

PHYSIOLOGICAL MECHANISMS OF AQUATIC PREY CAPTURE IN SUNFISHES: FUNCTIONAL DETERMINANTS OF BUCCAL PRESSURE CHANGES

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Abstract—1. Cranial muscle electromyograms, buccal pressures, and gill apparatus movements were measured simultaneously during prey capture in two species of sunfishes.

2. The gill apparatus of sunfishes functions as a dynamic resistance within the mouth cavity that regulates water flow during feeding.

3. Gill apparatus motion and activity of the levator operculi and epaxial muscles were the best statistical predictors of buccal pressure variables.

INTRODUCTION

The physiological mechanisms underlying the process of energy acquisition in vertebrates have been the subject of increasing study over the last 10 years (Gans and Gorniak, 1982; Gorniak *et al.*, 1982; Herring, 1976, 1980; Lauder and Shaffer, 1985; Liem, 1980). Comparative experimental studies of energy acquisition in aquatic vertebrates have focused attention on the mechanisms by which prey are captured and have emphasized the evolutionary conservatism of several key bone movement and muscle activity patterns involved in prey capture throughout lower vertebrates (Bemis and Lauder, 1986; Lauder, 1985). These studies have established that pressure reductions within the mouth cavity cause a primarily unidirectional flow of water through the mouth carrying the prey into reach of the jaws. This pressure reduction, which may reach -650 mm Hg (Lauder, 1980), is caused by several cranial muscles which mediate a precisely timed expansion of the mouth. Aquatic prey capture may be extremely rapid, occurring in as little as 10 msec (Grobecker and Pietsch, 1979).

Recent work on prey capture mechanisms in aquatic salamanders (*Ambystoma*) has also shown that movements of the gill apparatus appear to be critical in regulating water flow through the mouth cavity, and that the mainly unidirectional character of the flow regime during feeding is due primarily to the timing of gill apparatus motion (Lauder and Shaffer, 1985).

However, for ray-finned fishes, which make up over half of all vertebrate species, there are no quantitative analyses of the relationship between muscle electrical activity, mouth cavity pressure changes, and gill apparatus movement. In order to formulate detailed models of aquatic feeding in vertebrates and to expand the comparative basis of our understanding of vertebrate feeding physiology, it is important to obtain quantitative data from ray-finned fishes for comparison with other groups.

The goals of this paper are (1) to present experimental data on the mechanisms of prey acquisition in

one group of ray-finned fishes, the sunfish family Centrarchidae, (2) to examine the ability of muscle activity and gill apparatus movement recordings to predict variation in buccal pressure and (3) to test predictions of previous models of aquatic feeding concerning the role of the gill apparatus.

MATERIALS AND METHODS

Animals

Two species within the North American sunfish family Centrarchidae were chosen for analysis: the bluegill, *Lepomis macrochirus*, and the rockbass, *Ambloplites rupestris*. Simultaneous recordings of electromyograms, gill impedance, and buccal pressure were obtained on five bluegill and two rockbass, ranging in size from 15 to 20 cm. Additional pressure and electromyographic data were available from two other bluegill, from two pumpkinseed sunfish (*Lepomis gibbosus*), and from two bass (*Micropterus salmoides*). Since the recordings of pressure, muscle electromyograms, and gill impedance were performed without damage to the fish, several individuals were used again after a 4- to 14-month rest period to assess the repeatability of the data. All fish were housed individually at 18°C in an 80-l. aquarium.

Separate recording sessions were usually also used for each prey type. Because previous research showed a significant effect of prey type on muscle activity pattern used in feeding (Wainwright and Lauder, 1986), only one of two prey types was used in each experimental session. The two prey types were: 1-cm pieces of earthworm, and live minnows (*Pimephales*) 2-3 cm in length. Each experimental fish was fed one piece of prey at approx. 30-sec intervals until satiated. The experiment was terminated when a prey item was not eaten within 2 min. The number of prey items eaten in one session varied from 12 to 55 and depended on the type of prey (fish or worms) and the motivation of the predator.

