Suction feeding mechanics, performance, and diversity in fishes

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Synopsis Despite almost 50 years of research on the functional morphology and biomechanics of suction feeding, no consensus has emerged on how to characterize suction-feeding performance, or its morphological basis. We argue that this lack of unity in the literature is due to an unusually indirect and complex linkage between the muscle contractions that power suction feeding, the skeletal movements that underlie buccal expansion, the sharp drop in buccal suction pressure that occurs during expansion, the flow of water that enters the mouth to eliminate the pressure gradient, and the forces that are ultimately exerted on the prey by this flow. This complexity has led various researchers to focus individually on suction pressure, flow velocity, or the distance the prey moves as metrics of suction-feeding performance. We attempt to integrate a mechanistic view of the ability of fish to perform these components of suction feeding. We first discuss a model that successfully relates aspects of cranial morphology to the capacity to generate suction pressure in the buccal cavity. This model is a particularly valuable tool for studying the evolution of the feeding mechanism. Second, we illustrate the multidimensional nature of suction-feeding performance in a comparison of bluegill, *Lepomis macrochirus*, and largemouth bass, *Micropterus salmoides*, two species that represent opposite ends of the spectrum of performance in suction feeding. As anticipated, bluegills had greater accuracy, lower peak flux into the mouth, and higher flow velocity and acceleration of flow than did bass. While the differences between species in accuracy of strike and peak water flux were substantial, peak suction velocity and acceleration were only about 50% higher in bluegill, a relatively modest difference. However, a hydrodynamic model of the forces that suction feeders exert on their prey shows that this difference in velocity is amplified by a positive effect of the smaller mouth aperture of bluegill on force exerted on the prey. Our model indicates that the pressure gradient in front of a fish that is feeding by suction, associated with the gradient in water velocity, results in a force on the prey that is larger than drag or acceleration reaction. A smaller mouth aperture results in a steeper pressure gradient that exerts a greater force on the prey, even when other features of the suction flow are held constant. Our work shows that some aspects of suction-feeding performance can be determined from morphology, but that the complexity of the behavior requires a diversity of perspectives to be used in order to adequately characterize performance.

Introduction

For some years, the paradigm in fish feeding biomechanics has been that there are three basic techniques used by fish to capture prey: manipulation, ram, and suction (Liem 1980; Ferry-Graham and Lauder 2001; Wainwright and Bellwood 2002). To understand trophic diversity in fishes is largely to understand these three feeding methods, how fish use them, why fish use them, and the basis for differences among species in performance. While the basic mechanics of each of these mechanisms are known, recent years have brought a new realization of the surprising diversity, both mechanical and ecological, contained within each category (Alfaro and Westneat 1999; Wainwright et al. 2004; Collar et al. 2005; Konow and Bellwood 2005; Van Wasssenbergh et al. 2006a, 2006b). These new studies have challenged our understanding of the basis of feeding performance and the result is an urgent need to identify the morphological basis of feeding performance in fishes as a means of interpreting diversity.

In this article, we focus on suction feeding, the most widely used mechanism of prey capture in ray-finned fishes and in many other groups of aquatic vertebrates. Suction feeders rapidly expand their

buccal cavity, thereby creating a flow of water that engages the prey, and draws it into the mouth (Muller et al. 1982; Van Leeuwen 1984; Lauder 1980). There is, therefore, a notably complex connection between the powerful muscular contractions that drive expansion of the buccal cavity, the complex expansion of the skull, the suction pressure that is generated inside the buccal cavity, the pattern of water flow that is generated in front of the mouth, and ultimately, the forces that are exerted by that flow on the prey (Fig. 1). This complexity helps explain the historical diversity of the metrics of suction-feeding performance. Previous researchers have tended to simplify the problem by focusing solely on one or another aspect of this sequence of events. Generally, single metrics have been used to characterize suction-feeding performance, including peak suction-pressure capacity, peak velocity of flow, the distance traveled by the prey during the strike, and handling time (Werner 1974; Norton and Brainerd 1993; Nemeth 1997, Wainwright et al. 2001). Referring to Fig. 1, it is apparent that most previous metrics are linked mechanically, but there has been no previous attempt to unify the series of events that occur during suction feeding or to place it into the context of performance. In addition, only very recent work has begun to evaluate the mechanical events that result in forces experienced by the prey of suction feeders (Wainwright and Day 2007) and this element of the predator prey interaction shown in Fig. 1 has not been integrated into a broader view of performance.

