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PREY CAPTURE HYDRODYNAMICS IN FISHES: EXPERIMENTAL TESTS OF TWO MODELS

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SUMMARY

Three experimental modifications of the feeding mechanism in the bluegill sunfish (*Lepomis macrochirus* Rafinesque: Centrarchidae) were performed to distinguish between two alternative hydrodynamic models of the high-speed suction-feeding process in fishes. These two models make different predictions about the change in slope of the regression line representing the relationship between buccal and opercular cavity pressures, and the three experiments provide a critical test of the models. The results from all three tests unequivocally support (1) the concept of the gill bars as a resistant element within the mouth cavity functionally dividing it into buccal and opercular cavities, (2) the negligible role of lateral movement of the gill cover (operculum) in generating negative mouth cavity pressures, and (3) the large pressure differentials previously reported between the buccal and opercular cavities. Measured pressures conform neither in relative magnitude nor waveform with pressures predicted from theoretical mathematical models. Inertial effects and accelerational flows are key aspects of high-speed suction feeding.

INTRODUCTION

The process of fish respiration involves coordinated movements of many bones in the head to produce a flow of water over the gills. The mechanism of flow production has been the subject of extensive research since the classical experimental work of Hughes (1960) and Hughes & Shelton (1958). The major concepts that have emerged from these investigations are (1) that water flow over the gills is relatively continuous with perhaps a brief period of low or zero flow, (2) that the gills form a significant resistance to flow (see Hughes, 1965, 1976; Hughes & Morgan, 1973; Jones & Schwarzfeld, 1974; Shelton, 1970), and (3) that a 'double pump' mechanism involving a buccal force pump and an opercular suction pump is responsible for moving water over the gills. Holeton & Jones (1975) and Hughes (1978) have recently shown that flow velocities within the mouth cavity may be very unsteady and be significantly out of phase with pressure fluctuations.

Suction feeding in teleost fishes is a highly dynamic process lasting only 20–100 ms, involving large accelerations, and producing a single rapid pulse of water through the mouth cavity (Lauder, 1980*a*). Attempts to understand the hydrodynamic aspects of

teleost feeding have been hampered by the technical difficulties associated w~~ measuring rapidly fluctuating pressures, and have relied heavily on concepts borrowed from studies of fish respiration (Lauder, 1980*b*).

In a previous paper I established that very large and rapidly changing pressures are generated within the mouth cavity of teleosts during feeding and that correlations between kinematic and pressure patterns suggested an interpretation of feeding dynamics based on unsteady flows and inertial effects (Lauder, 1980*a*). The gill bars supporting the filaments were proposed as an important resistance to flow within the mouth cavity, and the gill cover (operculum) was suggested to play little or no role in generating negative opercular or buccal pressures. Osse & Muller (1980) and Muller, Osse & Verhagen (1982) have outlined a theoretical model of suction feeding in which the gill bars and filaments are not included (in contrast to models of fish respiration; Hughes & Woakes, 1970) and in which the operculum plays a prominent role in generating *both* buccal and opercular cavity negative pressures.

The purposes of this paper are (1) to present the results of three experimental tests of these two proposed roles of the gills and operculum, (2) to demonstrate that the use of new high-fidelity pressure transducers gives extremely similar recordings to those reported previously, (3) to show that the buccal and opercular cavity pressure waveforms and relative magnitudes in the bluegill sunfish, *Lepomis macrochirus*, the species used to test the two models of suction feeding, are not unique to that species, and (4) to compare measured pressure magnitudes and waveforms with those predicted by theoretical models.

