

Integrative and Comparative Biology

Suction feeding by small organisms: Performance limits in larval vertebrates and carnivorous plants

Journal:	Integrative and Comparative Biology
Manuscript ID	ICB-2020-0050.R1
Manuscript Type:	Symposium article
Date Submitted by the Author:	01-Jul-2020
Complete List of Authors:	Deban, Stephen ; University of South Florida, Integrative Biology Holzman, Roi; Tel Aviv University, Faculty of Life Sciences Muller , Ulrike ; California State University Fresno, Department of Biology
Keywords:	scaling, aquatic feeding, fluid dynamics, salamander, bladderwort

SCHOLARONE[™] Manuscripts

Suction feeding by small organisms: Performance limits in larval vertebrates and carnivorous plants

Stephen M. Deban^{1*}, Roi Holzman[†], and Ulrike K. Müller[‡]

^{*}Department of Integrative Biology, University of South Florida, 4202 E. Fowler Ave, SCA 110, Tampa, FL 33620, USA; [†]School of Zoology, Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel and the Inter-University for Marine Sciences in Eilat, Israel; [‡]Department of Biology, California State University Fresno, Fresno, CA 93740, USA.

From the symposium "Form, structure and function: How plants vs. animals solve physical problems," presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3-7, 2020 at Austin, Texas.

¹Corresponding author: Email: <u>sdeban@usf.edu</u>, Phone: 813-974-2242, Fax: 813-974-3263

Ulrike ORCID: 0000-0001-5338-9310

Steve ORCID: 0000-0002-7979-4346

Roi ORCID: 0000-0002-2334-2551

Keywords: scaling, aquatic feeding, fluid dynamics, salamander, bladderwort

Page 2 of 45

Suction feeding by small organisms

Abstract

Suction feeding has evolved independently in two highly disparate animal and plant systems, aquatic vertebrates and carnivorous bladderworts. We review the suction performance of animal and plant suction feeders to explore biomechanical performance limits for aquatic feeders based on morphology and kinematics, in the context of current knowledge of suction feeding. While vertebrates have the greatest diversity and size range of suction feeders, bladderworts are the smallest and fastest known suction feeders. Body size has profound effects on aquatic organismal function, including suction feeding, particularly in the intermediate flow regime that tiny organisms can experience. A minority of tiny organisms suction feed, consistent with model predictions that generating effective suction flow is less energetically efficient and also requires more flow-rate specific power at small size. Although the speed of suction flows generally increases with body and gape size, some specialized tiny plant and animal predators generate suction flows greater than those of suction feeders 100 times larger. Bladderworts generate rapid flow via high-energy and high-power elastic recoil and suction feed for nutrients (relying on photosynthesis for energy). Small animals may be limited by available muscle energy and power, although mouth protrusion can offset the performance cost of not generating high suction pressure. We hypothesize that both the high energetic costs and high power requirements of generating rapid suction flow shape the biomechanics of small suction feeders, and that plants and animals have arrived at different solutions due in part to their different energy budgets.

> Deban, Holzman, and Müller – Page 2 of 38 http://mc.manuscriptcentral.com/icbiol

Introduction

Suction feeding is widely used by aquatic vertebrate predators across a large size range from larval fish and frog tadpoles to toothed whales, as well as by one group of carnivorous plants, the bladderworts (Fig. 1) (Muller and Osse 1984; Drost and Boogaart 1986; Van Damme and Aerts 1997; Deban and Olson 2002; Lemell et al. 2002; Motta et al. 2002; Werth 2004; Bloodworth and Marshall 2005; Marshall et al. 2008; Kane and Marshall 2009; Vincent et al. 2011b; Bardet et al. 2013; Stinson and Deban 2017; Enstipp et al. 2018; Jacobs and Holzman 2018; Coates et al. 2019; Gidmark et al. 2019; Berg et al. 2020). Suction feeders generate sub-ambient pressure within the expanding volume of their mouth cavity, which drives strong flow into the mouth. That flow entrains prey, dragging it towards the mouth. Suction feeding in animals has been studied most extensively in adult teleost fish (Day et al. 2015; Wainwright et al. 2015; Jacobs and Holzman 2018) and is the predominant feeding mode in teleosts throughout their development from first-feeding larva to adult (China et al. 2017; Jacobs and Holzman 2018; Gidmark et al. 2019). This feeding mode is also found in many other aquatic predators such as sharks, amphibia, turtles, mammals, and aquatic carnivorous plants (Deban and Olson 2002; Motta et al. 2002; Bloodworth and Marshall 2005; Nauwelaerts et al. 2007; Wilga et al. 2007; Marshall et al. 2008; Stinson and Deban 2017; Jacobs and Holzman 2018; Coates et al. 2019; Gidmark et al. 2019). This review focuses on suction feeders that have received renewed attention, including aquatic amphibians and small suction feeders, with special attention given to bladderwort traps and larval fish. By

> Deban, Holzman, and Müller – Page 3 of 38 http://mc.manuscriptcentral.com/icbiol

comparing these suction feeders with adult teleosts, this review aims to highlight how size affects suction performance (i.e., flow speed), especially at the small end of the scale.

Body size has profound effects on biomechanical processes, and these effects can impose upper or lower size limits when these processes become no longer effective or efficient. In the case of organismal movement of and in fluids, viscous forces increasingly dominate over inertial forces as spatial scale decreases, effects to which organisms have evolved a variety of compensatory strategies (Denny 1993; Vogel 1994; Koehl 1996; Gazzola et al. 2014). The effects of increasing viscous forces are strongly felt by small suction-feeding animals, as reflected in their generally reduced prey-capture performance when compared with larger suction feeders (China and Holzman 2014; Yaniv et al. 2014; Jacobs and Holzman 2018). In contrast, small suction-feeding plants (i.e., bladderworts) capture prey effectively at small sizes (Berg et al. 2020) seemingly circumventing the limits imposed on tiny animals by fluid dynamic properties. Dickinson et al. (2000) pointed out, *"Biologists have long been attracted to … extremes because they provide especially clear examples from which to determine structure-function*

relations." Suction feeding in tiny organisms is where extreme size meets extreme speed: the fastest suction feeders are also among the smallest. Yet among small suction feeders, there are huge differences in performance; where the tiny traps of a carnivorous plant excel at speed and pressure, larval fish perform poorly (Fig. 2). This difference indicates that larval vertebrates and bladderworts solve the problem of suction feeding at small

> Deban, Holzman, and Müller – Page 4 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

size differently; plants use high energy whereas animals appear to use supplementary strategies [e.g., ram and mouth protrusion (Deban and Olson 2002)]. To understand what drives the differences in feeding strategy and capture performance between plant and animal suction feeders, we first review the literature on how morphology and behavior of organisms affects their suction performance and how body size affects this performance to establish the evidence for a lower size limit. Second, we examine the strategies that allow suction feeders to maintain performance near this limit. Third, we discuss the costs of those strategies and develop hypotheses about why animal and plant suction feeders might choose different strategies. Our focus is on the events leading up to and including prey capture, in particular the energetically costly and hydrodynamically challenging phase of generating suction flow.

Essentials of suction feeding

At its essence, suction can be defined as flow driven by sub-ambient pressure. Suction feeding organisms generate sub-ambient pressure within a chamber, such as the expanding buccopharynx of vertebrates or the spring-loaded traps of bladderworts (Muller and Osse 1984; Joyeux et al. 2011; Berg et al. 2019). The sub-ambient pressure causes water to flow into the chamber through an aperture or mouth. Solid objects such as prey items in this suction flow experience three types of forces that accelerate the prey towards the predator: pressure drag, viscous drag, and acceleration reaction (Holzman et al. 2007; Wainwright and Day 2007; Holzman et al. 2008b; Van Wassenbergh and Aerts 2009; Skorczewski et al. 2010). Of these three, pressure drag

Deban, Holzman, and Müller – Page 5 of 38 http://mc.manuscriptcentral.com/icbiol

caused by the spatial pressure gradient is the predominant force (Holzman et al. 2007; Wainwright and Day 2007; Holzman et al. 2008a; Van Wassenbergh and Aerts 2009; Skorczewski et al. 2010). The strength of the spatial pressure gradient depends on the sub-ambient pressure driving the flow and the size and shape of the aperture resisting the flow. By modulating the driving pressure (i.e., chamber expansion) and the resistance to the flow (i.e., mouth or aperture opening and closing), suction feeders can control the initiation, termination, and velocity-time profile of the suction flow. The relation between suction flow and prey capture success can be predicted from hydrodynamic theory. Mathematical models show that greater sub-ambient driving pressure produces a greater spatial pressure gradient in front of the aperture as well as faster flow and faster onset of flow, all else equal (Langhaar 1942). Both the pressure and the steepness of the pressure gradient diminish with distance from the aperture, limiting the strike range of suction feeders to roughly one gape diameter from the aperture (Jacobs and Holzman 2018; Müller et al. 2020). Circular gapes or stronger driving pressures increase flow speed (Van Wassenbergh et al. 2006; Skorczewski et al. 2012). Computational studies simulating animal suction feeders also show that the correlation between driving pressure and prey capture success is weakened by the effects of buccal morphology, making the flow speed in front of the aperture a more direct and readily observable predictor of prey capture success (Van Wassenbergh et al. 2006; Skorczewski et al. 2012).

