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## THE SUCTION FEEDING MECHANISM IN SUNFISHES (*LEPOMIS*): AN EXPERIMENTAL ANALYSIS

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### SUMMARY

The process of prey capture by inertial suction was studied in three species of sunfishes (*Lepomis auritus*, *L. macrochirus*, and *L. gibbosus*) by the simultaneous recording of buccal and opercular cavity pressures in order to test current hydrodynamic models of feeding in fishes. Synchronous high-speed films permitted the correlation of kinematic patterns of jaw bone movement with specific pressure waveforms. Opercular cavity pressures averaged one-fifth buccal pressures and pressure magnitude was correlated with prey type. Peak buccal and opercular pressures were  $-650$  cm  $H_2O$  and  $-150$  cm  $H_2O$  respectively; peak rate of pressure change was  $-100$  cm  $H_2O$ /ms. Buccal pressure magnitude varied inversely with degree of predator satiation.

Opercular pressure waveforms have an initial positive phase followed by a prolonged negative phase and then a final positive phase. The initial positive pressure may be absent during slow strikes at worms. Buccal pressure waveforms show considerable variability. The modal waveform consists of a sharp negative pressure pulse followed by a positive phase and finally by another pressure reduction. Delayed opercular abduction relative to mouth cavity compression correlates with the presence of a positive buccal phase. The second buccal negative pressure is the result of rapid mouth closing causing a pressure reduction (water hammer effect) as water flow continues posteriorly. These data indicate that (1) the buccal and opercular cavities are functionally separated by a gill curtain of high resistance, (2) that inertial effects of water are important in the description of the suction feeding process, (3) that a reverse flow of water (opercular to buccal cavity) may occur during the early phase of mouth opening prior to establishment of a buccal to opercular flow regime, and (4) current models of respiratory pressure and flow pattern cannot be applied to feeding. Current hydrodynamic models of suction feeding in fishes are re-evaluated in the light of this analysis.

### INTRODUCTION

Fishes capture their prey by using a wide variety of attack strategies. For example, prey may be grabbed between the jaws by a rapid lateral movement of the head as in many long-jawed fishes such as *Belone*, *Belonesox* (Karrer, 1967), or *Lepisosteus* (Lauder, 1980a; Lauder & Norton, 1980). This method of prey capture limits the distance from which the predator can strike to the range of lateral head excursion plus

the short distance covered by the predator during the final prestrike acceleration phase. Alternatively, planktivorous fishes (e.g. *Brevoortia*) may swim through the water filtering out particles with elongate gill rakers, while other fishes such as tuna (Walters, 1966) may capture prey primarily with forward body velocity. Planktivorous fishes may also use a different feeding method, remaining relatively stationary and rapidly expanding the mouth cavity to suck in small food items such as copepods (Werner & Hall, 1974). This method of feeding, *inertial suction*, allows a variable strike distance which may be determined by the relative mass of the predator and prey, the rapidity of predator mouth cavity expansion, and the volume change of the expanding mouth cavity. Feeding by inertial suction, i.e. the rapid expansion of the mouth cavity to create a flow of water into the mouth from in front of the head, is the dominant mode of prey capture by teleost fishes. The use of suction is often combined with forward body motion to varying degrees during prey capture. Osse & Muller (1980) have noted that the creation of a negative mouth cavity pressure is a necessary component of aquatic feeding because of the influence of a predator's movement on the position of the prey in a high density medium such as water.

For the most part, investigators over the last decade have used indirect techniques to analyse the functional anatomy and mechanics of suction feeding. The kinematic profile of fish jaw bone movements has been studied (Alexander, 1966, 1967; Anker, 1974; Dutta, 1968; Lauder, 1979; Liem, 1967; 1970; Nyberg, 1971; van Hasselt, 1978), and electromyographic techniques have allowed the analysis of cranial muscle activity during feeding (Ballintijn, van den Berg & Egberink, 1972; Elshoud-Oldenhave, 1979; Elshoud-Oldenhave & Osse, 1976; Lauder & Liem, 1980; Liem, 1973, 1978; Osse, 1969).

Of more direct interest to the analysis of suction feeding is the precise measurement of pressure changes in the mouth cavity during prey capture. Alexander (1969, 1970) made the first measurements of pressure change in the mouth cavity during feeding. His technique allowed the determination of the peak negative pressure in the buccal cavity but not the pressure waveform. Osse (1976) reported buccal and opercular cavity pressure magnitudes and Osse & Muller (1980) have presented pressure traces for *Amia calva*. Osse's technique (see Ballintijn, 1969) for the first time enabled the comparison of buccal and opercular cavity pressure waveforms during feeding. Liem (1978) discussed buccal cavity pressures during feeding in piscivorous cichlid fishes and Casinos (1973), using the technique of Alexander (1969), reported peak negative pressures in cod (*Gadus*). Lauder (1980b) has recently reviewed previous approaches to the hydrodynamics of feeding in fishes.

Previous work on suction feeding has involved only a limited number of pressure recordings and no attempt has been made to examine pressure waveform and magnitude variability or to test experimentally the present hydrodynamic hypotheses of suction feeding.

The goal of this paper is to characterize comprehensively mouth cavity pressure changes in a wide variety of feeding situations in order to (1) test current hypotheses of the hydrodynamics of prey capture in fishes, (2) examine the relationship of buccal and opercular cavity pressure magnitude to prey type, kinematic profile of jaw movement, and predator motivation, and (3) propose a new model of suction feeding in fishes based on these experimental data.

MATERIALS AND METHODS

*Fish*

Pressure recordings were made from three species of sunfishes (Family Centrarchidae): *Lepomis macrochirus* Rafinesque, the bluegill; *L. gibbosus* (Linnaeus), the pumpkinseed; and *L. auritus* (Linnaeus), the redbreast sunfish. Experimental subjects ranged from 12 to 23 cm total length and representative specimens have been deposited in the systematic collection of the Museum of Comparative Zoology, Department of Fishes. Most fishes were obtained by seining in local streams and ponds; larger individuals were caught in the Quabbin Reservoir in central Massachusetts. Fish were acclimated to laboratory water and temperature for over a month before experiments were conducted.

No interspecific differences in pressure patterns were noted and thus data for all individuals are discussed together (e.g. Fig. 3). All individuals were fed a mixed diet of earthworms (*Lumbricus*) and goldfish (*Carassius auratus*). During pressure cannula implantation, fishes were anaesthetized with tricaine methanesulfonate (TMS). Fish were removed from their tank, placed in a small plastic tray, and TMS was dissolved in the water to a concentration of 0.3 g/l. This solution was buffered with 0.2 g NaOH/g TMS to maintain neutral water pH. If the anaesthetic solution is not buffered, the water pH may be reduced to 3.0 when TMS is added. Buffering thus prevents rapid pH changes and greatly enhances recovery of the subject (also see Elshoud-Oldenhave, 1979). The cranial anatomy of the bluegill sunfish has been described previously (Lauder & Lanyon, 1980).

*Cinematography*

High-speed films (200 frames/s) were obtained with a Photosonics 16 mm IPL camera as described previously (Lauder & Norton, 1980; Lauder, 1980a). Fishes were trained to feed over a mirror inclined at a 45° angle to the film plane and thus lateral and ventral views were filmed simultaneously (see Fig. 4). Prey were not restrained or tethered in any way.

Control films were taken prior to pressure cannula implantation and no differences were observed between the excursions or type of jaw movements. Elshoud-Oldenhave (1979) observed a two-fold reduction in the speed of jaw movements following electrode or pressure cannula implantation but no such effect was found in sunfishes.

Pressures were recorded from 12 individuals and more than 350 feeding events were studied.

*Pressure recordings*

The technique used here for recording rapidly changing pressures has been briefly described previously (Lauder & Lanyon, 1980), but a detailed description of the apparatus, calibration technique, and potential pitfalls of this approach will be presented below as the nature of the recording apparatus has an important effect on the type of data obtained. Thus, pressures obtained using other, or undefined techniques, may not be comparable to data presented here.

Pressure transducer cannulae ('Intramedic' polyethylene tubing, 0.86 mm i.d. and 1.52 mm o.d.), were implanted in the buccal and opercular cavities by drilling through

the ethmoid region of the skull and cleithrum respectively. Semi-sterile technique was observed to reduce the chance of infection. Cannula size was chosen to be flexible enough to permit rapid and unrestricted pursuit of prey but with sufficiently thick walls to reduce compliance. Cannulae were each attached to a small plastic clamp anchored by a loop of stainless steel wire through the epaxial muscles (see Fig. 4), and were allowed to trail freely behind the fish. Cannula patency was generally maintained for up to two weeks. During recording sessions, these cannulae were attached to Statham P23 Gb (in later experiments) or P23 Db (in earlier experiments) pressure transducers. The transducer and cannula system was flushed with a mixture of 55% glycerine and 45% distilled water, both boiled to remove air bubbles. Great care was taken to remove air bubbles from the transducer and cannula during filling as even small bubbles greatly reduce the frequency response. Transducer output was recorded on FM tape at 37.5 cm/s and played back at 4.7 cm/s through a Gould 260 pen recorder for analysis.