EXPERIMENTAL TESTS

Three experimental tests were designed that would unambiguously distinguish the models of Lauder (1980*a*) and Osse & Muller (1980). In test one (see Fig. 1), the tendon of the dilator operculi muscle to the operculum was cut. I have previously argued that the role of gill cover abduction in generating negative mouth (and especially opercular cavity) pressures during high-speed suction is minimal (Lauder, 1980*a*) due to (1) the fact that the operculum is moving *medially* as the mouth is opened and maximum negative pressures are being produced, and (2) the small force applied to the gill cover by the dilator operculi, the only muscle capable of mediating active opercular abduction (Ballintijn & Hughes, 1965; Lauder, 1983; also see Alexander, 1969, who first raised this point). I predict that severing the dilator operculi tendon will result in a regression line representing the relationship between opercular and buccal pressures with a slope not significantly different from control recordings (Fig. 1). The alternative suggestion is that abduction of the operculum is crucial for generating negative pressures (Muller *et al.* 1982; p. 51), and Muller, Osse & van Leeuwen (1980) have even stated that the operculum 'is necessary to maximize the momentum given to water and prey *in front of the mouth*' (my emphasis). This model thus predicts that severing the dilator operculi tendon will greatly reduce the slope of the regression because only small opercular cavity pressures are expected to occur. Furthermore, the maximum negative buccal pressures achieved are predicted to be less than control values.
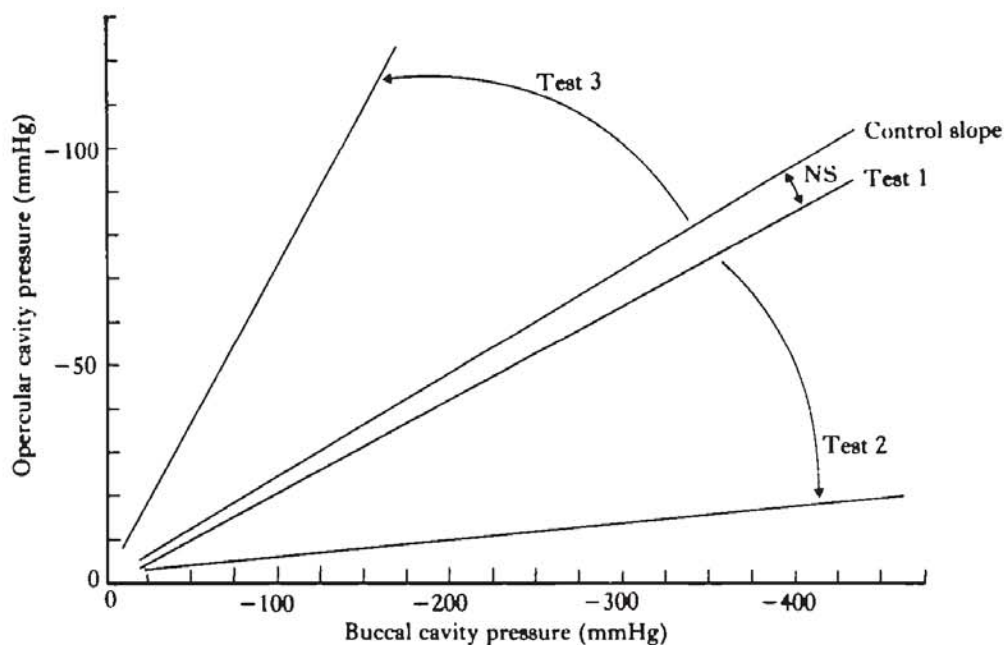
Fig. 1. Diagrammatic illustration of the three experimental tests designed to evaluate the predictions of two alternative models of the suction feeding mechanism in fishes. The model proposed by Lauder (1980a) predicts no change in slope of the opercular: buccal pressure regression line when the tendon of the dilator operculi muscle is cut (NS = not significant), test 1; a reduction in slope when a hole is cut in the opercular bone, test 2; and an increase in slope when spacers are placed between the gill bars to provide a passageway between the buccal and opercular cavities by eliminating the gill resistance, test 3.

The second test involves making a hole in the operculum so that the opercular cavity is in free communication with ambient water even when the gill cover is adducted. Care is taken not to interfere with the role of the gill cover in opening the mouth (see Materials and Methods). I predict that a hole in the operculum will result in a regression line with a significantly lower slope (Fig. 1) than the control regression, and that the peak magnitude of negative pressure within the buccal cavity will be unaffected because of the gill resistance. The alternative model predicts significantly reduced opercular *and* buccal pressures as an opening is made in the gill cover.

Finally, the third test examines the role of the gill bars (hypobranchial, cerato-branchial, and epibranchial bones and the associated soft tissues) in segregating the mouth cavity into two functional components. In this experiment, small spacers are attached to a section of the first three gill arches so that adduction of the gill bars cannot occur (this is illustrated in Fig. 2). The gills can still be abducted, but adduction is prevented by the spacers, and an open connection is established between the buccal and opercular cavities. The model of Lauder (1980a) predicts that the negative buccal and opercular cavity pressure magnitudes will tend to equalize, increasing the slope of the regression line (Fig. 1), while the alternative model predicts no change in the regression slope. Muller *et al.* (1982: p. 76) assert that it is 'inconceivable' that gill resistance could account for the different pressure magnitudes measured just anterior to and behind the gills. This test will decide the issue.

