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HYDRODYNAMICS OF PREY CAPTURE BY TELEOST FISHES

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SUMMARY

The dominant mode of prey capture in teleost fishes is inertial suction: rapid expansion of the mouth cavity creates a negative (suction) pressure relative to the surrounding water. This pressure differential results in a flow of water into the mouth cavity carrying in the prey. Previous models of the suction feeding process have predicted the pattern and magnitude of pressure change in the mouth cavity based on kinematic profiles of jaw bone movement and the application of the Bernoulli equation and the Hagen-Poiseuille relation. These models predict similar pressure magnitudes and waveforms in both the buccal and opercular cavities, and rely on the assumption of a unidirectional steady flow. In vivo simultaneous measurement of buccal and opercular cavity pressures during feeding in sunfishes shows that (1) opercular cavity pressures average one-fifth buccal pressures (which may reach $-650 \text{ cm H}_2\text{O}$), (2) the opercular and buccal cavities are functionally separate with distinct pressure waveforms, (3) a flow reversal (opercular to buccal flow) probably occurs during mouth opening, and (4) the kinetic energy of the water and inertial effects must be considered in hydrodynamic models of suction feeding.

INTRODUCTION

Despite the dramatic advances in our understanding of the hydrodynamics of fish locomotion in the last decade (Lighthill, 1969; Webb, 1975; Weihs, 1972, 1973), very

little work has been done on the hydrodynamics of fish prey capture. This may in part be due to experimental difficulties involved in studying feeding behavior. Water-tunnel respirometers allow the study of locomotion under controlled circumstances in a fixed location. The process of locomotion is cyclical and allows repeated measurements over an experimental trial. Investigators of fish locomotion have also greatly benefited from the input of hydrodynamic engineers and theoretical physicists who have applied a large body of relevant experimental and theoretical work to problems of fish locomotion. In contrast, prey capture by teleost fishes occurs extremely rapidly (often within 50 ms), is not cyclical, and the fish cannot be excessively restrained or subjected to experimental trauma without eliminating the feeding response.

The difficulties of studying the hydrodynamics of feeding in fishes have been ably summarized by Holeyton and Jones (1975: 547) (in the context of respiration). "The analysis of the breathing mechanics of fish is difficult because it involves the measurement of an unsteady flow of a dense fluid through a non-uniform system which is ill-defined. The compliance of the respiratory tract is variable, both spatially and temporally, and certain resistive elements (such as the gill filaments) are mobile, both actively and passively, throughout a breathing cycle." These difficulties are all compounded during feeding by the extremely short duration of the prey capture event.

In spite of these formidable problems, a number of investigators have modeled the process of prey capture using simple hydrodynamic equations and the kinematics of jaw bone movement to predict the pattern of pressure change in the mouth cavity. In this paper I will review these models and examine the few experimental studies with actual pressure measurements from the mouth cavity during feeding. I will then present new experimental data on the suction feeding mechanism in sunfishes and propose a new model of fluid flow and pressure change in the teleost mouth cavity.

II. ANATOMICAL BASIS OF THE SUCTION FEEDING MECHANISM

Prey capture in most teleost fishes occurs by inertial suction feeding. Mouth cavity volume is rapidly expanded by the contraction of certain jaw muscles (see Lauder and Liem,

1980; Liem, 1978), and this expansion results in the creation of a negative pressure (relative to the surrounding water) in the mouth cavity. This pressure differential creates a flow of water into the mouth from the region directly in front of the head and draws the prey in. The jaws are then closed trapping the prey in the mouth cavity while the water flows out over the gills.

The mouth cavity may be divided into an anterior buccal cavity and two posterolateral opercular cavities (Fig. 1B), separated from the buccal cavity by the gill curtain. The gills are supported on four gill arches and form a resistance to fluid flow within the mouth cavity. Changes in volume of the buccal and opercular cavities for the most part do not occur independently: anatomically they are coupled. Expansion of the buccal cavity may occur by elevation of the neurocranium, opening of the front jaws, depression of the hyoid apparatus, and lateral expansion of the suspensory apparatus (Fig. 1; also see Lauder and Liem, 1980; Liem, 1970, for a more detailed account of anatomical couplings). These movements may also effect opercular cavity expansion. However, some bone movements (such as opercular adduction) (Fig. 1) do predominantly affect only one cavity. In general, the dorsal, ventral, and lateral walls of the mouth cavity all rapidly expand to create a low pressure center during the attack at a prey item.