Careful static *and* dynamic calibration of the transducer-cannula system is essential for the recording of rapidly changing pressures. Three factors must be considered (Geddes & Baker, 1975): (1) linearity of amplitude, (2) adequate bandwidth of sine wave frequency response, and (3) linearity of phase shift. Amplitude linearity was monitored by calibration against a range of known pressures. Dynamic calibration was conducted following the procedure of Gabe (1972) and consisted of measuring the transducer response to a step decrease in pressure.

Strain gauge diaphragm transducers such as those used here have frequency response characteristics that tend to distort the recorded pressure waveform. When a step change in pressure is applied to an undamped transducer (Fig. 1 A), considerable overshoot occurs and the transducer oscillates about the new pressure before finally stabilizing. Increased damping of the resonant element will tend to reduce the overshoot but only at the cost of increasing the rise time. The transducer-cannula system is *critically damped* when, following a step pressure change, the new pressure is reached as rapidly as possible without overshoot. What degree of damping provides the best compromise between overshoot and rise time? Geddes & Baker (1975) note 'In practice, to obtain a good compromise... the damping of dynamic systems is usually adjusted to 0.65.' With the damping factor  $\beta = 0.65$  (see Gabe (1972) for an excellent review of pressure measurements and methods for calculating damping coefficients) the overshoot for a step pressure change is 7%, maximum phase error is 4%, bandwidth is from 0% to 108% of  $f_0$  ( $f_0$  is the undamped resonant frequency), and the rise time is  $1/2.1 \times f_0$ . Gabe (1972, p. 22) also noted that a damping factor of 0.65 is desirable and that at this value the phase lag is roughly linear from 0 to 70% of the natural frequency.

The results of a series of dynamic calibration experiments performed with the Statham pressure transducers used in this study are shown in Fig. 1. All pressure records reported here were made with the transducer-cannula system damped to  $\beta = 0.65$  and the response of this system to a step pressure change is shown in Fig. 1 D. Rise time (time from 10 to 90% response) for a step change ranging from 50 to 600 cm H<sub>2</sub>O was 5 ms or less. Transducer oscillations had the form of a damped sinusoid and were regarded as the product of a single degree of freedom system. Dynamic calibrations were performed prior to all recording sessions.

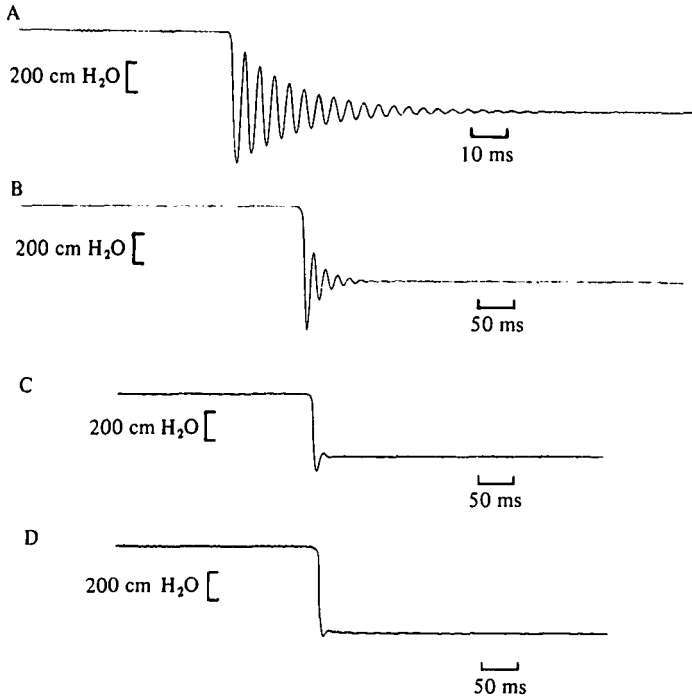


Fig. 1. Dynamic calibrations of Statham P23 Db and P23 Gb pressure transducers responding to a step change in pressure produced following the procedure of Gabe (1972) (see text). A: Statham P23 Db pressure transducer calibrated with a 2 cm long metal needle attached to the transducer dome and distilled water. Frequency of oscillation is 250 Hz; damping factor  $\beta = 0.054$ . B: same experimental arrangement as in A except that a 50 cm long polyethylene cannula is attached to the transducer (see text);  $\beta = 0.136$ . C: P23 Gb transducer. The transducer-cannula system is filled with a boiled mixture of 50% glycerine and 50% distilled water;  $\beta = 0.434$ . D: same as in C except that the solution is 55% glycerine and 45% water;  $\beta = 0.65$ . The system giving calibration D was used for all experiments in this paper. Note differences in time and pressure scales between calibrations.

Despite these precautions, a number of possible sources of error enter into pressure measurement with diaphragm transducers. (1) Rapid movements of the fish head such as head shaking from side to side may result in 'catheter whip' and introduce high-frequency artifacts into the pressure record. This was not a serious problem as these events were identified from the films and eliminated from the analysis. The fluid in the cannula can also act as an accelerometer during pursuit of the prey. At the damping factor used and because accelerations are perpendicular to the cannula axis, this effect was extremely small.

(2) A more serious problem results from the inadequate frequency response of the transducer-cannula system. Ideally, the experimental apparatus should have a flat amplitude response up to the tenth harmonic of the fundamental frequency for faithful reproduction of dynamic pressures. The frequency of feeding in sunfishes varies from about 2 to 20 Hz (expansive phase =  $1/2$  cycle; see Lauder & Lanyon, 1980) depending on prey type and degree of predator satiation, and thus the apparatus used in this study will only provide reasonably accurate pressure waveforms of events up to about 10 Hz in fundamental frequency. For very rapid mouth cavity expansion, the pressure

records must be regarded as giving only an approximation of the true waveform. A series of experiments was attempted with a catheter tip pressure transducer (Millar PC 470) with a kHz frequency response, but sunfishes proved unable to support the weight of the catheter. (3) Finally, the alignment of the cannula tip relative to the direction of flow may influence pressure records. In these experiments, great care was taken to measure hydrostatic pressure, and thus the axis of the cannula was oriented and fixed in a position perpendicular to the flow. If the cannula tip is oriented into the flow, then hydrodynamic pressures are recorded and the pressure magnitudes will be a partial function of flow velocity.

### *Stimulation experiments*

A series of muscle stimulation experiments was performed which involved back-stimulating selected cranial muscles in unanaesthetized free-swimming fishes while film (at 200 frames/s) and buccal and opercular cavity pressures were simultaneously recorded. Muscles were stimulated via fine-wire bipolar electrodes inserted by standard electromyographic techniques (see Lauder & Lanyon, 1980; Lauder, 1980*a*). A grass S 44 square wave muscle stimulator was used and monophasic single pulses at durations of 10 to 50 ms and magnitudes of 10 to 50 V elicited muscle twitches. The geniohyoideus, levator operculi, sternohyoideus, and levator arcus palatini were all stimulated bilaterally. The range of bone movement resulting from muscle stimulation was less than in normal feeding sequences.

## RESULTS

### *Pressure waveform patterns*

Buccal and opercular cavity pressures exhibit a variety of different waveforms. Most commonly (Fig. 2A, B, D: BU) buccal pressure decreases sharply just as the mouth begins to open. Peak negative pressure is reached within 10 to 60 ms after mouth opening begins. Pressure then increases as the mouth begins to close and a brief positive phase occurs followed by a final pressure reduction (Fig. 2A–D: BU). Opercular pressure usually becomes sharply positive just at the initiation of pressure decrease in the buccal cavity (Fig. 2A, B: OP). A negative phase then follows and peak negative opercular pressure is reached 10–25 ms after the negative buccal pressure peak. Pressure then returns to ambient and usually exhibits a final positive phase (Fig. 2A, D).

Variations of these modal pressure waveforms occur frequently. In contrast to the most common buccal pressure sequence of negative–positive–negative phases, recordings may show only the initial negative phase with buccal pressure rapidly returning to ambient (Fig. 2G, I: BU). Buccal pressures may also show a negative–positive pattern (Fig. 2I, J: BU) or a double pattern of negative pressure pulses (Fig. 2B, F: BU). Kinematic correlates of these waveform variations will be discussed below.