MATERIALS AND METHODS

The pressure recording technique used for these experiments represents a substantial improvement over the method used previously (Lauder, 1980a). Even when considerable care is taken to obtain the correct damping, diaphragm transducers such as the Statham P23 Db require a great deal of fluid within the transducer dome and the frequency response is 80 Hz at best. For this paper, two Millar PC-350 catheter-tip pressure transducers (1·67 mm o.d.) were used. Flexible polyethylene cannulae (0·86 mm i.d. and 1·52 mm o.d.) were implanted in the buccal and opercular cavities as described previously (Lauder, 1980a). The cannulae were between 15 and 20 cm in length (roughly one-third the length used before) and were connected directly to the Luer fitting over the catheter-tip transducer. With no catheter extension, Millar catheter-tip transducers have a frequency response of over 15 000 Hz, but with the catheters used here, frequency response is 300–500 Hz. The catheters were flushed regularly with distilled water, and in between experiments, fishes were allowed to swim freely trailing short lengths of tubing behind them. During pressure recording sessions, subjects were mildly hindered by the weight of the transducer catheter but were free to swim to all corners of the 80 l experimental aquaria. Buccal and opercular cavity pressures were always recorded simultaneously and more than 500 feeding events were available for analysis.
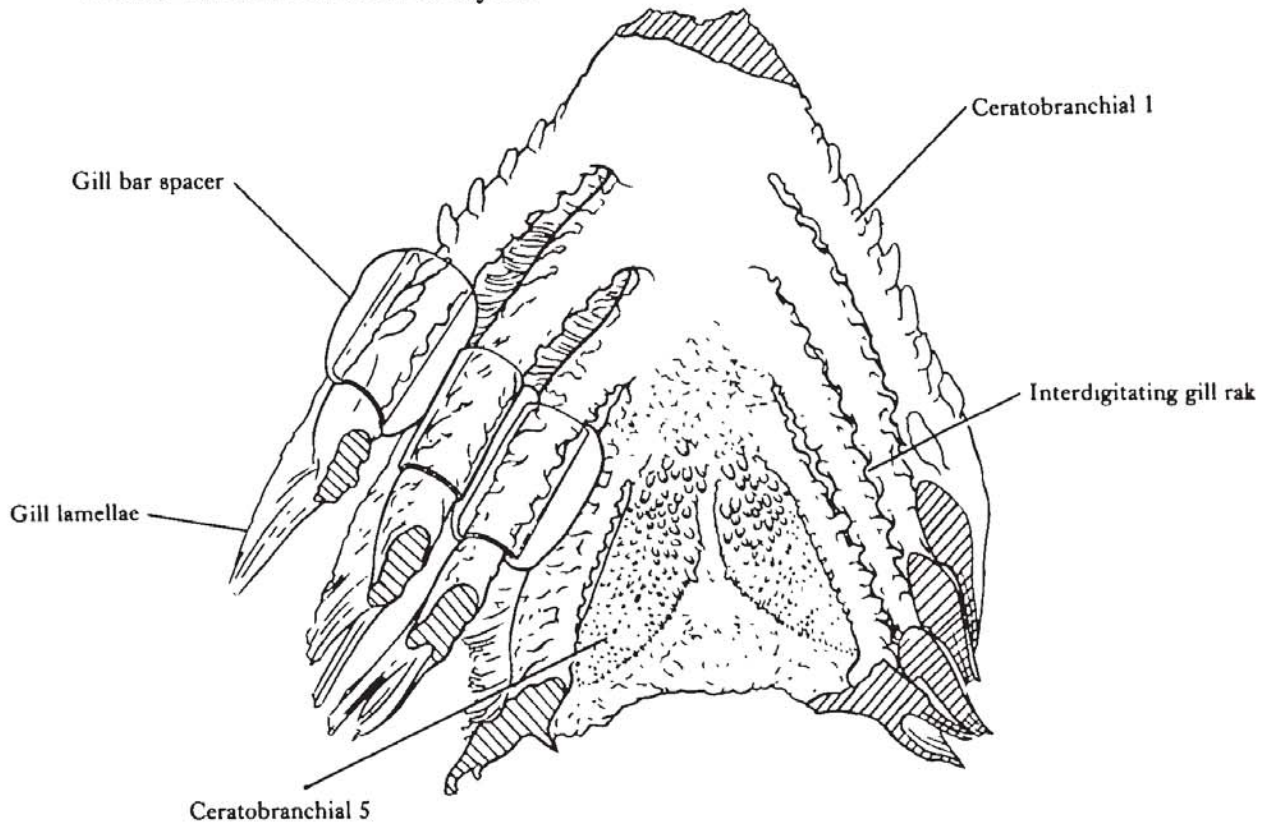

Fig. 2. Dorsal view of the ventral part of the branchial apparatus in *Lepomis macrochirus* × *cyanellus* to show the closely apposed gill arches on the right side (note the alternating short gill rakers on adjacent arches) and the effect on branchial resistance of placing spacer elements on the first three gill arches. The spacers open a connection between the buccal and opercular cavity by preventing gill arch adduction during the early stages of suction feeding.

Surgical modifications for the three experimental tests described above were performed with the specimens anaesthetized as described previously (Lauder & Norton, 1980). The dilator operculi tendon was severed lateral to the joint between the operculum and the hyomandibula just proximal to its attachment to the gill cover. *Post-mortem* dissections were performed to confirm that the tendon had been completely cut. For the second test, a piece (about $1 \cdot 0 \, cm^2$) was removed from the posteroventral margin of the operculum. Most of the bone was left intact so that the important role of this bone in opening the mouth (Liem, 1970) would not be disturbed. Gill filaments, and occasionally also the flared end of the opercular catheter, could be seen through the space in the operculum. The gill bar spacers for the third test were made out of lengths ($\leqslant 1$ cm) of polyethylene tubing ($2 \cdot 69$ mm i.d., $3 \cdot 5$ mm o.d.) with a longitudinal slit down one side. Small quantities of silicone rubber were applied to each side of the pieces of tubing to force the gill bars apart. Under anaesthesia, a spacer was unilaterally attached to each of the first three gill bars by slipping the slit tubing around the ceratobranchial so that tension in the tubing wall held the spacer to the gill arch. Spacers on adjacent arches abutted each other and created a free passageway between the buccal and opercular cavities above and below the spacers (Fig. 2). The gill arches could not be adducted, but could be (and were) abducted during feeding. The presence of spacers did not prevent the tips of primary gill lamellae from touching as is normal during respiration (Pasztor & Kleerekoper, 1962), and in no case did the presence of spacers clipped to the gill arches prevent the fish from closing the opercular or branchiostegal valves.