We attempt to present an integrated view of suction-feeding performance by linking recent insights into several of the events that occur during suction feeding (Fig. 1). We begin by discussing a morphological model of the basis of suction-pressure capacity and we illustrate how such a model can be especially useful to the study of the evolution of feeding mechanics in fishes. We then review a study that compared several aspects of suction feeding in two species of centrarchid fishes thought to represent extremes of performance. This study resulted in somewhat of a paradox because, although the ability to generate high velocity flow into the mouth was greater in the small-mouthed bluegill than in the largemouth bass, the magnitude of the difference was relatively small. Finally, we explore the implications of this difference in velocity of flow for the forces that are experienced by the prey of these two species. We show that mouth morphology interacts with the velocity and acceleration of flow and influences the magnitude of total force. When the difference between these species in the size of the
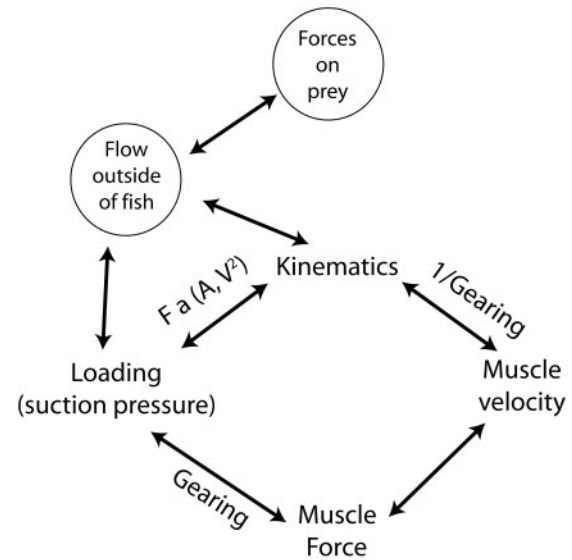
Fig. 1 Schematic overview showing the relationship between the series of mechanically linked events that occur during suction feeding. Cranial muscles contract with a given shortening velocity and force. Shortening velocity is transmitted through skeletal linkages into cranial expansion (referred to as kinematics) with output movement being related to input motion by the inverse of the mechanical advantage, or gearing, in the skeletal system. Muscle force is transmitted through the skeletal transmission system to buccal cavity expansion with a system-specific mechanical advantage. Force of expansion distributed around the expanding buccal cavity results in suction pressure inside the buccal cavity. The kinematics of expansion and the suction pressure are related by the terms shown in the arrow that connects them. Cranial expansion creates a flow of water into the mouth that is proportional in velocity to the suction pressure inside the buccal cavity. This flow field external to the mouth engages the prey item, exerting hydrodynamic forces on it that draw it into the predator's mouth. In this article, we consider (1) a model that attempts to simplify the musculoskeletal system to allow inferences about the relative capacity of different species to generate suction pressure, (2) we emphasize the value of considering several aspects of suction feeding performance that, taken together, may provide a relatively complete picture of suction feeding performance, and (3) we review recent insights from fluid mechanics concerning the nature of the forces that are exerted on prey by the suction flow.

mouth is taken into account, a 50% higher fluid speed in bluegill translates into a three-fold increase in the magnitude of the pressure gradient force. Our research has involved a combination of mathematical models and a variety of experimental methods in an attempt to understand the physical events that occur during suction feeding.
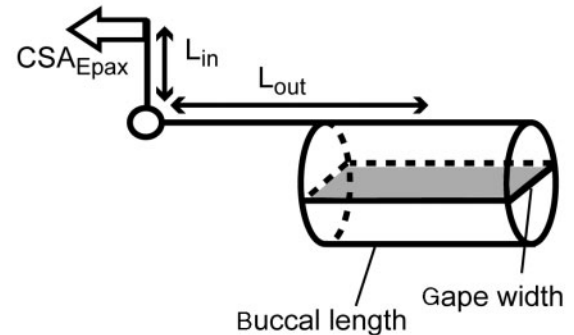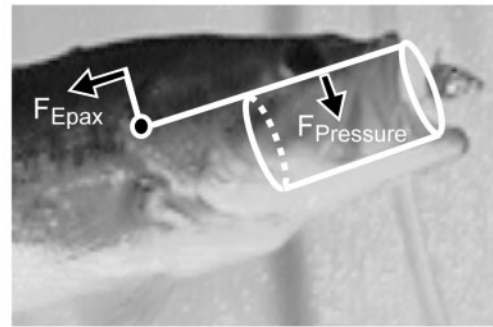
Morphological basis of suction-pressure capacity

Suction feeding involves rapid cranial expansion that brings about significant hydrodynamic loading and

results in a sharp drop in pressure inside the buccal cavity (Lauder 1980; Carroll 2004). This drop in pressure causes water to move rapidly from the regions of higher pressure, in front of the open mouth, into the buccal cavity (Muller et al. 1982). Although the exact relationship between buccal pressure and the velocity of flow is mediated by the size and shape of the buccal cavity (Van Wasssenbergh et al. 2006a), there will generally be a close relationship between the magnitude of the pressure drop that occurs during suction feeding and the peak velocitiy of flow that is generated (Higham et al. 2006b). Thus, a model that accounts for the capacity of the fish to generate suction pressure is potentially useful because it may help us understand the specific trade-offs involved in generating the diversity of suction feeders.