Experimental techniques

Electromyograms were recorded from four cranial muscles using standard procedures described previously (Lauder, 1980; Wainwright and Lauder, 1986). Briefly, bipolar stainless steel electrodes were inserted in four cranial muscles while the fish was anesthetized. These electrodes were glued together into a thin cable, sutured to the back of the fish for stability, leading to a connector above the aquarium, and from there to Grass P511J preamplifiers. Electromyograms, as well as all other analog signals, were

recorded on a Bell and Howell 4020A FM tape recorder at a speed 15 times faster than used for playing back the signals. This provided an effective chart frequency response of from 1 to 1000 Hz. Three muscles that function to open the mouth were recorded: the levator operculi (LOP), the epaxial muscles (EP), and the sternohyoideus (SH). Electromyograms were also obtained from the dominant jaw closing muscle, the adductor mandibulae part 2 (AM2). Anatomical descriptions of fish cranial morphology are provided in Lauder (1985) and Liem (1970).

Buccal pressures were recorded using the technique described in Lauder (1983). A plastic cannula (0.86 mm i.d.) was implanted through the skull near the anterior portion of the frontal bones. One end of the cannula was flanged and pulled flush with the roof of the mouth. A Millar PC-350 catheter-tipped pressure transducer was threaded down the cannula until the pressure sensor was within 1 cm of the mouth cavity. The frequency response of the pressure recordings was greater than 1000 Hz.

Gill bar movement occurs inside the head and thus cannot be directly visualized with traditional techniques such as high speed films. In order to measure the motion of the gill supports (ceratobranchial and epibranchial bones), a unipolar electrode was implanted on adjacent ceratobranchials and an impedance converter was used to transduce the distance between these elements. The impedance between the two electrodes on adjacent ceratobranchials is a function of the distance between them. The frequency response of the impedance recording system was 550 Hz, more than adequate for measuring the variables of interest.

Data analysis: variables and statistics

All three types of measurement, electromyograms, pressures and impedance, were obtained simultaneously from each individual. From these analog recordings a total of 17 variables were measured for each feeding. The complete data matrix consisted of 17 variables by 191 observations. (The abbreviations listed below are those used for the variables in the tables.) From the electromyograms, the duration of electrical activity in each cranial muscle was measured: LOP, duration of activity in the levator operculi muscle; EP, duration of activity in the epaxialis; SH, duration of activity in the sternohyoideus; AM2, duration of activity in the adductor mandibulae. The time each muscle started to become active relative to the onset of the reference muscle, the LOP, was also measured. The levator operculi is the major mouth opening muscle and has been used successfully in previous studies as a reference (Lauder, 1980; Wainwright and Lauder, 1986). The abbreviations for these variables are: LOP-EP, LOP-SH and LOP-AM2. In addition, the maximum amplitude of electrical activity was measured in each muscle: LOPA, EPA, SHA, AM2A.

From each pressure trace we measured the time taken to reach maximum negative pressure (TPRES), the magnitude of the maximum negative pressure (MPRES), and the area under the negative portion of the buccal pressure trace (APRES). This variable was measured because the integral of pressure over its duration is the impulse of the pressure (Lauder and Shaffer, 1986; Rouse, 1978) and reflects the change in momentum of the water involved in prey capture. The APRES variable thus provides an indication of the energy put into the water by the feeding mechanism.

Descriptive statistics were calculated for the individuals, and differences between individuals and species were assessed with one- and two-way analyses of variance (Sokal and Rohlf, 1981). The ability of electromyographic and gill impedance variables to predict buccal pressure variables was assessed with multiple regressions. We tested three sets of electromyographic (EMG) variables (durations of activity, relative onsets, and amplitudes) separately to determine which type of EMG data, if any, was best at predicting pressures during feeding. We also tested the ability of gill movement variables alone to predict feeding pressures.

Finally, we constructed a linear model consisting of selected variables from each type in an effort to obtain the best predictors of buccal pressure variables. Buccal pressures were selected as dependent variables because the pressure reduction within the mouth cavity measures the total effect of cranial muscles on the water (Lauder and Shaffer, 1985, 1986).

Considerable caution must be exercised in interpreting the results of multiple regression analyses when many independent variables are available and several linear models are constructed (Berry and Feldman, 1985). Because of the multiplicity of combinations of variables and patterns of intercorrelation between variables, it is possible to obtain significant linear models that may have little biological significance. In this study we have made every effort to minimize these problems by (1) keeping the number of independent variables small relative to the sample size for each regression, (2) replicating regression models in multiple individuals, (3) using variables that have an *a priori* physiological and biomechanical interpretation, (4) only drawing conclusions from results that are robust to individual differences and (5) assessing the biological relevance of significant regression models in light of independent physiological and biomechanical data.