Four replicates of each test were conducted on different individuals. Bluegill (*Lepomis macrochirus*) collected in the Mississippi River were used for most experiments. Several tests were conducted using hybrid sunfishes (L. *macrochirus* × *cyanellus* Rafinesque) because their large size facilitated experimental modifications. All pressures are reported in mmHg and were measured at a water temperature of 17–18 °C. Control pressure recordings were always made on the same individuals used for subsequent experimental modification and in most cases the same set of implanted catheters was used also. Catheters were left in place for up to 14 days with little difficulty. In the only reversible modification, test 3, the spacers were removed at the end of the recording session in two experiments and pressures were recorded again. No statistically significant difference in regression line slope was found between these data and the initial controls.

Linear regression analysis was performed on the University of Chicago's Amdahl computer. A least-squares method was rejected as inappropriate because neither buccal nor opercular cavity pressure could strictly be regarded as the independent variable. The appropriate method in cases such as this is the reduced major axis method (see Discussion in Miller & Kahn, 1962; Imbrie, 1956). A z-statistic for comparing reduced major axis regression slopes (Miller & Kahn, 1962: p. 206) was used to test for significant difference between two slopes. Two-tailed probabilities were used for experimental test 1 because no *a priori* prediction about the direction of experimental slope deviation from the control was possible. For tests 2 and 3, one-tailed probabilities were used because of a specific *a priori* prediction of the direction of slope change (see Fig. 1).

It is important to note that pressure magnitude is a function of both predator

Table 1. *Descriptive statistics for testing models of suction feeding dynamics*

Replicate	Pressures (mmHg below ambient)	Test 1		Test 2		Test 3	
		control	experimental	control	experimental	control	experimental
1.	Mean buccal	263	289	111	82	212	134
	s.d. buccal	95	103	63	62	133	82
	Mean opercular	78	89	61	21	62	56
	s.d. opercular	15	25	32	16	28	29
	Regression slope	0·16	0·24	0·51	0·26	0·21	0·36
	Statistical significance[1]		NS		P<0·001		P<0·01
2.	Mean buccal	139	85	99	115	141	90
	s.d. buccal	57	57	55	60	88	85
	Mean opercular	73	51	64	19	41	56
	s.d. opercular	28	33	29	12	18	48
	Regression slope	0·47	0·57	0·53	0·21	0·20	0·57
	Statistical significance[1]		NS		P<0·001		P<0·001
3.	Mean buccal	76	123	148	179	333	96
	s.d. buccal	29	65	88	120	126	63
	Mean opercular	56	72	49	25	77	67
	s.d. opercular	20	34	27	12	27	45
	Regression slope	0·69	0·53	0·30	0·10	0·21	0·72
	Statistical significance[1]		NS		P<0·001		P<0·001
4.	Mean buccal	75	73	136	155	222	140
	s.d. buccal	37	37	92	72	92	56
	Mean opercular	48	50	41	27	104	98
	s.d. opercular	21	25	33	15	45	46
	Regression slope	0·57	0·68	0·36	0·21	0·49	0·82
	Statistical significance[1]		NS		P<0·01		P<0·01

[1] Of difference between slopes of reduced major axis regression lines for control versus experimental buccal and opercular pressures (see text).
NS = not significant at 0·05 level.   s.d. = standard deviation.

satiation and prey type (Lauder, 1980a). During each experiment, a variety of prey was used (worms, crayfish and minnows) in an attempt to elicit a range of pressure magnitudes. Because predictions about change in the relative *mean* buccal and opercular pressures would be susceptible to minor variations in the types of prey eaten during each experiment, the regression *slopes* were chosen as the most robust discriminator of the two suction feeding models.

RESULTS

The variability and basic components of buccal and opercular pressure waveforms recorded with catheter-tip pressure transducers in bluegill sunfish are similar in all respects to those reported elsewhere (Lauder, 1980a,b). One additional feature is the occurrence of higher frequency components in many of the opercular pressure traces than was indicated by previous records.