Opercular pressures generally show less variation. During slower strikes at relatively stationary prey items such as worms (Fig. 2C, E: OP), the initial positive phase may be reduced or absent. This positive pressure is invariably present during rapid strikes

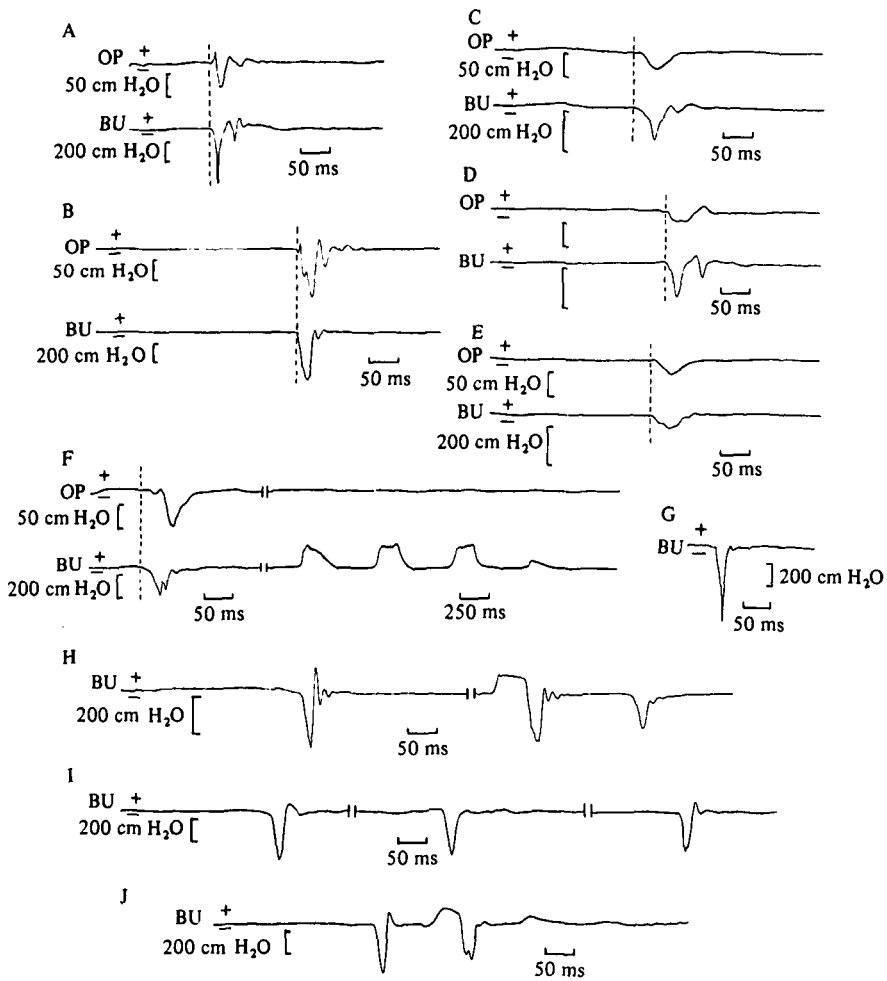


Fig. 2. Buccal and opercular cavity pressures synchronously recorded from sunfishes during feeding. BU: buccal cavity pressures; OP: opercular cavity pressures. A, B: pressure waveforms during feeding on goldfish. C, D, E: different pressure waveforms during feeding on earthworms. F: buccal and opercular cavity pressures during the strike (on left) and chewing (on right) following prey capture. Note differences in time scale. G: extremely rapid buccal pressure reduction during capture of a fish. H, I, J: variability in buccal pressure waveform during each of three recording sessions. Note the occurrence of a preparatory phase in two feeding attempts and variability in the waveform following the initial pressure reduction.

at elusive prey (goldfish). The same range of pressure waveforms is found in all three species of sunfishes. Peak negative opercular cavity pressure always follows or is coincident with the negative buccal peak.

A preparatory phase prior to buccal compression is occasionally present (Fig. 2H, J). The positive pressure lasts from 10 to 75 ms and its magnitude varies from +10 to +150 cm H<sub>2</sub>O. Buccal cavity pressure reduction can occur extremely rapidly (Fig. 2G) with pressures as low as -600 cm H<sub>2</sub>O achieved in 10 to 15 ms; peak rate of buccal pressure change is 100 cm H<sub>2</sub>O/ms.

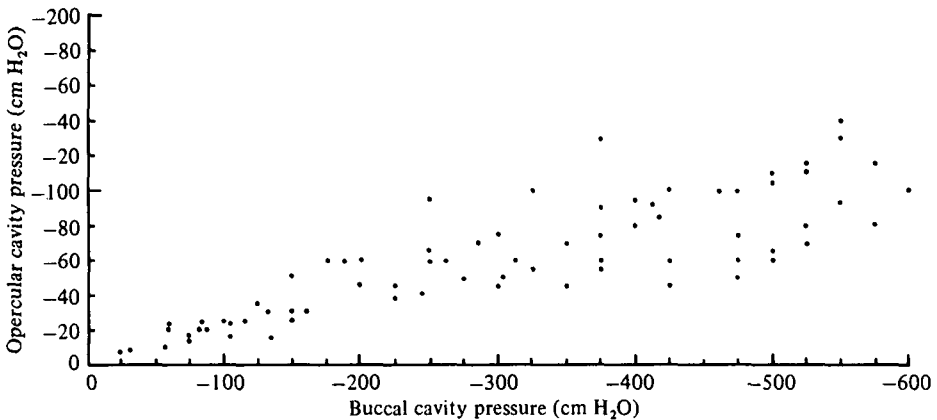


Fig. 3. Relationship between peak buccal and opercular cavity negative pressure during the strike. Each point represents synchronously recorded buccal and opercular cavity pressures. Note that buccal pressures average five times opercular pressure.

Following prey capture a series of positive buccal pressures are often recorded (Fig. 2 F) during chewing and maceration of the prey in the buccal cavity. Duration and magnitude of the pulses is variable but they range from 100 to 400 ms and from +20 to +250 cm H<sub>2</sub>O. No corresponding positive pressures are recorded from the opercular cavity (Fig. 2 F).

Buccal and opercular cavity pressure magnitudes show a consistent relationship in all three species: negative buccal pressures average five times the synchronously recorded corresponding opercular cavity pressures (Fig. 3). The maximum negative buccal pressure is -650 cm H<sub>2</sub>O, while the peak opercular cavity pressure is -150 cm H<sub>2</sub>O.

Simultaneous pressure recordings were also made from the anterior and posterior areas of the buccal cavity. The anterior cannula opening was located just posterior to the premaxilla while the posterior cannula pierced the buccal roof posterior to the adductor arcus palatini and just anterior to pharyngobranchial two. Pressure magnitudes at these two sites were not significantly different, although there was a slight tendency for the posterior site to show greater negative pressures. Waveforms recorded anteriorly and posteriorly were extremely similar and the positive and negative peaks occurred within 5 ms of each other.

#### *Motivational effects on pressure waveform*

The effects of predator motivation on buccal cavity pressure waveform and magnitude were studied by depriving one individual of food for 8 days and then placing small (300 mm<sup>3</sup>) uniformly sized pieces of earthworm in the tank at 30 s intervals. Twenty-five prey items were eaten in total (Fig. 5).

Buccal pressure magnitude declines non-linearly with the number of prey items eaten (Fig. 5) and after 10 prey items reaches a plateau of about -50 cm H<sub>2</sub>O. Rate of pressure decrease declines rapidly (Fig. 5 A, B, C), and the duration of the first negative phase increases with the amount of food eaten. Maximum recorded buccal cavity pressure is -460 cm H<sub>2</sub>O.



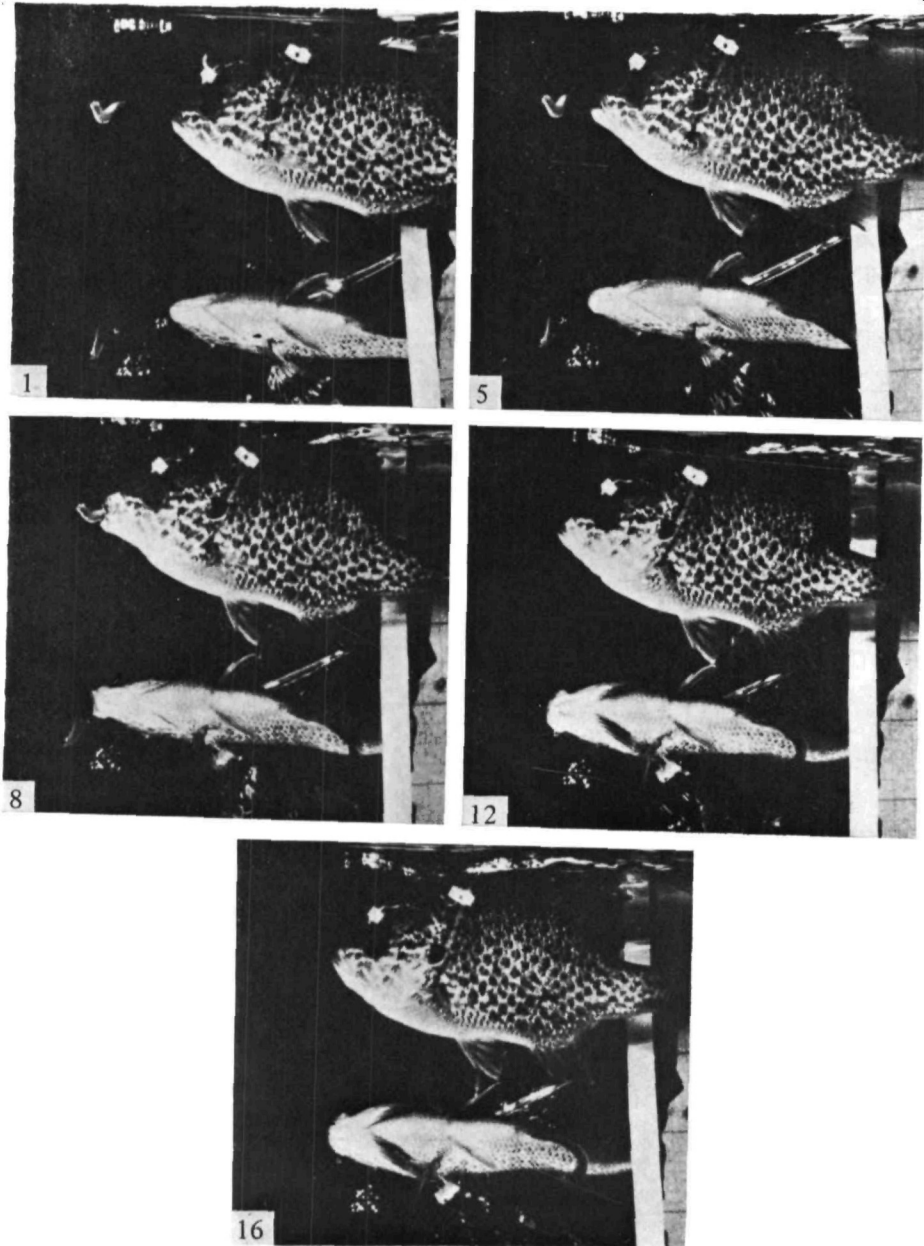


Fig. 4. Representative frames from a high-speed film of prey capture by the pumpkinseed (*Lepomis gibbosus*). Frame numbers correspond to those in Fig. 6. Time between sequential frames is 0.01 s. Note the buccal and opercular cavity pressure cannulae and the early stages of branchiostegal membrane opening in frame 16.