> Deban, Holzman, and Müller – Page 6 of 38 http://mc.manuscriptcentral.com/icbiol

 Manuscripts submitted to Integrative and Comparative Biology

Suction feeding by small organisms

Predictions from fluid dynamic theory are often borne out by experimental observations (Langhaar 1942; Muller et al. 1982; Berg et al. 2020). Experimental studies on animal suction feeders do indeed find that greater prey capture success correlates with greater flow speed and a shorter time to peak gape (Holzman et al. 2012). However, against predictions, circular gapes or stronger driving pressures do not always correlate with stronger pressure gradients and higher capture success (Van Wassenbergh et al. 2006; Skorczewski et al. 2012), possibly due to inter- and intraspecific differences in morphology and behavior, and organisms using compensatory strategies or simply varying their behavior (Van Wassenbergh et al. 2006; Skorczewski et al. 2012; Jacobs and Holzman 2018). An example for which we understand the cause for the discrepancy between prediction and experimental observation is the relation between gape and flow speed; whereas theory predicts that increasing gape reduces flow speed for a given driving pressure, suction feeders can and do increase flow speed even with wider gapes by generating greater suction pressure (Jacobs and Holzman 2018).

The behavior of the prey and its position in the suction flow also affect capture success: prey at a greater distance from the aperture and fast-swimming prey are less likely to be caught because they either experience a lower suction force or are able to resist the suction force (Holzman et al. 2012). Predators counter by controlling the timing of aperture opening (e.g., triggered by prey movement in bladderworts) as well as kinematics of their mouth and body (i.e., movement by animals) (e.g., Cundall et al. 1987; Van Wassenbergh et al. 2014).

> Deban, Holzman, and Müller – Page 7 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding vertebrates

Suction feeding is used by a wide range of vertebrates and is a dominant feeding mode among teleost fish and aquatic salamanders, accomplished via mouth opening, buccopharyngeal expansion, and mouth closing (van Leeuwen and Muller 1984; Muller and Osse 1984; Aerts et al. 1987; Deban and Wake 2000; de Lussanet and Muller 2007; Bishop et al. 2008). A common pattern seen in both fish and amphibians is mouth opening followed by buccopharyngeal expansion, with maximum gape achieved prior to maximum expansion such that mouth closing can occur even as expansion continues. This type of coordination ensures that flow only enters the open mouth during prey capture (as opposed to backflow out the mouth as it closes). However, such unidirectional flow is dependent upon the momentum of the water in inertial flow regimes, as evidenced by the backflow out the mouth in tiny fish operating in viscous flow regimes, fish that use similarly coupled kinematics (Yaniv et al. 2014; Krishnan et al. 2020).

Expansion of the buccopharynx is accomplished in teleost fish by a combination of elevation of the neurocranium, ventral and lateral movements of the hyobranchial apparatus, and retraction of the pectoral girdle (Van Wassenbergh et al. 2005b; Camp and Brainerd 2014; Camp and Brainerd 2015; Day et al. 2015; Wainwright et al. 2015). Elasmobranchs emphasize hyobranchial movements (Motta et al. 2002). In amphibian suction feeders, cranial elevation and hyobranchial depression expand the buccopharynx and in some frogs the pectoral girdle buckles ventrally to expand the

> Deban, Holzman, and Müller – Page 8 of 38 http://mc.manuscriptcentral.com/icbiol

Page 9 of 45

 Suction feeding by small organisms

enlarged buccopharynx that fills the entire trunk (Erdman and Cundall 1984; Elwood and Cundall 1994; Deban and Wake 2000; Deban and Olson 2002; Cundall et al. 2017; Stinson and Deban 2017).

Once chamber expansion and the resulting pressure gradient has imparted momentum to the water, the water can continue to enter the mouth even after the pressure in the chamber has reached (or exceeded) ambient pressure, at least in the larger organisms operating at high Re that have been the focus of most studies of suction feeding. The volume of water that is engulfed during a suction feeding event, and hence the time course of flow velocity profile at the mouth, is affected by the fate of the engulfed water (Van Leeuwen 2010; Van Wassenbergh 2015). The moving water can produce passive expansion of the chamber, as we see in some aquatic amphibians with large volumes (Miller and Larsen 1989; Elwood and Cundall 1994; Deban and O'Reilly 2005; Carreño and Nishikawa 2010; Cundall et al. 2017) or it can continue rearward to exit through gill slits, as in many fish and some amphibians (Muller and Osse 1984) increasing the total engulfed volume. At the lower Re of bladderworts and larval vertebrates, this inertial flow is likely to be less prominent, and storage or pass-through of engulfed water may be less important in its impact on suction performance and engulfed volume. Computational models suggest that total ingested volume in larval fish is 65% of the buccal volume, in contrast to 250 to 325% in adult fish (Sanford and Wainwright 2002; Ferry-Graham et al. 2003; Higham et al. 2006a; Higham et al. 2006b; China and Holzman 2014; Yaniv et al. 2014; Holzman et al. 2015; China et al. 2017; Sommerfeld and Holzman 2019; Krishnan et al. 2020).

> Deban, Holzman, and Müller – Page 9 of 38 http://mc.manuscriptcentral.com/icbiol

A feature observed in many species of vertebrate suction feeders is a nearly circular, planar aperture or mouth (Deban and Olson 2002; Wainwright et al. 2015). This shape is predicted to result in higher rates of flow than other shapes and also to center and enlarge the region of high flow, improving capture success (Skorczewski et al. 2012; Van Wassenbergh and Heiss 2016). Despite these benefits of a planar, circular opening, many suction feeders exhibit different mouth shapes, with elliptical shapes or notched profiles, signaling potential compromises with other functions that may reduce suction performance; alternatively, deficits may be compensated by other mechanisms or simply difficult to detect in organismal data (Jacobs and Holzman 2018).

In addition to buccopharyngeal expansion and mouth opening and closing, mouth protrusion is often exhibited by vertebrate suction feeders. Mouth protrusion of many suction feeding fish (Motta 1984; Muller and Osse 1984; Osse 1985; Dean and Motta 2004; Holzman et al. 2008c), also called jaw protrusion, enhances performance in a number of ways: it moves the mouth closer to the prey, increasing the velocity and pressure gradients (which are steeper near the mouth) across the prey, it extends the mouth beyond the bow wave created by forward movement, it increases the volume change within the mouth, it restricts flow anteriorly, and it reduces momentum transfer to the water (van Leeuwen and Muller 1984; Muller and Osse 1984; Deban and Olson 2002). These performance advantages of mouth protrusion are likely gained with relatively little energetic cost when compared with the cost of generating higher suction pressure to achieve the same performance. Increasing mouth protrusion velocity, in addition to distance, has been shown to increase suction performance in fish, and it has

> Deban, Holzman, and Müller – Page 10 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

been proposed that the increase in speed of movement of the flow velocity profile across the prey increases the acceleration of the prey towards the mouth (Holzman et al. 2008c), beyond the effects obtained by simply positioning the mouth closer to the prey. Movement of the mouth by moving the head or entire body forward, as seen in many fish, amphibians, and some reptiles, also enhances suction performance and ensures that the volume of engulfed water is in front of the predator (Nyberg 1971; Weihs 1980; Higham et al. 2005). Forward movement has disadvantages, however, in that it can produce an area of elevated pressure in front of the predator, a 'bow wave', that can startle prey. Mouth protrusion and forward head or body movement (i.e., ram) are often coupled temporally with compensatory suction such that the bow wave is reduced or eliminated (Van Damme and Aerts 1997).

Suction feeding plants

Bladderworts (*Utricularia*) are genus of carnivorous plants that catch prey in underwater or underground motile traps. The traps are modified leaf structures forming hollow bladders that are roughly lenticular in shape (Reifenrath et al. 2006; Whitewoods et al. 2020). Of the more than 200 bladderwort species, 35 species have underwater suction traps of the so-called *vulgaris* trap type (Poppinga et al. 2015; Westermeier et al. 2017). These traps are similar in gape size to early larval fish – their aperture diameters range from 0.2 to 1.3 mm (Friday 1991; Poppinga et al. 2017) (Fig. 3). An individual plant has a large number of operational traps, in some species several

> Deban, Holzman, and Müller – Page 11 of 38 http://mc.manuscriptcentral.com/icbiol

hundred traps per plant (Friday 1992), and the number and size range of these traps can vary seasonally and with nutritional status (Knight and Frost 1991; Guisande et al. 2000; Guiral and Rougier 2007) (Fig. 3a). Traps grow to their mature size and become functional within a few weeks; they remain functional for a several weeks, then senesce and decay (Friday 1991; Poppinga et al. 2017).