The comparative analysis of buccal and opercular pressure records in three other centrarchid species with different mouth sizes and shapes (Fig. 3) shows that buccal pressures always exceed opercular pressures. Of the four species studied, the bluegill possesses the greatest buccal pressures for a given opercular pressure with an avera
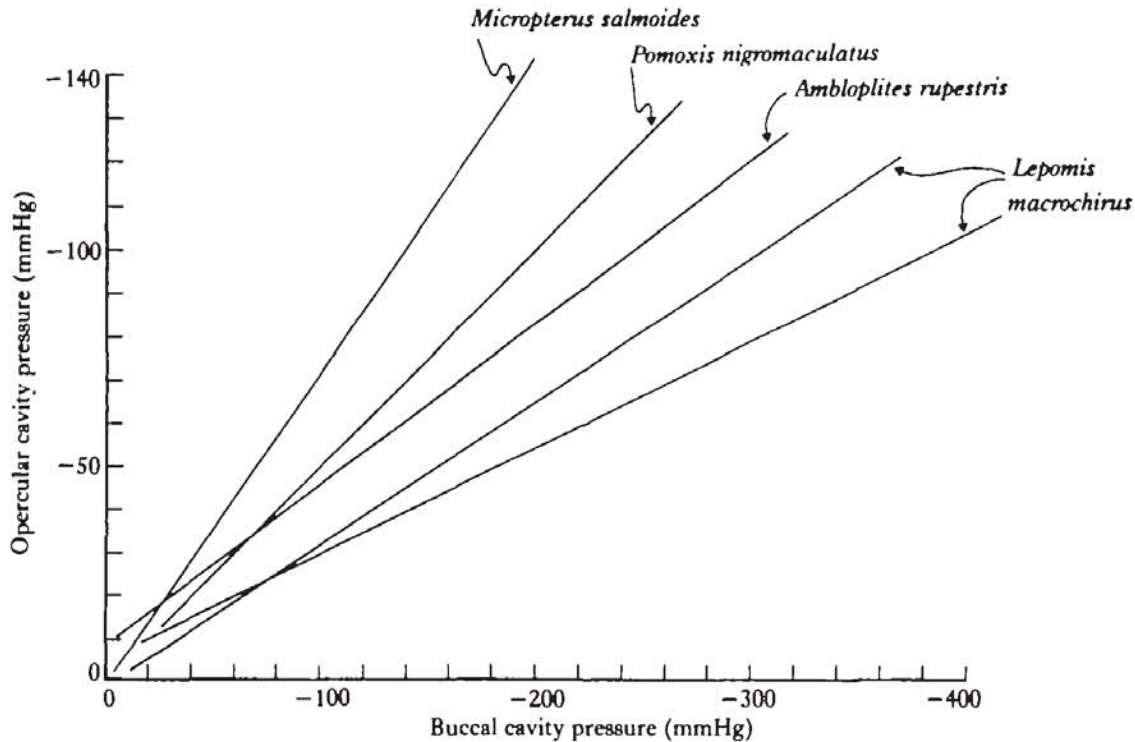
Fig. 3. Reduced major axis regressions (see text) for opercular and buccal pressures (simultaneously recorded) in four centrarchid species. The two lines for the bluegill, *Lepomis macrochirus*, illustrate the range of slopes that contains approximately 75 % of the individuals tested. The individuals in Table 1 with slopes over 0·50 were hybrids between the bluegill and green sunfish, *L. cyanellus*.

slope of 0·34. Opercular pressures greater than 130 mmHg are rarely recorded.

Representative scatterplots for each of the three experimental tests of the two suction feeding models are presented in Figs 4, 5 and 6 and descriptive statistics for the four replicates of each test are given in Table 1. The results are extremely clear and consistent. Severing the dilator operculi tendon to the operculum has no significant effect on the slope of the buccal and opercular pressure regression line. Cutting a hole in the operculum to establish a connection to ambient water (test 2) significantly reduces the slope (Fig. 5; Table 1). In none of the replicates performed was the reduction in slope significant at less than the 0·01 probability level, and three out of the four were significant at $P < 0·001$.

