

A Note From the Editor

From time to time the *Journal of Morphology* publishes special presentations that expand and define the current state of an area of research. In the accompanying article, *Aquatic Prey Capture in Ray-Finned Fishes: A Century of Progress and New Directions*, Drs. Lara A. Ferry-Graham and George V. Lauder "... trace the history of functional morphological analyses of suction feeding in ray-finned fishes, with a particular focus on the mechanisms by which suction is generated and present new data using a novel flow imaging technique that enables quantification of the water flow field into the mouth" as we continue this series.

Frederick W. Harrison
Editor

Aquatic Prey Capture in Ray-Finned Fishes: A Century of Progress and New Directions

Lara A. Ferry-Graham^{1*} and George V. Lauder²

¹*Department of Evolution and Ecology, University of California, Davis, California*

²*Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts*

ABSTRACT The head of ray-finned fishes is structurally complex and is composed of numerous bony, muscular, and ligamentous elements capable of intricate movement. Nearly two centuries of research have been devoted to understanding the function of this cranial musculoskeletal system during prey capture in the dense and viscous aquatic medium. Most fishes generate some amount of inertial suction to capture prey in water. In this overview we trace the history of functional morphological analyses of suction feeding in ray-finned fishes, with a particular focus on the mechanisms by which suction is generated, and present new data using a novel flow imaging technique that enables quantification of the water flow field into the mouth. We begin with a brief overview of studies of cranial anatomy and then summarize progress on understanding function as new information was brought to light by the application of various forms of technology, including high-speed cinematography and video, pressure, impedance, and bone strain measurement. We also provide data from a new technique, digital particle image

velocimetry (DPIV) that allows us to quantify patterns of flow into the mouth. We believe that there are three general areas in which future progress needs to occur. First, quantitative three-dimensional studies of buccal and opercular cavity dimensions during prey capture are needed; sonomicrometry and endoscopy are techniques likely to yield these data. Second, a thorough quantitative analysis of the flow field into the mouth during prey capture is necessary to understand the effect of head movement on water in the vicinity of the prey; three-dimensional DPIV analyses will help to provide these data. Third, a more precise understanding of the fitness effects of structural and functional variables in the head coupled with rigorous statistical analyses will allow us to better understand the evolutionary consequences of intra- and interspecific variation in cranial morphology and function. *J. Morphol.* 248: 99–119, 2001. © 2001 Wiley-Liss, Inc.

KEY WORDS: prey capture; suction feeding; technology; form; function; digital particle image velocimetry

The structure and function of the head in fishes is an area of vertebrate morphology that has a long and distinguished history (Russell, 1916; Hanken and Hall, 1993). In the 19th century, anatomical study of the skull and jaws of fishes began in earnest and such noted anatomists as Louis Agassiz and Richard Owen provided new insights into the composition of the skull in fishes, an analysis that was aided by the contributions of German vertebrate anatomists such as Gegenbaur (1865) and Vetter (1874). In the 20th century the anatomical tradition of research on the skull of fishes was continued by

such workers as W.K. Gregory (1933), E.P. Allis (1909, 1922), Sir G. DeBeer (1937), and F.H. Edgeworth (1935), all of whom provided significant in-

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*Correspondence to: Lara A. Ferry-Graham, Department of Evolution and Ecology, University of California, Davis, CA 95616.
E-mail: laferry@ucdavis.edu

sights into the comparative structure or development of the head in fishes.

Virtually all who have examined the structure of head in fishes have commented on its organizational complexity. An exemplary statement of this kind was made by Richard Owen in his treatise on the skeleton of vertebrates (1854, p. 173): "It may well be conceived, then, that more bones enter into the formation of the skull in fishes than in any other animals; and the composition of this skull has been rightly deemed the most difficult problem in Comparative Anatomy." Quoting the German anatomist Oken, he continues "It is truly remarkable ... what it costs to solve any one problem in Philosophical Anatomy. Without knowing the *what*, the *how*, and the *why*, one may stand, not for hours or days, but weeks before a fish's skull, and our contemplation will be little more than a vacant stare at its complex stalactitic form."

In the 20th century the study of the head of fishes was characterized above all else by the march of technology and the application of this technology to problems in comparative functional anatomy (e.g., Liem, 1970). Techniques such as high-speed film and video greatly increased our appreciation for the actual motions exhibited by skull and jaw bones during natural behaviors such as feeding and respiration. The advent of the ability to record muscle electrical activity directly and to correlate activity patterns with movements of associated bones not only allowed previous hypotheses of muscle function to be tested directly, but also provided ample evidence that assessing function experimentally reveals many previously unsuspected patterns and that inferring function from anatomy alone is a hazardous proposition (e.g., Osse, 1969).

Now, at the beginning of the 21st century, it is appropriate to assess past progress and to define the areas where both technical and conceptual advances are likely to contribute to our understanding of the form and function of the head in fishes. Our goals in this article are twofold. First, we review progress in the century just ended and provide an overview of the interplay between technological advances and new concepts central to understanding form and function during feeding in fishes. Second, we consider several techniques that promise to provide new data on the function of the head in fishes. We focus particularly on a novel technique not previously applied to the study of prey capture, with the aim of showing the potential of this technique for future research: digital particle image velocimetry (DPIV). DPIV allows quantification of the water flow field around the head of fishes as prey are captured, and hence allows us to directly address for the first time many questions that could previously be only indirectly studied.

A number of reviews of specific aspects of the structure and function of the head in fishes have appeared in recent years, and it is beyond the scope

of our analysis here to address topics such as feeding mechanisms other than suction feeding (i.e., suspension feeding, Sanderson and Wassenburg, 1993; van den Berg et al., 1994; or pharyngeal jaw function, Sibbing, 1982; Wainwright, 1989; Galis, 1992; Vandewalle et al., 1994), or details of the feeding mechanism in other fish taxa (i.e., elasmobranchs, Motta and Wilga, 2000; or sarcopterygians, Bemis and Lauder, 1986). Furthermore, we have not addressed comparative studies of suction feeding in other vertebrate taxa (e.g., Erdman and Cundall, 1984; Shaffer and Lauder, 1985; Lauder and Shaffer, 1986; Lauder and Prendergast, 1992; Vandamme and Aerts, 1997; Summers et al., 1998), although many of the principles discussed here are broadly applicable to understanding aquatic feeding systems (Lauder, 1985a). Feeding in tetrapods has been recently reviewed comprehensively in Schwenk (2000). Instead, we limit this overview to the process of suction feeding in ray-finned fishes, the techniques used to study suction feeding, and the broader implications of analyses of prey capture mechanics in ray-finned fishes.

Many of the examples that we provide are our own as the original data were available to us. However, in using such examples we do not mean to imply that ours is the only relevant work in this field. Tremendous advances in the study of suction feeding in fishes have been made by researchers from all over the world.

A CENTURY OF PROGRESS The Era of Morphological Inference

In a time when modern techniques for visualizing the movement of bones and recording functional variables such as muscle activity, fluid pressure, and bone strain had not been developed, the only available approach to studying the form and function of the feeding mechanism was anatomical study and manipulation of fresh and preserved specimens. Given the limitations of this approach it is remarkable how much progress was made in understanding the function of the head in ray-finned fishes. Indeed, since the technology associated with studying function directly has become more complex and time-consuming to apply, there has been something of a decline in the quality and intensity of morphological research (with notable exceptions such as Grande and Bemis, 1991, 1998). Such tradeoffs are perhaps unavoidable, but it is nonetheless true that the quality of morphological description present through the 1970s is not often available today.

While there are a number of outstanding morphological analyses of the head in fishes which include at least some functional interpretations (a selection of the many possible references includes Allis, 1909, 1917; Gregory, 1933; Edgeworth, 1935; van Dobben, 1935; Lightoller, 1939; Kirchhoff, 1958; Kayser, 1962; Jarvik, 1963; Karrer, 1967; Nelson, 1969; Gos-

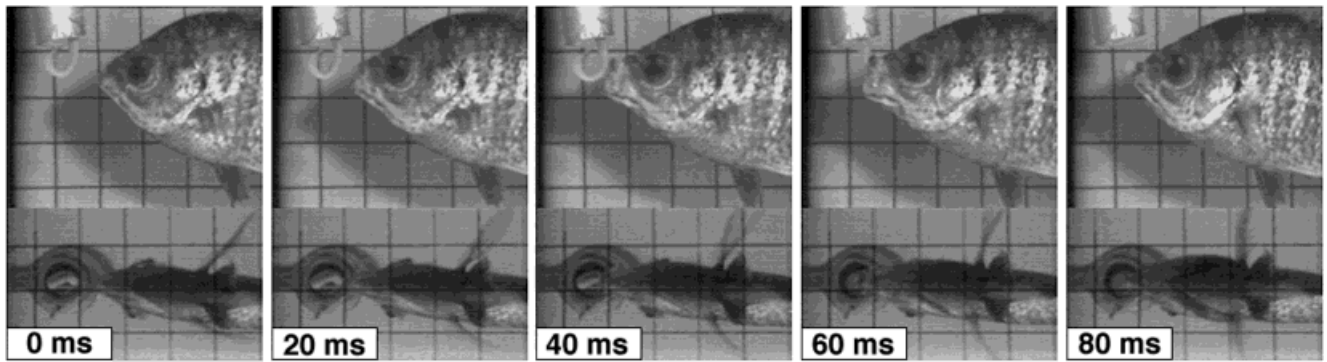


Fig. 1. Fields from high-speed video footage of a feeding bluegill sunfish (*Lepomis macrochirus*) successfully capturing an earthworm (*Lumbricus*) that has been dropped through a tube. Synchronized lateral and ventral views are shown for each time. The time (in ms) relative to the initiation of mouth opening is shown for each field. The grid in the background is 2×2 cm. Modified after Gillis and Lauder (1995).

line, 1971; Greenwood, 1971; Winterbottom, 1974; Patterson, 1975; Kershaw, 1976), the focus of most of this work was on descriptive anatomy and the examination of possible musculoskeletal homologies among taxa. Notable among morphological articles that have an explicit functional focus is the remarkable analysis of the feeding mechanism in the deep sea fish *Chauliodus* by Tchernavin (1953). Tchernavin presented a detailed morphological study of the head and hypothesized movements that would be involved in prey capture. Furthermore, he conducted a wide-ranging comparative analysis of skull structure and function, and included hypothesized movements of the head in pike, cod, salmon, and even snakes and bulldogs. Among Tchernavin's many contributions was the identification, from anatomical study alone, of the importance of cranial elevation and pectoral girdle rotation in suction feeding in *Salmo*. He further clearly explained the anatomical mechanisms involved in lateral buccal and opercular expansion, as well as the contribution of hyoid rotation to suction generation.