Bladderwort traps are hollow bladders sealed by a dome-shaped door (Friday 1991; Reifenrath et al. 2006; Westermeier et al. 2017) (Fig. 3d). A mature bladderwort trap is set by elastically loading the trap walls as water is removed from the trap lumen, causing the trap walls to bow inward and generating a sub-ambient pressure inside the trap (Sasago and Sibaoka 1985; Singh et al. 2011; Poppinga et al. 2015) (Fig. 3b,c). Trap sub-ambient pressures range from 10 to 17 kPa (Sydenham and Findlay 1975; Sasago and Sibaoka 1985; Singh et al. 2011). When prey touches trigger hairs on the trap door, the trap door snap-buckles inward and prey is sucked into the trap within a few milliseconds (Vincent et al. 2011b; Poppinga et al. 2015), and the trap walls spring outward (Fig. 3e). Suction events are brief and last typically 5 to 15 ms from triggering the trap door to door closure (Poppinga et al. 2015; Westermeier et al. 2017), and the time from onset of flow to maximum gape or prey capture is even shorter, typically less than 3 ms (Poppinga et al. 2015). Peak flow speeds inside the trap mouth reach 5 m/s(Berg et al. 2020). Traps reload after firing; they can fire again within 10 to 15 minutes, yet evacuation of water continues considerably longer (Sydenham and Findlay 1975; Sasago and Sibaoka 1985; Singh et al. 2011).

> Deban, Holzman, and Müller – Page 12 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

Bladderwort traps differ from fish in that traps generate sub-ambient pressure many minutes to hours before the suction event (Sasago and Sibaoka 1985; Adamec 2011; Singh et al. 2011; Poppinga et al. 2015; Berg et al. 2019) and in that the trigger mechanism is purely mechanical (Adamec 2012). Bladderwort traps generate similar suction pressures to adult fish (11-57 kPa) (Carroll et al. 2004; Van Wassenbergh et al. 2005a; Higham et al. 2006a). Traps generate their suction by releasing elastic energy, affording them brief onset times, similar to onset times observed in seahorses and pipefish, which also use elastic recoil (Van Wassenbergh et al. 2008; Roos et al. 2009), and briefer than the onset times of fish using muscle-driven suction (Sanford and Wainwright 2002; Ferry-Graham et al. 2003; Higham et al. 2006a; Higham et al. 2006b). Compared with larval fish, bladderwort traps generate stronger pressures and higher flow speeds (Drost et al. 1988; Pekkan et al. 2016).

Suction feeding is effective only within one gape diameter from the plane of the mouth, so fish increase their reach using supplementary strategies such as ram and mouth protrusion (Motta 1984; Osse 1985; Jacobs and Holzman 2018). Bladderworts can mimic some of the effects of the mouth protrusion of vertebrates by positioning the prey closer to the aperture within the flow field through the use of trigger hairs that initiate suction when prey are in a particular position (Joyeux et al. 2011; Vincent et al. 2011a; Vincent et al. 2011b). However bladderworts do not rapidly move their aperture towards the prey and therefore cannot benefit from the performance boost this action provides. This accords with the observation that bladderworts simply generate high suction pressure to achieve their high performance.

Deban, Holzman, and Müller – Page 13 of 38 http://mc.manuscriptcentral.com/icbiol

Challenges of small suction feeders

Small animal and plant suction feeders must deal with hydrodynamic constraints as the dominance of viscous forces at small scale dampens movement and resists flow (Denny 2015). Small animal suction feeders additionally face physiological constraints because the maximum shortening velocity of muscle tissue reduces the velocity of movement for tiny animals that have muscles with fewer sarcomeres in series than larger animals (Bennet-Clark and Lucey 1967; McNeill Alexander 2003).

Suction performance is strongly affected by flow regime, which can be characterized by Reynolds number (Re) computed as the product of gape diameter and flow speed divided by water's kinematic viscosity. Hence the two parameters that correlate most strongly with suction performance (gape and flow speed) also determine suction flow regime (Holzman et al. 2012). Suction feeders typically operate in the inertial flow regime (Re > 300), where viscous forces play a negligible role and suction flow mechanics can be approximated by the Bernoulli equation, with bulk flow speed proportional to the square root of the suction pressure (Langhaar 1942) (Fig. 4). However, as gape diameter drops below a critical limit, suction feeders enter the creeping flow regime, where for a given pressure differential, flow speed is inversely proportional to the fourth power of gape diameter, causing flow speed to drop precipitously as gape decreases (Yaniv et al. 2014; True and Crimaldi 2017). Hence flow regime imposes a lower size limit on suction feeding and no suction feeders have been reported with gapes smaller than 50 microns (Hernández 2000; Deban and Olson 2002;

> Deban, Holzman, and Müller – Page 14 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

Yaniv et al. 2014). Hydrodynamic laws predict that in the inertial flow regime, suction flow speed is dominated by the magnitude of the suction pressure; in the creeping flow regime, flow speed is severely limited due to viscous dissipation (Yaniv et al. 2014; True and Crimaldi 2017). Larval fish, tadpoles, and bladderwort traps operate at gapes near the critical size limit (100 to 300 microns), which positions them within the so-called intermediate flow regime between the inertial and creeping flow regime at Re ranging from 30 to 900 (Deban and Olson 2002; Vincent et al. 2011b; China and Holzman 2014). The challenges that small animal suction feeders face have been studied most extensively in early fish larvae. Like adult fish, larval fish achieve suction by buccopharyngeal expansion combined with mouth opening and closing (Hernández 2000). Comparative studies on adult fish have identified correlates of high suction performance, such as large gape size, short time to peak gape, and high peak flow speed (Holzman et al. 2012; Jacobs and Holzman 2018). Larvae resemble adult fish in some of those characteristics, such as time to peak gape, but not in others. Larval times to maximum gape range from 8 to 110 ms (Hernández 2000)(China and Holzman 2014; Yaniv et al. 2014; Holzman et al. 2015; China et al. 2017; Sommerfeld and Holzman 2019; Krishnan et al. 2020)(Hernández 2000)(China and Holzman 2014; Yaniv et al. 2014; Holzman et al. 2015; China et al. 2017; Sommerfeld and Holzman 2019; Krishnan et al. 2020)(Hernández 2000), which are similar to adult teleost fish values that range from 6 to 104 ms (Sanford and Wainwright 2002; Ferry-Graham et al. 2003; Higham et al. 2006a; Higham et al. 2006b) (Fig. 5). But larval fish operate at smaller gapes and weaker

> Deban, Holzman, and Müller – Page 15 of 38 http://mc.manuscriptcentral.com/icbiol

suction pressures than adults (Drost et al. 1988; Hernández 2000), differences which have important consequences for the hydrodynamics of suction feeding. In contrast to adult teleost suction feeders, which operate in the inertial flow regime, fish larvae operate at the transition from viscous to inertial flow regime. Early-feeding fish larvae face multiple hydrodynamic challenges that impair their prey capture performance (China and Holzman 2014; Yaniv et al. 2014; Holzman et al. 2015; China et al. 2017; Sommerfeld and Holzman 2019; Krishnan et al. 2020). Their feeding success correlates highly with an increase in Re (China et al. 2017). Lowering Re by artificially increasing water viscosity reduces the success rate of feeding strikes of older larvae to a level similar to that of younger larvae at equivalent Re, demonstrating that the low success rate of early-feeding larvae is not due to inexperience or immature motor control, but due to hydrodynamic constraints on performance (China and Holzman 2014). Even ingestion of prey does not always equal capture: experiments and flow simulations show that prey can be washed out of the mouth after ingestion when the larva closes its mouth, due to backwash (Krishnan et al. 2020). Fish larvae must generate strong and brief suction flows to catch their preferred prey and doing so means that larvae are successful when they operate close to the inertial flow regime (Sommerfeld and Holzman 2019).

In contrast to early larval fish, bladderwort traps appear to be effective suction feeders despite their similarly small gape diameters because they operate at considerably higher Re than early fish larvae (Deban and Olson 2002; Vincent et al. 2011b; China and

> Deban, Holzman, and Müller – Page 16 of 38 http://mc.manuscriptcentral.com/icbiol

Manuscripts submitted to Integrative and Comparative Biology

Suction feeding by small organisms

Holzman 2014). A comparison of suction characteristics (gape diameter, peak flow speed, time to peak gape, sub-ambient driving pressure) between animal and plant suction feeders reveals that bladderworts generate flow speeds and sub-ambient driving pressures that are similar to large animal suction feeders (Fig. 5; Supplementary Table 1). Available data for adult teleosts suggest that fish generate a narrow range of peak suction flow speeds centered around 0.5 m/s at a distance of one half of gape diameter from the mouth (Higham et al. 2006a; Holzman et al. 2008a; Staab et al. 2012) with corresponding suction pressures centered around -30 kPa, while larval fish generate flows and pressures that are orders of magnitude weaker (Pekkan et al. 2016) (Fig. 5). Adult amphibians range in buccopharyngeal pressures from -0.6 to -3.3 kPa (Lauder and Shaffer 1985; Carreño and Nishikawa 2010). In summary, bladderworts' strong driving pressures allow their tiny traps to generate suction flows as fast as those of animals with much larger gapes (Sydenham and Findlay 1975; Sasago and Sibaoka 1985; Singh et al. 2011; Adamec and Poppinga 2016; Westermeier et al. 2017).