The role of the gills as a resistant element separating the buccal and opercular cavities was first recognized by Woskoboynikoff and Balabai (1937) and van Dam (1938), and the concept of gill resistance to water flow has received considerable attention in recent studies of fish respiration (Ballintijn, 1972; Hughes and Morgan, 1973; Hughes and Shelton, 1958; Jones and Schwarzfled, 1974; Pasztor and Kleerekoper, 1962; Shelton, 1970). The resistance of the gills to flow is not equal in both directions: flow directed anteroposteriorly (i.e., from the buccal to opercular cavity) encounters less resistance than reverse flow from the opercular cavity into the buccal cavity due to the orientation of the gill filaments (Fig. 1). While several attempts have been made to measure gill resistance to anteroposterior flow (e.g., Brown and Muir, 1970; Davis and Randall, 1973; Hughes and Umezawa, 1968; Jones and Schwarzfled, 1974), no data exist on the values of gill resistance to reverse flow. It is well established, however, that gill configuration (and thus resistance) may be actively modified by intrinsic gill

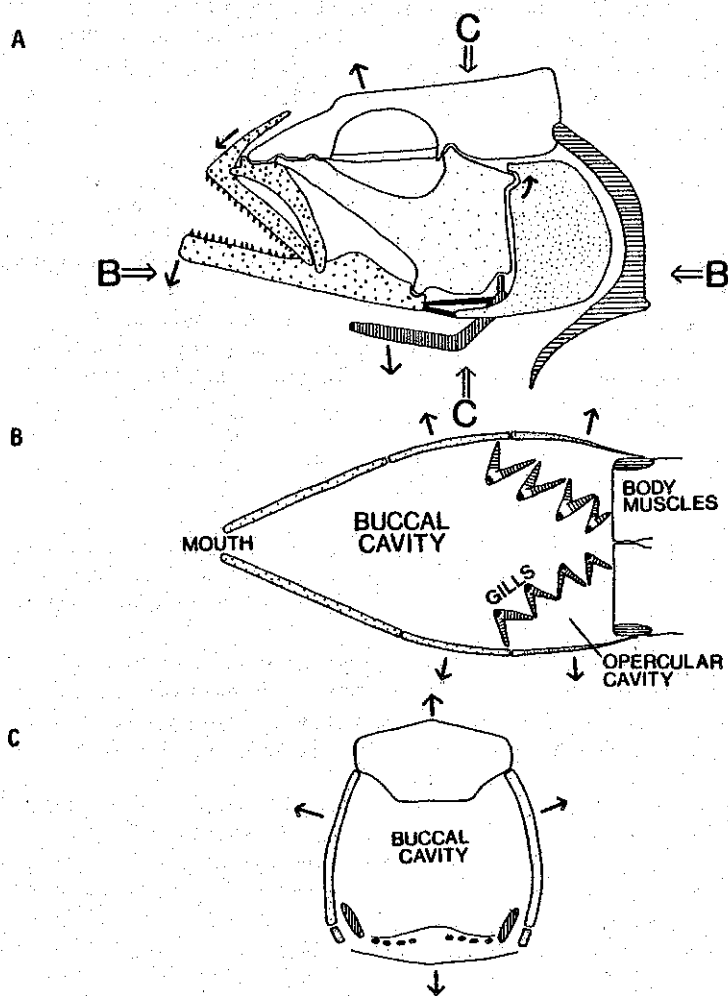


Fig. 1. Diagrammatic view of the head of an advanced teleost fish with protrusible jaws. B and C represent sections of the head at the level indicated in A. Arrows indicate major bony movements during prey capture. Key: white = neurocranium; vertical lines = hyoid apparatus; horizontal lines = pectoral girdle; dense stipple = opercular apparatus; fine stipple = suspensorium; large stipple = jaw apparatus.

arch musculature (Pasztor and Kleerekoper, 1962). Other resistance to flow occurs at the mouth opening and at the opercular and branchiostegal valves where water exits through a narrow slit of high resistance. Osse (1969: 371) and Alexander (1967) have suggested that gill resistance is very low during feeding.

III. RESPIRATORY HYDRODYNAMICS

Research on respiratory hydrodynamics has provided the conceptual basis for current models of fluid flow during feeding. The early work of Hughes (1960), Hughes and Shelton (1958), and Saunders (1961) established that water flow through the teleost mouth cavity is unidirectional and is regulated by two "pumps." An opercular suction pump draws water through the gill resistance by lateral expansion of the operculum which creates a pressure differential from the buccal to the opercular cavities. Shortly after opercular expansion has reached its peak, the buccal pressure pump is initiated by jaw closure and suspensorial adduction (Ballintijn and Hughes, 1965). This creates a positive buccal pressure (of 1-2 cm H₂O) which drives water through the gills and into the opercular cavity where it exits to the outside. Throughout this process buccal pressure is nearly always positive with respect to opercular pressure.

The key points established by studies of respiratory hydrodynamics are (1) that the gill cover functions as a fundamental element of the "opercular suction pump," drawing water over the gills, (2) that pressures in the opercular cavity are negative with respect to buccal cavity pressures, (3) that this pressure differential must exist if water is to flow unidirectionally through the mouth cavity (Saunders, 1961).