While Tchernavin's hypothesized functions of head bones and muscles were based primarily on manipulations of cranial morphology, other investigators such as Vrba (1968) went further and implanted small metal markers at various locations in the head and used X-ray photographs of the head manipulated into various positions to depict the potential motion of cranial elements.

Such attempts to understand the function of the head in fishes were extended into the evolutionary and historical realm by Schaeffer and Rosen (1961), whose article first defined the major trends in structural and functional evolution within ray-finned fishes. Schaeffer and Rosen identified perhaps the single most significant trend in the evolution of the feeding mechanism in ray-finned fishes: the increasing biomechanical independence of bony elements and functional linkage systems in the suspensorium and upper jaw.

The Study of Movement

As impressive as articles such as Tchernavin (1953) and Schaeffer and Rosen (1961) were at the time, some of their conclusions did not withstand the advent of our ability to directly measure the movement of skull bones and head expansion during prey capture. Several of the hypothesized movements of individual jaw bones (such as the maxilla in *Salmo*) by Tchernavin, for example, have been shown to be incorrect (Lauder, 1979; Lauder and Liem, 1980), and several hypothesized functions of the head in ray-finned fishes by Schaeffer and Rosen have been changed along with their evolutionary interpretations with the advent of direct measurements of prey capture kinematics (Lauder, 1980b, 1982). The actual quantification of function is the first step in understanding how the feeding mechanism evolves.

In this regard, one of the most influential early kinematic analysis of an acanthopterygian feeding mechanism was the comprehensive study of Liem (1970) on the feeding mechanism of nandid fishes. Although earlier articles exist that use photography to record movements of the jaws (e.g., Alexander, 1966; Liem, 1967; Osse, 1969; Alexander, 1970), Liem's (1970) article represents the first comprehensive kinematic study of both lateral and ventral head elements and also presents the first kinematic experimental test of proposed mechanical linkage systems in the head. Liem (1970) recorded kinematic patterns during prey capture and then anesthetized individuals and severed ligamentous connections between bony elements of mechanical linkage systems. Subsequent recording of head movements allowed the effect of eliminating such linkages to be quantified. Liem (1970) provided the first direct test of the function of the operculum and hyoid in causing mouth opening, and in that article he elaborated the notion of mechanical units and couplings that are still used today to describe the function of the head. Liem's work also served as the

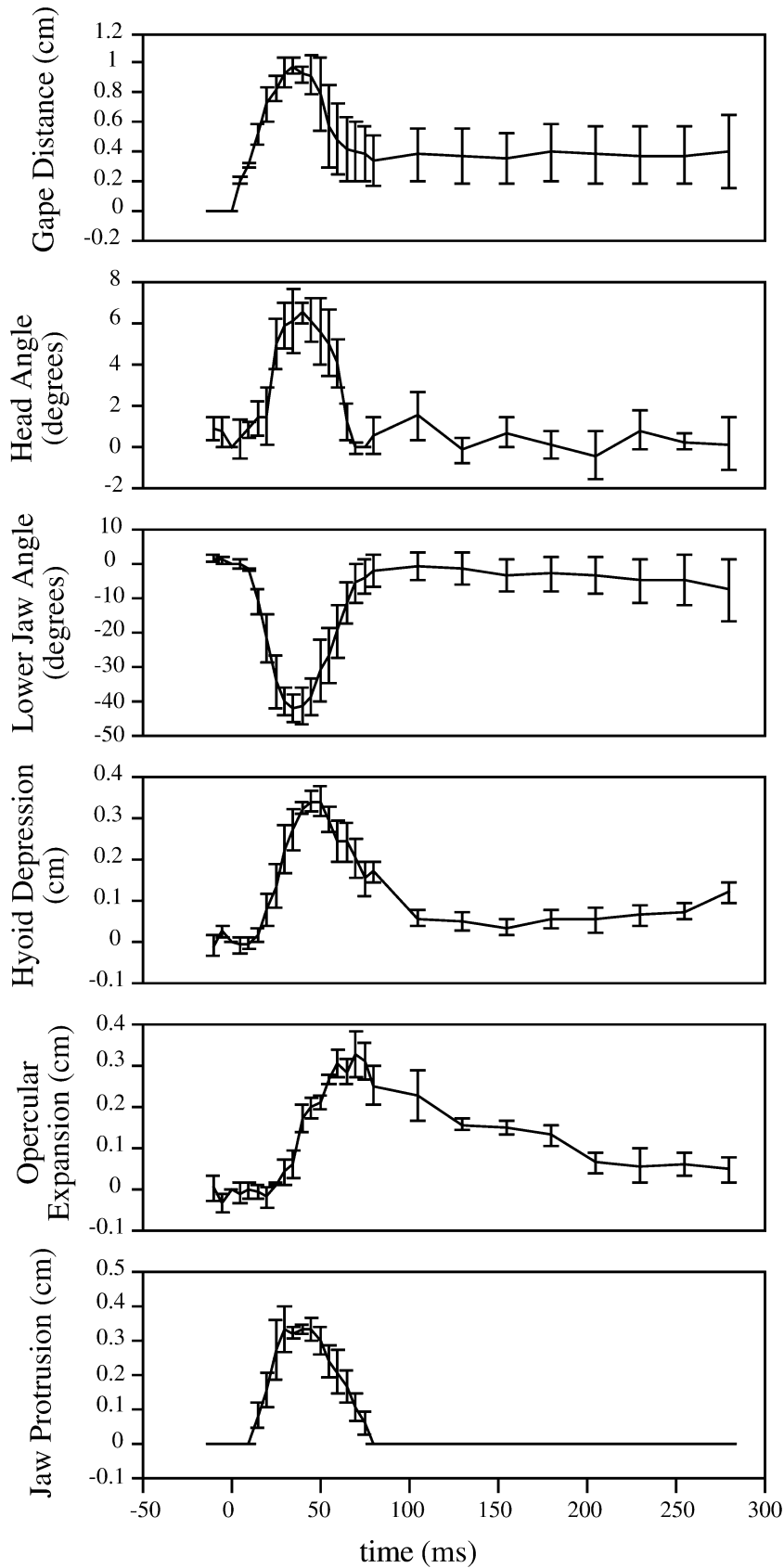


Fig. 2. Mean kinematic profiles (± 1 SE) for six variables typically quantified during prey capture. This profile represents the average of five feeding events from a bluegill sunfish (*Lepomis macrochirus*) feeding on worms (see Fig. 1). Modified after Gillis and Lauder (1995).

stimulus for a large number of early studies documenting the diversity of feeding kinematics of fishes and testing hypotheses based on comparative morphological and kinematic data (Nyberg, 1971; Elshoud-Oldenhavé and Osse, 1976; Anker, 1978; Elshoud-Oldenhavé, 1979; Grobecker and Pietsch, 1979; Lauder, 1980b; Lauder and Liem, 1981; Grobecker, 1983).

With the advent of high-speed video equipment and the ability to electronically synchronize two cameras so that both lateral and ventral views of the head during prey capture could be obtained, the nature of data acquisition changed considerably from the early days of film-based movies of feeding in the 1970s (e.g., Gibb, 1995, 1996). High-speed video image acquisition now allows the rapid review of sequences and the easy transfer of images into a digital format, greatly facilitating quantitative analysis of movement patterns. Figure 1 illustrates sample data obtained from prey capture in a bluegill sunfish (*Lepomis macrochirus*) by Gillis and Lauder (1995). By training fish to feed on relatively immobile prey that emerged from the end of a tube, Gillis and Lauder (1995) were able to quantify the pattern of jaw movement in two simultaneous views during both initial prey capture and the subsequent transport of prey.

Quantification of kinematic data from a variety of ray-finned fish taxa has shown that in many cases there is a clear progression of expansion from anterior to posterior as prey are captured using inertial suction (Liem, 1970; Lauder, 1983b, 1985a; Muller and Osse, 1984): peak gape is typically followed by maximal hyoid depression and cranial elevation which is in turn followed by opercular expansion (Fig. 2). This movement pattern is presumed to be associated with creating a unidirectional flow of water through the buccal cavity (see below) and with fluid inertia resulting from acceleration of water in front of the mouth into the buccal and opercular cavities.

The Advance of Technology

While new techniques sometimes become an end in and of themselves, the history of 20th century vertebrate functional morphology has shown clearly that technological progress and conceptual progress in understanding form and function often go hand-in-hand. The study of prey capture mechanics in fishes is no exception, and as a variety of techniques have been brought to bear on the complex mechanics of the head, our understanding of how prey capture is accomplished has been greatly enhanced.

Perhaps one of the most useful techniques to be added to the recording of movement using high-speed films was the direct measurement of pressures within the mouth cavity. Beginning with the first measurements using fluid-filled pressure transducers, Alexander (1969, 1970) showed that buccal

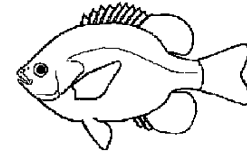
cavity pressure decreases sharply as the mouth opens, drawing water and prey into the mouth. Subsequent work demonstrated the possibility of measurement error involved in using fluid-filled transducer tubes (Lauder, 1980a; Van Leeuwen and Muller, 1983), although improvements in pressure measurement quality by using catheter-tipped pressure transducers confirmed the basic result of Alexander for buccal cavity pressures (Lauder, 1983a; van Leeuwen and Muller, 1983; Muller and Osse, 1984; Norton and Brainerd, 1993; Nemeth, 1997b).

Simultaneous measurement of pressure within both the buccal and opercular cavities of feeding fishes in conjunction with simultaneous high-speed film records of head movement and impedance recordings to transduce gill bar movements demonstrated several features of the suction feeding mechanism (Lauder, 1983b, 1985a): 1) pressure magnitudes vary with predator motivation and show considerable variation as prey type and feeding motivation change (Fig. 3); 2) buccal cavity pressure may reach extremely low values, approaching the pressure at which water cavitates (although most prey capture events are associated with more moderate negative pressures); and 3) pressures in the opercular cavity may be only one-fifth of the negative buccal pressure. The use of an impedance converter to directly transduce the distance between adjacent gill bar elements suggests that the gill bars play a role in segregating the opercular cavity from the buccal cavity as the mouth opens (Lauder, 1983a,b; Lauder et al., 1986). The gill bar elements display a pattern of adduction followed by abduction which is associated with effectively unidirectional water flow into the mouth and out of the opercular openings posteriorly (Fig. 4A).