Strategies of small suction feeders and their costs

A comparison of small animal and plant suction feeders suggests that the main difference between the two is peak suction flow speed in front of the mouth or trap entrance, which is a strong predictor of prey capture success (Van Wassenbergh et al. 2006; Skorczewski et al. 2012). Despite operating at similar gape diameters as early larval fish, bladderwort traps show no strongly depressed suction performance and instead generate peak flow speeds similar to adult fish, possibly because they operate at

> Deban, Holzman, and Müller – Page 17 of 38 http://mc.manuscriptcentral.com/icbiol

sub-ambient driving pressures similar to adult fish and much higher than larval fish. This raises the question how small organisms produce suction flow.

Studies on large suction feeders have shown that generating effective suction flows requires substantial hydrodynamic power, which can be provided by a large muscle volume or through rapid elastic recoil (Aerts et al. 1987; Van Wassenbergh et al. 2009; Camp et al. 2015; Poppinga et al. 2015; Westneat and Olsen 2015; Berg et al. 2019). More than 80% of the required power for suction feeding goes to the generation of subambient pressure by buccopharyngeal expansion in catfish (gape ~ 2 cm), while inertia and drag account for the remainder (Van Wassenbergh et al. 2005a). Buccopharyngeal expansion, and consequently suction performance, is power limited in vertebrates that use direct muscle shortening for expansion (Aerts et al. 1987; Carroll and Wainwright 2009), which includes most suction feeding vertebrates that have been examined. Largemouth bass recruit the anterior third of their axial musculature during the suction event, greater than the mass of the cranial musculature (Camp et al. 2015), a testament to the high hydrodynamic power requirements of suction feeding. Exceptional fish that do not use direct muscle power are the pipefish, seahorses and snipefish, which are especially rapid feeders whose movements require power in excess of that which muscle shortening can provide directly; they use elastic recoil of tendons previously stretched by axial muscles, combined with latching morphology that couples head pivoting and hence snout movement with buccal expansion (Van Wassenbergh et al. 2008; Van Wassenbergh et al. 2014; Longo et al. 2018). The long snouts and small gapes

> Deban, Holzman, and Müller – Page 18 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

in these fish may necessitate power that only an elastic-recoil mechanism can efficiently provide.

In addition to requiring high power (i.e., rate of energy delivery), suction feeding performance is limited by the quantity of energy delivered to the water. The energy requirements and hydrodynamic efficiency of suction feeding can be predicted using mathematical models of flow through pipes (Langhaar 1942; Singh et al. 2020). The energy that suction feeders must invest to generate suction flows can be divided into three contributions: the energy required to overcome viscous friction (Fig. 4a), the energy to accelerate the water inside the buccal cavity or the channel leading into the trap (internal acceleration, Fig. 4b), and the energy required to accelerate the water outside the mouth or trap (external acceleration, Fig. 4c). While the first two types are losses, the third is what generates the spatial pressure gradient in front of the mouth or aperture that accelerates prey toward the predator. Thus, the ratio of 'external acceleration' energy to total energy can be used as a measure of hydrodynamic efficiency. A mathematical model that estimates the relative contribution of these three energies to the total hydrodynamic energy required for a suction event shows that the contribution of these three energies to total energy strongly depends on gape diameter and strength of the generated flow, i.e. flow speed (Fig. 4) (Berg et al. 2020). In large suction feeders, muscle or elastic energy is largely converted into kinetic energy of the water sucked into the predator's mouth cavity (Higham et al. 2006a; Van Wassenbergh et al. 2008; Camp and Brainerd 2014). In contrast, small suction feeders face large viscous losses, resulting in weaker suction flows (Pekkan et al. 2016; Berg et al. 2019)

> Deban, Holzman, and Müller – Page 19 of 38 http://mc.manuscriptcentral.com/icbiol

(Fig. 4), and the losses due to internal acceleration of water are highest at gape diameters typical for small animal and plant suction feeders (Fig. 4b). Suction flow speed and hydrodynamic efficiency drop sharply while the energetic costs of suction feeding increases sharply as pipe diameter (gape) drops below 0.1 mm (Sasago and Sibaoka 1985; Adamec 2011; Singh et al. 2011; Poppinga et al. 2015; Berg et al. 2019) (Fig. 4).

Smaller suction feeders not only face the challenge that the relative cost of generating suction flows is higher at smaller gapes; the proportion of their energetic investment that goes towards generating suction flows outside their mouth decreases with decreasing size (low hydrodynamic efficiency). But small suction feeders also face higher absolute costs; the amount of energy required to move a given volume of water within a given time (high flow-rate specific power) increases with decreasing size (Fig. 4d).

Small suction feeders can overcome these challenges by investing the energy required to generate strong suction flows or by reducing the energetic cost relative to capture success by using morphological or behavioral adaptations or supplementary strategies such as mouth protrusion and ram, or a combination of these. Bladderwort traps and seahorses appear to converge on the first strategy, investing considerable energy and storing this energy elastically to release the high power required to create strong sub-ambient suction flows (Van Wassenbergh et al. 2009; Poppinga et al. 2015; Berg et al. 2019). Tadpoles of *Hymenochirus* appear to at least use the second and third strategy;

Deban, Holzman, and Müller – Page 20 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

their funnel-shaped mouth can reduce viscous drag, and the mouth protrudes, so these tadpoles achieve flow velocities comparable to much larger suction feeders (Deban and Olson 2002).

Conclusions

Theoretical predictions and experimental observations suggest that organisms with gape sizes between 50 to 500 microns and sub-ambient driving pressures between 0.2 and 10 kPa may face dramatic changes in performance as a function of their gape size and suction pressure. Experiments on larval fish show that small animal suction feeders can be severely impacted in their suction and prey capture performance (China and Holzman 2014; China et al. 2017; Sommerfeld and Holzman 2019). Among small suction feeders within the predicted critical range of gape sizes, bladderwort traps stand out for their sub-ambient driving pressures above 10 kPa, which allow them to enter the inertial flow regime, in contrast to early fish larvae which operate in the intermediate flow regime. Although larval fish and bladderwort traps have similar gapes that are two to three orders of magnitude smaller than adult fish, bladderworts achieve flow speeds and hydrodynamic efficiencies that are only one order of magnitude lower than large suction feeders (Fig. 5). By operating at Re above 100, bladderworts lose 17% of the generated power to friction, compared with 2% in adult fish (Aerts et al. 1987; Van Wassenbergh et al. 2005b; Van Wassenbergh et al. 2009; Camp et al. 2015; Poppinga et al. 2015; Berg et al. 2019), and achieve peak flow speeds at half gape from the aperture of 0.2 to 0.3 m/s compared with 0.68 to 1.4 m/s in adult fish (Ferry-Graham et al. 2003;

> Deban, Holzman, and Müller – Page 21 of 38 http://mc.manuscriptcentral.com/icbiol

Higham et al. 2006a; Higham et al. 2006b; Singh et al. 2020). In contrast, early zebrafish larvae achieve flow speeds that are four orders of magnitude lower than adult fish, and their hydrodynamic efficiency is calculated to be below 60% (Aerts et al. 1987; Van Wassenbergh et al. 2009; Camp et al. 2015; Poppinga et al. 2015; Berg et al. 2019). Bladderwort traps outperform similar sized zebrafish larvae by generating faster suction flows that allows them to operate in the inertial flow regime (traps: Re 200 to 500; zebrafish larvae: Re 1)(Müller et al. 2020), but bladderworts do so at considerable energetic cost. The sharp decrease in hydrodynamic efficiency and sharp increase in energetic costs might place energetic limits on suction feeding that are more relevant to heterotrophs that must feed for energy than to autotrophs that suction feed mainly to acquire nutrients. Autotrophic organisms such as bladderworts can afford the energetic cost of suction feeding at small size because they obtain energy through photosynthesis and feed primarily for nutrients. In contrast, tiny heterotrophic organisms such as tadpoles and larval fish may favor supplementary strategies such as ram and mouth protrusion over pure suction feeding at the elevated energetic costs associated with generating fast suction flows.

Acknowledgments

This research was supported by the University of South Florida, the National Science Foundation (NSF-BIO-IOS 1352130 to UKM), and California State University Fresno. This manuscript resulted from a symposium presentation, funded by NSF-BIO-IOS

> Deban, Holzman, and Müller – Page 22 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

1930744 and the Company of Biologists. Otto Berg did the calculations for Fig. 4. We thank four anonymous reviewers for helpful suggestions.

References

Adamec L. 2011. Functional characteristics of traps of aquatic carnivorous Utricularia species. Aquat Bot. 95(3):226–233.

Adamec L. 2012. Firing and resetting characteristics of carnivorous Utricularia reflexa traps: physiological or only physical regulation of trap triggering. Phyton. 52:281–290.