We developed such a model (Fig. 2), based on the feeding mechanism of centrarchid fishes. The model treats the feeding mechanism as a lever system that transmits force and movement from the contracting epaxial muscles to the expanding buccal cavity (Carroll et al. 2004). We assumed that the ability to generate a buccal pressure gradient is limited by the forces that the muscles can generate and the resistance of the skeletal elements to those forces. The expanding buccal cavity of centrarchids can be modeled as an expanding cylinder with pressure being distributed across its surface. The magnitude of the expansion force is equal to the magnitude of the buccal pressure multiplied by the projected area of the buccal cavity. This force exerts a torque on the neurocranium, directed ventrally at the buccal cavity. If one ignores the forces required to accelerate skeletal elements and water external to the head (which appear to be minor; Van Wassenbergh et al. 2006a, 2006b), the force generated by the epaxial muscles (and matched, through an antagonistic skeletal transmission system, by the ventral sterno-hyoideus muscle) must be balanced by the resolved force of buccal pressure as it is transmitted through the lever system of the neurocranium (Fig. 2).

The magnitude of the pressure gradient that a fish can create is therefore a function of the amount of force that the epaxial muscles can generate (proportional to physiological cross sectional area, PCSA), the moment arm of the epaxialis (L_{in}), the moment arm of the buccal cavity (L_{out}), and the projected area of the buccal cavity (buccal length times buccal width). Generation of force by the epaxial muscles is based on force per unit of cross-sectional area and PCSA; omitting the former from the equation allows one to generate a Suction Index (Fig. 2) that involves the morphological parameters of the relationship,


$$\text{Suction index} = \frac{(CSA_{Epax} \times (L_{in} / L_{out}))}{(\text{gape width} \times \text{buccal length})}$$

Fig. 2 A model of the morphological basis of the capacity to generate suction pressure in the buccal cavity (Carroll et al. 2004). The parameters of the model are described in the text. The model allows one to relate morphological variation among individual fish, or species of fish, to relative capacity to generate suction pressure.

but does not make assumptions about how force per unit area of the muscle may vary among feeding events and across taxa.

This model was tested by making measurements of peak suction pressure in 45 individual centrarchid fishes across five species and differing by a factor of 2.5 in body length. Morphological measurements were made from each specimen to parameterize the model and the predictions were compared against realized performance. The predictions of the model provided a strong fit to the empirical data ($r^2 = 0.71$) suggesting that this framework accounts for differences in suction capacity among individual fish and among species (Fig. 3). Additionally, the epaxial muscle stress estimated by the model in this study as well as in a separate study (Carroll and Wainwright 2006) is similar to that measured from epaxial muscle fibers *in vitro* under realistic conditions of activation and strain (Coughlin and Carroll 2006). This realistic absolute estimation of muscle function,
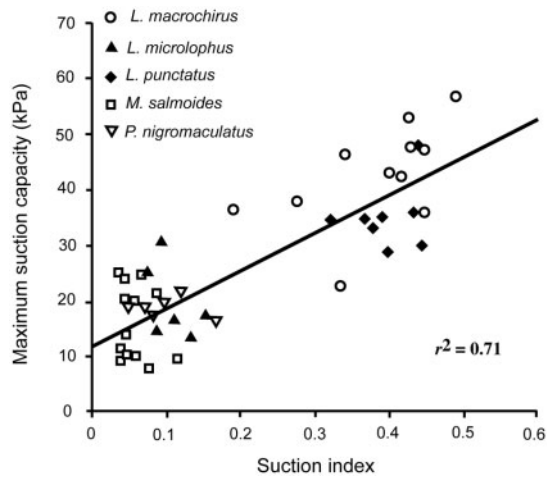
Fig. 3 A comparison of predictions from the suction-feeding model and empirical measurements of peak capacity for suction pressure [modified after data from Carroll et al. (2004)]. Data are from 41 individual fish (one data point per fish) across five species of Centrarchidae and over a wide range of body sizes. Suction Index is a strong predictor of actual variation in the capacity to generate suction pressure.

Table 1 Ranking of model parameters of the Suction Index from a multiple regression analysis of phylogenetically standardized, independent contrasts of the Suction Index, and the parameters measured in 27 species of centrarchid fishes

Variable	Sum of squares
Gape width	0.117
Buccal length	0.056
L_{out}	0.015
CSA	0.047
L_{in}	0.031

Note that gape width accounted for the largest amount of variation in the Suction Index.

as well as relative predictions of individual performance, provides support for the mechanical analysis underlying the model and suggests that it may be used in any group of fishes for which the assumptions apply.

A model that permits estimates of relative performance from morphological variation is a potentially powerful tool in the study of diversity in suction feeding. Physiologists and biomechanicians often feel limited in their ability to gain insights into diversity and evolution because of the need to conduct detailed investigations on many species, in order to develop a large comparative database. Models such as this one simplify the mechanics of the system and yet they may permit researchers to identify major trends in key functional traits. By reducing the system to its essential mechanical elements, the model addresses diversity in suction feeding through a few specific morphological measurements that can readily be made either on fresh or fixed specimens.