RESULTS

Representative data from a single prey capture event are shown in Fig. 1. Prey capture in sunfishes can be extremely rapid, especially when feeding on minnows, and all four cranial muscles become active within about 5 msec. The sternohyoideus muscle tends to have the shortest activity duration, while the adductor mandibulae continues to be active well after the other three muscles stop. The impedance trace clearly shows that the gill bars are being adducted as the pressure drops, that the adduction starts just after mouth cavity pressure drops below ambient, and that the gill bars are maintained in an adducted position for an extended period of time after pressure returns to ambient.

The timing of six events during prey capture, relative to the onset of electrical activity in the levator operculi muscle, is shown for representative experimental series in *Lepomis* (Fig. 2) and *Ambloplites* (Fig. 3). The sternohyoideus and epaxial muscles are the first to become active, followed less than 10 msec later by the adductor mandibulae. Maximum gill bar adduction is achieved synchronously with (Fig. 2), or slightly before (Fig. 3) maximum negative pressure is reached. Maximal abduction of the gill bars occurs well after all other kinematic and electromyographic events have terminated, with a mean of 73.4 msec (SE = 3.6) in *Lepomis* and 71.1 msec (SE = 3.6) in *Ambloplites*. While timing of gill bar abduction is similar in both species, it is noteworthy that peak negative pressure is reached significantly earlier in *Lepomis* (mean TPRES = 26.7 msec, SE = 1.5) than in *Ambloplites* (mean TPRES = 47.3 msec, SE = 3.9).

Multiple regressions using amplitude, duration, and relative onset EMG variables to predict both TPRES, the time to maximum negative pressure (Table 1), and APRES, the area under the pressure trace (Table 2) showed that none of these three types of EMG variables was significantly better than the others at predicting pressure variables. On average, all types of models accounted for about half of the variance in the two dependent pressure variables. The