Similarly, inserting spacers between the gill bars produced a highly significant increase in regression line slope in all four replicates (Table 1). The example illustrated in Fig. 6 shows the effects of gill spacers particularly well. In normal bluegills feeding by high-speed inertial suction, opercular pressures reach a maximum of about −120 mmHg when buccal pressures attain values of −500 mmHg. These large negative pressures are achieved only during very rapid strikes at elusive prey. With spacers opening a passage between the buccal and opercular cavities and allowing pressures in the two chambers to more nearly reach equilibrium, opercular pressure reaches −145 mmHg at a buccal pressure of only −160 mmHg. Opercular pressures never exceed buccal pressures as a result of spacer implantation, but the two do approach an equilibrium value (regression slope of 1). Thus, the gill spacers reduce the differential in negative pressure between the two cavities and produce a statistically highly significant increase in regression line slope.
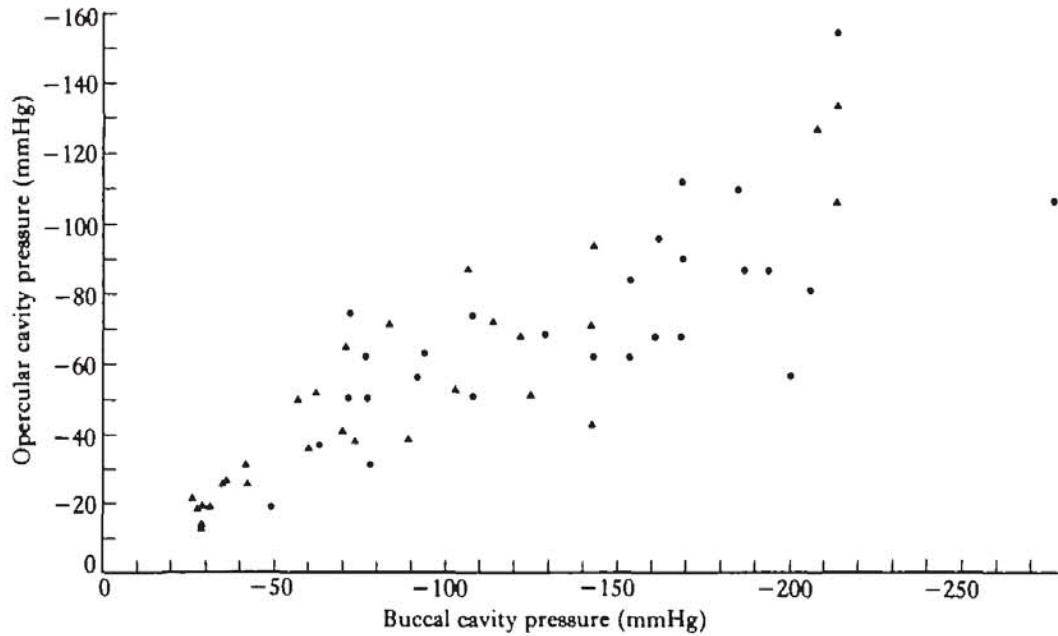
Fig. 4. Scatterplot of opercular and buccal pressures in *Lepomis macrochirus* × *cyanellus*. Circles are control points and triangles represent the pressures obtained after the tendon of the dilator operculi muscle to the operculum was severed (test 1). There is no significant difference in the slopes of reduced major axis regression lines through the control and experimental points (Table 1).
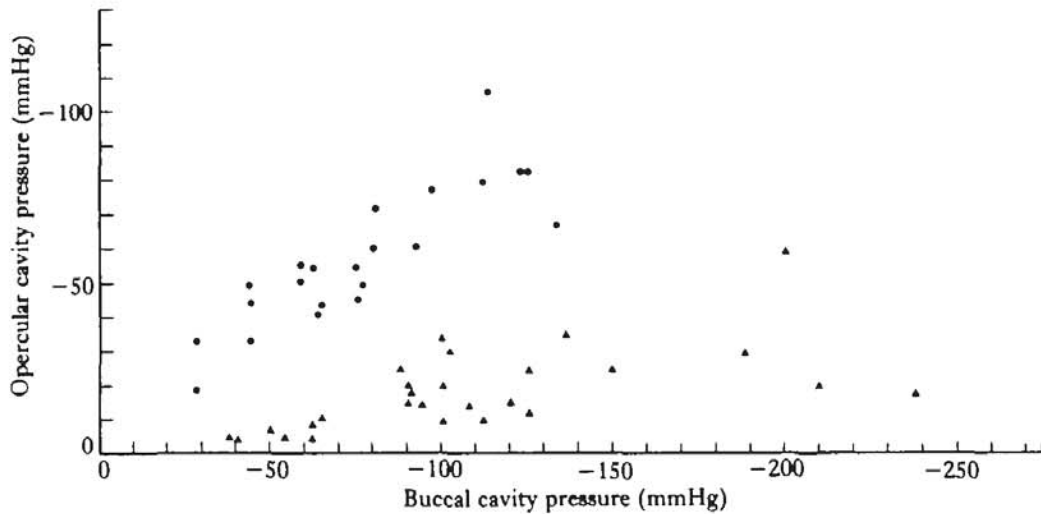

Fig. 5. Scatterplot of opercular and buccal pressures in *Lepomis macrochirus*. Circles are control points and triangles represent the pressures obtained after a hole (about 1 cm²) was cut in the operculum (test 2). There is a highly significant reduction in slope of the reduced major axis regression through the experimental points (Table 1).

In two experiments, the fish was reanaesthetized after pressures had been recorded with the spacers in place and the spacers were removed. In both cases the slope decreased and was statistically not significantly different from the initial control slope.

DISCUSSION

The results of all three experimental tests of the two suction feeding models indicate unambiguously that (1) the gill bars can function as a resistant element within the mouth cavity and (2) that abduction of the operculum by the dilator operculi plays little role in generating negative mouth cavity pressures. The data thus support neither the basic assumption of Muller *et al.* (1982) that the gills and gill bars can be ignored in models of suction feeding, nor their use of the gill cover as a fundamental element of the head regulating negative opercular *and* buccal cavity pressures.