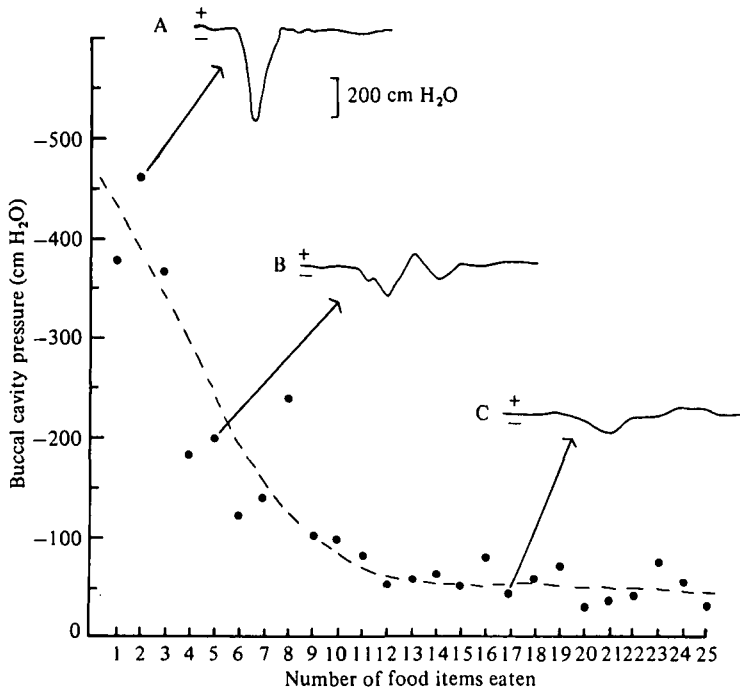


Fig. 5. Effect of motivational state on buccal cavity pressure waveform and magnitude. Food was 300 mm<sup>3</sup> pieces of earthworm introduced individually into the tank at thirty second intervals. A, B, and C show representative waveforms for the points indicated.

#### *Kinematic correlates of pressure waveform*

The most consistent aspect of buccal pressure waveform is the presence of two negative phases. Fig. 4 shows representative frames from a prey capture sequence in *Lepomis gibbosus* and Fig. 6 the kinematic and pressure profiles from the same sequence. The second negative pressure consistently follows closing of the mouth opening (Figs. 6, 7, 8), and the magnitude of the second negative phase correlates with the speed of mouth closure. Absence of a second negative pulse is associated with a delay in mouth closing (Fig. 9). Mouth closure consistently occurs near the peak of the positive buccal pressure pulse in those records having a second negative phase (e.g. Fig. 7). Delayed mouth closure has little effect on the occurrence of a positive phase.

Adduction of the mandible either occurs against protruded premaxillae (Figs. 6, 7) or the lower jaw is adducted against retracted premaxillae (Figs. 8, 9). Delayed premaxillary retraction primarily occurs in slower feeding sequences (on the order of 100 ms for mouth opening and closure, Figs. 4, 6), whereas following rapid mouth cavity expansion the premaxillae and lower jaw return to the rest position nearly simultaneously.

The positive phase of the buccal pressure waveform correlates with delayed opercular abduction relative to mouth cavity compression following peak gape. Opercular abduction commences most often at the negative buccal pressure peak (Figs. 6, 8, 9) but occasionally begins earlier (Fig. 10) or later (Fig. 7). Delayed opercular abduction

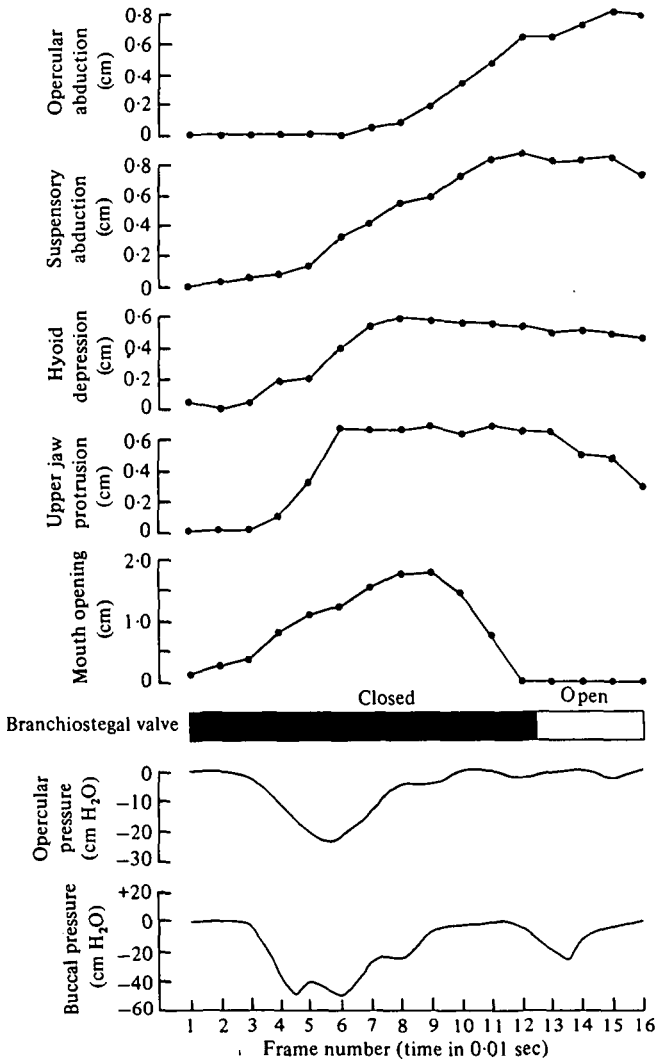


Fig. 6. Kinematic profile and synchronously recorded buccal and opercular cavity pressures during capture of a worm. Note the double negative buccal pressure pattern. The black bar indicates closure of the branchiostegal valve; white bar means the valve is open. The opercular valve opens synchronously with the branchiostegal membrane except as indicated in Figs. 8, 9, and 10 by diagonal hatching.

coupled with the onset of buccal compression near or at the negative buccal pressure peak (Figs. 8, 9) results in the occurrence of a positive pressure phase. Mouth closing and hyoid adduction are the aspects of buccal volume compression that correlate most closely with the positive phase. Suspensorial abduction is usually maintained at near peak levels until after mouth cavity pressures return to ambient values. Absence of a positive phase correlates with either continued buccal cavity expansion after the peak negative pressure (Fig. 6) or with a steady opercular abduction from the onset of mouth opening (Fig. 10).

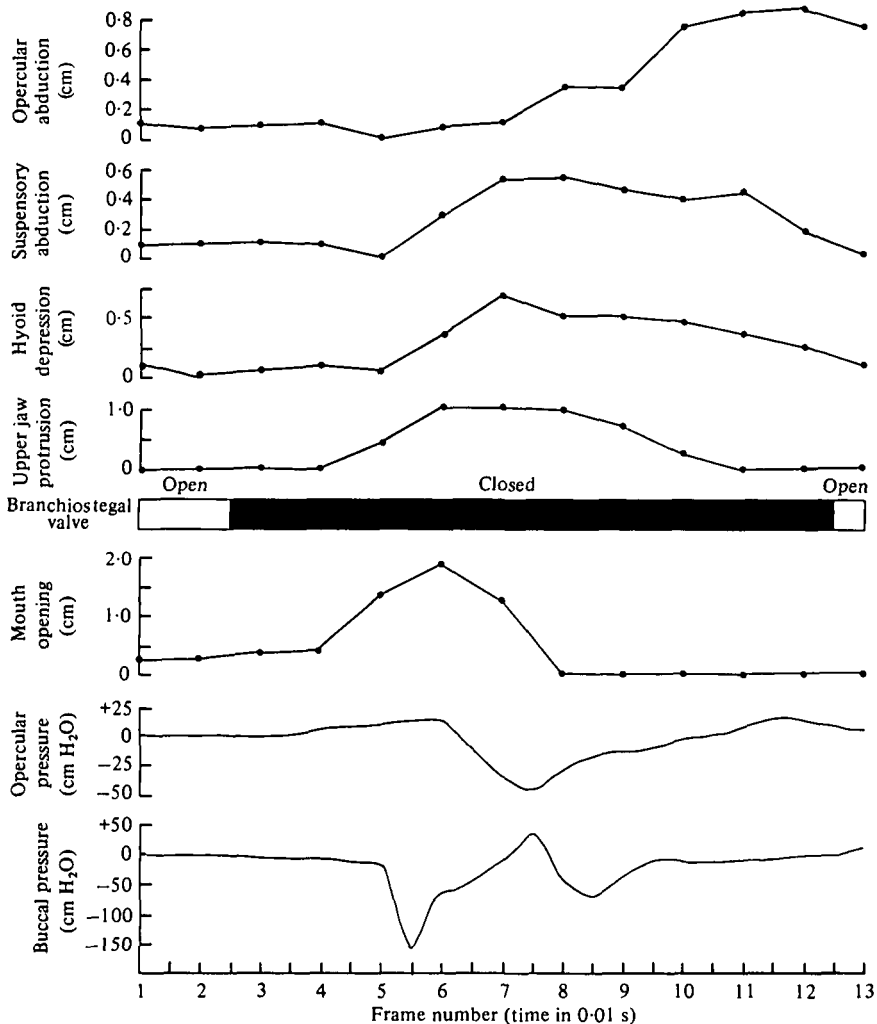


Fig. 7. Kinematic profile of selected jaw movements and synchronously recorded buccal and opercular cavity pressures during the capture of a fish. Note the positive phase in the buccal pressure waveform, the delay in peak negative opercular pressure, and the timing of opercular abduction. Scale of the abscissa for kinematic events is relative in this and subsequent figures.