Holeton and Jones (1975) provided the first velocity measurements of flow during respiration and noted that water velocity varied within the buccal cavity. Velocities of up to 38 cm/sec were recorded during normoxic respiration.

IV. PREVIOUS MODELS OF SUCTION FEEDING IN FISHES

A. Pressure Waveforms and Magnitudes: Predictions

Osse (1969) first attempted to predict the magnitude of mouth cavity pressures in fishes using simple hydrodynamic

relationships between velocity and pressure. The equation

$$\frac{P_1}{\rho g} + \frac{\frac{1}{2}V^2}{g} = \frac{P_0}{\rho g}$$

(where P_1 is the pressure near the mouth within the mouth cavity, P_0 the pressure of the surrounding water, V the velocity of water entering the mouth, ρ the density of the liquid, and g the acceleration due to gravity) was applied to the fish head with $V=200$ cm/sec, and a buccal pressure of -20 cm H_2O was calculated. Velocity of water flow was calculated from the estimated change in buccal volume, the estimated rate of volume change, and the mean cross-sectional area of the mouth during mouth opening. This approach was indicated as a first approximation to problems of fluid flow in the mouth cavity and involved a number of assumptions. The most important of these is the assumption of steady flow in the Bernoulli equation, a condition that is certainly not met during feeding. Lauder (1979) also assumed steady flow conditions during his consideration of the effect of mouth geometry on flow rate. Osse (1969: 371) concluded that expansion of both the buccal and opercular cavities contributes to suction feeding: "The suction force due to enlargement of the opercular cavity is directly applied to the water entering the buccal cavity, thus increasing the quantity of water and the velocity of the current."

More recently, Pietsch (1978) has applied the Bernoulli equation and the Hagen-Poiseuille relation to the tubular mouth of *Stylophorus* to calculate the buccal cavity pressure and flow velocity during feeding. Assumptions of the Hagen-Poiseuille relation, none of which apply to fishes, include (1) a small pipe diameter, (2) steady flow, (3) absence of particles (i.e., prey) in the flow, and (4) that the relationship is not valid near the pipe entrance (see Prandtl, 1949; Streeter and Wylie, 1979). The predicted buccal pressure was -53 cm H_2O with a flow velocity of 325 cm/sec.

Muller and Osse (1978) and Osse and Muller (in press) have developed an elegant hydrodynamic model to predict the pattern of pressure and velocity change with time during feeding. The fish head is modeled as a radially symmetrical cone that expands to reduce the pressure inside. The timing

of expansion of both the anterior and posterior bases of the cone can be varied to simulate the timing of mouth opening and opercular expansion respectively. Flow velocity is obtained from the equation of continuity

$$\frac{\partial u}{\partial x} + \frac{1}{r} \cdot \frac{\partial(vr)}{\partial r} = 0$$

where u is the component of velocity along the body axis, x the distance along the body axis, v is the velocity component perpendicular to the body axis (along the radius of the cone), and r is the radius of the cone at the point of interest. By solving this equation for velocity and substituting into the equation of motion (Navier-Stokes, for frictionless flow),

$$\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} = \frac{-1}{\rho} \cdot \frac{\partial p}{\partial x}$$

where p is pressure and ρ is density, the pressures generated by the expanding cone can be calculated. This procedure does not assume steady fluid flow through the mouth cavity.

Three major hydrodynamic assumptions have been made (Muller and Osse, 1978): (1) friction is neglected, (2) the fish head is assumed to be radially symmetrical, and (3) the prey is assumed to behave as an element of the water.

Elshoud-Oldenhav and Osse (1976: 411-412) have made the most specific predictions of pressure waveform in the teleost mouth cavity and correlated the hypothesized pressure changes with kinematic events to produce a theoretical model of suction feeding. Figure two summarizes the present hypothesis of pressure change in the buccal and opercular cavities and is drawn from discussions in Alexander (1969, 1970), Elshoud-Oldenhav and Osse (1976), Lauder (1979), Nyberg (1971), and Liem (1978).

A preparatory phase occurs first as the fish approaches the prey (Fig. 2:P). The volumes of both the buccal and opercular cavities are reduced and the pressure goes positive relative to the surrounding water. The mouth cavity then begins to expand (Fig. 2:mce) while the front jaws remain closed, and this results in a pressure decrease in both cavities. The mouth then opens (Fig. 2:mo), pressures reach their peak negative value, and compression of the