Adamec L, Poppinga S. 2016. Measurement of the critical negative pressure inside traps of aquatic carnivorous *Utricularia* species. Aquat Bot. 133:10–16.

Aerts P, Osse JWM, Verraes W. 1987. Model of jaw depression during feeding in *Astatotilapia elegans* (Teleostei: Cichlidae): Mechanisms for energy storage and triggering. J Morphol. 194(1):85–109.

Bardet N, Jalil N-E, de Lapparent de Broin F, Germain D, Lambert O, Amaghzaz M. 2013. A giant chelonioid turtle from the late Cretaceous of Morocco with a suction feeding apparatus unique among tetrapods. PLoS One. 8(7):e63586.

Bennet-Clark HC, Lucey E. 1967. The jump of the flea: a study of the energetics and a model of the mechanism. J Exp Biol. 47(1):59–76.

Berg O, Brown MD, Schwaner MJ, Hall MR, Müller UK. 2020. Hydrodynamics of the bladderwort feeding strike. J Exp Zool A Ecol Integr Physiol. 333(1):29–37.

Deban, Holzman, and Müller – Page 23 of 38 http://mc.manuscriptcentral.com/icbiol

Berg O, Singh K, Hall MR, Schwaner MJ, Müller UK. 2019. Thermodynamics of the bladderwort feeding strike – suction power from elastic energy storage. Integr Comp Biol. 59(6):1597–1608. Bishop KL, Wainwright PC, Holzman R. 2008. Anterior-to-posterior wave of buccal expansion in suction feeding fishes is critical for optimizing fluid flow velocity profile. J R Soc Interface. 5(28):1309–1316.

Bloodworth B, Marshall CD. 2005. Feeding kinematics of *Kogia* and *Tursiops* (Odontoceti: Cetacea): characterization of suction and ram feeding. J Exp Biol. 208(Pt 19):3721–3730.

Camp AL, Brainerd EL. 2014. Role of axial muscles in powering mouth expansion during suction feeding in largemouth bass (*Micropterus salmoides*). J Exp Biol. 217(8):1333–1345.

Camp AL, Brainerd EL. 2015. Reevaluating musculoskeletal linkages in suction-feeding fishes with x-ray reconstruction of moving morphology (XROMM). Integr Comp Biol. 55(1):36–47.

Camp AL, Roberts TJ, Brainerd EL. 2015. Swimming muscles power suction feeding in largemouth bass. Proc Natl Acad Sci U S A. 112(28):8690–8695.

Carreño CA, Nishikawa KC. 2010. Aquatic feeding in pipid frogs: the use of suction for prey capture. J Exp Biol. 213(Pt 12):2001–2008.

Carroll AM, Wainwright PC. 2009. Energetic limitations on suction feeding performance in centrarchid fishes. J Exp Biol. 212(Pt 20):3241–3251.

Carroll AM, Wainwright PC, Huskey SH, Collar DC, Turingan RG. 2004. Morphology predicts suction feeding performance in centrarchid fishes. J Exp Biol. 207(Pt 22):3873–3881.

China V, Holzman R. 2014. Hydrodynamic starvation in first-feeding larval fishes. Proc Natl

Deban, Holzman, and Müller – Page 24 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

Acad Sci U S A. 111(22):8083-8088.

China V, Levy L, Liberzon A, Elmaliach T, Holzman R. 2017. Hydrodynamic regime determines the feeding success of larval fish through the modulation of strike kinematics. Proc Biol Sci. 284(1853):20170235.

Coates MI, Tietjen K, Olsen AM, Finarelli JA. 2019. High-performance suction feeding in an early elasmobranch. Science Advances. 5(9):eaax2742.

Cundall D, Fernandez E, Irish F. 2017. The suction mechanism of the pipid frog, *Pipa pipa* (Linnaeus, 1758). J Morphol. 278(9):1229–1240.

Cundall D, Lorenz-Elwood J, Groves JD. 1987. Asymmetric suction feeding in primitive salamanders. Experientia. 43(11):1229–1231.

Day SW, Higham TE, Holzman R, Van Wassenbergh S. 2015. Morphology, kinematics, and dynamics: the mechanics of suction feeding in fishes. Integr Comp Biol. 55(1):21–35.

Dean MN, Motta PJ. 2004. Feeding behavior and kinematics of the lesser electric ray, Narcine brasiliensis (Elasmobranchii: Batoidea). Zoology. 107(3):171–189.

Deban SM, Olson WM. 2002. Suction feeding by a tiny predatory tadpole. Nature. 420(6911):41– 42.

Deban SM, O'Reilly JC. 2005. The ontogeny of feeding kinematics in a giant salamander *Cryptobranchus alleganiensis*: Does current function or phylogenetic relatedness predict the scaling patterns of movement? Zoology. 108(2):155–167.

Deban SM, Wake DB. 2000. Aquatic feeding in salamanders. In: Schwenk K, editor. Feeding:

Deban, Holzman, and Müller – Page 25 of 38 http://mc.manuscriptcentral.com/icbiol

Page 26 of 45

Suction feeding by small organisms

> form, function and evolution in tetrapod vertebrates. San Diego: Academic Press. p. 65–94. Denny M. 2015. Ecological mechanics: principles of life's physical interactions. Princeton University Press.

Denny MW. 1993. Air and water: the biology and physics of life's media. Princeton University Press.

Dickinson MH, Farley CT, Full RJ, Koehl MA, Kram R, Lehman S. 2000. How animals move: an integrative view. Science. 288(5463):100–106.

Drost MR, Boogaart JGM. 1986. The energetics of feeding strikes in larval carp, Cyprinus carpio. J Fish Biol. 29(3):371–379.

Drost MR, Muller M, Osse JWM. 1988. A quantitative hydrodynamical model of suction feeding in larval fishes: the role of frictional forces. Proc R Soc Lond B Biol Sci. 234(1276):263–281.

Eaton RC, Bombardieri RA, Meyer DL. 1977. The Mauthner-initiated startle response in teleost fish. J Exp Biol. 66(1):65–81.

Elwood JRL, Cundall D. 1994. Morphology and behavior of the feeding apparatus in *Cryptobranchus alleganiensis* (Amphibia: Caudata). J Morphol. 220(1):47–70.

Enstipp MR, Descamps S, Fort J, Grémillet D. 2018. Almost like a whale – first evidence of suction feeding in a seabird. The Journal of Experimental Biology. 221(13):jeb182170. doi:10.1242/jeb.182170. http://dx.doi.org/10.1242/jeb.182170.

Erdman S, Cundall D. 1984. The feeding apparatus of the salamander *Amphiuma tridactylum*: morphology and behavior. J Morphol. 181(2):175–204.

Deban, Holzman, and Müller – Page 26 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

Ferry-Graham LA, Wainwright PC, Lauder GV. 2003. Quantification of flow during suction feeding in bluegill sunfish. Zoology . 106(2):159–168.

Friday LE. 1991. The size and shape of traps of Utricularia vulgaris L. Funct Ecol. 5(5):602-607.

Friday LE. 1992. Measuring investment in carnivory: seasonal and individual variation in trap number and biomass in Utricularia vulgaris L. New Phytol. 121(3):439–445.

Gazzola M, Argentina M, Mahadevan L. 2014. Scaling macroscopic aquatic locomotion. Nat Phys. 10:758.

Gidmark NJ, Pos K, Matheson B, Ponce E, Westneat MW. 2019. Functional morphology and biomechanics of feeding in fishes. In: Bels V, Whishaw IQ, editors. Feeding in vertebrates: evolution, morphology, behavior, biomechanics. Cham: Springer International Publishing. p. 297–332.

Guiral D, Rougier C. 2007. Trap size and prey selection of two coexisting bladderwort (*Utricularia*) species in a pristine tropical pond (French Guiana) at different trophic levels. EDP Sciences (Annales de Limnologie-International Journal of Limnology).

Guisande C, Andrade C, Granado-Lorencio C, Duque SR, Núñez-Avellaneda M. 2000. Effects of zooplankton and conductivity on tropical *Utricularia foliosa* investment in carnivory. Aquat Ecol. 34(2):137–142.

Hernández LP. 2000. Intraspecific scaling of feeding mechanics in an ontogenetic series of zebrafish, Danio rerio. J Exp Biol. 203(Pt 19):3033–3043.

Higham TE, Day SW, Wainwright PC. 2005. Sucking while swimming: evaluating the effects of

Deban, Holzman, and Müller – Page 27 of 38 http://mc.manuscriptcentral.com/icbiol

ram speed on suction generation in bluegill sunfish *Lepomis macrochirus* using digital particle image velocimetry. J Exp Biol. 208(Pt 14):2653–2660.

Higham TE, Day SW, Wainwright PC. 2006a. The pressures of suction feeding: the relation between buccal pressure and induced fluid speed in centrarchid fishes. J Exp Biol. 209(Pt 17):3281–3287.

Higham TE, Day SW, Wainwright PC. 2006b. Multidimensional analysis of suction feeding performance in fishes: fluid speed, acceleration, strike accuracy and the ingested volume of water. J Exp Biol. 209(Pt 14):2713–2725.