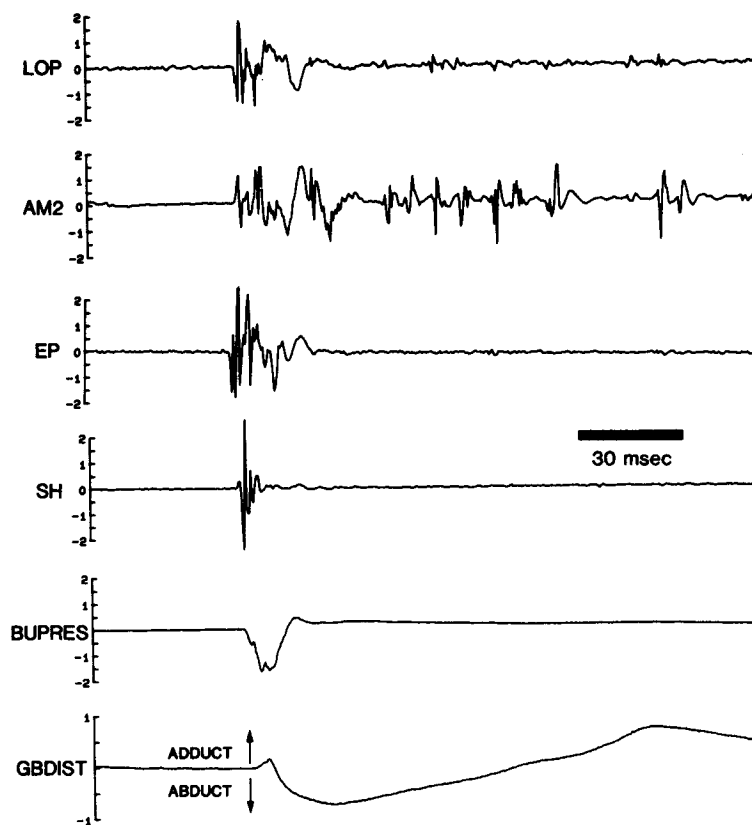


Fig. 1. Representative data obtained from one feeding by a bluegill (*Lepomis macrochirus*) on a minnow. Note the synchrony in onset of the four electromyograms, the pressure drop 10 msec later, and the adduction of the gill bars as the pressure drops. Scale on left indicates voltage in $\mu\text{V} \times 10^2$. Abbreviations: AM2, part 2 of the adductor mandibulae muscle; BUPRES, pressure in the buccal cavity; EP, epaxial muscles; GBDIST, distance between two adjacent gill bars (ceratobranchials 2 and 3); LOP, levator operculi muscle; SH, sternohyoideus muscle. Scale for BUPRES is $\times 200$ mm Hg.

gill bar variables accounted for 81% of the variance in TPRES on average, but did no better than the EMG variables in predicting the area under the pressure curve. The time to peak gill bar abduction (TADD) emerged as a significant variable in predict-

ing the time to maximum negative pressure in all three individuals (Table 1).

In *Ambloplites*, the only genus for which complete data on relative muscle timing was available, the difference in the onset of contraction in the levator

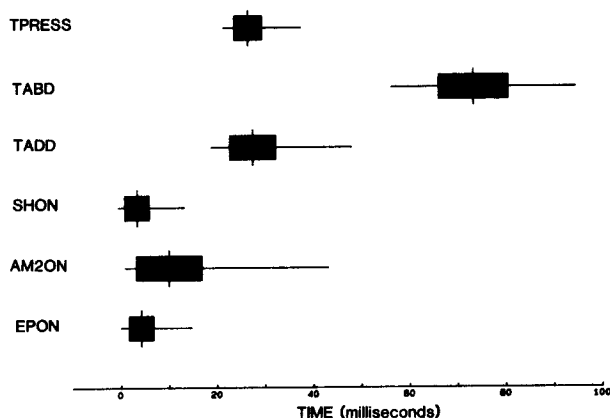


Fig. 2. Relative timing of events during feeding by *Lepomis macrochirus* on fish ($N = 11$). The time of maximum gill bar adduction (TADD) is not significantly different from the time of maximum negative pressure (TPRES). The vertical line indicates the mean for each variable, the width of the black bar, two standard errors on either side of the mean, and the thin horizontal line, the range. Other abbreviations: TABD, time of maximal gill bar abduction; SHON, time of onset of electromyographic activity in the sternohyoideus muscle relative to the start of activity in the levator operculi; AM2ON, onset of activity in the adductor mandibulae; EPON, onset of activity in the epaxial muscles.

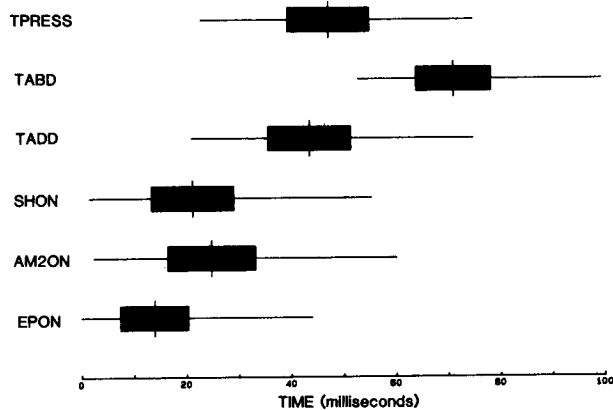


Fig. 3. Relative timing of events during feeding by *Ambloplites rupestris* on fish ($N = 18$). Maximal gill bar adduction, TADD, occurs significantly earlier than maximum negative pressure (P , two-tailed, $=0.01$). Abbreviations as in Fig. 2.

operculi and adductor mandibulae (LOP-AM2) muscles was consistently a significant variable in all four linear models. Sternohyoideus amplitude (SHA) emerged as significant in three of the four individuals tested (Table 2). Similarly, the duration of electrical activity in the levator operculi muscle (LOP) had a significant coefficient in three of the four models used to predict TPRES (Table 1).

When the complete data set, with subsets of variables selected from all classes of models, was used to predict the two dependent pressure variables (Table 3), considerably more of the variation in pressure was accounted for. Using a maximum of five variables, these models had an average R^2 of 75.3. Gill bar movement variables contributed significantly to the two models with the highest R^2 values, but not at all

to the models for *Ambloplites* number 2. For feedings by *Lepomis* (Table 3), the epaxial muscles stand out as being a particularly consistent contributor to predicting both time to negative pressure and pressure area.