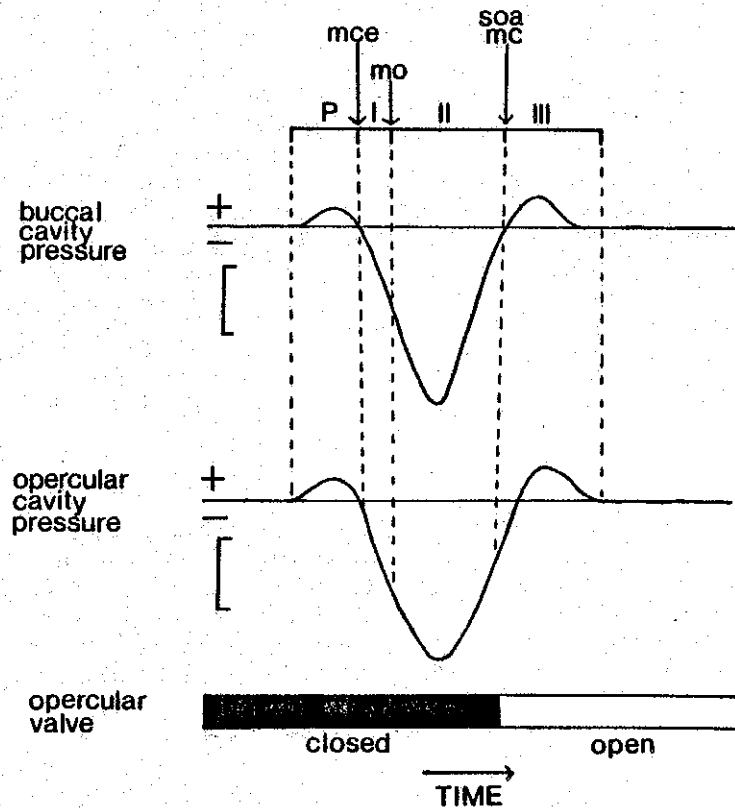


Fig. 2. Current model of buccal and opercular cavity pressure change with time during suction feeding. Phases P, I, II, and III are defined after Elshoud-Oldenhavé and Osse (1976), as are the kinematic correlates of pressure change: mce, mouth cavity expansion; mo, mouth opening; soa, suspensorial and opercular adduction; mc, mouth closing. Note the close similarity in both waveform and magnitude (see arbitrary scale bar on left) between buccal and opercular cavity pressures.

mouth cavity occurs. Finally, as the buccal pressure reaches zero, suspensorial and opercular adduction commences and the mouth closes (Fig. 2: soa, mc), resulting in a positive pressure as water is forced out the opercular slit.

The key elements of this model are (1) the close similarity between buccal and opercular pressure waveforms and magnitudes, (2) the role of opercular abduction in the generation of a negative opercular cavity pressure, (3) pressure decrease before the mouth begins to open, and (4) unidirectional flow through the mouth cavity. O'Brien (1979:579) has also emphasized the importance of opercular expansion in contributing to the unidirectional flow of fluid through the mouth.

B. Experimental Data

Alexander (1969, 1970) provided the first direct measurements of pressures in the teleost mouth cavity. He used a pressure transducer attached to a nylon tube which was fixed in the aquarium. A small piece of food was attached to the tube and the fishes were trained to suck off the food by placing their mouths around the tube. Pressures were measured during the feeding act.

A survey of nine different species showed that the maximum negative pressure varied from $-80 \text{ cm H}_2\text{O}$ to $-400 \text{ cm H}_2\text{O}$ in the buccal cavity. Pressure waveforms typically showed a sharp negative pressure drop shortly after the mouth opened and a slight positive pressure pulse of $+1$ to $9 \text{ cm H}_2\text{O}$ as "water which has been sucked in with the food is ... driven out through the opercular openings" (Alexander, 1969). These pressure traces agree well with the pattern of buccal pressure change hypothesized from kinematic analyses (Fig. 2), although data on the occurrence of a preparatory phase were not available since the fish had to open its mouth before pressures could be recorded. Casinos (1977) using similar equipment recorded pressures of $-150 \text{ cm H}_2\text{O}$ in cod (*Gadus*).

Osse (1976) presented preliminary pressure measurements from the buccal and opercular cavities of *Amia calva* and reported pressures as low as $-170 \text{ cm H}_2\text{O}$ and $-95 \text{ cm H}_2\text{O}$ respectively. Most recently, Liem (1978) measured buccal pressure profiles in two cichlid fishes and found a preparatory pressure pulse corresponding to phase P in Fig. 2.