We used the model to explore the evolution of capacity for suction feeding in centrarchid fishes (Collar and Wainwright 2006). Change in any parameter of the model can cause changes in Suction Index and we were interested in which model parameter accounted for the most evolutionary variation in suction capacity among centrarchid species. To address this question, we measured the parameters of the model in several specimens of each of 27 centrarchid species and calculated Suction

Index (Collar and Wainwright 2006). We then used a phylogeny of centrarchid fishes, developed in our previous research with DNA sequences from a mixture of mitochondrial and nuclear genes (Near et al. 2005), as the basis for calculating standardized, independent contrasts of the parameters of the model and Suction Index. We ran a multiple regression analysis with the contrasts of Suction Index as the dependent variable and contrasts of the parameters of the model as the independent variables. While Suction Index is strictly determined by the five model parameters, this analysis allowed us to ask which variables accounted for the most evolutionary change in Suction Index. The result was that mouth diameter contributed more than twice as much to the evolution of Suction Index as did any of the other parameters, although every parameter was involved (Table 1).

This analysis can be viewed as a model for a commonly asked question in evolutionary biomechanics: how is the mechanism altered during evolution in ways that produce diversity in some important emergent property. In this case, the emergent property is the capacity to develop suction pressure. The finding that mouth diameter accounts for more than twice the variation in Suction Index of any other variable is concordant with the longstanding feeling among students of suction feeding that mouth diameter is an important axis of diversity among suction feeders (Werner 1977; Keast 1978; Van Leeuwen and Muller 1984; Norton 1991). By simplifying aspects of the necessary analyses, models can greatly enhance the analysis of the evolutionary dynamics in complex functional systems.

Multidimensional analysis of performance in suction feeding

The sharp drop in buccal pressure that occurs during suction feeding is associated with a rapid flow of
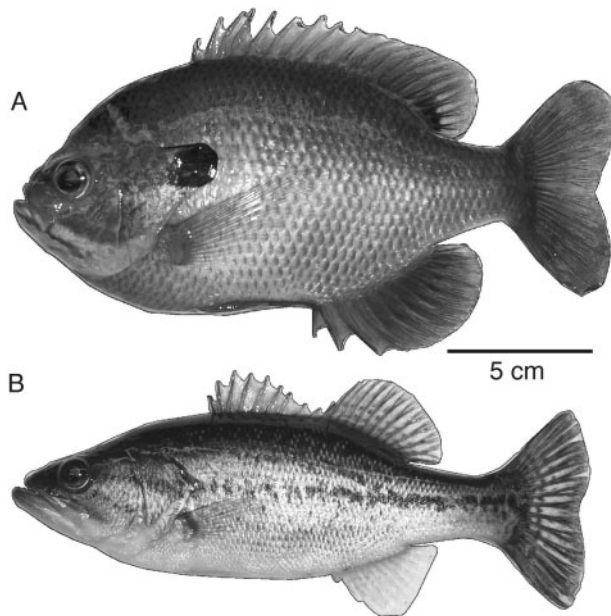
Fig. 4 Photographs of (**A**) a bluegill, *Lepomis macrochirus*, and (**B**) a largemouth bass, *Micropterus salmoides*. Several aspects of the water flow patterns generated during suction feeding by these two species were compared. These species represent a classical contrast between a taxon thought to be specialized for suction feeding (bluegill) and one adapted to feeding by ram–suction (largemouth bass). Note the more slender body and larger mouth of largemouth bass, as compared to the deep body and small mouth of bluegill.

water that fills the expanding buccal cavity (Muller et al. 1982). Several aspects of this flow of water may impact the effectiveness of the feeding fish. The spatial scale over which the flow extends will limit the range over which suction can be effective. In addition, the accuracy of the predator in positioning the prey in the center of the water mass that is ingested may affect the chances of escape for a mobile prey. The time period over which the flow is generated will affect the duration of the period over which it might be effective (Van Leeuwen and Muller 1984). Perhaps what has intrigued researchers most over the years is the idea that the velocity of water flow into the mouth may strongly influence the ability to overcome the various avoidance responses of prey (Van Leeuwen and Muller 1983; Wainwright et al. 2001; Van Wassenbergh et al. 2006a).

Interestingly, it appears that there may be trade-offs between pairs of these properties of the suction-flow field. Our research has shown that the spatial scale of the flow field is largely a function of the size of the mouth aperture (Day et al. 2005)—the larger the mouth opening, the larger the flow field.

In contrast, thought exercises have concluded that a smaller mouth aperture may result in higher flow velocities; if the rate of expansion of the buccal cavity is held constant, then a smaller aperture will result in a higher velocity of flow entering the mouth (Norton 1991). The model discussed in the previous section also suggests that there may be a general trade-off, in which large mouth apertures result in lower velocity of flow.