Holzman R, China V, Yaniv S, Zilka M. 2015. Hydrodynamic constraints of suction feeding in low reynolds numbers, and the critical period of larval fishes. Integr Comp Biol. 55(1):48–61.

Holzman R, Collar DC, Day SW, Bishop KL, Wainwright PC. 2008a. Scaling of suction-induced flows in bluegill: morphological and kinematic predictors for the ontogeny of feeding performance. J Exp Biol. 211(Pt 16):2658–2668.

Holzman R, Collar DC, Mehta RS, Wainwright PC. 2012. An integrative modeling approach to elucidate suction-feeding performance. J Exp Biol. 215(Pt 1):1–13.

Holzman R, Day SW, Mehta RS, Wainwright PC. 2008b. Integrating the determinants of suction feeding performance in centrarchid fishes. J Exp Biol. 211(Pt 20):3296–3305.

Holzman R, Day SW, Mehta RS, Wainwright PC. 2008c. Jaw protrusion enhances forces exerted on prey by suction feeding fishes. J R Soc Interface. 5(29):1445–1457.

Holzman R, Day SW, Wainwright PC. 2007. Timing is everything: coordination of strike

Deban, Holzman, and Müller – Page 28 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

kinematics affects the force exerted by suction feeding fish on attached prey. J Exp Biol. 210(Pt 19):3328–3336.

Jacobs CN, Holzman R. 2018. Conserved spatio-temporal patterns of suction-feeding flows across aquatic vertebrates: a comparative flow visualization study. J Exp Biol. 221(Pt 7):jeb. 174912.

Joyeux M, Vincent O, Marmottant P. 2011. Mechanical model of the ultrafast underwater trap of *Utricularia*. Phys Rev E Stat Nonlin Soft Matter Phys. 83(2 Pt 1):021911.

Kane EA, Marshall CD. 2009. Comparative feeding kinematics and performance of odontocetes: belugas, Pacific white-sided dolphins and long-finned pilot whales. J Exp Biol. 212(Pt 24):3939– 3950.

Knight SE, Frost TM. 1991. Bladder control in *Utricularia macrorhiza*: lake-specific variation in plant investment in carnivory. Ecology. 72(2):728–734.

Koehl M. 1996. When does morphology matter? Annu Rev Ecol Syst. 27(1):501-542.

Krishnan K, Nafi AS, Gurka R, Holzman R. 2020. The hydrodynamic regime drives flow reversals in suction-feeding larval fishes during early ontogeny. J Exp Biol. 223(Pt 9). doi:10.1242/jeb.214734. http://dx.doi.org/10.1242/jeb.214734.

Langhaar LH. 1942. Steady flow in the transition length of a straight tube. J Appl Mech. 9:55.

Lauder GV, Shaffer HB. 1985. Functional morphology of the feeding mechanism in aquatic ambystomatid salamanders. J Morphol. 185(3):297–326.

van Leeuwen JL, Muller M. 1984. Optimum sucking techniques for predatory fish. J Zool.

Deban, Holzman, and Müller – Page 29 of 38 http://mc.manuscriptcentral.com/icbiol

37(2):137-169.

Lemell P, Lemell C, Snelderwaard P, Gumpenberger M, Wochesländer R, Weisgram J. 2002. Feeding patterns of Chelus fimbriatus (Pleurodira: Chelidae). J Exp Biol. 205(Pt 10):1495–1506.

Lenz PH, Hartline DK. 1999. Reaction times and force production during escape behavior of a calanoid copepod, Undinula vulgaris. Mar Biol. 133(2):249–258.

Lenz PH, Hartline DK, Davis AD. 2000. The need for speed. I. Fast reactions and myelinated axons in copepods. J Comp Physiol A. 186(4):337–345.

Longo SJ, Goodearly T, Wainwright PC. 2018. Extremely fast feeding strikes are powered by elastic recoil in a seahorse relative, the snipefish, *Macroramphosus scolopax*. Proc Biol Sci. 285(1882):1–1.

de Lussanet MHE, Muller M. 2007. The smaller your mouth, the longer your snout: predicting the snout length of *Syngnathus acus*, *Centriscus scutatus* and other pipette feeders. J R Soc Interface. 4(14):561–573.

Marras S, Killen SS, Claireaux G, Domenici P, McKenzie DJ. 2011. Behavioural and kinematic components of the fast-start escape response in fish: individual variation and temporal repeatability. J Exp Biol. 214(Pt 18):3102–3110.

Marshall CD, Kovacs KM, Lydersen C. 2008. Feeding kinematics, suction and hydraulic jetting capabilities in bearded seals (Erignathus barbatus). J Exp Biol. 211(Pt 5):699–708.

McNeill Alexander R. 2003. Principles of Animal Locomotion. Princeton University Press.

Miller BT, Larsen JH Jr. 1989. Feeding performance in aquatic postmetamorphic newts (Urodela:

Deban, Holzman, and Müller – Page 30 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

Salamandridae): are bidirectional flow systems necessarily inefficient? Can J Zool. 67(10):2414–2421.

Motta PJ. 1984. Mechanics and functions of jaw protrusion in teleost fishes: a review. Copeia. 1984(1):1–18.

Motta PJ, Hueter RE, Tricas TC, Summers AP. 2002. Kinematic analysis of suction feeding in the nurse shark, *Ginglymostoma cirratum* (Orectolobiformes, Ginglymostomatidae). Copeia. 2002(1):24–38.

Muller M, Osse JWM. 1984. Hydrodynamics of suction feeding in fish. Trans Zool Soc London. 37(2):51–135.

Muller M, Osse JWM, Verhagen JHG. 1982. A quantitative hydrodynamical model of suction feeding in fish. J Theor Biol. 95(1):49–79.

Müller UK, Berg O, Schwaner MJ, Brown MD, Li G, Voesenek CJ, van Leeuwen JL. 2020. Bladderworts, the smallest known suction feeders, generate inertia-dominated flows to capture prey. New Phytol. doi:10.1111/nph.16726. http://dx.doi.org/10.1111/nph.16726.

Nauwelaerts S, Wilga C, Sanford C, Lauder G. 2007. Hydrodynamics of prey capture in sharks: effects of substrate. J R Soc Interface. 4(13):341–345.

Nyberg DW. 1971. Prey capture in the largemouth bass. Am Midl Nat. 86(1):128–144.

Osse JWM. 1985. Jaw protrusion, an optimization of the feeding apparatus of teleosts? In: Zweers GA, editor. Architecture in Living Structure. Dordrecht: Martinus Nijhoff/Dr W. Junk P. p. 113–126.

> Deban, Holzman, and Müller – Page 31 of 38 http://mc.manuscriptcentral.com/icbiol

Pekkan K, Chang B, Uslu F, Mani K, Chen C-Y, Holzman R. 2016. Characterization of zebrafish larvae suction feeding flow using µPIV and optical coherence tomography. Exp Fluids. 57(7):112.

Poppinga S, Daber LE, Westermeier AS, Kruppert S, Horstmann M, Tollrian R, Speck T. 2017. Biomechanical analysis of prey capture in the carnivorous Southern bladderwort (Utricularia australis). Sci Rep. 7(1):1776.

Poppinga S, Weisskopf C, Westermeier AS, Masselter T, Speck T. 2015. Fastest predators in the plant kingdom: functional morphology and biomechanics of suction traps found in the largest genus of carnivorous plants. AoB Plants. 8:lv140.

Reifenrath K, Theisen I, Schnitzler J, Porembski S, Barthlott W. 2006. Trap architecture in carnivorous Utricularia (Lentibulariaceae). Flora - Morphology, Distribution, Functional Ecology of Plants. 201(8):597–605.

Roos G, Van Wassenbergh S, Herrel A, Aerts P. 2009. Kinematics of suction feeding in the seahorse *Hippocampus reidi*. J Exp Biol. 212(Pt 21):3490–3498.

Sanford CPJ, Wainwright PC. 2002. Use of sonomicrometry demonstrates the link between prey capture kinematics and suction pressure in largemouth bass. J Exp Biol. 205(Pt 22):3445–3457.

Sasago A, Sibaoka T. 1985. Water extrusion in the trap bladders of *Utricularia vulgaris* I. A possible pathway of water across the bladder wall. The Botanical Magazine Tokyo (Shokubutsu-gaku-zasshi). 98(1):55–66.

Singh AK, Prabhakar S, Sane SP. 2011. The biomechanics of fast prey capture in aquatic bladderworts. Biol Lett. 7(4):547–550.

Deban, Holzman, and Müller – Page 32 of 38 http://mc.manuscriptcentral.com/icbiol

Suction feeding by small organisms

Singh K, Reyes RC, Campa G, Brown MD, Hidalgo F, Berg O, Müller UK. 2020. Suction flows generated by the carnivorous bladderwort *Utricularia* – comparing experiments with mechanical and mathematical models. Fluids Barriers CNS. 5(1):33.

Skorczewski T, Cheer A, Cheung S, Wainwright PC. 2010. Use of computational fluid dynamics to study forces exerted on prey by aquatic suction feeders. J R Soc Interface. 7(44):475–484.