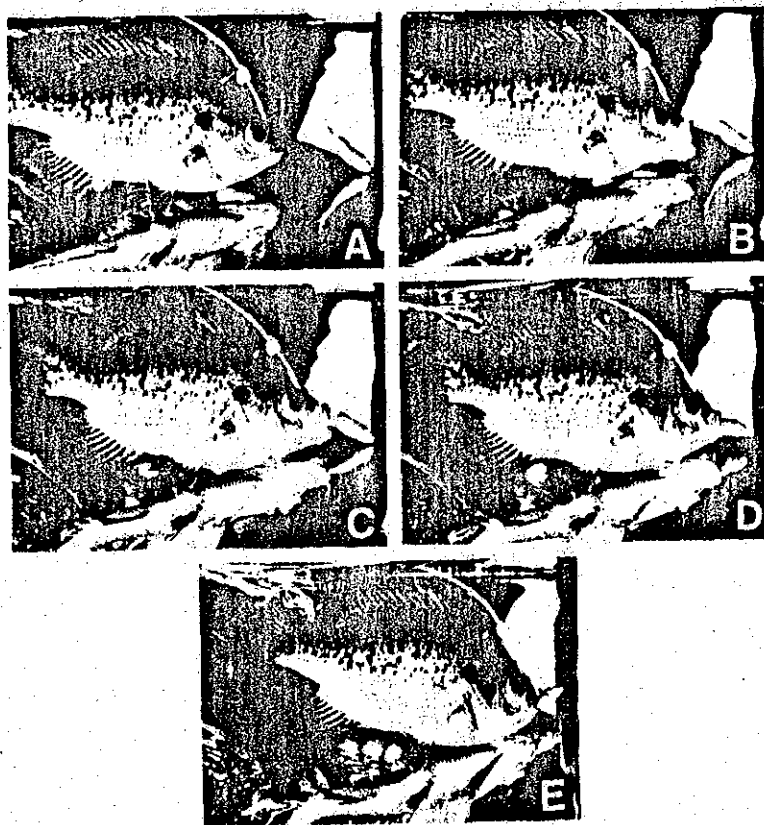


Fig. 3. Representative frames from a high-speed film (200 frames per second) of the bluegill (*Lepomis macrochirus*) capturing a goldfish. Note the plastic cannula leading into the buccal cavity and the attachment of the cannula to the clamp. Also note abduction of the gill filaments as seen in the ventral view of frame E. Frames A, B, C, D, and E correspond to frames 1, 4, 6, 8, and 15 from the film.

V. EXPERIMENTAL ANALYSIS OF FEEDING IN SUNFISHES

A. Materials and Methods

The suction feeding mechanism in the bluegill sunfish *Lepomis macrochirus* (Family Centrarchidae) was studied by

the simultaneous recording of buccal and opercular cavity pressures together with a high-speed film (200 frames per second) of jaw movements. A detailed description of the recording apparatus and calibration technique may be found in Lauder (1980). Briefly, plastic cannulae (o.d. 1.52 mm, i.d. 0.86 mm) were chronically implanted in the buccal and opercular cavities (see Fig. 3) and attached to Statham P23 Gb pressure transducers filled with a mixture of 53% boiled (degassed) glycerine and 47% boiled distilled water. This mixture resulted in a transducer damping factor of 0.65 and a frequency response of 75 Hz. Films were then taken of the fish feeding over a mirror to allow accurate measurement of kinematic events. The fishes were fed a variety of prey types, from live goldfish (*Carassius auratus*) to earthworms and mealworms.

B. Results

The patterns of buccal and opercular cavity pressure recorded during feeding are shown in Fig. 4 and typical jaw movements occurring during capture of a goldfish in Fig. 3. There is tremendous variability in the pressure waveform between different feeding events and these variations correlate with specific kinematic patterns (Lauder, 1980).

Buccal pressures very rarely exhibit a preparatory phase. A pressure drop is recorded immediately after the mouth begins to open and peak gape occurs before the maximum negative pressure. The maximum recorded buccal cavity pressure was $-650 \text{ cm H}_2\text{O}$. Pressure magnitudes correlate with prey type (goldfish elicit the greatest negative pressures, mealworms the least), and pressure varies inversely with the degree of satiation (Lauder, 1980). The most common buccal pressure waveform contains an initial large negative peak followed by a smaller positive pressure pulse and then by a final negative phase (see Fig. 4A: 1, 5, 7, 9). Occasionally the positive pulse or the second negative is absent (Fig. 4: 2, 10).

Opercular pressure waveforms exhibit an initial sharp positive phase which is followed by a negative pressure peak that may reach a maximum of about $-130 \text{ cm H}_2\text{O}$ (Fig. 4B). A positive pulse may follow the negative (Fig. 4B: 1, 2, 4, 5, 7) or it may be absent (Fig. 4B: 3, 8, 9). Feeding on stationary prey produced opercular pressures in the -10 to -40