In their discussion of gill resistance, Muller *et al.* (1982: p. 76) have confused the resistance due to the gill filaments (primary and secondary lamellae) during respiration and the resistance due to the gill bars and rakers during feeding. Remarkably, these authors suggest that during fish respiration the gill lamellae do not constitute a resistance to water flow, a view in contrast to the conclusions of numerous and well documented investigations into fish respiration (see e.g., Hughes, 1972: p. 4; Hughes & Morgan, 1973: pp. 452–454; Saunders, 1961: p. 650; Shelton, 1970: pp. 300–301, who comments that 'the concept of the dual pump rests on a gill curtain offering appreciable resistance to water flow'). During suction feeding, the gill *bars* (not filaments) constitute the resistance. Kinematic records of jaw bone movement in a wide variety of teleosts as well as in *Amia calva* (reviewed in Lauder, 1982) demonstrate that as the mouth begins to open the operculum is adducted. Gill bar resistance is very high at this time and decreases rapidly as the sides of the head expand during the middle and late stages of feeding. Fig. 2 illustrates that the gill bars fit closely against neighbouring arches and that the short stubby gill rakers of adjacent arches
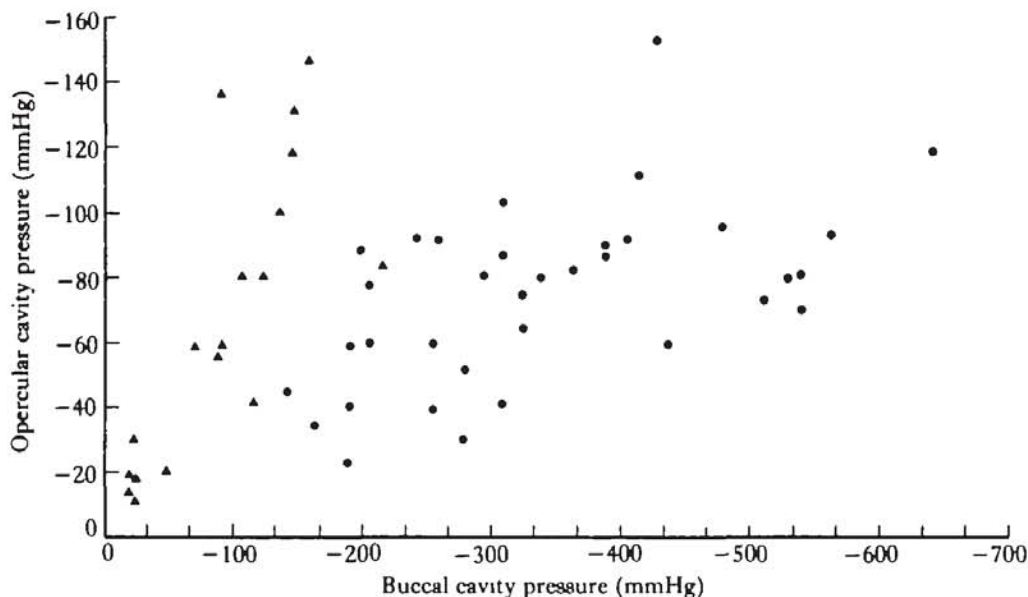

Fig. 6. Scatterplot of opercular and buccal pressures in *Lepomis macrochirus*. Circles are control points and triangles represent the pressures obtained after spacers were unilaterally placed between gill bars one, two and three (test 3). See text and Fig. 2 for discussion and illustration of the spacers. There is a highly significant increase in slope of the reduced major axis regression through the experimental points (Table 1), indicating that the branchial apparatus is an important resistance within the mouth cavity.

alternate in position when the arches are adducted. It is the formation of a near
continuous barrier as illustrated in the right side of Fig. 2 that constitutes the gill
resistance during the early phases of prey capture.

Further evidence of the role of the gill bars as a resistance during high-speed inertial
suction is derived from the results of test 2. When a hole was cut in the operculum,
opercular pressures declined to a mean of 13 mmHg while mean buccal pressure was
unaffected (Table 1). Opening a channel from the opercular cavity to the ambient
water thus has no effect on buccal pressure magnitudes.

These conclusions on gill resistance apply mainly to fishes feeding by high-speed
suction using extremely unsteady flows. Species that use body velocity to overtake
prey will probably exhibit a somewhat different pattern of buccal and opercular cavity
pressure change. Alexander (1967) proposed three simple categories for fishes feeding
on aquatic prey: (1) species that primarily use suction feeding and thus remain nearly
stationary relative to the prey, a method used by many ambush hunting fishes, (2)
species that actively pursue prey and thus are moving rapidly through the water when
food is engulfed, and (3) species using both body velocity and suction. Only high-
speed suction feeding fishes and fishes using a slow to moderate approach velocity are
likely to exhibit large pressure differentials across the gills. Pike (*Esox*), for example,
utilize rapid accelerations from rest and large amplitude body movements during prey
capture (Webb & Skadsen, 1980). The mouth opens well before the prey is reached
and the final stages of the strike occur with *both* the mouth and operculum at near
maximal abduction (Rand & Lauder, 1981). In addition, the gill bars are long and
slender and do not lie snugly against each other in the adducted position. Pressure
measurements during prey capture by *Esox* (G. V. Lauder, unpublished results)
confirm that no pressure differential exists across the gills: the mean ratio of buccal
to opercular peak negative pressures is 1 : 1. If the gills did possess a high resistance
and were held in the adducted position as the pike accelerated toward the prey, very
large drag forces would be produced.