Skorczewski T, Cheer A, Wainwright PC. 2012. The benefits of planar circular mouths on suction feeding performance. J R Soc Interface. 9(73):1767–1773.

Sommerfeld N, Holzman R. 2019. The interaction between suction feeding performance and prey escape response determines feeding success in larval fish. J Exp Biol. 222(Pt 17):1–8.

Staab KL, Holzman R, Hernandez LP, Wainwright PC. 2012. Independently evolved upper jaw protrusion mechanisms show convergent hydrodynamic function in teleost fishes. J Exp Biol. 215(Pt 9):1456–1463.

Stinson CM, Deban SM. 2017. Functional trade-offs in the aquatic feeding performance of salamanders. Zoology. 125:69–78.

Sydenham PH, Findlay GP. 1975. Transport of solutes and water by resetting bladders of *Utricularia*. Funct Plant Biol. 2(3):335–351.

True AC, Crimaldi JP. 2017. Hydrodynamics of viscous inhalant flows. Phys Rev E. 95(5-1):053107.

Van Damme J, Aerts P. 1997. Kinematics and functional morphology of aquatic feeding in Australian snake-necked turtles (Pleurodira; Chelodina). J Morphol. 233(2):113–125.

> Deban, Holzman, and Müller – Page 33 of 38 http://mc.manuscriptcentral.com/icbiol

Van Leeuwen JL. 2010. A quantitative study of flow in prey capture by Rainbow trout, *Salmo gairdneri* with general consideration of the actinopterygian feeding mechanism. The Transactions of the Zoological Society of London. 37(2):171–227.

Van Wassenbergh S. 2015. A solution strategy to include the opening of the opercular slits in moving-mesh CFD models of suction feeding. Integr Comp Biol. 55(1):62–73.

Van Wassenbergh S, Aerts P. 2009. Aquatic suction feeding dynamics: insights from computational modelling. J R Soc Interface. 6(31):149–158.

Van Wassenbergh S, Aerts P, Herrel A. 2005a. Scaling of suction-feeding kinematics and dynamics in the African catfish, *Clarias gariepinus*. J Exp Biol. 208(11):2103–2114.

Van Wassenbergh S, Aerts P, Herrel A. 2006. Hydrodynamic modelling of aquatic suction performance and intra-oral pressures: limitations for comparative studies. J R Soc Interface. 3(9):507–514.

Van Wassenbergh S, Dries B, Herrel A. 2014. New insights into muscle function during pivot feeding in seahorses. PLoS One. 9(10):e109068.

Van Wassenbergh S, Heiss E. 2016. Phenotypic flexibility of gape anatomy fine-tunes the aquatic prey-capture system of newts. Sci Rep. 6:29277.

Van Wassenbergh S, Herrel A, Adriaens D, Aerts P. 2005b. A test of mouth-opening and hyoiddepression mechanisms during prey capture in a catfish using high-speed cineradiography. J Exp Biol. 208(Pt 24):4627–4639.

Van Wassenbergh S, Roos G, Genbrugge A, Leysen H, Aerts P, Adriaens D, Herrel A. 2009.

Deban, Holzman, and Müller – Page 34 of 38 http://mc.manuscriptcentral.com/icbiol

Suction is kid's play: extremely fast suction in newborn seahorses. Biol Lett. 5(2):200–203.

Van Wassenbergh S, Strother JA, Flammang BE, Ferry-Graham LA, Aerts P. 2008. Extremely fast prey capture in pipefish is powered by elastic recoil. J R Soc Interface. 5(20):285–296. Vincent O, Roditchev I, Marmottant P. 2011a. Spontaneous firings of carnivorous aquatic Utricularia traps: temporal patterns and mechanical oscillations. PLoS One. 6(5):e20205. Vincent O, Weisskopf C, Poppinga S, Masselter T, Speck T, Joyeux M, Quilliet C, Marmottant P. 2011b. Ultra-fast underwater suction traps. Proc Biol Sci. 278(1720):2909–2914. Vogel S. 1994. Life in moving fluids: the physical biology of flow. Princeton University Press. Waggett RJ, Buskey EJ. 2008. Escape reaction performance of myelinated and non-myelinated calanoid copepods. J Exp Mar Bio Ecol. 361(2):111–118. Wainwright PC, Day SW. 2007. The forces exerted by aquatic suction feeders on their prey. J R Soc Interface. 4(14):553-560. Wainwright PC, McGee MD, Longo SJ, Hernandez LP. 2015. Origins, Innovations, and Diversification of Suction Feeding in Vertebrates. Integr Comp Biol. 55(1):134–145. Webb PW. 1980. Does schooling reduce fast-start response latencies in teleosts? Comp Biochem Physiol A Physiol. 65(2):231–234. Weihs D. 1980. Hydrodynamics of suction feeding of fish in motion. J Fish Biol. 16(4):425-433.

Werth AJ. 2004. Functional morphology of the sperm whale (*Physeter macrocephalus*) tongue, with reference to suction feeding. Aquat Mamm. 30(3):405–418.

Deban, Holzman, and Müller – Page 35 of 38 http://mc.manuscriptcentral.com/icbiol

Werth AJ. 2006. Mandibular and dental variation and the evolution of suction feeding in Odontoceti. J Mammal. 87(3):579–588.

Westermeier AS, Fleischmann A, Müller K, Schäferhoff B, Rubach C, Speck T, Poppinga S. 2017. Trap diversity and character evolution in carnivorous bladderworts (Utricularia, Lentibulariaceae). Sci Rep. 7(1):12052.

Westneat MW, Olsen AM. 2015. How fish power suction feeding. Proceedings of the National Academy of Sciences of the United States of America. 112(28):8525–8526.

Whitewoods CD, Gonçalves B, Cheng J, Cui M, Kennaway R, Lee K, Bushell C, Yu M, Piao C, Coen E. 2020. Evolution of carnivorous traps from planar leaves through simple shifts in gene expression. Science. 367(6473):91–96.

Wilga CD, Motta PJ, Sanford CP. 2007. Evolution and ecology of feeding in elasmobranchs. Integr Comp Biol. 47(1):55–69.

Yaniv S, Elad D, Holzman R. 2014. Suction feeding across fish life stages: flow dynamics from larvae to adults and implications for prey capture. J Exp Biol. 217(Pt 20):3748–3757.

Figure Captions

Figure 1. The enormous size range of suction feeding organisms on a logarithmic scale. Data for figure taken from the literature (Cundall et al. 1987; Drost et al. 1988; Deban and Wake 2000; Hernández 2000; Werth 2004; Bloodworth and Marshall 2005; Werth 2006; Marshall et al. 2008; Westermeier et al. 2017).

Figure 2. Predator and prey speeds on a logarithmic scale. Note the extreme time to peak flow in bladderworts. Data for figure taken from the literature (Eaton et al. 1977; Webb 1980; Lenz and Hartline 1999; Lenz et al. 2000; Ferry-Graham et al. 2003; Higham et al. 2006b; Waggett and Buskey 2008; Marras et al. 2011; Pekkan et al. 2016; Stinson and Deban 2017; Singh et al. 2020).

Figure 3. Bladderwort morphology including (A) a strand of bladderwort traps (*Utricularia australis*); scale bar 1 cm. *Utricularia* trap in frontal view (B) pre-trigger and (C) post-trigger, and (D) in lateral view. (E) Illustration of trap with open door showing position of trigger hairs; scale bar 0.2 mm.

Figure 4. Steady-state model of transitional flow into a finite pipe, simulating suction feeding (Langhaar 1942). The fraction of total energy input that goes to (A) friction (rather than acceleration of water), (B) acceleration of water inside the pipe (C) and acceleration of water outside (contributing to prey capture), and the flow-rate specific power required (D), all plotted as a function of gape diameter and peak flow speed. Note the increasing energy loss to friction at the expense of external acceleration and

Deban, Holzman, and Müller – Page 37 of 38 http://mc.manuscriptcentral.com/icbiol

the increasing power required as pipe diameter decreases. These calculations arbitrarily assume a ratio of pipe length to pipe diameter of 5:3 throughout.

Figure 5. Summary of suction feeding performance in vertebrates and plants. Note the peak flow of bladderworts is faster than that of larval fish and similar to that of adult amphibians and fish. Light grey area with the salamander icon contains both salamanders and fish. Note that for bladderworts the longest dimension of a single trap is taken as body length. Data shown as one average value per size class per species per cited study; see Table S1 (Muller and Osse 1984; Drost and Boogaart 1986; Hernández 2000; Sanford and Wainwright 2002; Ferry-Graham et al. 2003; Van Wassenbergh et al. 2005a; Higham et al. 2006b; Wainwright and Day 2007; Kane and Marshall 2009; Roos et al. 2009; Staab et al. 2012; Yaniv et al. 2014; Pekkan et al. 2016; China et al. 2017; Stinson and Deban 2017; Jacobs and Holzman 2018; Singh et al. 2020; Müller et al. 2020).