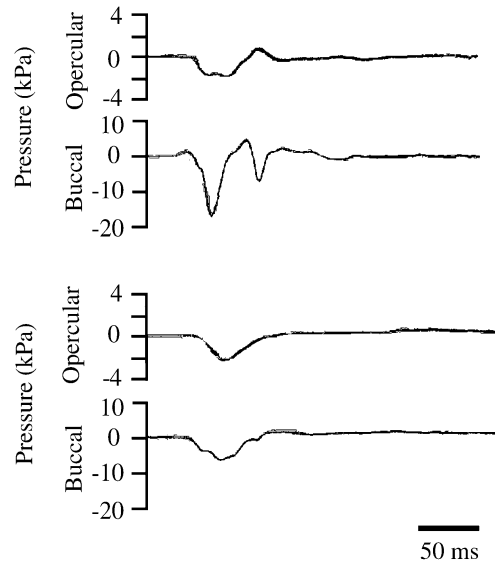
To our knowledge, only one article (Lauder and Lanyon, 1980) has used strain gauge technology (commonly used to study the mechanics of terrestrial locomotion) as a technique to further clarify the mechanics of suction feeding. Lauder and Lanyon (1980) implanted rosette strain gauges on the opercular bones of bluegill sunfish and were able to record deformation of the operculum along three axes as pressure decreased within the buccal cavity during prey capture. Strain measurements showed that the operculum bends medially and twists as opercular cavity pressure decreases, and these data provide an explanation for the perpendicularly oriented ridges on the medial surface of the operculum in many teleost fishes.

Probably the most widely used technique for the study of function during suction feeding is that of electromyography (Fig. 4). The rise of electromyography as a tool for understanding the suction feeding mechanism began in earnest with the work of Osse (1969), and subsequently numerous investigators have recorded muscle electrical activity in feeding fishes (see reviews in Lauder, 1985a; Lauder and Shaffer, 1993). The goals of these articles have in-

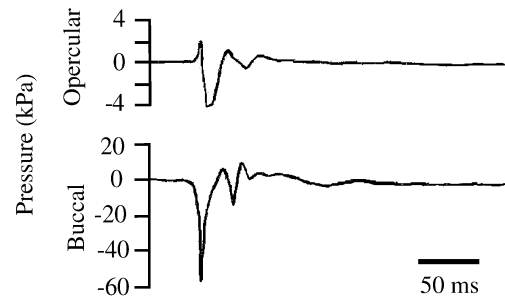
Earthworm prey



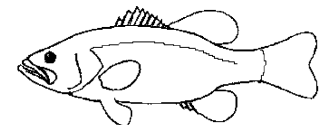
Bluegill sunfish



Goldfish prey



Goldfish prey



Largemouth bass

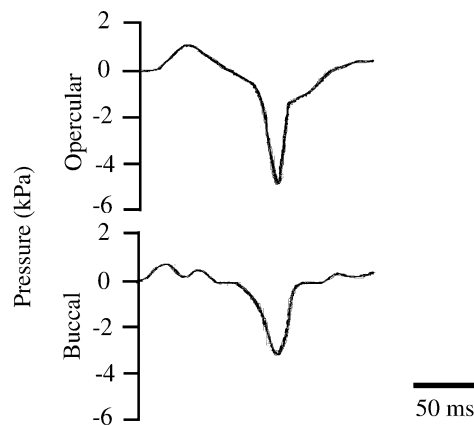
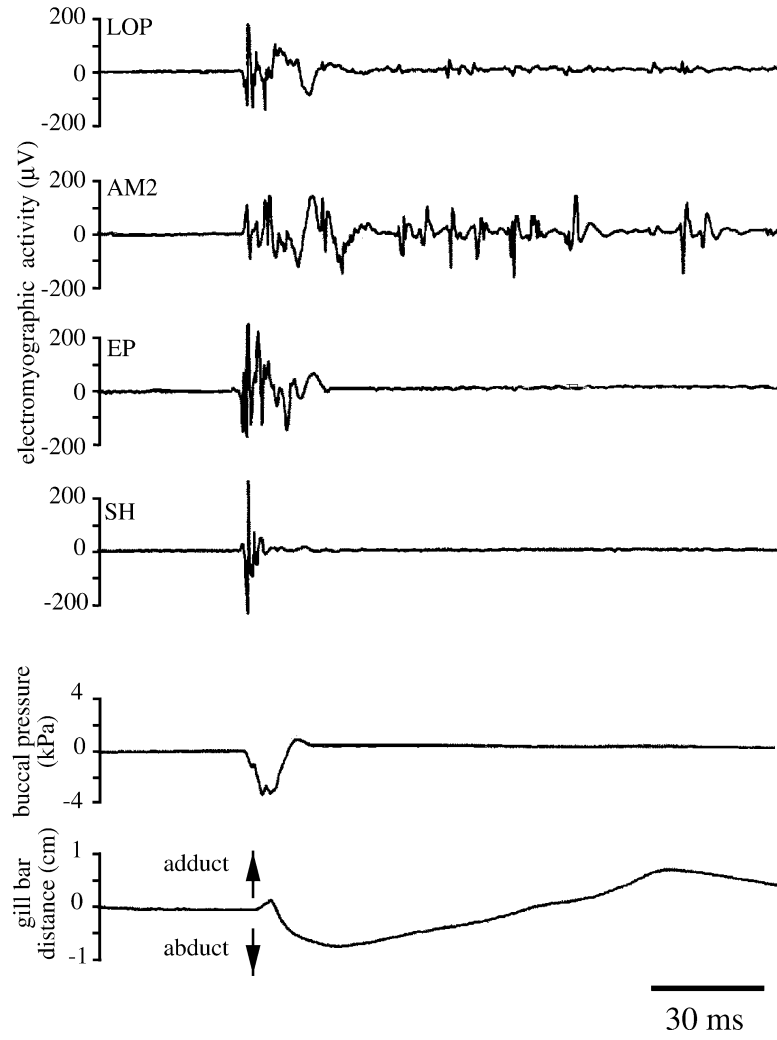


Fig. 3. Buccal and opercular cavity pressures from a bluegill sunfish (*Lepomis macrochirus*) feeding on earthworm (*Lumbricus*) and goldfish (*Carassius*) prey, and from a largemouth bass (*Micropterus salmoides*) feeding on goldfish prey. The largemouth bass, as its name indicates, is a large-mouthed predator compared to the small-mouthed bluegill. It has been suggested that the bluegill-like morphology is better for suction production (Norton and Brainerd, 1993). Note that bluegill produce much larger negative pressures (relative to ambient) during prey capture. Bluegill data from Lauder (1980a); largemouth bass panel modified after Norton and Brainerd (1993) with permission of E.L. Brainerd.

A.



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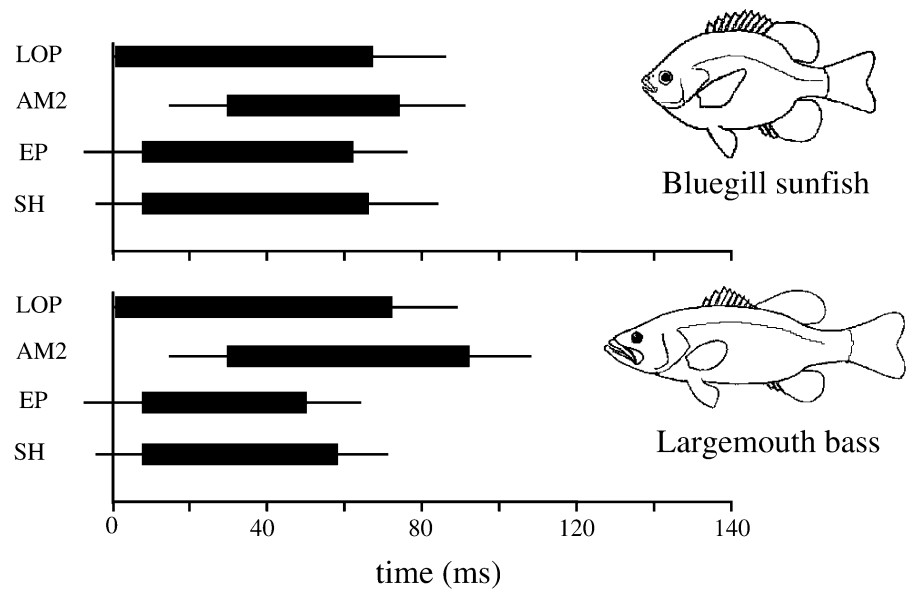


Figure 4.

cluded quantifying the timing and sequence of activation of cranial muscles to understand the basic mechanics and neuromuscular control of the feeding mechanism (Elshoud-Oldenhave and Osse, 1976; Elshoud-Oldenhave, 1979; Lauder, 1980b; Lauder and Liem, 1980), and measuring muscular activity that underlies the generation of negative pressure within the mouth cavity (Lauder et al., 1986; Grubich and Wainwright, 1997). The anterior-to-posterior pattern of kinematic expansion in the head of feeding fishes is most likely caused by a sequential pattern of activation of the cranial musculature (Osse, 1969; Liem, 1978). The reduction in pressure generated in the buccal cavity will be affected by the magnitude of activity of the cranial musculature and the subsequent amount of expansion of the head during feeding (Lauder et al., 1986; Grubich and Wainwright, 1997). More rapid expansion of the head will lead to greater decreases in pressure, as indicated by pressure transducers, and presumably increases in suction production (Grubich and Wainwright, 1997).