Using exemplar species from the Centrarchidae, we sought to empirically measure key aspects of the flow field that we felt represented determinants of the performance by fish in capturing prey (Higham et al. 2006a). We compared bluegill, *Lepomis macrochirus*, and largemouth bass, *Micropterus salmoides* (Fig. 4). Bluegill are the most zooplanktivorous of all centrarchid species but they also feed on benthic insects (Collar et al. 2005). This species has a mouth diameter that is about half that of largemouth bass of the same body length. Bluegill were predicted by the model to have the greatest capacity for generating suction pressure of all centrarchids, and the pressures that have been measured from them are among the strongest yet recorded in any teleost fish. In contrast, largemouth bass feed on large elusive prey, primarily other fish, often chasing their quarry. The large mouth and relatively small epaxial moment arm indicate that bass have a relatively modest capacity to generate buccal pressure, and this has been confirmed experimentally (Carroll et al. 2004).

We studied the flow field generated by these two species using digital partical image velocimetry (Day et al. 2005; Higham et al. 2006a, 2006b). Briefly, our method involves shining a sheet of laser light up through the bottom of an aquarium to illuminate near-neutrally buoyant glass beads. The fish is trained to feed in this sheet of light and the event is recorded in lateral view with a video camera operating at 500 images per second. The glass beads move as particles of water and successive images from the video allow us to calculate the two-dimensional field of flow. Additional details of this method and our particular implementation can be found in papers by Higham et al. (2006a, 2006b) and Day et al. (2005).

We measured four quantities from the flow field in experiments in which fish were challenged with highly elusive prey (small shrimp). Many sequences were recorded from each fish and the highest performance of each individual fish was used and averaged across three individuals for each of the two species. By viewing the videos of particle motion in front of feeding fish, we developed an accuracy index

in which we first calculated the distance of prey from the center of the parcel of ingested water and created a ratio of this distance to the distance from the center of the water parcel to the edge of the ingested volume. This ratio was subtracted from one to give an index that approached one as prey were positioned closer to the center of the ingested volume of water. We also used the videos to calculate the peak flux of water into the mouth, or the highest rate of volume flow into the mouth during the strike. In addition, we measured the peak flow velocity and acceleration at a distance of one half of peak mouth diameter on the central axis extending directly in front of the mouth of the feeding fish. This homologous location was chosen to make values of peak speed of flow comparable across fish with different-sized mouths and was necessary because of the very strong spatial gradient of flow. Peak flow velocity and acceleration were first calculated in the earth-bound frame of reference, but a large difference between the species in swimming speed at the time of the strike suggested to us that it would also be important to compare suction velocity and acceleration in the predator's frame of reference. The fish used in the experiments were all matched by body length.

Bluegill showed twice the accuracy of largemouth bass (Table 2), positioning prey within 20% of the distance from the center of the captured water parcel to the edge of the parcel. In contrast, largemouth bass had peak flux values about five times that of bluegill. As expected, bluegill generated higher peak flow velocities and accelerations than did largemouth bass, but their superiority was rather modest, being only 50% better than bass for both metrics (Table 2). This difference in performance between the species completely disappeared when velocity and acceleration were calculated in the frame of reference of the attacking fish. When combining swimming speed and velocity of suction flow, largemouth bass actually generated higher speeds closing on the prey. In other words, the time taken to bring the prey to the margin of the mouth was actually slightly shorter for bass.

To a large extent these results were consistent with previous expectations. Bluegill have been widely viewed as a superior suction feeder based largely on recordings of exceptionally strong suction pressure in this species. Largemouth bass have been viewed as a combination ram–suction feeder that trades-off high suction performance (previously measured as weak suction pressure) by using high attack velocity and a large mouth to capture elusive prey. The superior accuracy of bluegill may be partly

Table 2 Metrics of performance in suction feeding measured in bluegill and largemouth bass. Values are averages of peak values for three individual fish per species. Initial values of velocity and acceleration indicate measurements in the earthbound frame of reference. "Fish frame" refers to measurements in the attacking fishes' frame of reference

Performance metric	Largemouth Bass	Bluegill
Fluid speed (cm s^{-1})	46	71*
Fluid speed (fish frame)	116	86
Acceleration (m s^{-2})	45	66*
Acceleration (fish frame)	63	79
dV/dt (cm^3 s^{-1})	2605	442
Accuracy index	0.4	0.8*

*=Significantly larger in bluegill at $P < 0.005$.

due to the dexterity that comes with slower swimming speeds during attack, and a smaller jaw apparatus. Bluegill also have the highest visual acuity known among centrarchids, a property that is thought to be related to their status as zooplanktivores (Hawryshyn et al. 1988). We found that peak flux scaled directly with the size of the mouth aperture, both within species and between the two species, so the superior peak flux of largemouth bass can be seen as a direct result of their larger buccal cavity. Bluegill also achieved 50% higher velocitiy of flow than did largemouth bass, but this difference disappeared when flow was calculated in the frame of reference of the attacking fish. It appears that the different mechanics of feeding in these two species result in only a modest enhancement of suction flow speed for bluegill.

