

SHORT COMMUNICATION

PREY CAPTURE HYDRODYNAMICS IN FISHES: TWO APPROACHES

BY M. MULLER, J. L. VAN LEEUWEN, J. W. M. OSSE AND
M. R. DROST

*Department of Experimental Animal Morphology and Cell Biology,
Agricultural University, Marijkeweg 40, 6709 PG Wageningen,
The Netherlands*

Accepted 20 May 1985

Suction feeding is widely used in teleost fish (>20 000 species). It is accomplished by rapid expansion and contraction (<100 ms) of the buccal and opercular cavities and results in movement of both the prey and the fish itself. Suction is often combined with jaw protrusion and swimming. During a single suction movement the volume of water passing through the mouth aperture may exceed, by more than five times, the volume of the fully expanded mouth cavity, since after a given moment water leaves the mouth through the opercular slits. The generated flow is highly unsteady, i.e. large local accelerations ($>50 \text{ m s}^{-2}$) occur and streamline patterns change rapidly with time.

Muller & Osse (1978) and Muller, Osse & Verhagen (1982) have constructed a quantitative hydrodynamical model of the fish's sucking system, in which the buccal and opercular cavities ('mouth cavity') are represented by an expanding and contracting cone ('profile'). The posterior end can expand with different phase and amplitude compared to the anterior end, the mouth aperture. The dimensions and the movements of the fish are the inputs of the model. The velocities of the water inside and in front of the mouth are calculated from expansion, compression and forward motion of the profile. The pressures are calculated from these velocities and accelerations and compared with experimental data (van Leeuwen & Muller, 1983). Gill resistance was ignored in our calculations. In fact, this resistance will vary with time.

On the basis of this model and measurements on nine fish species of different families, several feeding types were distinguished, characterized by the shape of the flow, time of valve opening, relative contribution of forward motion and presence or absence of jaw protrusion. The streamlining of the mouth cavity, pectoral girdle and gills was explained in relation to water flow during feeding. Changes in fish head construction during evolution were interpreted as improvements of the hydrodynamic efficiency of suction feeding (Muller & Osse, 1984). Finally, conditions for optimal prey-suction were derived (van Leeuwen & Muller, 1984). Our goal was to formulate

a quantitative theory, giving hypotheses for the options fish of different form and ecological niche have to manipulate the flow during prey capture (see above references). *Hypotheses from our model about pressures can only be based on very accurate measurements of the expansion of the buccal and opercular cavities (i.e. movement curves, accurate up to the second derivative are required).*

Lauder (1983) compared this approach with that from his own qualitative model (Lauder, 1980*a,b*). The approach of Lauder is based on pressure waveforms, measured in the buccal and opercular cavities of *Lepomis*. The flow direction is deduced from these recordings by comparing the instantaneous values of these pressures. From the quite variable recordings, a typical one was chosen for this purpose. Lauder (1983) presented three experimental tests, the results of which were claimed to support his approach alone. The present paper examines the two approaches and the merits of the experiments to test their validity.

Formulation of hypotheses

Based on his approach Lauder (1983) formulated two hypotheses. (1) Opercular abduction plays a negligible role in generating negative buccal or opercular cavity pressures and (2) gill resistance, dividing the mouth cavity into buccal and opercular cavities is the main cause of pressure differentials between the cavities in suction feeding.

To compare his approach with ours, Lauder formulated two corresponding hypotheses for the model of Muller *et al.* (1982). These were: (1) abduction of the operculum is 'crucial for generating negative pressures' and (2) that gill lamellae do not constitute a resistance to water flow.

Our suggestions are as follows.

(1) the contribution of gill cover abduction can be simulated with our model, by varying the input parameters of the posterior expansion (delay time, amplitude and speed). An example of the influence of the delay time and the expansion rate on the pressure halfway along the fish's mouth is given by van Leeuwen & Muller (1984). *Specific predictions about the influence of gill cover abduction on the pressure, for a particular specimen of a particular species, cannot be made without quantitative data of the dimensions of the fish and its expansion movements.* Obviously, negative pressures can be generated by buccal expansion alone. So, we do not accept Lauder's first suggestion for our model.

(2) Any object placed in a flow will act as a resistant element. The question is thus *not* whether the gills act as a resistant element, but how much they influence the flow as a function of the time (owing to their changing positions and shapes). We did not state that the resistance is zero, but we simplified our model by ignoring its influence. Simulations of feeding events of four fish species provided a satisfactory similarity between measured and calculated pressures (van Leeuwen & Muller, 1983), suggesting that gill resistance has little influence on pressure fluctuations in these species. These findings may not be confirmed for all fish, since the anatomy of the gill filaments and bars is quite variable. Therefore, a further elaboration of our model, which takes account of gill resistance, may be worthwhile.