DISCUSSION

These results provide convincing evidence that the gill apparatus of ray-finned fishes, long supposed to have a role in regulating water flow during respiration (Holeton and Jones, 1975; Hughes and Morgan, 1973; Lauder, 1984), plays an important role in regulating the nature of fluid flow through the mouth during feeding. Such a role during feeding was proposed previously on both biomechanical evidence

Table 1. Multiple regression analyses with time to peak negative buccal pressure (TPRES) as the dependent variable

Fish	Model type							
	EMG durations R^2	Significant variables	EMG relative onsets R^2	Significant variables	EMG amplitudes R^2	Significant variables	Gill bar movements R^2	Significant variables
Ambloplites 1	0.47	LOP	0.76	LOP-SH, LOP-AM2, LOP-EP	0.43	EPA, LOPA	0.97	TADD
Ambloplites 2	0.33	LOP, AM2	0.36	LOP-AM2, LOP-EP	0.17	AM2	—	—
Lepomis 1	0.81	LOP	—	—	0.79	AM2A	0.81	TADD, MADD
Lepomis 2	0.49	none	—	—	0.78	EPA, SHA, AM2A	0.65	TADD
Mean R^2	0.53		0.56		0.54		0.81	

R^2 is the proportion of variation in the dependent variable explained by the regression model.

— indicates missing data.

Table 2. Multiple regression analyses with the area under the negative portion of the buccal pressure curve (APRES) as the dependent variable

Fish	Model type							
	EMG durations R^2	Significant variables	EMG relative onsets R^2	Significant variables	EMG amplitudes R^2	Significant variables	Gill bar movements R^2	Significant variables
Ambloplites 1	0.51	SH, AM2, LOP	0.56	LOP-SH, LOP-AM2	0.70	LOPA	0.53	MADD, MABD
Ambloplites 2	0.33	none	0.55	LOP-AM2	0.62	AM2A, SHA	—	—
Lepomis 1	0.38	AM2, EP, SH	—	—	0.39	AM2A, SHA	0.28	TABD
Lepomis 2	0.29	none	—	—	0.64	EPA, SHA	0.76	MABD, MADD, TADD
Mean R^2	0.38		0.55		0.58		0.52	

— indicates missing data.

Table 3. Summary models using independent variables selected from all classes of models to predict two dependent variables, time to maximum negative buccal pressure and the area under the pressure curve

Fish (degrees of freedom)	Dependent variable		
	Time to neg. buccal pressure R^2	Significant variables	Pressure area Significant variables
Ambloplites 2 (54)	0.70	LOP-AM2, LOP, AM2	0.70 AM2A, LOP-AM2
Lepomis 4 (33)	0.85	TADD, MADD, EPA	0.63 SHA, EP, TABD, AM2A
Lepomis 5 (16)	0.79	EPA	0.85 MABD, EPA, MADD

and simultaneous pressure measurements on both sides of the gill bars (Lauder, 1983), but direct, *in vivo*, measurements of the pattern of gill apparatus movement in relation to other important physiological events during feeding in fishes have not been obtained previously. As Figs. 1, 2 and 3 indicate, maximum adduction of the gill bars occurs synchronously with, or slightly before maximum negative pressure is reached in the mouth cavity. Also, the pressure decrease precedes the beginning of gill bar adduction by 5–15 msec.

These data are consistent with proposed models of feeding based only on high-speed films and pressure recordings (Lauder, 1983; Liem, 1978). This previous research, in conjunction with the results presented here, permits clarification of the events occurring during prey capture and delineation of the following sequence of events. As the prey is approached by the fish, mouth expansion causes a pressure reduction within the buccal cavity relative to the surrounding water that results in a water influx into the mouth. As the mouth begins to open as a result of cranial muscle activity, the gill bars at the back of the buccal cavity begin to move together (adduct). There is a delay between the time pressure starts to drop and the time the gill bars adduct, so that there is probably a small reverse flow (posterior to anterior) of water into the mouth from the opercular cavity. When maximum negative pressure in the mouth is reached, the gill bars are maximally adducted, completely closing off the opercular cavities on each side of the head from the buccal cavity. During this time, water is flowing into the mouth and passing posteriorly to the back of the buccal cavity. Then, as pressure begins to return to ambient, the gill bars abduct, the opercular cavity expands, and water drawn into the mouth cavity continues to move posteriorly between the gill bars to exit out of the opercular openings at the back of the head. The gill bars remain abducted for up to 120 msec after the mouth has opened (Fig. 1).

