouth, little is known about these flows.

There have been several studies that empirically characterized the pressure within the buccal cavity of fish by cannulating the skull and these predate PIV measurements of flow. Some species generate large negative pressures (-65 kPa). The magnitude of peak negative pressure has been used as a metric of suction-feeding performance and is correlated with between-species variation in measured speeds of flow (Holzman et al. 2008a). The magnitude of peak negative buccal pressure is also highly correlated with strike-to-strike variation of speed of flow within an individual as predicted by simple fluid mechanics (Day et al. 2007).

Detailed quantitative kinematics

Kinematics of skeletal elements visible from the outside of the fish have been quantified from a two-dimensional perspective, using high-speed video in several species and two-dimensional X-ray videography has been used for a more limited number of species. However, many of the skeletal motions, such as the hyoid apparatus contributing both to depression and lateral expansion of the lower jaw, are complex and three-dimensional. Sonomicrometry has been used to track the relative three-dimensional position of several key landmarks within the skull in at least one study (Sanford and Wainwright 2002). New techniques provide novel ways to assess both

three-dimensional morphology and movement. For example, based on bi-planar X-ray videos, X-ray Reconstruction of Moving Morphology (XROMM) enables the visualization of rapid skeletal movement under *in vivo* conditions, making it an excellent technique for examining the rapid, three-dimensional movements involved in suction feeding (Gidmark et al. 2012). This tool can be used in future studies to reveal aspects of movement that are associated with unique morphologies and/or ecology. Sophisticated morphological analyses using CT scanning, especially when coupled with functional studies, can provide an incredible amount of information regarding the mechanisms underlying feeding (Roos et al. 2009a). XROMM measurements of one species of fish are presented in an article within these proceedings (Camp and Brainerd 2015).

Conclusion

Our understanding of suction-feeding mechanics and fluid mechanics has grown substantially over the past several years, mainly due to the application of advanced visualization methods and numerical models. These quantitative mechanistic models, however, focus on very specific aspects of suction feeding, such as the spatial patterns of the flows, or the force exerted on the prey. Our current understanding of the suction-feeding mechanism, and the computational tools available, make it possible to construct a mechanistic model that would integrate the entire process. Ideally, the model would prescribe only morphology and muscle contraction and solve for the movement of bones, flows, and pressures inside and outside the mouth, the consequent forces exerted on the prey, and perhaps even the responses by prey. This could be achieved by the integration and simultaneous solution of existing models presented here, although it may require some of the knowledge described in our limitations of understanding before this can be done comprehensively for a significant range of morphology and behavior. Eventually, this type of truly integrative understanding and predictive modeling will, we hope, allow a better understanding of the general relationships between cranial morphology and the capture of prey that might be used for comparative or paleontological studies.

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