Experimental tests

Lauder tests the influence of: (1) transection of the m. dilatator operculi, (2)

perforation of the operculum, and (3) the placing of spacers between gill bars, on the measured pressures in the buccal and opercular cavities. The peak negative values of the pressures were plotted against each other and the slope of the regression line chosen as 'the most robust discriminator of the two suction feeding models'. According to Lauder the two models would predict different changes in the slopes for each of the three cases. This approach presents a series of problems. The following comments are concerned with the prediction of changes of slopes, the influences of experimental treatment of the animals, the accuracy of pressure measurements and the statistical significance of the tests. The validity of specific tests will be discussed briefly.

Predictions of changes of slope

To predict a change of slope with our model we would need to know the movements of the individual snaps for both the control situation and the test situation. From these movements, the peak negative values of the pressures could be calculated for all snaps and from these values the regression lines could be calculated. *The data presented by Lauder are not sufficient to enable predictions to be made from our model and Lauder's suggestions for them may be mistaken.*

Manipulations with the fishes

During a test, preferably only one parameter should change and all other parameters should remain rather constant. Lauder's tests involve serious manipulations (including mutilation) of the fish, such that the entire movements will be different before and after treatment. *Therefore, predictions about the functioning of the system after manipulation or severing parts of it are hard to give.* We emphasize that, in a system as complex as the head of a sucking fish (with many variables of form and movement) it is tempting to adapt the reasoning to validate either model.

Accuracy of pressure measurements

Fluid-filled catheters should be avoided in measuring pressures, since *accelerations of the fluid in the catheter seriously distort the records* (even exceeding 100%) (van Leeuwen & Muller, 1983, Fig. 8). Also, *the bandwidth of the pressure transducer is much reduced* (10- to 100-fold), thus affecting the accuracy of amplitude and phase recording. Therefore, catheter tip transducers should be used, with the tip directly inserted at the measuring position. As Lauder (1983) connected his catheter tip transducer *via* a fluid-filled cannula to the fish's mouth cavity, the pressure data obtained were similar to those obtained earlier with Statham transducers. With this technique, different tube orientations alone can induce considerable differences in the two synchronously measured pressure waveforms from buccal and opercular cavities.

Statistical significance

Most of Lauder's experiments were done with *Lepomis macrochirus*. For this species a range of control slopes is shown in his Fig. 3 of 0.24–0.33 for 75% of the individuals tested. Surprisingly, in Lauder's table (containing the test results) only *one* of the eight control slopes for *L. macrochirus* lies in this range. *Thus the range is apparently much greater* (at least 0.16–0.65, 0.65 was calculated by us for the control

data of Fig. 5). Lauder's figures show that many times, for individual snaps, the peak opercular pressure is more negative than the peak buccal pressure. *This is in contradiction with Lauder's model.* Additionally, for the same species, the change of slopes in tests 2 and 3 shown in the table *falls within the range of control slopes in four of the six cases.* Lauder's Table 1 contains only a *sample* of the data (e.g. data from Fig. 5 are omitted). The control slope in Fig. 5 (0.65) is closer to the experimental slope in Fig. 6 (0.78) than to the control slope in Fig. 6 (0.21).

Finally, *the variation in control slopes between the species* (Lauder, 1983, Fig. 3) *is as big as the (great) difference in slopes which test 3 is expected to produce* (Fig. 1) *and indeed produces* (Fig. 6).

Discussion of the individual tests

Test 1. Test 1 involves cutting of the m. dilatator operculi (m.d.o.), stated by Lauder (1983, p.2) to be 'the only muscle capable of active opercular abduction'. In respiration it is indeed important. In feeding, however, the power needed for caudal expansion of the head is delivered by the body musculature (Osse, 1969; Alexander, 1983). Cutting the tendon of the m.d.o. does not therefore disable active opercular expansion through the ventral kinematic chain. So test 1 was invalid.

Test 2. In test 2 the operculum was perforated. Lauder's (1983, p.3) model predicts that the opercular pressure should drop and 'the peak magnitude of negative pressure within the buccal cavity will be unaffected'. He suggests that the model of Muller *et al.* (1982) would predict that both peak buccal pressure (P_{bu}) and peak opercular pressure (P_{op}) should drop. This suggestion is incorrect since it is based on steady flow assumptions. In fact, the model of Muller *et al.* takes unsteady flow features into account, such that water can move against a pressure gradient. Calculations with this model show, that in a fish mouth profile without gills, the buccal pressure can have a more negative value than the opercular pressure when water flows from the buccal to the opercular cavity (Muller & Osse, 1984). As movement analyses are not provided by Lauder (1983), we cannot make predictions for *individual* snaps.

Lauder's (1983) Fig. 5 shows no control data with a value of P_{bu} more negative than -135 mmHg, while for about 25 % of the experimental data P_{bu} is more negative than this value. This *could* mean that the mutilated fish compensates its decreased suction ability with a more powerful buccal expansion, resulting in a more negative buccal pressure peak and a less negative opercular peak.