The initial positive pressure phase in the opercular pressure waveform, one of the most consistent waveform attributes, correlates with opercular adduction at the onset of mouth opening (Figs. 7, 11). Absence of the initial positive phase (Fig. 6) can be attributed to a lack of opercular adduction and suspensorial abduction.

A preparatory positive phase in the buccal cavity is due to hyoid protraction and synchronous mandibular adduction. Both of these kinematic events are difficult to measure in light films but electromyographic recordings indicate activity in the adductor mandibulae and geniohyoideus during the preparatory phase.

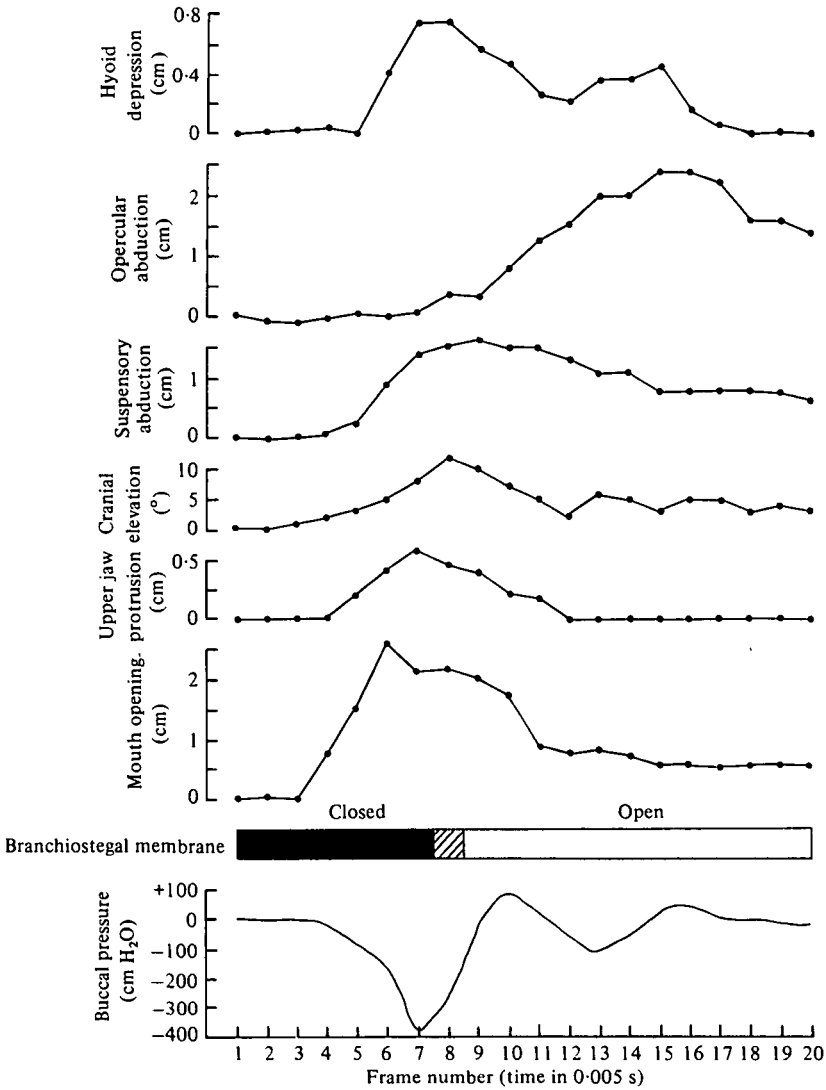


Fig. 8. Kinematic profile of selected jaw movements and synchronously recorded buccal cavity pressure. Diagonal hatching indicates the time when the opercular valve is open but the branchiostegal membrane is still closed (also see Fig. 9).

### Stimulation experiments

Bilateral stimulation of the sternohyoideus muscle evokes buccal and opercular cavity pressure waveforms that closely approximate those recorded during feeding (Fig. 12). Mouth opening (mandibular depression *and* upper jaw protrusion), suspensory abduction, and hyoid depression all result from sternohyoideus stimulation. The buccal pressure waveform shows the characteristic positive phase that correlates with delayed opercular abduction relative to buccal compression. Opercular abduction, probably caused by water flowing out over the gills, is delayed until the buccal position

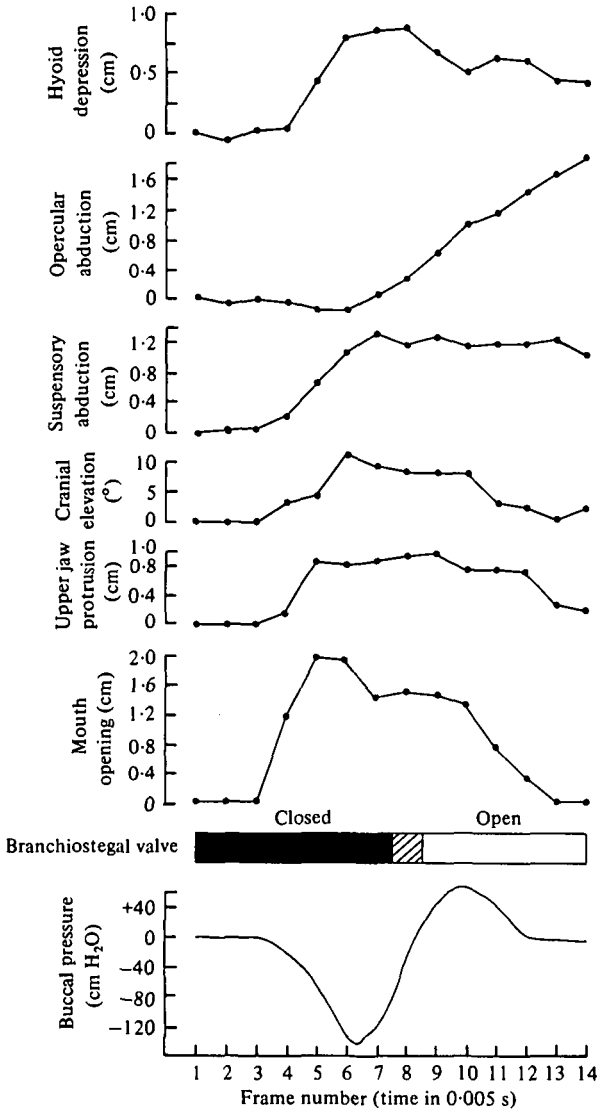


Fig. 9. Kinematic profile of selected jaw movements and synchronously recorded buccal cavity pressure. Compare the buccal waveform and associated kinematic pattern in this figure with Fig. 8.

pressure peak. The peak opercular cavity negative pressure follows the buccal peak by 5 ms and shows the characteristic initial positive phase (Fig. 12).