These data are strikingly similar to results obtained on aquatic feeding dynamics in ambystomatid salamanders (Lauder and Shaffer, 1985; Fig. 12). In *Ambystoma mexicanum*, for example, maximal gill bar adduction occurs synchronously with maximum negative buccal pressure, and gill bar abduction reaches a maximum 90 msec after the mouth starts to open. The morphology of the gill supports in *Ambystoma* is also very similar to the sunfishes studied here, with interdigitating gill rakers providing a high resistance to flow when the branchial apparatus is adducted.

These results indicate that the process of aquatic

prey capture using pressure reductions in the mouth cavity to create a flow of water, appears to be quite similar in the aquatic salamanders and ray-finned fishes studied to date. In both groups, movement of the gill apparatus permits a unidirectional flow through the mouth cavity by preventing water influx posteriorly as the mouth opens. This increases the velocity of water entering the mouth and presumably, also the probability of capturing prey. The branchial apparatus thus functions as a dynamic resistance within the mouth cavity.

Despite considerable variability from individual to individual in the coefficients of the multiple regression models, several general patterns do emerge. First, it is clear that measurements of gill bar movement have considerable value in predicting both the time to peak negative pressure and the area under the pressure curve (Tables 1, 2 and 3). In one recording session, the time to peak adduction of the gill bars alone accounted for over 90% of the variance in time to peak negative pressure (Table 1). This lends support to *a priori* biomechanical predictions that the gill apparatus is mechanically capable of forming a dynamic resistance at the posterior end of the buccal cavity.

Secondly, the levator operculi muscle appears as a significant variable in most of the models. This indicates the potential importance of the speed and extent of mouth opening itself (as distinct from other movements that increase the volume of the mouth, such as depression of the hyoid) as a factor that must be considered in any attempt to understand the multiplicity of causal mechanisms underlying feeding performance.

Finally, one surprising result was the lack of significant coefficients associated with the sternohyoideus muscle in many of the models. In salamanders, the sternohyoideus muscle controls the major mechanical system that produces pressure change in the mouth cavity—the hyoid apparatus. In ray-finned fishes, there are several mechanical linkages that contribute to expansion of the mouth cavity, and the hyoid is only one system (Liem, 1970). However, because the hyoid has been demonstrated to contribute significantly to volume changes within the mouth cavity, we expected that some variables associated with this muscle would prove to correlate highly with pressure variables. There are three possible explanations for this result.

(1) The EMG from the sternohyoideus could be an inaccurate reflection of the function of the hyoid system in its entirety.

(2) The variables chosen for measurement from

the sternohyoideus EMG do not accurately characterize those aspects of muscle activity relevant to hyoid function. Perhaps the integrated electrical activity of the sternohyoideus would be a better predictor of pressure patterns.

(3) The hyoid apparatus in these species actually does not contribute to pressure changes in the mouth cavity.

We feel that previous experimental studies (Lauder, 1980; Liem, 1970, 1978) rule out the third explanation, and that one or both of the other explanations apply.

Although there are other muscles that are potentially capable of influencing buccal pressure, and despite the relative simplicity of the variables measured from the experimental data, overall predictability of pressure patterns from the variables measured is quite high (Table 3). An average of 75% of the variance in pressure is accounted for by five or fewer independent variables.

The feeding mechanism of most ray-finned fishes is a complex functional system with over 60 muscles and more than 40 independently movable body elements (Lauder, 1985). Many experimental and descriptive avenues are needed to tease apart the complicated functional relationships between mechanical components of the skull and to provide causal explanations, physiological mechanisms, and useful models of feeding function. The approach taken in this paper extends previous experimental and descriptive approaches by using a data set that contains a number of simultaneous measurements of relevant physiological parameters, and by using a simple statistical approach to examine the relationship between variables in the data set. In a complex morphological system such as the feeding mechanism, there are a large number of potential morphological and functional bases of even a simple dependent variable such as time to maximum negative pressure. The number of possible experimental manipulations that could be performed (such as surgically eliminating one morphological system by cutting ligaments, etc.) is huge. The approach taken here promises to facilitate discovery of the important functional factors that underlie prey capture dynamics, and to contribute to clarifying the interrelationships between the many morphological systems that contribute to the feeding mechanism.