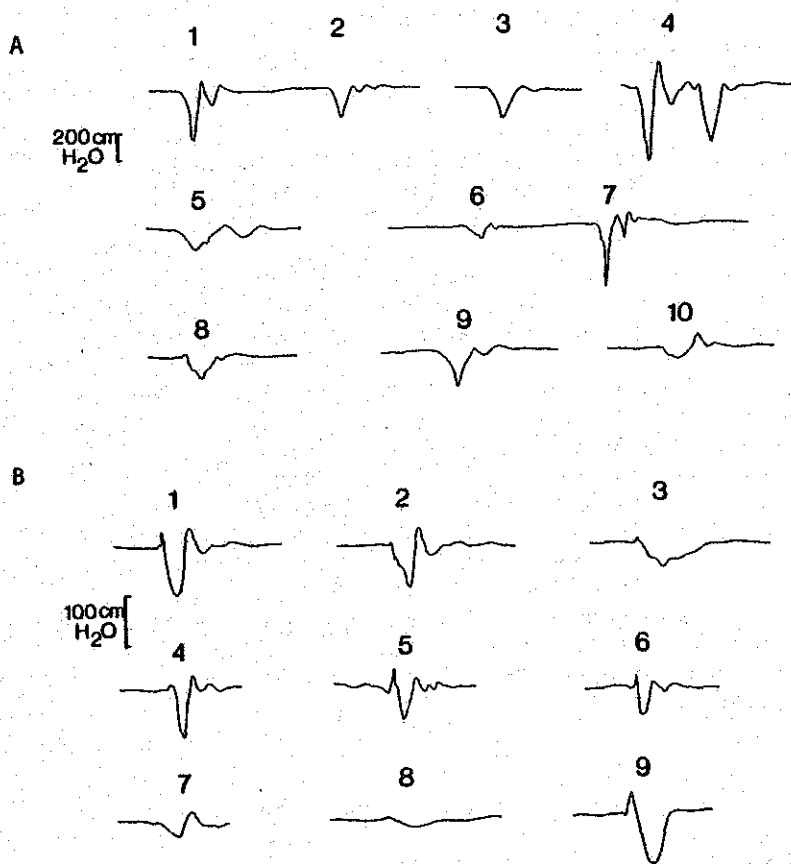


Fig. 4. Representative traces of pressure change in the buccal cavity (A) and the opercular cavity (B) in bluegill (*Lepomis macrochirus*) during feeding. Note the differing scales and the variation in pressure waveform and magnitude. See text for discussion.

cm H₂O range and tended to flatten out the pressure profile (Fig. 4B: 3, 8).

The temporal relationship between the buccal and opercular pressures is shown in Fig. 5A. Buccal cavity pressure begins to decrease immediately after the mouth

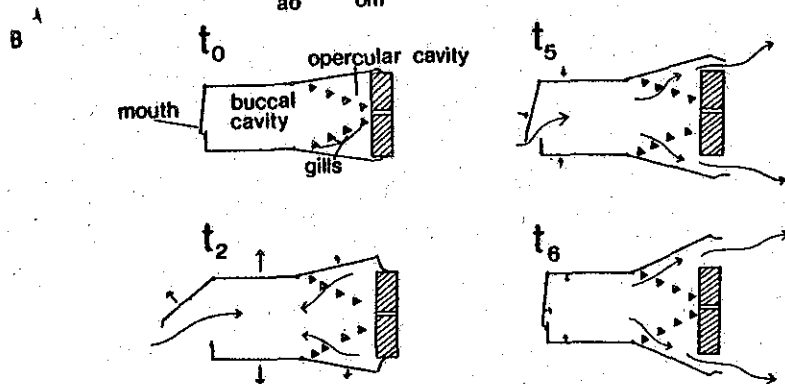
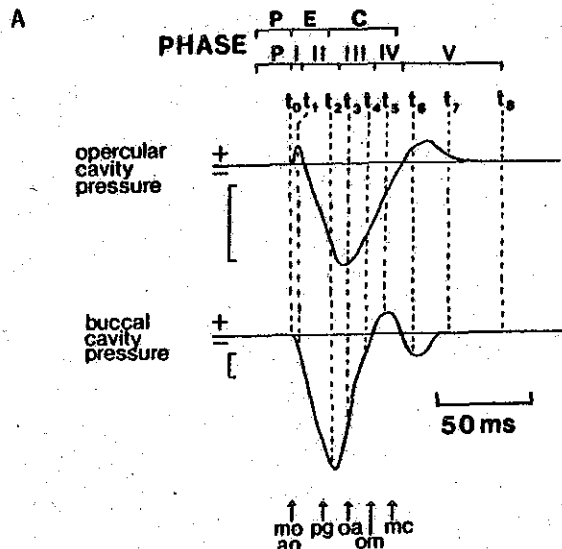
starts to open (Fig. 5A: t_0 to t_1). During this same time interval, the operculum is adducted and opercular cavity pressure actually rises. Buccal pressure reaches its peak (usually 5 times the peak opercular pressure) 5 to 10 ms prior to the opercular pressure peak although the two peaks are occasionally temporally coincident. Buccal pressure then starts to rise and passes through zero while the opercular cavity pressure is still negative. The positive phase of the buccal waveform (Fig. 5: phase IV) occurs while the opercular cavity pressure is negative. In phase V, opercular pressure goes positive as the second negative buccal pressure pulse occurs. Opercular abduction is initiated at the peak in opercular cavity pressure (Fig. 5: oa); throughout the first third of the feeding sequence the operculum exhibits no lateral movement (see ventral view in Fig. 3B). Considerable opercular abduction occurs before the opercular and branchiostegal valves open (Figs. 3B; 5:om). Mouth closure, usually against partially protruded premaxillae, occurs before opercular pressure passes zero and at or near the peak of the positive buccal pressure pulse (Fig. 5:mc). The operculum often remains abducted after the mouth has closed and the pressures have returned to their ambient values (Fig. 5: t_7 , t_8). At this point the gill filaments from adjacent arches are clearly seen to be abducted (Fig. 3E: ventral view) and gill resistance is presumably low.