Modeling the forces exerted by suction feeders on their prey

How do the differences in pattern of suction flow between bluegill and largemouth bass translate into the forces they each exert on their prey? In other words, we would like to close the final gap in the framework illustrated by Fig. 1. Here, we turn away from empirical work and consider the problem with a mathematical model. Ultimately, the ideas and hypotheses generated by this model can be tested with feeding fishes. One interesting feature of suction feeding is that the predator does not touch its quarry, but instead, prey capture is accomplished by the flow field that is generated by the predator. This flow exerts forces that cause the prey to be drawn into the predator's mouth.

We employed a mathematical model to estimate the forces generated by suction feeders (Wainwright and Day 2007). There are three forces that the flow

can exert on the prey. The velocity of fluid moving relative to the prey item will generate a drag force. A fluid velocity increasing through time, as characterizes suction feeding (Day et al. 2005), will also generate an acceleration reaction. Finally, because fluid velocity will both vary in space (being higher at the mouth aperture and decreasing with distance from the mouth) and in time, the pressure in front of the mouth will also vary spatially. A pressure gradient exists with the lowest pressures at or inside the mouth and increasing away from the predator. This pressure gradient creates a force that moves the prey toward the mouth.

If the velocity field in front of the mouth is known for all times during the feeding event, then all components of force that act on a prey may be calculated or estimated. The sum of these component forces is the net force acting on the prey, from which we calculated the resultant kinematics, velocity, and position of prey, as a function of time. Additionally, comparison of the magnitudes of the three forces lends insights into the fundamental mechanisms whereby force is generated. What is the dominant force that acts on the prey of suction feeders?

The input to the model consists of aspects of a fluid flow field generated by the predator and the physical properties and initial position of the prey. We have shown previously that the pattern of flow speed in front of a feeding fish is a function of the magnitude of fluid speed at the mouth and of the gape of the fish. We parameterized our model with details of the flow field from our previous research on bluegill (Day et al. 2005). The reader is referred to our original publication for formulation of the equations used to calculate the three forces (Wainwright and Day 2007). In our initial calculations, we assumed the diameter of the fully opened mouth to be 15 mm and the prey to be a 5 mm-diameter sphere. We explored three scenarios that span the range of realistic conditions of encounter but here we focus only on the situation when the prey item is fixed, e.g., clinging to the substratum. We calculated the magnitude of the three forces at intervals of time throughout the strike.

The acceleration and velocity of the prey are equal to zero and its position remains constant, as shown in Fig. 5. In this simulation, the distance between the predator's mouth and the prey remained a constant 15 mm because the predator was not approaching the prey. The largest force was due to the pressure gradient (about 55% of total), followed by acceleration reaction (about 40% of total) and drag (about 10% of total). There was also a difference in the
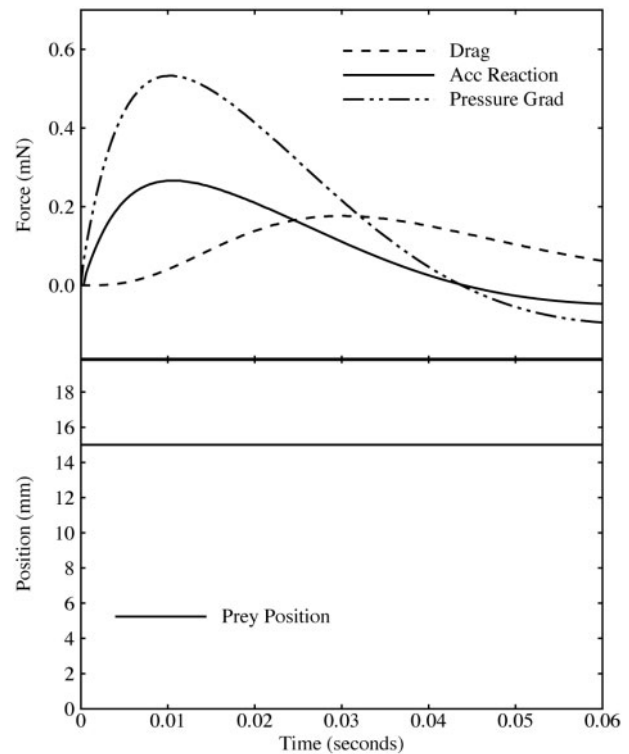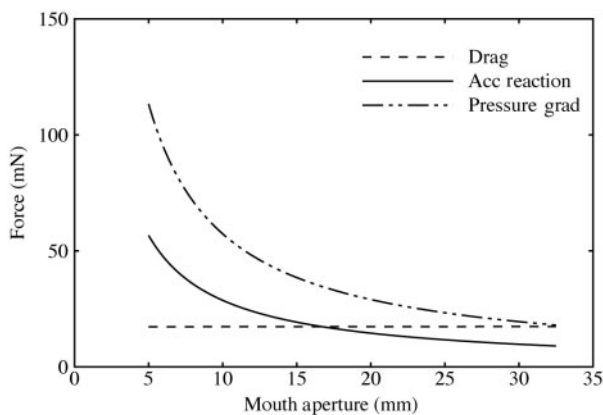

Fig. 5 Calculations of the forces exerted by a suction feeder on a hypothetical spherical prey that is fixed to the substrate (from Wainwright and Day 2007). The largest of three forces is the pressure gradient force, that is caused by the spatial and temporal gradient of pressure that occurs in front of the predator's mouth during feeding. Note also that drag peaks much later in the strike than does the pressure gradient force or the acceleration reaction.

timing of the forces, in which acceleration reaction and pressure gradient both peak in about a third of the time required for drag to reach its peak.