Test 3. Test 3 involves mounting of spacers on the gill bars. Lauder (1983, p.3) predicts that 'the negative buccal and opercular cavity pressure magnitudes tend to equalize, increasing the slope of the regression line'. Under this prediction we would expect that the effect on P_{op} should be most dramatic because it is said that P_{bu} is at least four times greater in amplitude than P_{op} . Lauder (1983, Fig. 6) indeed shows that P_{bu} becomes less negative, but apparently the ranges of control and experimental values of P_{op} remain quite similar. Also in his Table 1 P_{op} becomes less negative in three of the four cases!

Lauder predicts from our model that the slope should not change. Again, *without motion data we cannot give a definitive prediction.* We note, however, that the spacers increase the initial volume of the mouth cavity. Pressure is reversibly and non-linearly proportional to initial volume (Muller & Osse, 1984). Because the volume of the

mouth cavity is much smaller at the moment of peak buccal than at peak opercular pressure, the relative increase of the volume is greatest at the moment of the buccal peak. The effect of the spacers will thus be much greater on P_{bu} than on P_{op} (this agrees with Lauder's Table 1).

Concluding remarks

Lauder's (1980*a,b*) methodology, presents a number of problems. (1) His approach is based on steady flow assumptions by deducing the flow direction from the pressures, whereas the flow in suction feeding is unsteady. (2) Pressure measurements were used to construct a model, which has to reproduce these pressures. (3) The pressure fluctuations were correlated with movement data which were not shown to be simultaneously recorded with the typical recording used for his model. The movements differ markedly in the two papers describing his model (Lauder, 1980*a*, Fig. 15; 1980*b*, Fig. 5). (4) The input parameters are not defined for his model and the forward motion of the fish is not considered. (5) In Fig. 5B (Lauder, 1980*b*), the opercular expansion with closed opercular valves occurs synchronously with a reverse flow *out of the opercular cavities!* Because water is incompressible this is impossible.

Lauder (1983, p.1) concludes that the results of his experiments 'unequivocally support' his approach and that 'measured pressures conform neither in relative magnitude nor waveform with pressures predicted from theoretical mathematical models'. We conclude that the tests performed by Lauder are subject to enough criticism to reject his claim that an unequivocal decision in favour of his model is justified. Lauder (1983) does not compare his pressure waveforms with those derived from theoretical mathematical models. The latter use the movements and dimensions of the fish to determine pressure waveforms. Since no data are provided on movements and dimensions of the fish used in his experiments, a direct comparison as suggested by Lauder is impossible.

Lauder's hypothesis (p.390) about the negligible role of opercular abduction in generating negative mouth cavity pressures is not supported by his tests. In fact, it ignores the kinematic linkage between the gill covers and the trunk *via* the pectoral girdle and the hyoids. The hypothesis may be studied as outlined above (p.390). Lauder's tests do not provide unambiguous answers about the role of the gills (bars and filaments). Elaboration of theoretical models in combination with experimental work is needed for fundamental new insight in this respect. In our opinion the explanation of pressure waveforms is not a goal in itself. Many other important problems remain to be solved, such as the ecological significance of the great diversity of feeding adaptations in fish.

We thank anonymous referees for their most useful comments.

REFERENCES

- ALEXANDER, R. McN. (1983). *Animal Mechanics*. Oxford, London: Blackwell Scientific Publishers.
 LAUDER, G. V. (1980*a*). The suction feeding mechanism in sunfishes (*Lepomis*): an experimental analysis. *J. exp. Biol.* **88**, 49–72.
 LAUDER, G. V. (1980*b*). Hydrodynamics of prey capture by teleost fishes. *Proceedings of the Second Conference on Bio-Fluid Mechanics*, Vol. 2, pp. 161–181. New York: Plenum Press.

- LAUDER, G. V. (1983). Prey capture hydrodynamics in fishes: experimental tests of two models. *J. exp. Biol.* **104**, 1–13.
- MULLER, M. & OSSE, J. W. M. (1978). Structural adaptations to suction feeding in fish. In *Proceedings of the ZODIAC Symposium on Adaptation*, pp. 57–60. Wageningen, The Netherlands: Pudoc.
- MULLER, M. & OSSE, J. W. M. (1984). Hydrodynamics of suction feeding in fish. *Trans. zool. Soc. Lond* **37**, 51–135.
- MULLER, M., OSSE, J. W. M. & VERHAGEN, J. H. G. (1982). A quantitative hydrodynamical model of suction feeding in fish. *J. theor. Biol.* **95**, 49–79.
- OSSE, J. W. M. (1969). Functional morphology of the head of the perch (*Perca fluviatilis* L.): an electromyographic study. *Neth. J. Zool.* **19**, 289–392.
- VAN LEEUWEN, J. L. & MULLER, M. (1983). The recording and interpretation of pressures in prey sucking fish. *Neth. J. Zool.* **33**, 425–475.
- VAN LEEUWEN, J. L. & MULLER, M. (1984). Optimum sucking techniques for predatory fish. *Trans. zool. Soc. Lond* **37**, 137–169.