C. New Model of Fluid Flow in the Mouth Cavity

A comparison of simultaneously recorded buccal and opercular cavity pressure waveforms and magnitudes (Fig. 5A) strongly suggests the hypothesis that flow is not unidirectional in the mouth cavity. Figure 5B illustrates the hypothesized flow pattern at representative stages of the feeding cycle.

During phase I, the period when opercular cavity pressure is positive (Fig. 5A), buccal cavity pressures may reach -150 cm H₂O. Between t_1 and t_2 (Fig. 5A) the ratio of buccal to opercular cavity pressure is about 8. This large pressure differential and the lack of opercular abduction indicate a reverse flow from the opercular to buccal cavity between t_0 and t_2 (Fig. 5). After the end of phase II, opercular abduction occurs and the direction of flow is hypothesized to be from the buccal into the opercular cavity. This change is due both to opercular cavity volume increase

and the momentum of water entering the mouth. The branchiostegal membrane opens at t_4 and this allows flow between the opercular cavity and the exterior. If opercular abduction were delayed beyond t_3 , then the anteroposterior flow pattern would likely not be established by t_4 , and opening of the branchiostegal valve (by the hyohyoideus inferioris muscle) should actually result in water flow into the opercular cavity from the outside. This anterior flow would be temporary because by t_5 (Fig. 5B) the anteroposterior flow is well established as buccal pressure becomes positive with respect to that of the opercular cavity. At this point,



resistance of the opercular slit is high because of its small cross-sectional area.

The mouth closes during the buccal positive pulse (phase IV) and this event is followed by a rapid pressure decrease in the early part of phase V. This second buccal negative pressure is hypothesized to be due to the water hammer effect. Rapid closing of the mouth acts like the closing of a valve in a pipeline during flow. On the upstream side of the valve the pressure rapidly increases and a high pressure wave is propagated upstream. On the downstream side, the pressure is rapidly reduced (a cavity forms and the fluid returns with the same velocity) and a low pressure wave travels downstream. This tends to reduce the velocity of fluid flow and to contract the pipe downstream of the valve. The analogous situation during feeding is depicted in Fig. 5B: t_6). The mouth rapidly closes, water tends to continue flowing posteriorly causing a pressure reduction just inside the mouth (early phase V). Positive pressures are often recorded as water flows anteriorly after the pressure reduction (Fig. 4A: 1, 7, 9, 10). This phenomenon is analogous to events causing the dichrotic notch in the mammalian cardiac pressure waveform. Finally, by t_8 both the buccal and opercular cavities have returned to ambient pressure.

Fig. 5. A, simultaneous recordings of buccal and opercular cavity pressures during a typical strike at a goldfish. Scale bar equals 100 cm H₂O. P, E, and C refer to the preparatory, expansive, and compressive phases of the strike as conventionally defined (see Liem, 1978). Phases below are those proposed in this paper. Note the dissimilarity of pressure waveforms and magnitudes in the two cavities: e.g., the lack of a preparatory phase and the two negative phases in the buccal waveform. 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 in A. Small arrows indicate movements of the mouth cavity. Note the hypothesized reverse flow between t_1 and t_2 . Kinematic events are: mo, mouth opening; ao, opercular adduction; pg, peak gape; oa, opercular abduction; om, branchiostegal valve opens; mc, mouth closure.

VI. DISCUSSION

The assumptions and predictions of previous models of pressure change and fluid flow in the teleost mouth cavity during feeding are not supported by the experimental analysis of suction feeding in sunfishes presented here; no previous simultaneous buccal and opercular cavity pressure measurements exist. Current conceptions of the hydrodynamics of teleost feeding have been framed by the large body of data on respiratory mechanics and hydrodynamics. Thus, flow is assumed to be unidirectional, inertial effects have been generally neglected (but see Holeyton and Jones, 1975; Muller and Osse, 1978), and the process of creating suction during feeding is viewed as a modification of the respiratory two-pump system. In particular, the operculum is suggested to be of key importance in creating negative mouth cavity pressures (Alexander, 1967; Muller and Osse, 1978; Nyberg, 1971; O'Brien, 1979; Osse, 1969), in a manner analogous to the opercular suction pump during respiration. Additional elements of current concepts of feeding hydrodynamics are the close similarity between buccal and opercular cavity pressure waveforms and magnitudes, the correlated view that the buccal and opercular cavities are a functional unit, and the assumption that gill resistance is low during feeding.