Whereas drag depends only on the magnitude of relative flow speed, acceleration reaction and pressure gradient forces depend on the spatial pattern of the flow. We wanted to know what effect the difference between bluegill and largemouth bass in size of the aperture of the mouth would have on these forces. Because the flow field is known to scale linearly with the size of the mouth, it could be expected that the smaller mouth of the bluegill would generate a steeper pressure gradient. Our simulations showed that a steeper pressure gradient, and the accompanying velocity gradient, do result in higher pressure-gradient forces and higher acceleration reaction forces exerted on the prey (Figs 6 and 7). We can then account for the difference in mouth diameter between the bluegill and largemouth bass that were used to generate the flow field data in Table 2. These fish were size-matched for body length, but the diameter of the
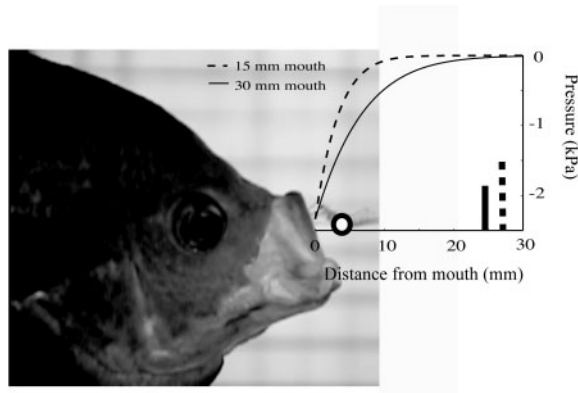
Fig. 6 The effect of mouth diameter on the pressure gradient force experienced by a spherical prey item fixed to the substratum. The spatial gradients of pressure in front of a 15 mm mouth and a 300 mm mouth are shown. The smaller mouth generates a steeper pressure gradient and hence a larger pressure gradient force. This difference in mouth size allows bluegill to generate three times the total force on prey that largemouth bass generate even when the velocity of peak flow is the same in boh species.

Fig. 7 The effect of mouth diameter on the relative magnitude of the three forces exerted by a suction feeder on prey (from Wainwright and Day 2007). In these simulations, the mouth diameter was 15 mm and the prey was a 5 mm sphere. Note that the pressure gradient force and acceleration increase with decreasing mouth diameter, even when the velocity of peak flow, and hence drag, are constant.

mouth of the bluegill in these experiments was almost exactly half that of the largemouth bass. As a result, although bluegill generated only 50% greater flow velocities than did largemouth bass, the difference in mouth diameter means that the bluegill would generate over three times the total forces on the 5 mm spherical prey in our simulations.

Researchers have recognized for some time that species that appear to be modified for high-performance suction feeding often have relatively

small mouths (Norton and Brainerd 1993; Wainwright and Richard 1995; Carroll et al. 2004). Most explanations for this have focused on the potential advantage of the small mouth in concentrating flow so that velocities might be higher than in fish with larger mouths. Our experiments with bluegill and largemouth bass suggest that this advantage is rather modest (Higham et al. 2006b). Our inference that a smaller mouth aperture results in relatively higher pressure gradient and higher acceleration-reaction forces, when the time course and peak values of the flow field remain the same (Fig. 7), represents a previously unrecognized way in which morphology enhances this key element of performance in suction feeding (Wainwright and Day 2007).

An integrated view of performance in suction feeding

Like other aspects of animal performance, suction feeding can be viewed in a hierarchical fashion. If we consider success in capturing prey under natural conditions as a high level in this hierarchy, it is clear that several aspects of the mechanics of suction feeding are involved in this integrated level of performance. Strike success depends on the ability of the predator to stalk and approach the prey without startling it. During the strike, the fish must move the aperture of the mouth close enough to expose the prey to the influence of the flow of water that it generates. The flow of water must be sufficient to overcome any escape response by the prey. Furthermore, the predator must time its approach such that the highly ephemeral flow that is generated encounters the prey at a point where high forces can be exerted with that flow. High-acceleration flow is clearly important in the performance of suction feeding. The ability to coordinate aspects of locomotion and vision with jaw movements also play a major role in feeding success. One important area of future research on suction feeding will concern the nature of this integration of the different organ systems involved in feeding behavior.