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REFERENCES

- Bemis W. and Lauder G. L. (1986) Morphology and function of the feeding apparatus of the lungfish, *Lepidosiren paradoxa* (Dipnoi). *J. Morph.* **187**, 81–108.
- Berry W. D. and Feldman S. (1985) *Multiple Regression in Practice*. Sage Publications, Beverly Hills.
- Gans C. and Gorniak G. C. (1982) Functional morphology of lingual protrusion in marine toads (*Bufo marinus*). *Am. J. Anat.* **163**, 195–222.
- Gorniak G. C., Rosenberg H. I. and Gans C. (1982) Mastication in the Tuatara, *Sphenodon punctatus* (Reptilia: Rhynchocephalia): structure and activity of the motor system. *J. Morph.* **171**, 321–353.
- Grobecker D. B. and Pietsch T. W. (1979) High-speed cinematographic evidence for ultrafast feeding in antennariid anglerfish. *Science* **205**, 1161–1162.
- Herring S. W. (1976) The dynamics of mastication in pigs. *Archs Oral Biol.* **21**, 473–480.
- Herring S. W. (1980) Functional design of cranial muscles: comparative and physiological studies in pigs. *Am. Zoologist* **20**, 283–293.
- Holeton G. F. and Jones D. R. (1975) Water flow dynamics in the respiratory tract of the carp (*Cyprinus carpio* L.). *J. exp. Biol.* **46**, 317–327.
- Hughes G. M. and Morgan M. (1973) The structure of fish gills in relation to their respiratory function. *Biol. Rev.* **48**, 419–475.
- Lauder G. V. (1980) The suction feeding mechanism in sunfishes (*Lepomis*): an experimental analysis. *J. exp. Biol.* **88**, 49–72.
- Lauder G. V. (1983) Prey capture hydrodynamics in fishes: experimental tests of two models. *J. exp. Biol.* **104**, 1–13.
- Lauder G. V. (1984) Pressure and water flow patterns in the respiratory tract of the bass (*Micropterus salmoides*). *J. exp. Biol.* **113**, 151–164.
- Lauder G. V. (1985) Aquatic feeding in lower vertebrates. In *Functional Vertebrate Morphology* (Edited by Hildebrand M., Bramble D. M., Liem K. F. and Wake D. B.), pp. 210–229. Harvard University Press, Cambridge.
- Lauder G. V. and Shaffer H. B. (1985) Functional morphology of the feeding mechanism in aquatic ambystomatid salamanders. *J. Morph.* **185**, 297–326.
- Lauder G. V. and Shaffer H. B. (1986) Functional design of the feeding mechanism in lower vertebrates: unidirectional and bidirectional flow systems in the tiger salamander (*Ambystoma tigrinum*). *Zool. J. Linn. Soc. Lond.* (in press).
- Liem K. F. (1970) Comparative functional anatomy of the Nandidae (Pisces, Teleostei). *Fieldiana, Zool.* **65**, 1–166.
- Liem K. F. (1978) Modulatory multiplicity in the functional repertoire of the feeding mechanism in cichlid fishes. I. Piscivores. *J. Morph.* **158**, 323–360.
- Liem K. F. (1980) Acquisition of energy by teleosts: adaptive mechanisms and evolutionary patterns. In *Environmental Physiology of Fishes* (edited by Ali M. A.), pp. 57–91. Plenum Press, New York.
- Rouse H. (1978) *Elementary Mechanics of Fluids*. Dover, New York.
- Sokal R. and Rohlf F. J. (1981) *Biometry*. W. H. Freeman, San Francisco.
- Wainwright P. C. and Lauder G. V. (1986) Feeding biology of sunfishes: patterns of variation in prey capture. *Zool. J. Linn. Soc. Lond.* (in press).