Comparatively, electromyography has also been used to understand the functional, ecological, and evolutionary significance of inter- and intraspecific variation among individuals at a level that high-speed video has not (Liem, 1978, 1979, 1980; Wainwright and Lauder, 1986; Wainwright, 1986; Sanderson, 1988, 1990, 1991; Wainwright et al., 1991; Turingan et al., 1995; for high-speed video see Motta, 1988; Cook, 1996; Gibb, 1997; Ferry-Graham et al., 2001). The ability to assess the timing and amplitude of activity in homologous muscles across a broad range of taxa has provided important insights into the evolution of function (Wainwright et al., 1989; Wainwright and Lauder, 1992; Friel and Wainwright, 1999). For example, the basic pattern of head expansion is largely conserved among ray-finned fishes, and the mechanical function of any one muscle in the head often remains similar from taxon to taxon (Lauder, 1985b). Such data are now being extended beyond ray-finned fishes facilitating an integrated view of the evolution of muscle function and its role in suction feeding across a broader range of vertebrates (e.g., Motta and Wilga, 2000). In addition, patterns of variation within individuals induced by different prey, or modulation, have now been quantified in a variety ray finned-fishes (Wainwright, 1986; Aerts and DeVree, 1993; Galis et al., 1994; Friel and Wainwright, 1999, for high-speed video see Nemeth, 1997a,b). Liem's (1978, 1979) original ideas regarding the ability of fishes to consistently modify the basic pattern of head expansion in response to different prey types have largely held true for electromyographic and other types of studies.

The increasing availability of high-speed computing resources in the late 1970s also provided workers interested in the mechanics of suction feeding with an additional powerful tool: the ability to generate theoretical models of suction generation. Models of suction feeding can be divided into two general categories: mechanical models of cranial musculoskeletal elements and linkage systems (e.g., Anker, 1974; Aerts et al., 1987; van Leeuwen and Spoor, 1987; Westneat, 1994) and theoretical calculations of feeding hydrodynamics (e.g., Weihs, 1980; Muller et al., 1982; Muller and Osse, 1984; Drost et al., 1988). Both approaches have added to our understanding of how suction is generated by fishes feeding in a dense and viscous medium.

Models of musculoskeletal elements and the linkages between such elements have helped us to understand how the movements that we measure using tools like high-speed video and electromyography facilitate suction prey capture. The work of Wainwright and Richard (1995), for example, presented in Figure 5, generated predictive expectations from simple mechanics. These predictions were then tested against experimental data. Wainwright and Richard (1995) were able to conclude that in-lever to out-lever ratios could accurately predict feeding modes (Fig. 5). High-lever ratios indicated that the jaws could effectively transmit force more efficiently; the species with high ratios were biting and grasping predators of benthic prey. Lower ratios facilitate a greater jaw closing velocity, and species with lower ratios fed on prey in the water column (Wainwright and Richard, 1995); presumably relying more on suction to capture the prey item. Modeling the skull as a series of mechanical linkages also has proven useful for understanding how the elements work together to perform a function (Aerts and Verraes, 1984; Aerts, 1990; Muller, 1996). Westneat (1990), for example, provided direct experimental tests of mechanical models of bony linkage systems in the head of suction feeding teleost fishes

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Fig. 4. **A:** Electromyographic, pressure, and impedance data from a bluegill (*Lepomis macrochirus*) during a rapid strike at a minnow (*Pimephales*). LOP, levator operculi; AM2, adductor mandibulae part 2; EP, epaxials; SH, sternohyoideus. Buccal pressure is measured using a catheter-tipped pressure transducer inserted through a cannula into the buccal cavity. Gill bar distance is transduced using a calibrated impedance converter. Note the synchrony in muscle activity onset followed by a pressure drop and gill bar adduction during the pressure decrease. Modified from Lauder (1986). **B:** Electromyographic bar diagrams showing average duration of muscle activity in the bluegill sunfish compared with the largemouth bass (*Micropterus salmoides*), two very different predators in terms of mouth size and body morphology. Both are feeding on live fish. Note the overall similarity of patterns of muscle activation during suction feeding. Sample sizes range from two to seven individuals and from 21–63 feedings per species. Thin lines are one standard deviation in onset and offset times. Modified after Wainwright and Lauder (1992).

and combined modeling with experimental kinematic data. Using four-bar linkage models, Westneat (1990) was able to predict the amount of upper jaw protrusion, hyoid depression, and opercular rotation that should occur. Kinematic data were used to confirm that predictions for the upper jaw and hyoid were accurate, but Westneat also showed that the model of opercular rotation failed to predict realistic movements (Westneat, 1990, 1994, 1995). Such theory complements the data we are able to collect using modern techniques, and will hopefully in turn be complemented by the application of additional techniques like sonomicrometry and endoscopy that are currently being tested and applied to related questions in functional morphology (see Future Directions, below).

Models that consider hydrodynamics, on the other hand, have been useful for trying to conceptualize how all of the parts of the head work as a whole to affect the aquatic medium and lead to the generation of suction. Muller and Osse (1978) and Muller et al. (1982) were among the first to develop comprehensive hydrodynamic models of how suction might be generated by a feeding fish. The expanding head was modeled as an expanding cone, with the inside of the buccal cavity modeled as the frustum of a cone, with the base at the posterior end of the buccal cavity (see Liem, 1990, for most recent explanation). Van Leeuwen and Muller (1983), Muller and Osse (1984), and van Leeuwen and Muller (1984) elaborated on this model and compared selected empirical measurements with predictions generated by the model. The model could subsequently be altered to yield predictions of flow that more closely matched the empirical data for the species studied. These were the first articles to show why small mouths with large expandable buccal cavities behind the mouth aperture should be most effective at generating suction for prey capture (see also Norton and Brainerd, 1993). Powerful buccal expansion and rapid mouth opening are associated with extreme suction generation. More recent modelers have utilized a geometric or kinematic model that takes into account dimensions inside the head of the fish (De Visser and Barel, 1996, 1998; Bouton et al., 1999). While they do not always calculate hydrodynamics explicitly, such models have led to precise predictions regarding the movement of kinematic elements and the consequence for suction prey capture (Aerts et al., 1987; Aerts, 1991). De Visser and Barel (1996) suggest that the right and left hyoid bars should be close to one another medially, which allows them to depress the hyoid apparatus causing no outward rotation of the suspensorium and presumably producing suction more efficiently. Such positioning of the hyoid represents a tradeoff in that large biting forces can no longer be produced. De Visser and Barel (1996) and Bouton et al. (1999) predicted that predators that feed on prey requiring suction for capture will possess closely apposed left and right hyoid bars, but species that feed on at-

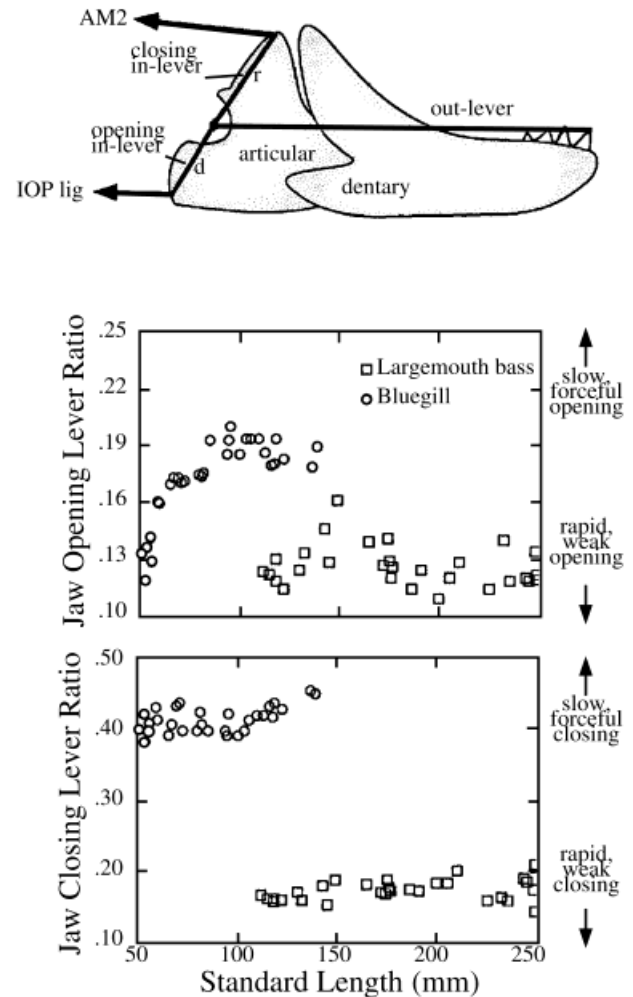


Fig. 5. Diagram of a generalized teleost lower jaw with measurements of lever arms used for modeling the mechanics of force production during mouth opening and closing. AM2, adductor mandibulae part 2; IOPlig, interoperculo-mandibular ligament. Black lines indicate measurements taken from fish jaws. The IOPlig operates to pull in the direction shown by the arrow and attaches to the articular bone at the base of the arrow drawn. A line is drawn from the center of the lower jaw joint to the IOPlig attachment site creating the distance, d , that serves as a representation of the opening in-lever. The AM2 attaches via Meckel's cartilage at the top of the articular bone, at the base of the drawn arrow. Connecting this attachment site with the center of the jaw joint creates the closing in-lever, r . The out-lever is measured as the distance from the center of the jaw joint to the anteriormost tooth row. The graphs indicate the relationship between in- and out-lever ratios and body length during jaw opening (top) and closing (bottom) for the bluegill sunfish (*Lepomis macrochirus*; open circles) and the largemouth bass (*Micropterus salmoides*; open squares). Modified after Wainwright and Richard (1995) with permission of P.C. Wainwright.

tached prey will not. Both have largely found support for their predictions. The techniques described above all have focused on defining the mechanics of the feeding system and on understanding how suction is generated by cranial bones and muscles. However, such techniques have not been able to reveal the pattern of fluid flow in front of the mouth