The regressions illustrated in Fig. 1 are consistent with the notion of gill resistance
and mouth cavity pressure differentials bearing an inverse relationship to body veloc-
ity at the strike. The bass, *Micropterus*, attacks prey with a velocity of from
20–200 cm s^{-1} (Nyberg, 1971). This species also exhibits the smallest pressure differ-
ence across the gills (Fig. 1). Bluegill have much slower attack velocities (5–40 cm s^{-1})
and have the highest pressure differentials, while the rock bass (*Ambloplites*) and
crappie (*Pomoxis*) are intermediate in both respects.

The gill bars in bluegill are constructed so as to fit tightly up against each other in
the adducted position with the gill rakers of adjacent arches alternating in position
(Fig. 2). In the normal rest position during quiet respiration, only a small opening is
present between each pair of gill bars, while in the early stages of suction feeding, the
gill bars are adducted as the gill cover and suspensorium move medially (Lauder,
1980a). There is thus a clear morphological basis for the branchial apparatus func-
tioning as a resistance to flow within the mouth cavity.

Muller *et al.* (1980, 1982) consider the operculum to be a key element in generating
negative pressures within the mouth cavity of high-speed suction-feeding fishes.
Active opercular abduction is incorporated into their model as part of the 'expanding
cylinder' that serves as an analogue of the fish head. The results of experimental test

and 2 clearly indicate that lateral movement of the operculum plays essentially no role in generating buccal or opercular negative pressures (Table 1).

This conclusion is in agreement with three previous discussions of the role of the operculum, all based on different lines of evidence. (1) Alexander (1969) calculated the pressure against which the dilator operculi muscle of the orfe, *Idus idus*, could abduct the operculum, based on the cross-sectional area, fibre length, and moment arm of the dilator muscle. He concluded that a pressure of only -7 cmH$_2$O within the gill cavity was sufficient to prevent opercular abduction. Since opercular cavity pressures may reach -140 cmH$_2$O and are invariably more negative than -10 cmH$_2$O for nearly 70 % of the time that the mouth is open, it should not be expected that active opercular abduction would occur during the early and middle stages of suction feeding.

(2) Lauder & Lanyon (1980) measured bone strain in three directions on the lateral surface of the operculum during suction feeding and found that this bone was being deformed *medially* and twisted as opercular pressure decreased. The bone strain evidence thus also indicates that the gill cover is not moving laterally and contributing to negative opercular pressures during high-speed suction feeding.

Finally (3), the broad range of kinematic data now available on bone movement during suction feeding in fishes clearly indicates that the operculum moves medially or stays stationary during at least the first half of mouth opening, and often does not begin to abduct until peak gape has been reached (Lauder, 1980*a*, 1982). Even the data published by Osse & Muller (1980: Fig. 3b) demonstrate this point: opercular abduction in *Pterois* does not begin until mouth opening has reached 70 % of its peak value, and maximum opercular abduction occurs after the mouth has closed to 50 % of peak gape. In sum, the kinematic profile in high-speed suction-feeding fishes is extremely consistent (also see Alexander, 1970; Grobecker & Pietsch, 1979) and in all cases the gill cover exhibits delayed abduction and peak excursion relative to mouth opening.

One final aim of the theoretical model of Muller *et al.* (1982) is to predict accurately actual pressures within the buccal and opercular cavities. Now that a considerable body of comparative data has been obtained from a variety of species (Alexander, 1969, 1970; Lauder, 1980*a,b*, 1983, this paper; Liem, 1978) it is possible to compare the predicted pressures against those actually measured. (Predictions of flow velocity will be compared with measured values in a forthcoming paper.) The pressures within the mouth cavity predicted from the mathematical model have the following six salient characteristics (see Muller *et al.* 1982: Fig. 11): (1) negative opercular pressure is twice as large as pressure in the anterior portion of the buccal cavity; (2) pressure increases (in the opercular region) and decreases (in the buccal cavity) may reach 80 % of their peak values before mouth cavity expansion has progressed to even 5 % of its peak value (these figures were measured from Fig. 11 of Muller *et al.* 1982); (3) buccal cavity pressures show only a single negative phase; (4) all predicted pressures for the (normal) feeding situation in which water is allowed to exit over the gill cover decline asymptotically towards a limit considerably less than ambient pressure; (5) peak negative buccal and opercular pressures occur synchronously and (6) pressure at the mouth opening declines rapidly and remains at its peak value, never returning ambient.

None of these features characterize pressure traces obtained from living fishes. As emphasized above, buccal pressures in all high-speed suction-feeding fishes studied to date exceed opercular pressures. Also, mouth cavity pressures begin to change only 5–10 ms after buccal expansion begins (Lauder, 1980a), buccal pressures commonly exhibit two negative phases (the second due to flow momentum causing a local pressure decrease inside the mouth as the jaws rapidly close – the water hammer effect, Lauder, 1980a,b), measured pressures always return to ambient after a feeding event, and peak negative buccal pressure occurs before the maximum pressure reduction in the opercular cavity.

At least for rapid prey capture by inertial suction, predictions derived from current mathematical models of the feeding mechanism, despite adjustments by assuming relevant biological constraints, fail to characterize, even generally, the relative magnitudes and waveforms of pressures measured experimentally.

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