Bilateral stimulation of the levator arcus palatini (Fig. 13) produces a significant degree of mouth closing, rapid suspensorial and opercular abduction, and slight hyoid depression. Both pressure waveforms show an initial very slight positive phase due to mandibular adduction. Peak negative pressure is reached first in the opercular cavity (Fig. 13) and is maintained for 10 ms or more due to continued suspensorial and opercular expansion. The buccal pressure waveform lacks a second positive and

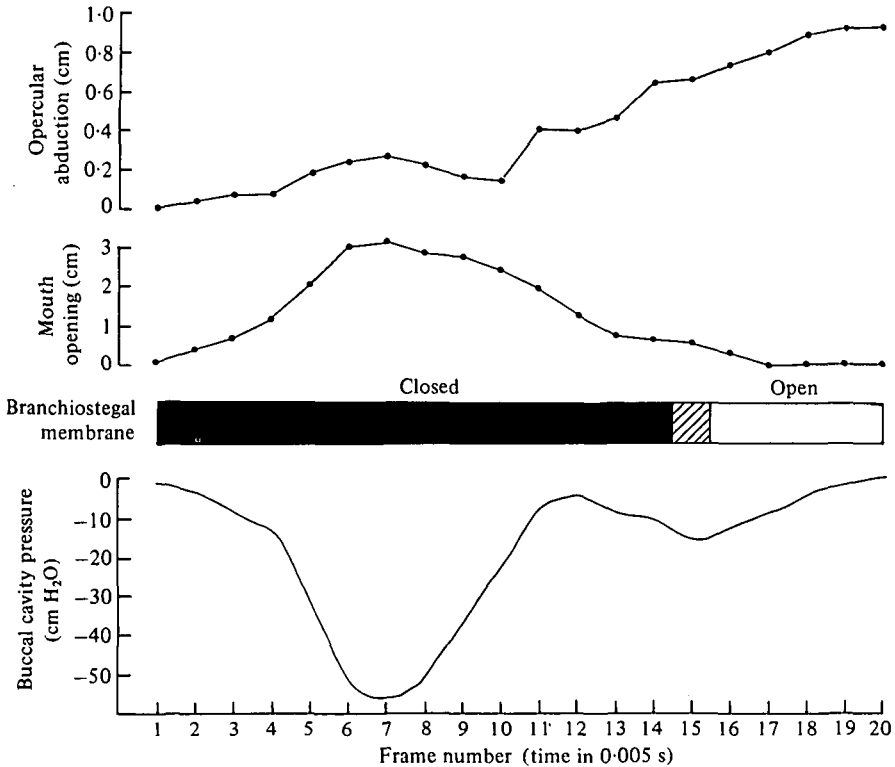


Fig. 10. Kinematic profile of selected jaw movements and synchronously recorded buccal cavity pressure. Compare opercular abduction and pressure waveform with Figs. 8 and 9.

negative phase because of early opercular expansion and the lack of rapid mouth closing during flow through the mouth cavity.

Stimulation of the geniohyoideus muscle alone (Fig. 14) produces a pressure pattern extremely similar to that seen during chewing and maceration of the prey following capture (see Fig. 2 F). A sharp rise in buccal pressure occurs (Fig. 14) with concomitant mouth closing and suspensory adduction. Opercular abduction, the result of water forced out through the gills by the positive buccal pressure, is delayed 10 ms after the buccal positive peak. Only a very slight positive pressure is recorded in the opercular cavity, corresponding closely to the chewing pattern observed *in vivo*.

#### DISCUSSION

##### *Previous models of suction feeding*

Previous models of suction feeding in fishes (Elshoud-Oldenhave & Osse, 1976; Lauder, 1979; Muller & Osse, 1978; Osse, 1969; Osse & Muller, 1980; Pietsch, 1978) have recently been reviewed by Lauder (1980b). Buccal and opercular cavity pressure waveforms and magnitudes have been predicted by these workers on the basis of kinematic analysis of jaw bone movement and the timing of cranial muscle electrical activity as determined by electromyography. Key predictions of current models regarding mouth cavity pressures and their kinematic correlates are (1) a close



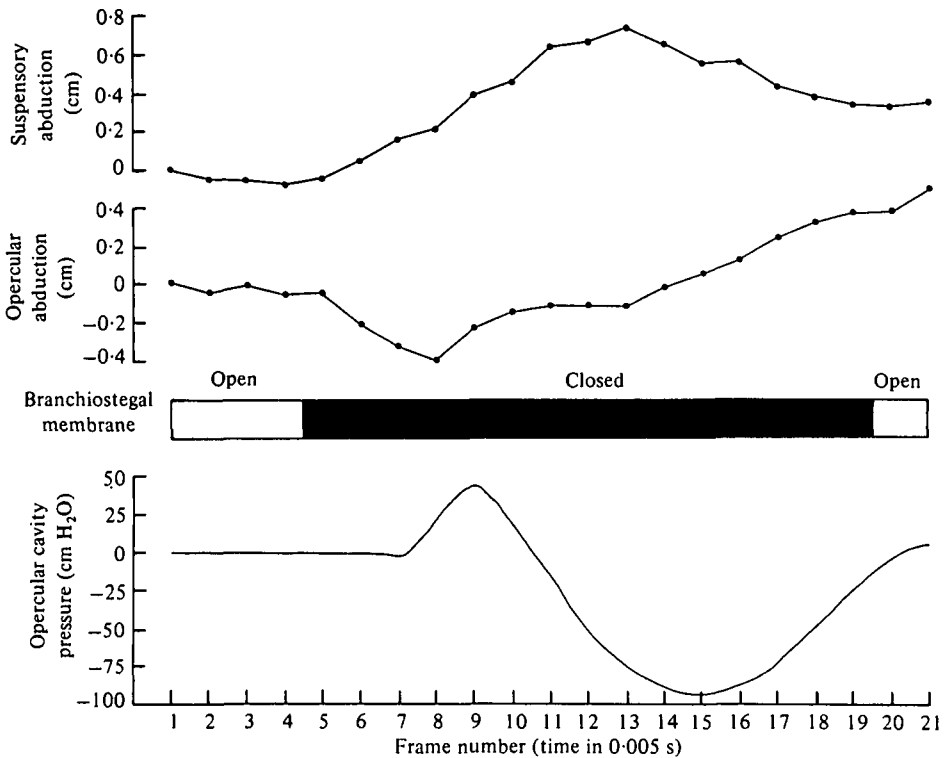


Fig. 11. Kinematic profile of selected jaw movements and synchronously recorded opercular cavity pressure. Note the initial positive pressure and opercular adduction.

similarity between buccal and opercular cavity pressure waveform and magnitude, (2) onset of a pressure decrease in the mouth cavity before the mouth actually opens as a result of buccal expansion with the jaws closed, (3) the important role of the opercular apparatus in generating negative opercular cavity pressures and contributing to the velocity of water flow during feeding (see Osse, 1969, p. 371; O'Brien, 1979, p. 579), and (4) flow through the mouth cavity is assumed to be unidirectional (anterior to posterior). Other aspects of current models of suction feeding include the presence of a preparatory phase (positive pressure) in both the buccal and opercular cavity waveform and a positive phase as the mouth closes. The branchiostegal valve, held against the pectoral girdle during mouth opening, opens as the pressure in the mouth cavity goes positive as a result of mouth closing, and water exits posteriorly between the opercular apparatus and the pectoral girdle.

If the operculum does play a fundamental role in generating negative mouth cavity pressures then a positive correlation would be predicted between the speed of opercular abduction and negative gill cavity pressure.

A number of authors have also hypothesized that movements of the pectoral girdle can contribute to suction feeding (Anker, 1974; Hutchinson, 1973; Osse, 1969; Tchernavin, 1953): pectoral girdle retraction mediated by the hypaxial muscles (*obliquus inferioris*) is assumed to enlarge the mouth cavity and increase the suction pressure.

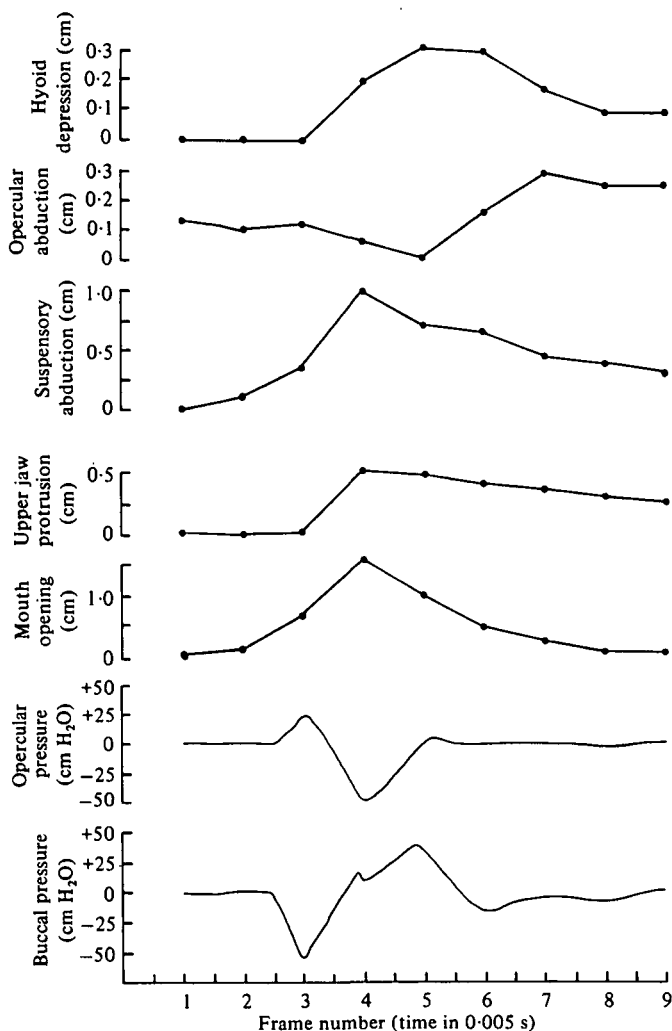


Fig. 12. Buccal and opercular cavity pressure and the pattern of jaw bone movement resulting from a twitch stimulus (40 ms duration) applied bilaterally to the sternohyoideus muscle. Note the close similarity of the pressure waveforms to those obtained during feeding.