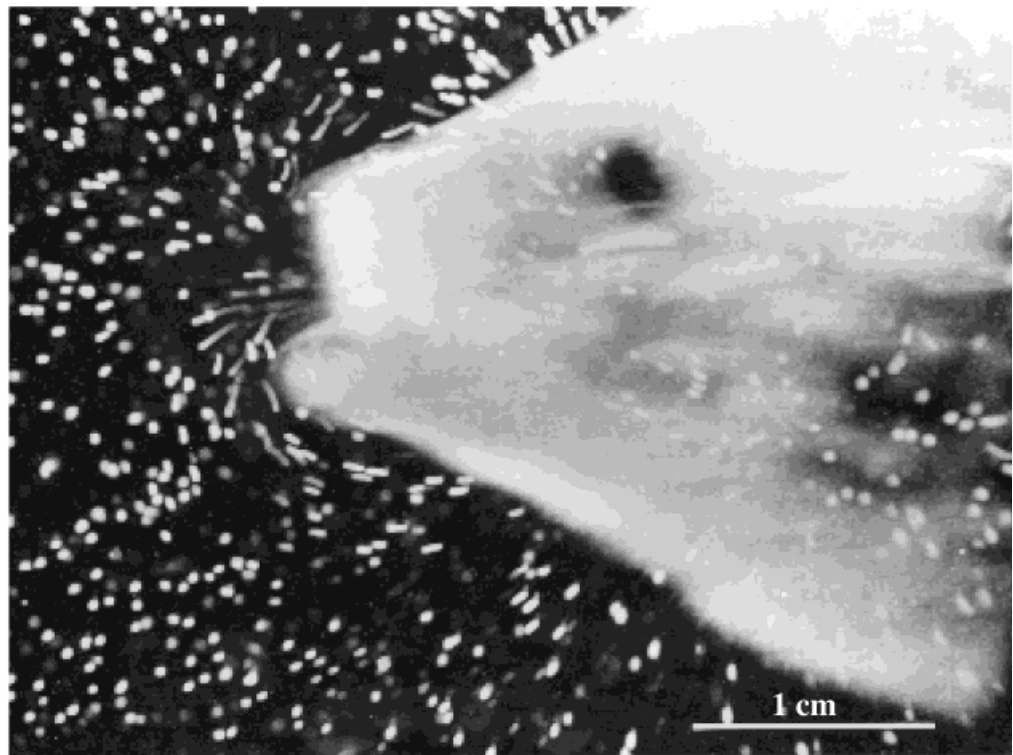
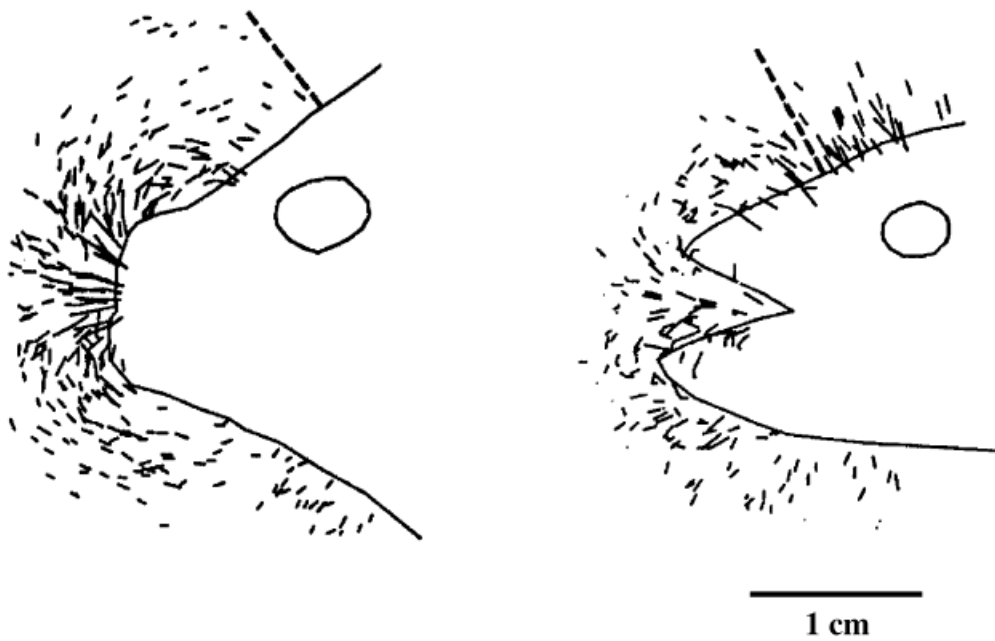
A.**B.**

Fig. 6. Water flow patterns into the mouth of a bluegill sunfish (*Lepomis macrochirus*) capturing an earthworm piece as revealed by tracking of individual particles. **A:** Streak photograph showing individual particle tracks at the moment of maximal mouth opening. **B:** Summary of particle motion at peak gape and during mouth closing. Figure modified after Lauder and Clark (1984).

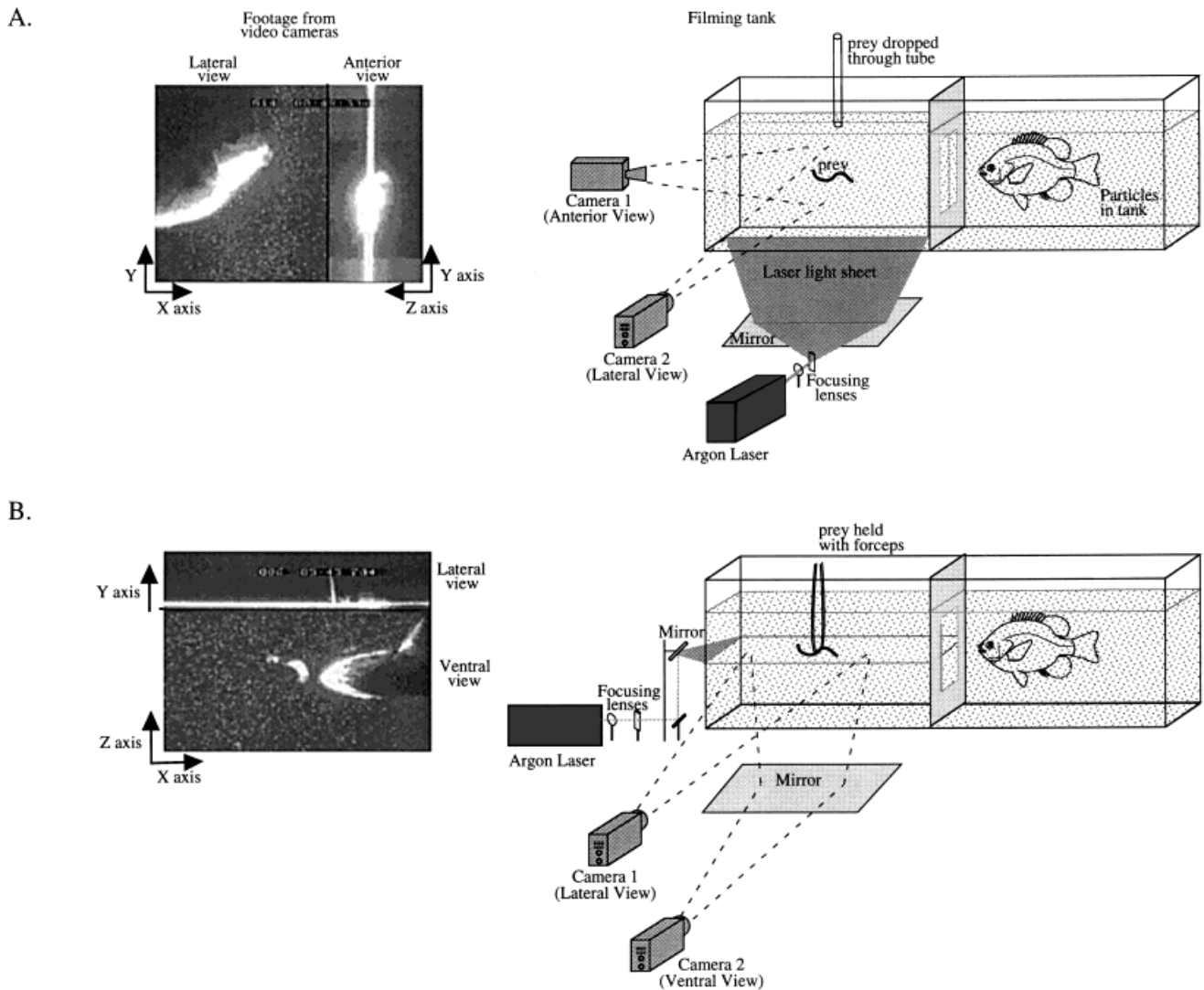


Fig. 7. Schematic diagrams of the experimental arrangements used for DPIV imaging of flow into the mouth of feeding fishes. For each experiment, the fish is confined to the right side of an aquarium which is divided in half by a partition with a trap door. When the door is opened, the fish swims through the opening to retrieve a prey item that has been dropped through a tube into the experimental portion of the aquarium on the left. A laser light sheet is focused into either a vertical (upper panel) or horizontal light sheet (lower panel) and the capture of the prey when it is located in the light sheet produces a flow of water into the mouth that is recorded with a high-speed video camera, camera 2. Another (synchronized) video camera, camera 1, is used to image the location of the prey and predator relative to the light sheet. A sample image from each laser light sheet orientation is shown to the left of the corresponding experimental arrangement.

and in the vicinity of the prey. Quantifying patterns of fluid flow during suction feeding is critical to understanding the effect of muscle activity, bone movement, and pressure changes on the prey item and ultimately prey capture. To this end, a number of attempts have been made to define flow into the mouth. Muller and Osse (1984) placed small polystyrene spheres in the water to visualize flow. Lauder and Clark (1984) used *Artemia* as particles to visualize and quantify flow into the mouth of feeding fishes, and a sample of the data from that article is shown here as Figure 6. Individual particles form streaks as they move, and particle streaks can be summed from the flow field to reveal an

overall pattern of water movement in the region of the head. Yet, these data are clearly inadequate for modern quantitative studies of suction feeding. New techniques are needed to address this important deficiency in our understanding of suction feeding, and below we present a new approach designed to address this issue.