60



Figure 1. The enormous size range of suction feeding organisms on a logarithmic scale. Data for figure taken from the literature (Cundall et al. 1987; Drost et al. 1988; Deban and Wake 2000; Hernández 2000; Werth 2004; Bloodworth and Marshall 2005; Werth 2006; Marshall et al. 2008; Westermeier et al. 2017).

127x79mm (600 x 600 DPI)

Predator and prey performance



Figure 2. Predator and prey speeds on a logarithmic scale. Note the extreme time to peak flow in bladderworts. Data for figure taken from the literature (Eaton et al. 1977; Webb 1980; Lenz and Hartline 1999; Lenz et al. 2000; Ferry-Graham et al. 2003; Higham et al. 2006b; Waggett and Buskey 2008; Marras et al. 2011; Pekkan et al. 2016; Stinson and Deban 2017; Singh et al. 2020).

127x73mm (600 x 600 DPI)



Bladderwort morphology including (A) a strand of bladderwort traps (Utricularia australis); scale bar 1 cm. Utricularia trap in frontal view (B) pre-trigger and (C) post-trigger, and (D) in lateral view. (E) Illustration of trap with open door showing position of trigger hairs; scale bar 0.2 mm.

91x75mm (600 x 600 DPI)





Figure 4. Steady-state model of transitional flow into a finite pipe, simulating suction feeding (Langhaar 1942). The fraction of total energy input that goes to (A) friction (rather than acceleration of water), (B) acceleration of water inside the pipe (C) and acceleration of water outside (contributing to prey capture), and the flow-rate specific power required (D), all plotted as a function of gape diameter and peak flow speed. Note the increasing energy loss to friction at the expense of external acceleration and the increasing power required as pipe diameter decreases. These calculations arbitrarily assume a ratio of pipe length to pipe diameter of 5:3 throughout.

36x98mm (600 x 600 DPI)



Figure 5. Summary of suction feeding performance in vertebrates and plants. Note the peak flow of bladderworts is faster than that of larval fish and similar to that of adult amphibians and fish. Light grey area with the salamander icon contains both salamanders and fish. Note that for bladderworts the longest dimension of a single trap is taken as body length. Data shown as one average value per size class per species per cited study; see Table S1 (Muller and Osse 1984; Drost and Boogaart 1986; Hernández 2000; Sanford and Wainwright 2002; Ferry-Graham et al. 2003; Van Wassenbergh et al. 2005a; Higham et al. 2006b; Wainwright and Day 2007; Kane and Marshall 2009; Roos et al. 2009; Staab et al. 2012; Yaniv et al. 2014; Pekkan et al. 2016; China et al. 2017; Stinson and Deban 2017; Jacobs and Holzman 2018; Singh et al. 2020; Müller et al. 2020).

126x67mm (600 x 600 DPI)

http://mc.manuscriptcentral.com/icbiol

Supplementary Table 1

Published data on suction feeders. Means are given with SEM. All references are listed in the References of the main manuscript.

9 10 11 12	Species	Body length [mm]	Gape size [mm]	Time to peak gape [ms] (*time to prey capture)	Flow speed [m/s]	location or type	Reference
13 14	Fish			. , . ,		/i	
14	Micropterus salmoides	174±2.5	26±1	22.4±1.4	0.46±0.01	half gape	Higham et al. 2006b
16	Lepomis macrochirus	152±0.7	13±1	28.3±3.2	0.71±0.04	half gape	Higham et al. 2006b
17	Lepomis macrochirus	200	22±1	22	0.2	unknown	Ferry-Graham et al. 2003
18 19	Carassius auratus	N/A	17	38	0.24	half gape	Staab et al. 2012
20	Lepomis macrochirus	57	3	12	0.1	half gape	Holzman et al. 2008
21	Lepomis macrochirus	88	7	14	0.24	half gape	Holzman et al. 2008
22	Lepomis macrochirus	190	15	12	0.42	half gape	Holzman et al. 2008
23 74	Polypterus endlicheri	153-166	5.0-16.1	30-189	0.027-0.396	half gape	Jacobs and Holzman 2018
2 . 25	Danio rerio	30.1-35.4	1.4-3.02	6-145	0.004-0.057	half gape	Jacobs and Holzman 2018
26	Carassius auratus	205-247	10.9-20.4	8-109	0.085-0.623	half gape	Jacobs and Holzman 2018
27	Apteronotus albifrons	65.3-87.3	1.4-4.5	3-50	0.001-0.104	half gape	Jacobs and Holzman 2018
28 29	Hemigrammus pulcher	62.7-70.4	3.1-6.3	7-57	0.007-0.085	half gape	Jacobs and Holzman 2018
30	Pimelodus pictus	73.6-81.0	3.9-7.4	24-99	0.018-0.058	half gape	Jacobs and Holzman 2018
31	Nimbochromis venustrus	74.8	3.4-7.1	48-152	0.014-0.033	half gape	Jacobs and Holzman 2018
32	Nastronotus ocellatus	113-142	10.5-20.4	8-52	0.040-0.351	half gape	Jacobs and Holzman 2018
33 34	Poecilia sphenops	58.9	3.0-4.9	9-47	0.010-0.042	half gape	Jacobs and Holzman 2018
35	Dascyllus marginatus	52.6	2.3-3.9	15-57	0.018-0.110	half gape	Jacobs and Holzman 2018
36	Chromis viridis	44.8-59.1	2.3-4.3	8-92	0.008-0.038	half gape	Jacobs and Holzman 2018
37	Chromis pelloura	51.3	2.1-3.6	30-86	0.006-0.032	half gape	Jacobs and Holzman 2018
38 20	Lepomis macrochirus	59.0-190.0	3.8-21.4	4-60	0.030-0.486	half gape	Jacobs and Holzman 2018
40	Clarias gariepinus	110-923	7-57	52	1.0-1.8	at mouth	van Wassenbergh et al. 2005a
41	Hippocampus reidi	33-34	4.3-4.6	3.5-3.7	2.87	buccal	Roos et al. 2009

1 2							
3	Amia calva	365	26.5	32.5-55	3.37	at mouth	Muller and Osse 1988
4 5	Gadus morhua	375	30.7	49-64.5	3.58	at mouth	Muller and Osse 1988
6	Pterois russelli	138	16.1	17-24	0.5-2.0	at mouth	Muller and Osse 1988
7	Danio rerio	4	0.125	9	0.0005	at mouth	Pekkan et al. 2016; Hernandez 2000
8	Danio rerio	8	0.6	18	0.002	at mouth	Pekkan et al. 2016; Hernandez 2000
9 10	Danio rerio	10	0.7	20	0.002	at mouth	Pekkan et al. 2016; Hernandez 2000
11	Danio rerio	20	1.05	18	0.01	at mouth	Pekkan et al. 2016; Hernandez 2000
12	Cyprinus carpio	5.8	0.5	4*	0.28	prey speed	Drost and van den Boogaard 1986
13 14	Cyprinus carpio	6.5	0.6	6*	0.35	prey speed	Drost and van den Boogaard 1986
14	Cyprinus carpio	9.5	1.1	8*	0.43	prey speed	Drost and van den Boogaard 1986
16	Sparus aurata	5-7	0.2-0.8	12*	0.07	prey speed	China et al. 2017
17	Amphibians						
18 10	Hymenochirus boettgeri	2.64	0.67	2 (4*)	0.03-0.3	prey speed	Deban and Olson 2002
20	Pleurodeles waltl	73.4	5.15±0.47	44±2	0.276±0.002	at mouth	Stinson and Deban 2017
21	Notophthalmus viridescens	46.1	5.31±0.19	67±14	0.204±0.019	at mouth	Stinson and Deban 2017
22	Triturus dobrogicus	73	3.9±0	38±1	0.256±0.009	at mouth	Stinson and Deban 2017
23 24	Cynops cyanurus	57.5	4.51±0.49	38±1	0.212±0.009	at mouth	Stinson and Deban 2017
25	Paramesotriton labiatus	74.2	6.06±0.24	28±1	0.515±0.012	at mouth	Stinson and Deban 2017
26	Ambystoma tigrinum	180-231	8.0-18.3	15-49	0.220-0.434	half gape	Jacobs and Holzman 2018
27	Ambystoma mexicanum	71.22	4.9	22-25	1.142-1.154	at mouth	Hidalgo (unpublished data)
28 29	Cetaceans						
30	Delphinapterus leucas	3320±439	63.5±3.6	277±38	2.19±0.19	prey speed	Kane and Marshall 2009
31	Lagenorhynchus obliquidens	1930±278	64.5±4.6	14±16	0.89±0.15	prey speed	Kane and Marshall 2009
32	Globicephala melas	4500±323	79.7±4.7	241±20	1.20±0.16	prey speed	Kane and Marshall 2009
33 34	Plants						
35	Utricularia gibba	0.7-1.4	0.27-0.42	0.3-1.4	0.02-0.18 (5.2)	at mouth (inside)	Singh et al. 2020
36 37	Utricularia australis	0.8-2.9	0.25-0.34	0.4-2.6	0.08-0.27	at mouth	Müller et al. 2020