### *A new proposal*

The hypothesized attributes of buccal and opercular cavity pressure waveforms outlined above and the proposed kinematic correlates do not agree with the measured pressure waveform patterns and kinematic events in sunfishes. Although there is variability in pressure waveform pattern, the buccal and opercular cavity pressure changes correspond neither in magnitude (Fig. 3) nor in waveform (Fig. 2). Buccal pressures in sunfishes average five times the opercular cavity negative pressures. The modal buccal waveform lacks a preparatory phase and exhibits a sharp initial pressure decrease as the mouth opens followed by a positive phase and then a final negative phase (see Fig. 15 for a summary). The positive pressure pulse in the buccal waveform

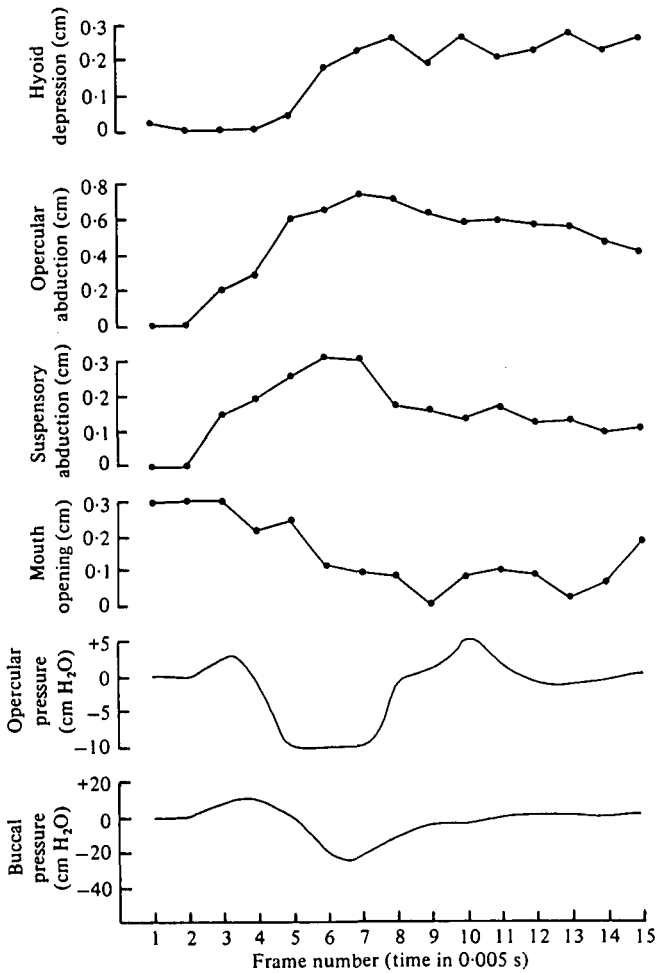


Fig. 13. Buccal and opercular cavity pressure and the pattern of jaw bone movement resulting from a twitch stimulus applied bilaterally to the levator arcus palatini muscle.

correlates with delayed opercular abduction relative to the timing of buccal compression (mouth closing and hyoid protraction). The rapid inflow of water created by buccal cavity expansion enters the mouth cavity and, if opercular expansion does not closely follow the negative buccal pressure peak, a positive pressure in the buccal cavity is created as the mouth closes. The second negative phase in the buccal waveform consistently follows mouth closing and is hypothesized to be due to the *water hammer effect* (Lauder, 1980b). When a rapid flow in a pipe is interrupted suddenly (as by a valve closing) the pressure is rapidly reduced on the downstream side of the valve and a low pressure wave travels downstream. This pressure reduction reduces the velocity of fluid flow and tends to cause a contraction of the downstream section of the pipe. This same phenomenon appears to occur during suction feeding. The rapid flow induced by buccal cavity expansion is shut off as the mouth closes. The time from

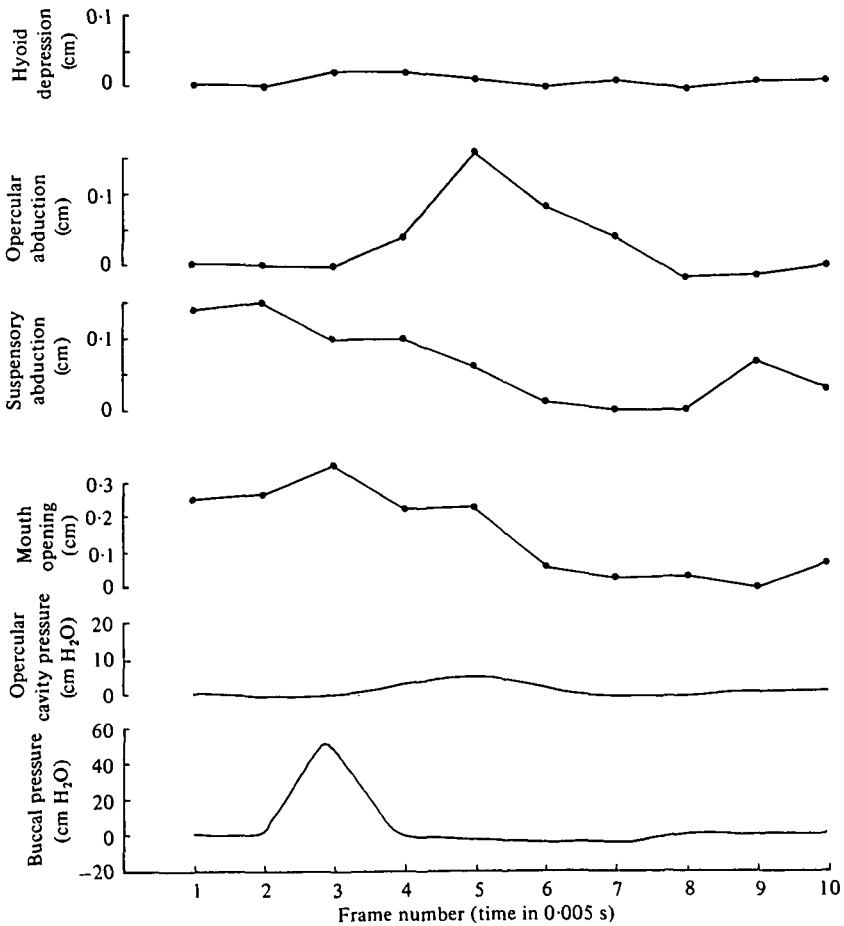


Fig. 14. Buccal and opercular cavity pressure and the pattern of jaw bone movement resulting from a twitch stimulus applied bilaterally to the geniohyoideus muscle. Note the close similarity in pressure waveform to chewing pressures (Fig. 2 F).

peak gape to complete mouth closure may be as little as 20 ms. When slow mouth closing occurs, the second negative phase is reduced or absent.

In the opercular cavity, pressure usually rises sharply just as the mouth opens due to opercular adduction (Figs. 7, 11). A negative pressure then follows the initial positive one (Fig. 15), and during rapid strikes, opercular cavity pressure is still equal to ambient when buccal pressure has reached  $-200$  cm H<sub>2</sub>O. The opercular cavity pressure reduction is hypothesized to be primarily the result of buccal cavity expansion as there is little kinematic evidence for opercular cavity expansion during mouth opening. Opercular cavity pressures generally average one-fifth the buccal pressures, due to the high gill resistance which functionally segregates the mouth cavity.

The timing of branchiostegal valve opening during feeding is of importance because it gives an indication of the time the water flow begins to exit from the opercular

cavity to the exterior. During rapid strikes, the branchiostegal valve opens during the first buccal negative phase (Figs. 8, 9), whereas in slow strikes at invertebrate prey (Figs. 6, 7), branchiostegal valve opening may be delayed until up to 50 ms after mouth closing at which time mouth cavity pressures have reached near-ambient values.

Pressures recorded during chewing of prey corroborate the interpretation of the buccal cavity as functionally segregated from distinct posterior opercular chambers. Sharp pulses of positive pressure in the buccal cavity are associated with prey maceration while synchronously recorded opercular cavity pressures show little change (Fig. 2F). These positive pressures correspond to the periods of geniohyoideus activity noted by Lauder & Lanyon (1980). Gill resistance appears to damp out pressure variations produced in the buccal cavity.

The patterns and correlates of pressure change in sunfishes discussed above may be summarized by the following conclusions: (1) the opercular and buccal cavities are functionally separated by a gill curtain of high resistance and each cavity has distinctive pressure waveforms, and (2) the operculum appears to contribute little to the generation of negative mouth cavity pressures or flow velocity, but does effectively prevent an influx of water into the posterior aspect of the mouth cavity during the initial stages of suction feeding (also see Lauder & Lanyon (1980) and Liem (1978) for a discussion of this point).

Stimulation of certain jaw muscles was conducted to test the observed correlation between kinematic events and pressure waveform attributes. Activation of the geniohyoideus muscle (Fig. 14) produces highly similar pressure waveforms to those observed during chewing and corroborates the functional separation of the buccal and opercular cavities. Sternohyoideus stimulation results in remarkably similar pressure waveforms to those observed during feeding and the predicted kinematic correlates are also present (Fig. 12).