A New Technique for Flow Visualization

Despite the ability to track individual particles that represent water flow during feeding, characterization of the full flow field around the jaws of fishes

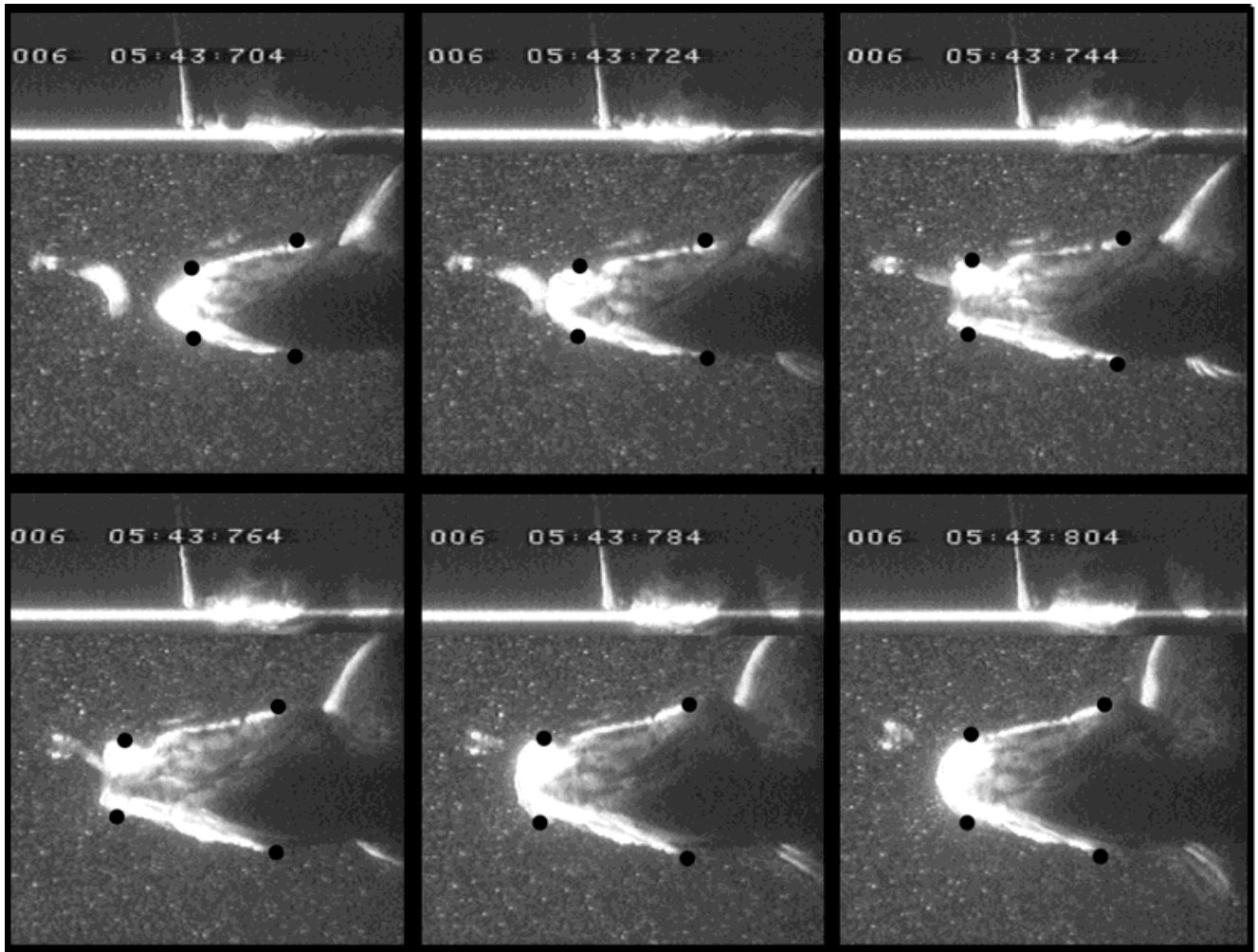


Fig. 8. Composite image from high-speed video footage of a bluegill sunfish (*Lepomis macrochirus*) feeding on a worm piece held released from forceps within a horizontal laser light sheet for digital particle image velocimetry (DPIV). Each frame consists of a lateral and a ventral view, with real times shown (min:s:ms). The lateral view is to verify fish position relative to the laser light sheet and is not scaled equivalently to the ventral view. The ventral view is used for analysis of particle images and water flow patterns are calculated from these images. The water has been seeded with silver-coated glass beads (see text), the reflections of which can be seen in the ventral view. For reference, points have been indicated on the ventral view of the feeding fish. These are the right and left sides of the jaw, and the right and left margins of the operculae.

during the process of prey capture has remained elusive. Following individual particles provides valuable information on the flow of water into the mouth, but particle streak photographs such as shown in Figure 6 provide only a snapshot of the flow at a single point in time and often do not provide a uniform picture of flow in the entire region around the mouth due to nonuniform particle distribution. And yet, characterization of the flow field around the mouth is precisely what is needed both for functional studies of the head and jaws and for ecomorphological analyses of the effect of different predator head morphologies on feeding performance. Until we quantify the *effect* of different muscle activity patterns or pressure profiles on water flow into the mouth, it will be difficult to understand the functional significance of variation in factors

such as head morphology and the motor patterns underlying feeding behaviors. DPIV is a technique that has the potential to resolve these issues, and allow us for the first time to directly measure dynamic flow variables and quantify precisely the flow field around the mouth of a feeding fish.

METHODS

Detailed general discussions of the technique of DPIV are available elsewhere (Willert and Gharib, 1991; Nieuwstadt, 1993; Fincham and Spedding, 1997), and application of this technique to the functional morphology of locomotion in fishes is presented by Drucker and Lauder (1999, 2000), Lauder (2000), Müller et al. (1997), and Wolfgang et al. (1999). Here we present an overview of the method-

ology to: 1) illustrate how the DPIV technique can be applied to the study of prey capture in fishes, and 2) facilitate understanding of our experimental results and the promise of this technique for future studies of the functional morphology of fish feeding.

We used DPIV to visualize water flow patterns created by bluegill sunfish (*Lepomis macrochirus*) expanding the buccal cavity during prey capture. The primary advantage of DPIV was that it allowed us to visualize the volume of water affected by the feeding fish and to simultaneously quantify flow parameters such as water velocity at any given position and fluid vorticity around the head. DPIV data were collected from four size-matched bluegill sunfish (*Lepomis macrochirus*, mean total length 20 cm) to establish general flow parameters.

To visualize flow into the buccal cavity each fish was placed into an experimental aquarium measuring $30 \times 76 \times 20$ cm (Fig. 7). The water in the aquarium was seeded with $12\text{ }\mu\text{m}$ silver-coated glass beads at a density of 1.3 g cm^{-3} , and a 5W argon-ion laser was used to separately create horizontal and vertical planar light sheets following the methods described in Drucker and Lauder (1999). The two light sheets were not created simultaneously and separate feeding experiments were conducted with each light sheet orientation (Fig. 7). Each plane of light was created by directing the laser beam through a series of focusing lenses that acted to spread the beam into a sheet of light approximately 10 cm wide and 0.1 cm thick. Mirrors placed at 45° angles served to direct the light sheet through the center of the experimental aquarium (Fig. 7). Care was taken to ensure that the light sheets were precisely horizontal or vertical relative to the aquarium walls.

To ensure that the bluegill fed within the illuminated sheet, it was necessary to constrain the position of both the prey and the predator without actually interfering with the feeding event. To position the prey within the vertical light sheet a small plastic tube was placed over the aquarium so that prey items (1–2 cm earthworm pieces, *Lumbricus*) could be dropped through the tube allowing them to fall slowly and vertically to the tank bottom, generally without moving laterally out of the light sheet before being devoured (Fig. 7A). Forceps were used to lightly hold the prey within the horizontal light sheet (Fig. 7B). To position the predator, a sliding trap door was placed in the center of the aquarium, effectively dividing it into two halves, a “resting” portion and an experimental portion. Individual bluegills were housed in the “resting” half of the aquarium whenever experiments were not being performed. Bluegills were trained to swim through the trap door to the experimental half by offering food held on forceps whenever the trap door was raised. All bluegills quickly came to associate the raising of the trap door with the offering of food and would readily swim through the open door regard-

less of whether or not the laser light sheet was illuminated. The trap door served to passively direct the bluegills’ attacks into the center of the aquarium and prevented the fish from approaching the prey to the extreme right or left of the vertical light sheet, or from far above or below the horizontal light sheet (Fig. 7).

Flow patterns within the light sheets were quantified by imaging the laser light reflected off the silver-coated glass beads with two synchronized NAC high-speed video cameras filming at 250 Hz (Fig. 7). One camera was used to capture the movement of the particles during the strike while the second camera was used to verify the predator’s position and orientation within the light sheet. Images were combined on a split screen. Feeding sequences were analyzed if the predator and prey remained visible throughout the strike, perpendicular to the camera, and the laser light sheet intercepted the head at the midline. Four prey captures from each of the four fish feeding in the horizontal light sheet were subsequently analyzed. Four prey captures from a single fish feeding in the vertical light sheet were also analyzed to determine if this plane provided additional or different information (discussed below).

From these images, the velocity of water around the mouth and jaws were quantified throughout the strike. Such data were calculated at 20-ms intervals during the strike by downloading image pairs. Image pairs consisted of a given image and the image that followed it in time on the high-speed videotape ($\Delta t = 4$ ms). At least five image pairs per strike were collected and related to the following stages of the gape cycle: mouth opening, prey capture, peak gape, peak opercular expansion (when detectable), and mouth closure. Intervals just prior to mouth opening and immediately after mouth closure were also analyzed. Image pairs were analyzed using two-frame cross-correlation (Raffel et al., 1998) and subsequently interrogated over a consistent 15×15 grid using the computer software Insight (v. 3.0, TSI, St. Paul, MN) (also see Drucker and Lauder, 1999, 2000; Wilga and Lauder, 1999, 2000; Lauder, 2000). For each laser plane a two-dimensional array of velocity vector profiles was generated; u and v and w are the velocity components parallel to the X, Y, and Z axes, respectively, and each could be estimated from one of the two laser light planes. The profile area was roughly 6–8 cm on a side and consisted of 225 uniformly distributed vectors. The velocity vectors were validated with a dynamic mean value algorithm (TSI Inc.) and also visually validated. Vectors that grossly and obviously misrepresented the flow were deleted. Such errors typically occurred at the margins of the data field or on the fish body where laser light tended to be intensely reflected. Gaps in the vector field were filled by interpolation using a least-squares estimate from neighboring particles in a 3×3 grid.