Our efforts have been directed toward understanding the linkage between the predator's morphology and the forces that are exerted on the prey. Making this connection requires that one understands the morphological and mechanical basis of the capacity to generate high suction pressure and high velocity of flow. Identification of the features of the flow of water that is generated during suction feeding are most important in determining the magnitude of forces that are exerted on the prey. One important

issue is whether pressure, which is mechanically related to flow velocity, can be taken as an accurate indicator of the latter. Recent modeling work (Van Wassenbergh et al. 2006b) revealed that the relationship between suction pressure and velocity of flow depends on the shape of the buccal cavity. This result suggests that peak suction pressure may be a misleading indicator of relative velocity of flow across markedly different buccal cavities, but empirical data on two species of centrarchid fishes that differ in buccal cavity morphology, largemouth bass and bluegill, indicated that peak suction pressure is an accurate predictor of flow velocity across these species (Higham et al. 2006b). Nevertheless, it seems that the magnitude of suction pressure should not be entirely relied upon as an indicator of flow velocity, especially when buccal cavity shape is highly divergent.

During suction feeding (Fig. 1) the predator's muscles contract, generating forces and movements that are translated through complex linkages into an expanding buccal cavity (de Visser and Barel 1998; Carroll and Wainwright 2006). Buccal expansion causes a flow of water into the mouth aperture. Capture of prey by suction feeders requires that the predator position this flow field in the vicinity of the prey so that the flow field can generate sufficient forces to cause the prey to be drawn into the mouth (de Jong et al. 1987). Working backward from the forces experienced by the prey, our studies highlight the fact that these forces depend not only on the peak velocity and acceleration of flow, but also on the spatial pattern of the flow field, a feature that is strongly influenced by the size and shape of the predator's mouth. Suction feeders with a smaller mouth aperture will exert higher forces on their prey for a given velocity and acceleration of water, because the compressed spatial scale of the flow pattern results in a steeper gradient in pressure and greater force (Wainwright and Day 2007).

Researchers are beginning to appreciate some ways in which the predator can manipulate the flow field and the forces that are exerted upon the prey (Nauwerlaerts et al. 2007), but a thorough exploration of parameter space has not yet been achieved. It seems likely that there will be other ways in which the various mechanical aspects of suction feeding interact to influence success by the predator. What is clear at this time is that strong suction feeders exert high forces on prey because they generate high velocity of flow and especially high accelerations of water. High velocities and accelerations are based on the ability to rapidly expand the buccal cavity and to generate a strong pulse of suction pressure. Fish that generate strong suction pressure tend to have a high cross-sectional area in the epaxial muscles inserting on the back of the cranium, high mechanical advantage of the linkage system that transmits epaxial force to the buccal cavity, and a small buccal cavity over which this force is distributed. Thus, there appears to be a strong framework in place for interpreting morphological diversity in terms of the capacity for suction pressure, and to a considerable extent, the forces that suction feeders can generate.

The discussions above help identify what makes a strong suction feeder. Why aren't all suction feeders characterized by this phenotype? What accounts for the diversity seen in nature? An important trade-off involves the size of the buccal cavity and the amount of water that is influenced by the suction feeder. The argument above actually suggests that the highest forces are generated by suction feeders with extremely small mouths, but a very small mouth does not generate a region of flow sufficiently large to capture larger prey. One of the clearest patterns in the feeding ecology of predatory fishes is a strong correlation between size of the prey and size of the predator's mouth (Werner 1974; Keast 1978; Wainwright and Richard 1995). Relatively large prey are also often more elusive. Included in the category of large prey fed upon by fish are many fish, cephalopods, and decapod crustaceans and these are quite evasive animals. Predators that specialize on these prey types often have a relatively large mouth and make use of rapid swimming to overtake their elusive quarry. With this strike strategy, much of the distance between predator and prey is closed by locomotion or jaw protrusion, rather than by suction. In this case, a large mouth is advantageous in helping intercept the prey and suction may primarily serve to eliminate a bow wave and impart momentum to the prey entering the mouth (Wainwright et al. 2001). Such ''ram'' feeders show a high flux of water into the mouth during the strike and, as some water begins to exit the opercular region during the strike, a volume of water may be engulfed that is more than three times the buccal volume (Higham et al. 2005, 2006a). The importance of mouth size as a key determinant of both feeding mechanics and feeding ecology has been shown in comparative analyses with centrarchids and other groups (Collar et al. 2005; Hulsey and de Leon 2005; Collar and Wainwright 2006; Bellwood et al. 2006). Thus, a basic trade-off among suction feeders seems to involve the ability to exert a high force over a small region of water

versus the ability to move a high volume of water and capture relatively large prey. It also appears that smaller mouths are associated with greater accuracy, faster speed of jaw movement and perhaps better skill in timing than is exhibited by close relatives with larger mouths.

The past decade of research on suction feeding now allows a more complete picture of the connections between the various stages indicated in Fig. 1. The mechanical linkages between muscle contractions in the fish and the force exerted on prey by suction feeders have been sufficiently resolved to allow considerable insight into the consequences of morphological diversity for variation in performance by suction feeders. These advances now set the stage for more powerful studies of the evolution of suction-feeding systems and the basis of trophic diversity in fishes.

Acknowledgments

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