Based on the mouth cavity pressures recorded in sunfishes, I propose a new model of fluid flow in the mouth cavity during feeding by high-speed inertial suction (Fig. 15). As the mouth opens, the ratio of buccal to opercular pressure increases and peaks at about 8:1. The large pressure differential and opercular adduction at this time indicate a reverse flow from the opercular into the buccal cavity (posterior to anterior flow) (Fig. 15  $t_2$ ). As peak negative buccal pressure is reached, flow direction reverses and becomes anteroposterior due to both opercular cavity volume increase and the momentum of water entering the mouth. The branchiostegal membrane generally opens about  $t_4$  (Fig. 15) and water may start to exit from the opercular cavity at this time. Lauder (1980b) hypothesized that if opercular abduction is delayed beyond  $t_3$ , the peak negative buccal pressure, the anteroposterior flow pattern might not have become established and opening of the branchiostegal valve might actually result in water flow *into* the opercular chamber from the outside. This hypothesis is corroborated here by the observation of particles suspended in the water. Particles near the opercular margin were carried into the gill cavity as the valve first opened, only to be swept out 5 to 10 ms later with the anteroposterior flow.

Mouth closure ( $t_5$ ) is immediately followed by the second (water hammer) negative pulse and the opercular waveform shows a positive phase at this time ( $t_6$ - $t_7$ ) as flow

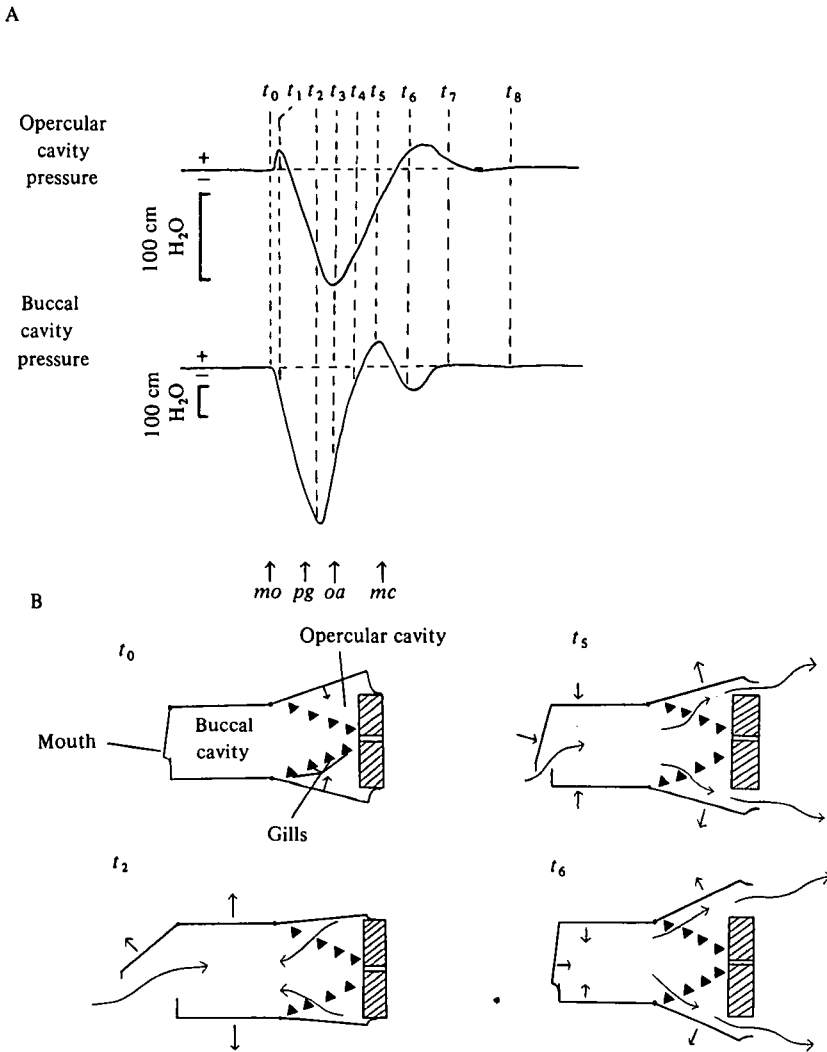


Fig. 15. A. Most common pattern of buccal and opercular cavity pressure change during a strike at a goldfish. Scale bar is 100 cm H<sub>2</sub>O. Note the dissimilarity of pressure waveforms and magnitudes in the two cavities (see text). B. Proposed pattern of fluid flow through the mouth cavity during feeding.  $t_0$ ,  $t_2$ ,  $t_5$ , and  $t_6$  correspond to the times indicated in A. Small arrows indicate kinematic events and large arrows depict the hypothesized flow pattern. Note the ratio of buccal to opercular pressure between  $t_1$  and  $t_2$  and that a flow reversal is proposed to occur in the opercular cavity between  $t_2$  and  $t_5$ , as momentum of water entering the mouth imposes an anteroposterior flow pattern. Abbreviations:  $mc$ , mouth closure;  $mo$ , mouth opening;  $oa$ , opercular abduction;  $pg$ , peak gape.

is forced through a region of high resistance, the opercular slit. Resistance decreases as lateral opercular expansion increases ( $t_8$ ).

The two key elements of this model, (1) initial reverse flow and (2) the importance of inertial effects in governing flow patterns, indicate that the process of high-speed suction feeding in the sunfish is best modelled as a powerful *buccal suction pump*.

Water is drawn in both from the area in front of the mouth and also from the opercular cavity by the rapid volume change of the buccal cavity. The operculum functions mostly as a passive element preventing the posterior influx of water. The inertia of water drawn in through the mouth may primarily govern the transition from the initial reverse flow to the dominant anteroposterior pattern. The asymmetry of opercular and buccal cavity pressures and the bidirectional flow pattern are due to gill resistance. Configurational and structural modifications of gill arches and filaments may thus play a major role in determining patterns of mouth cavity pressure change in fishes.

Osse & Muller (1980) and Elshoud-Oldenhave (1979) have recently presented preliminary pressure data for *Amia calva* and *Stizostedion lucioperca* respectively. Osse & Muller (1980) and Osse (1976) report that in *Amia* buccal cavity negative pressures generally are two to three times those in the opercular cavity (buccal pressure peaks at  $-170$  cm H<sub>2</sub>O), and the pressure waveforms appear to exhibit similar phases to those reported here for sunfishes. Elshoud-Oldenhave (1979) recorded buccal pressures of  $-50$  to  $-115$  cm H<sub>2</sub>O and noted that opercular cavity negative pressures were 5 to 10% higher than buccal pressures. The occurrence of a greater negative pressure in the opercular cavity may indicate an initial rapid opercular cavity expansion as the mouth opens and a reduced gill resistance to flow.

Two kinematic aspects of the sunfish feeding mechanism are particularly relevant to previous models of suction feeding in fishes. First, movement of the pectoral girdle appears to contribute little to orobranchial expansion. In fact, the pectoral girdle is actually protracted both in sunfishes (Lauder & Lanyon, 1980) and in char (Lauder & Liem, 1980) during the strike. Pectoral girdle movements would thus decrease the volume of the buccal cavity.

Secondly, considerable plasticity was observed in the relative timing of mandibular adduction and premaxillary protrusion. During rapid strikes at fish, the mandible was adducted against retracted premaxillae while during slow strikes at worms the lower jaw closed against protruded premaxillae (see Fig. 4). These data do not corroborate the hypothesis that one of the functions of jaw protrusibility is to allow more rapid mouth closure (Alexander, 1967) and indicate that the mechanisms and functions of protrusion may be more subtle than previously supposed.

#### *Respiration versus feeding: comparative hydrodynamics*

One of the main concepts to emerge from this analysis is the complete distinction between feeding and respiratory hydrodynamics. In teleost respiration, pressure differential between the buccal and opercular cavities ranges from about 0.2 to 2 cm H<sub>2</sub>O (Holeton & Jones, 1975; Hughes & Shelton, 1958; Hughes & Umezawa, 1968; Muir & Buckley, 1967; Saunders, 1961), and buccal pressure is positive with respect to opercular pressure for most of the respiratory cycle. Respiration in fishes has thus been modelled as a *buccal force (pressure) pump* coupled with an *opercular suction pump* (Hughes & Shelton, 1958).

During feeding, pressure relationships in the sunfish are nearly the reverse of those during respiration. Buccal cavity pressures average five times more negative than opercular cavity pressures (Fig. 3). The pressure differential across the gills is thus

*much* greater, and neither the buccal force nor opercular suction pumps are present. Movements of the operculum do not contribute to the generation of negative pressures, and the rapid buccal expansion constitutes a suction pump. During chewing and manipulation of prey, movements of the gill cover also appear to play a limited role (see Fig. 2F) and opercular pressure remains at near ambient levels. Kinematic and hydrodynamic studies of forced respiration (Ballintijn & Hughes, 1965) thus reveal little about the pressure and flow profiles occurring during suction feeding.

### *Prospectus*

The kinematic correlates determined above of the wide range of sunfish buccal and opercular cavity pressure waveforms, represent only the first step toward a more complete understanding of the hydrodynamics of prey capture in fishes. The predicted kinematic causes of specific waveform features need to be tested in other fishes with different movement profiles and waveform patterns. The relative timing and magnitude of opercular and buccal cavity pressure change is particularly interesting in relation to jaw kinematics and predator attack strategy. The ratio of predator to prey velocity at the strike may also be related to the pattern of pressure change in the mouth cavity and the ratio of buccal to opercular pressures.

The functional significance of different waveform attributes also remains to be investigated. What effect does the presence of a positive or second negative phase in the buccal waveform have on flow velocity, and how do different patterns relate to the efficiency of prey capture? Comparative investigations of actinopterygian feeding hydrodynamics are needed before a general theory of aquatic prey capture dynamics can be formulated.

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