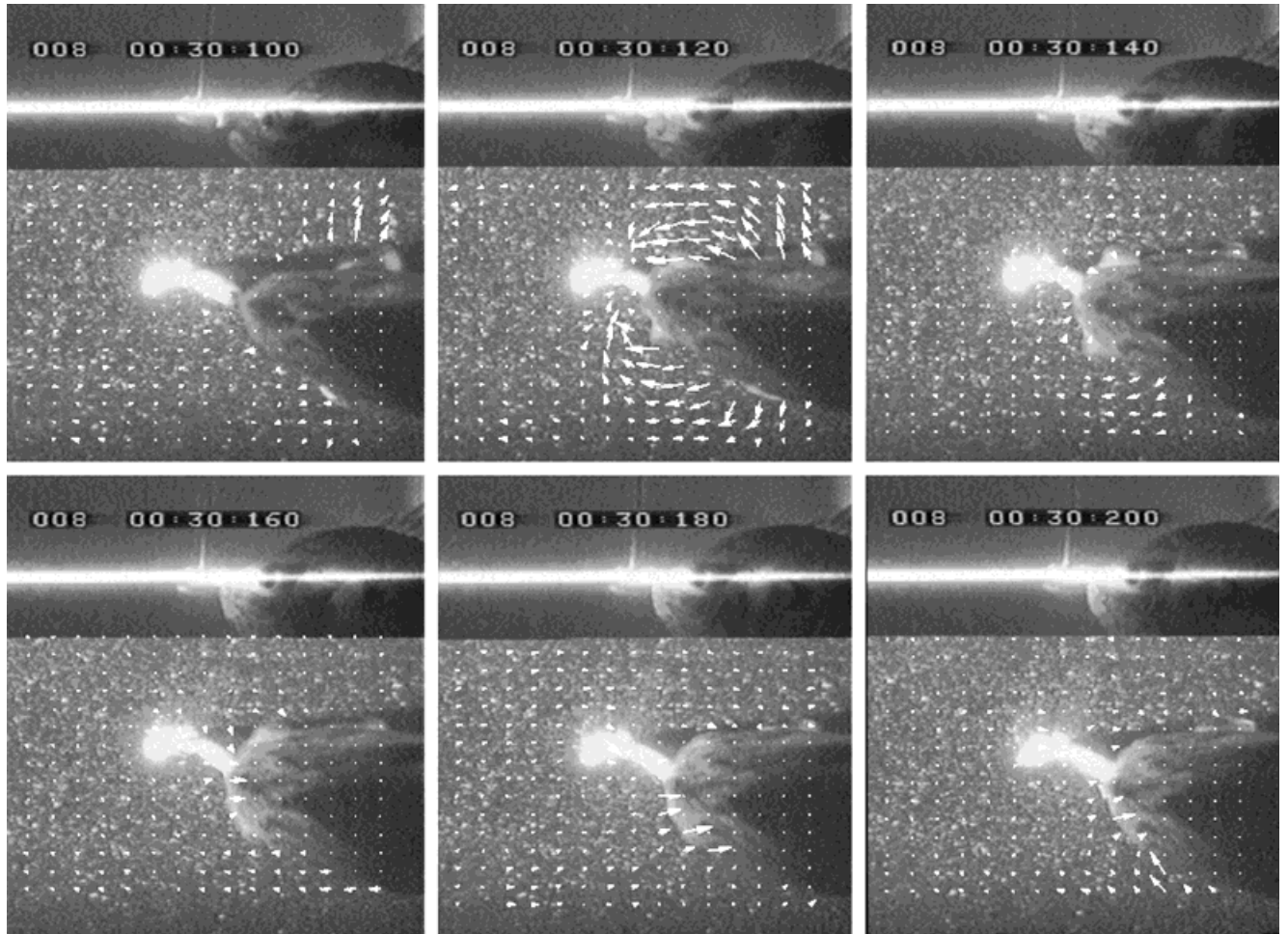


Fig. 9. Velocity vector profiles generated by a bluegill sunfish (*Lepomis macrochirus*) feeding on a worm piece held suspended by forceps within a horizontal laser light sheet. The velocity vectors (white arrows) are superimposed on high-speed video images from the same feeding event at the same points in time. Times are indicated on each field (min:s:ms). Peak gape occurred at 140 ms, 40 ms after the onset of the strike (at 100 ms). Note that the velocity vectors pointed to the right at 160 and 180 ms result from water attached via drag forces to the retreating bluegill, and not suction-generated for prey capture.

Velocity vector profiles were used to compute vorticity (ω), a measure of fluid angular velocity (also see Drucker and Lauder, 1999, 2000; Wilga and Lauder, 1999, 2000). Calculation of vorticity facilitates the visualization of rotational flow in the local flow field, the area of the fish head. The total strength of a vortex is measured in terms of the circulation of that vortex (Γ). We also used the velocity vector profiles to extract single, maximum values of velocity for each frame in a feeding sequence. Maximum velocity (U) was taken as the largest single vector generated in the X-direction, or into the open buccal cavity. For each feeding sequence, a single maximum was then obtained. These maximum values were used only so that we had a way of scoring individual strikes, and provided a variable that we could use to compare strikes statistically among individuals.

RESULTS

DPIV data collected from both vertical and horizontal laser light sheets indicated that the horizontal light sheet provided the most useful information for the quantification of flow velocity profiles into the mouth. The typical stages of prey capture and head expansion are most evident in the ventral view of the feeding bluegill, although data on gape distance were also collected from the lateral views. Thus, most of the data presented here resulted from the horizontal laser light sheet.

A prey capture sequence illustrating velocity vector profiles is presented in Figure 9. At the time of mouth opening, head expansion is evident as the vectors indicate that water is being displaced laterally. Twenty milliseconds later water has started to enter the buccal cavity, as indicated by velocity vectors curving anteriorly and medially. At the time of

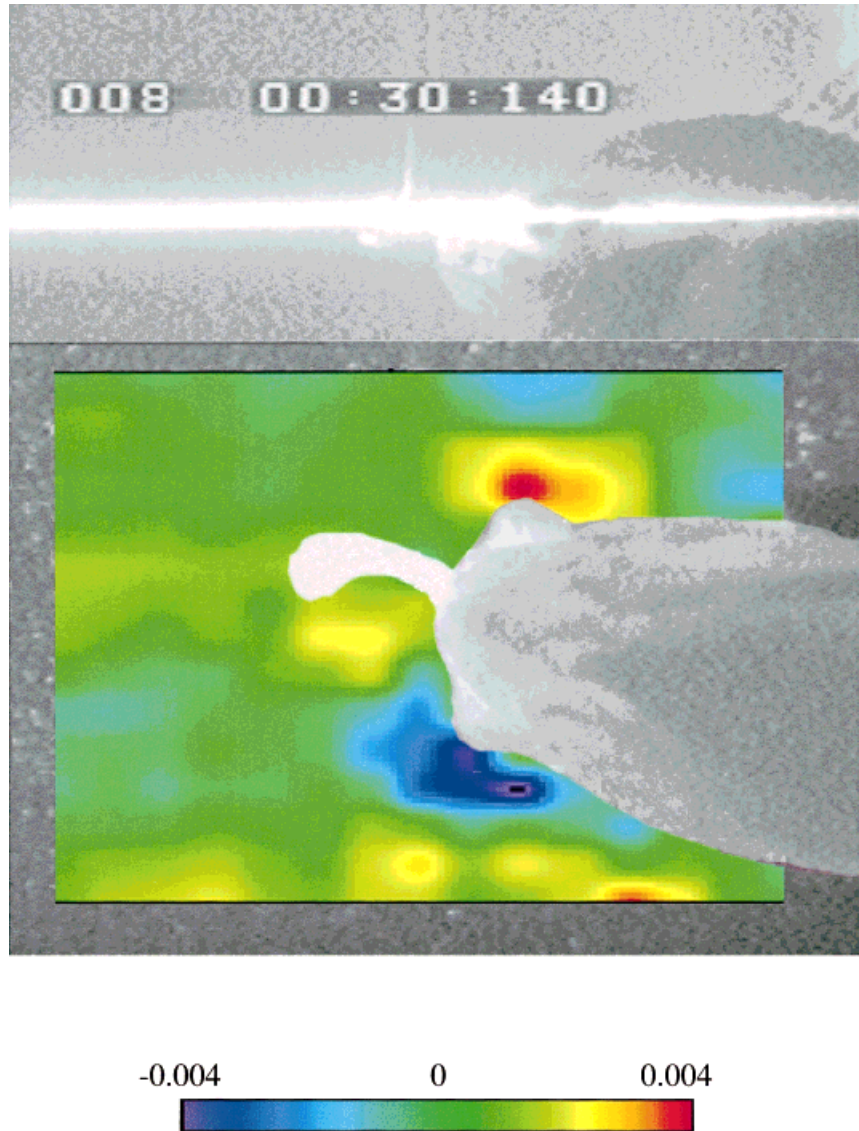


Fig. 10. Plot of fluid vorticity (in radians/sec) for a single frame from Figure 9, the time of peak gape. Areas of green are regions of no vorticity while blue color reflects clockwise fluid rotation and red/yellow color indicates counterclockwise fluid rotation. Note the two counterrotating vortices on either side of the bluegill's mouth.

peak gape (Fig. 9, 140 ms) water velocity has slowed, as indicated by the shortened velocity vectors, but water continues to enter the buccal cavity. The continued existence of counterrotating vortices directing water into the buccal cavity can be seen in a vorticity plot of the same image in time (Fig. 10). As the mouth begins to close on the prey item (Fig. 9, 160 ms), the jaws are retracting and water is drawn toward the head by the retracting jaws, as indicated by the posteriorly directed flow. The mouth is closed by 180 ms and the recovery phase nearly completed by the last frame (Fig. 9, 200 ms).

Maximum U (horizontal velocity) data collected for 15 feeding events analyzed from the horizontal light sheet suggest that the velocity imparted onto the water by the feeding bluegill is highly variable.

The mean for all strikes was 0.079 m sec^{-1} (± 0.057 SD). However, no trends were detected to suggest that any differences among feedings could be attributed to individual differences (one-factor ANOVA $F = 1.29$, $P = 0.28$).

DISCUSSION

DPIV images of water flow into the mouth of suction-feeding bluegills show that fluid flows toward the mouth both from anterior and from as far posteriorly as the operculae. Water flow into the mouth is not well characterized by simply considering the region immediately anterior to the jaws. Rather, water flows toward the opening mouth from a spherical region that extends posteriorly as well as

anteriorly (e.g., Fig. 9, time 120), and the overall flow pattern in three dimensions most likely represents a torus (similar to those observed during fish locomotion; Drucker and Lauder, 1999; Lauder, 2000) centered on the mouth with the central jet flow aimed into the buccal cavity. This pattern of water flow is relevant ecologically when considering the region of water flow that prey might detect as well as for analyses of suction-feeding efficiency and the effect of mouth size and shape on suction performance. Future DPIV studies of suction feeding might profitably investigate the effect of different mouth shapes on the three-dimensional flow field.

Variation in the flow field within and among individual bluegills existed and likely reflects variability in suction performance among feeding events. This variation was in the form of differences in the magnitude of velocity produced, rather than in the shape of the flow field or in the direction of circulation. No significant patterns of among-individual variation were detected in the maximum velocities that we quantified. Thus variation in velocity can likely be attributed to factors such as the distance at which the individual strike is initiated and variation in feeding motivation, all factors previously identified as causing interfeeding variation (Lauder, 1980a, 1985a; Wainwright and Lauder, 1986; Norton and Brainerd, 1993). It is not the goal of this study to understand why the magnitude of suction might vary; a number of authors have attempted to address that subject in detail and we will not reiterate those ideas here (see Wainwright, 1986; Norton and Brainerd, 1993; Summers et al., 1998).