None of these assumptions appear to be true. Buccal cavity pressures in sunfishes consistently average five times the opercular pressures (Fig. 5). In addition, pressure waveforms from the two cavities differ significantly and do not agree with expected patterns (Fig. 2). Flow reversal also appears to occur while the mouth is opening.

Inertial effects play a fundamental role in the hydrodynamics of feeding. The process of creating suction is best viewed as being composed of a powerful buccal suction pump that draws water into the buccal cavity from both the area in front of the mouth and from the opercular cavity. The operculum functions only as a passive element at this stage, preventing water influx from the outside. Flow from in front of the mouth is much greater than from the opercular cavity because the mouth opening is much less resistant to flow than the gill curtain. The inertia of the water drawn in through the mouth is primarily responsible for the transition to the anteroposterior flow pattern and the exit of water out over the gills to the exterior. Opercular abduction appears to contribute relatively little

to the direction of fluid flow, the magnitude of opercular cavity negative pressure, or flow velocity.

The asymmetry of gill resistance plays a key role in this model. In the early stages of feeding, the drop in opercular cavity pressure is due both to the buccal cavity pressure reduction and perhaps also to expansion of opercular cavity volume as a result of anatomical couplings between the two cavities, not to opercular abduction. Opercular cavity pressures do not equal those in the buccal cavity because of gill resistance, and the filaments of adjacent arches may be adducted. As the inertia of water sucked in through the mouth results in flow into the opercular cavity, the gill filaments are abducted and resistance becomes low.

Based on the synchronously recorded buccal and opercular cavity pressures and the hydrodynamic considerations outlined above, a number of kinematic correlates of pressure waveform attributes may be predicted (Table I). The correspondence between the occurrence of different kinematic patterns and variations in pressure waveform will be considered in detail elsewhere (Lauder, 1980), but variations during phases IV and V (Figs. 4, 5A) may be correlated with the timing of opercular abduction and mouth closing.

The large negative pressures recorded in the mouth cavity (up to -650 cm H_2O) invite considerations of the structural demands imposed on the teleost head. Lauder and Lanyon (1979) have considered the morphology of the sunfish operculum to be primarily a response to deformation induced by negative opercular cavity pressures. Two prominent orthogonal bony struts on the operculum were hypothesized to resist bending and twisting moments imposed by the pressure reduction. This view of the role of the operculum is consistent with the model of suction feeding presented here: the gill cover acts primarily as a passive element preventing fluid influx from the exterior.

A number of clearly defined areas may now be outlined for future work. Of particular interest is a characterization of the velocity field, both anterior to the mouth in the vicinity of the prey, and within the buccal and opercular cavities. Opercular cavity flow velocity determinations would provide a test of the reverse flow hypothesis. The pressure -- velocity relationship during feeding is also of importance. Because of the prominence of inertial effects

TABLE I
Predicted Kinematic Correlates of Pressure Waveform Attributes

Pressure Waveform Characteristic (See Fig. 5A)	Predicted Kinematic Correlate
BUCCAL PRESSURE	
Phase P: Positive	Hyoid protraction; suspensorial adduction.
Phase I, II: Negative	Mouth opening; suspensorial abduction; hyoid depression.
Phase III: Negative → 0	Mouth closing; start of hyoid and suspensorial adduction.
Phase IV: Positive	Delay in opercular abduction relative to mouth closing; hyoid, suspensorial adduction.
Phase V: Negative	Rapid closing of jaws relative to mouth cavity expansion.
OPERCULAR PRESSURE	
Phase P: Positive	Opercular adduction; suspensorial adduction; hyoid protraction.
Phase I: Positive	Opercular adduction.
Phase II: Negative	Mouth opening; suspensorial abduction; hyoid depression.
Phase III: Negative	Opercular abduction; mouth closing.
Phase IV: Negative → 0	Opercular abduction; mouth closing; hyoid and suspensorial adduction.
Phase V: Positive	Hyoid and suspensorial adduction.

and changing gill resistance during the strike, calculation of flow velocity from measured pressures is unlikely to yield satisfactory results. Finally, correlation of attributes of the suction feeding mechanism (such as volume flow rate, pressure, velocity) with morphological features, feeding efficiency, and prey type in a number of closely related taxa, may provide insights into the evolutionary mechanisms governing changes of shape and function in teleost fishes.

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