To our knowledge, the DPIV approach that we present here is the only attempt to directly measure the flow velocity field produced by the expanding buccal cavity during prey capture. And DPIV as a technique can be used to measure not only the velocity field itself, but also a number of other primary variables resulting from water flow patterns measured during suction feeding. For example, aspects of maximal flow magnitude can be calculated from the two orthogonal velocity components in a given two-dimensional light sheet and maximal vorticity can be extracted from the calculated vorticity field, as can fluid strain and streamlines. Such metrics provide the basis for reconstruction of the global three-dimensional pattern of fluid flow into the mouth and can be used to compare results from DPIV with data obtained with other techniques, such as pressure transducers or modeling, and can also be used as statistical variables in an analysis of the effects of prey type on water flow patterns or of interspecific differences in feeding function. In addition, more complex flow characterizations are possible by extracting velocity components along the centerline of the buccal cavity extending anteriorly into the region in front of the mouth and fitting functions to these values to quantify the rate of change of velocity with distance from the mouth opening.

DPIV is not the only way to measure variables like velocity and DPIV possesses its own set of limitations. In our experiments, we found that not all individuals were amenable to feeding in the laser light sheet. This reduced the sample size available to us and limited our ability to make some inferences regarding flow patterns. The sections of prey had to be sufficiently large for the bluegill to see them (1–2 cm), which surely prevented the measurement of some of the fine-scale flow patterns in the immediate area of the prey. Further, the locomotor activity of fish had to be seriously restricted in order to catch the feeding movements on camera with the proper magnification and depth of field. While the fish were not actually restrained in any way, we suspect that many species of fish might be even more resistant to feeding under the conditions created by DPIV than to the rather contrived conditions that functional morphologists use for techniques like high-speed video and electromyography. We maintain, however, that continual refinement of this technique will allow us to move beyond these obstacles. DPIV should be added to the functional morphologist's toolbox as another means of measuring physical variables associated with suction feeding.

However, we feel DPIV is most useful for the combined and integrated information that it provides about the feeding event as a whole. Quantitative synthetic measures of the flow field and the velocity profile will allow for new metrics of comparison among species. For example, reconstruction of the three-dimensional shape of the volume of water drawn into the mouth for species with different suction production would be extremely informative. The consequence of changes to kinematic, electromyographic, or other movement patterns for actual suction generation could then be determined directly. In addition, the primary advantage of DPIV is that it is not invasive in the manner of pressure transducers, velocity probes, and even electromyography. Thus, some levels of experimental artifact may be removed by this technique. DPIV will be a useful tool for understanding suction feeding in fishes more completely.

WHAT WE STILL NEED TO KNOW How Is Suction Generated?

Despite the considerable progress that has been made in the concepts and techniques used to study suction feeding in fishes, there are two key areas in which we still need quantitative data. First, we lack a comprehensive picture of the three-dimensional movements of the head during prey capture. Second, patterns of water flow into the mouth during prey capture remain obscure.

Knowledge of the three-dimensional movements of the head during prey capture is critical for moving beyond the simple two-dimensional plots of bone excursions that have been the standard to date.

Only rarely are data even collected in three dimensions (e.g., Gillis and Lauder, 1995) and even then analyses of movements are usually presented as two-dimensional graphs rather than as x, y, z plots. Plots in two dimensions of bones moving in three dimensions can be extremely misleading (see Lauder, 2000, for a specific example) and movements shown as excursions do not reflect the motion of bony *surfaces* that interact with the water to produce changes in fluid pressure. In order to analyze the motion of surface elements, such elements (minimally triangular) need to be defined by specific markers and the orientation of each element calculated with respect to each of three perpendicular planes (xy, xz, and yz) through time. Analyses of the motion of surface elements of fishes have been used in studies of fish propulsion (e.g., Ferry and Lauder, 1996; Lauder and Jayne, 1996) but no such analyses have been undertaken for bony elements involved in prey capture. X-ray cinematography, while extremely useful for the study of respiration in which the medium of interest (air) has a very different density from that of the animal (Liem, 1989; Brainerd, 1998) has only been applied in a limited way to prey capture (Anker, 1978; Lauder, 1979) as the rapidity of motion and density similarities limit resolution. Furthermore, simultaneous views in two planar orientations are not available and hence three-dimensional reconstruction is difficult and better accomplished with conventional two-camera high-speed video.

Although a comprehensive three-dimensional kinematic study of the movement of the head during prey capture would be extremely valuable, such data are not fully adequate to quantify volumetric changes during prey capture; changes in buccal and opercular cavity volumes are best measured by quantifying the movement of the internal oral surfaces which cannot be done via external measurements. For such analyses, a technique that provides a direct transduction of the distance between bony elements is needed. The use of impedance converters provided such a technique in the early 1980s when they were first used to transduce distances between gill bar elements during fish feeding and respiration (Lauder, 1983a, 1984). But impedance converters are difficult to calibrate to absolute distance and for the most part only a single distance measurement can be transduced at one time.

The technique of sonomicrometry provides a direct method of transducing the distance between two implanted crystals. Excluding clinical applications, it has been used by functional morphologists in studies of animal locomotion (see Coughlin et al., 1995; Dial et al., 1997; Roberts et al., 1997, among many possible references) and in a single respiration study (Ferry-Graham and Summers, 1999). Sonomicrometry can be extended into three dimensions using an implanted array of crystals and hence could

provide direct measurements of volumetric changes in the buccal and opercular cavities during prey capture. There are no existing sonomicrometric data that provide measurement of distances or volume changes during prey capture, and yet we consider such data critical to future progress on the biomechanics of suction feeding. When combined with techniques such as intraoral pressure measurement, three-dimensional sonomicrometric data could contribute significant insights into the mechanisms by which suction is generated. These might include differences between opercular and buccal cavity function during prey capture, the significance of hyoid depression and lateral expansion of the opercular elements, and the function of the gill bars during feeding.

Similarly, endoscopy provides a direct view of the inside of the head of a feeding fish. This approach has been applied successfully to study suspension feeding in fishes (for example, Sanderson et al., 1991, 1996), and has been used in conjunction with tools such as velocity probes inserted into the buccal cavity (Sanderson et al., 1994), and mathematical models of flow around gill rakers (Sanderson and Cheer, 1993) to more completely understand how particles are entrapped by the gills and their associated elements. Analogous data illuminating the internal features at work during suction feeding have not been published. As with potential sonomicrometric data, the combination of endoscopic data with existing techniques will also help us to understand more about the physical mechanisms responsible for suction generation, as well as the potential for visualizing water flow within and through the buccal cavity during suction feeding.

Data describing patterns of water flow into the mouth during prey capture are critical for understanding the impact of movements of the head on the volume of water surrounding the prey, and hence for linking biomechanical analyses of prey capture mechanics with ecomorphologically oriented hypotheses (*sensu* Norton and Brainerd, 1993; Motta et al., 1995a; Turingan et al., 1995). Although the DPIV data presented above provide a first analysis to illustrate the promise of this technique, much remains to be done. We consider this technique to be a critical addition to the array of approaches that will form the next generation of studies of prey capture in fishes. While the accurate use of DPIV requires attention to a number of technical details, the neglect of which can lead to inaccurate data and erroneous results, and while DPIV requires considerably more equipment and analytical expertise than many of the techniques used in the past study of prey capture in fishes, the need for analytical tools that allow the quantification of water flow near the prey is critical, and the effort needed to obtain such information will be well spent.

Which Variables Have Fitness Consequences?

Motta and Kotrschal (1992), Motta et al. (1995b), and Wainwright and Reilly (1994) suggest a move beyond simple correlative studies of form and function in fishes and advocate measuring performance in functional morphological studies. Traditional functional tests (e.g., Liem, 1970; Lauder, 1980a) will always have a place in functional morphology as they provide the means of testing the causal basis for the correlation between form and function, and in the past such experimental approaches have been instrumental in refuting theoretical models. But performance tests can and should go a step further by indicating actual consequences for organismal fitness (Motta et al., 1995b). A number of functional studies on the feeding mechanism in fishes have measured performance in some manner (Wainwright, 1986, 1987; Nemeth, 1997a; Bouton et al., 1998). But, it is not always clear which variables need to be measured to provide correlates with fitness that have a causal relationship (see Jayne and Bennett, 1990, for an example from locomotion studies).

Herein lies the problem for the researchers who study the functional morphology of feeding. Functional morphological researchers studying locomotion utilize traits like maximum sprint speed. One can demonstrate the link between sprint speed and the ability to escape predators and therefore increased survival and presumably fecundity. Further, we can directly connect a measurement of organism speed with an energetic cost of performing at that speed. What does one measure about feeding that has a performance consequence? Can we detect a fitness difference among individuals in which the length of the lower jaw varies by 5%? What can we measure that we can directly then translate to a cost of feeding? One approach is to quantify "prey capture success" as performance. One can clearly see that a missed meal will equal a cost in terms of energy allocated to growth, reproduction, and survival. But, how much energy? What does one missed meal cost? And what energy is expended during a prey capture event regardless of capture success?

We suggest that while the amount of suction produced by a feeding fish can be indirectly quantified using methods like DPIV and expressed in physical units of velocity (m sec^{-1}) or vorticity (sec^{-1}), and further equated to notions of force and work, we need to go further and directly evaluate the cost of prey capture and the absolute performance cost of a missed meal. Using the new approaches described above, we can distinguish the kinds of suction produced by fishes which rely on it to capture prey (i.e., inertial suction; see Summers et al., 1998) and suction that is produced merely to compensate for the predators' forward locomotion (i.e., compensatory suction; see Van damme and Aerts, 1997) and per-

haps compute the costs of generating inertial and compensatory suction. Further, in fishes that rely on inertial suction to capture prey, like bluegills, we can evaluate differences in suction production among strikes and determine the cost of failed attempts and successful prey captures both from an energetic and evolutionary perspective. Ultimately, our understanding of the significance of interspecific differences in prey capture mechanics stands on a foundation of measured variables with demonstrated performance consequences. Such demonstrations are far from trivial, and yet are an essential component of future research on prey capture mechanics in fishes.

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