

SHORT COMMUNICATION

AQUATIC PREY CAPTURE IN FISHES: EXPERIMENTAL
AND THEORETICAL APPROACHES

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In our attempts to understand how animals work, the diversity of animal design and the physiological basis of animal behaviour it is common to make theoretical models of animal function and to conduct experiments to test these models. Experimental analyses often provide a direct test of competing models, evaluate the accuracy of assumptions of models and, at a more descriptive level, simply provide increased observational precision. On the other hand, theoretical models may play an important heuristic role in suggesting new experiments and may provide a general predictive framework within which research can progress.

The value of a theoretical model of animal function is judged on both the validity of the assumptions that go into the model and on the accuracy of predictions from the model. If it can be shown that a model's assumptions are invalid *and* that it makes inaccurate predictions, then we must question the utility of the model for furthering our understanding of organismal design.

In this journal, Muller, Leeuwen, Osse & Drost (1985) have recently responded to an earlier paper of mine (Lauder, 1983) that outlined three experimental tests of their theoretical model of aquatic prey capture in fishes (Muller, Osse & Verhagen, 1982). These authors suggest that my tests of their model do not invalidate it. In this paper, I will (1) briefly review the key features of this debate, (2) evaluate the experimental tests of the Muller *et al.* (1982) model and reconsider its validity, and then (3) adduce additional evidence against both the assumptions and predictions provided by Muller *et al.* (1982).

Models of aquatic prey capture

Aquatic prey capture in fishes (and many other lower vertebrates) predominantly occurs by suction feeding in which the volume of the mouth is rapidly increased and the intraoral pressure thus decreased (Alexander, 1969; Lauder, 1980a; Liem, 1970). This produces a flow of water that carries the prey into the mouth. At least three reasons underlie the interest in this feeding system over the last 20 years: it is the dominant mode of energy acquisition in vertebrates, the biomechanical basis of the feeding mechanism is extremely complex with over 50 independently mobile

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bony elements controlled by as many muscles, and feeding can be very rapid with prey capture occurring within 10 ms. There are two main points of contention with regard to the mechanics of suction feeding. First, what is the role of the opercular bone in generating the negative pressure within the mouth cavity? Second, how significant are the gill supports within the mouth cavity in determining the pattern of intraoral pressure change?

My 1983 paper was designed to provide simple experimental tests of the two current views on these questions. Muller *et al.* (1980, 1982) proposed that lateral motion of the operculum contributes to negative pressure within the mouth cavity. I have suggested otherwise (Lauder, 1980*a,b*). Muller *et al.* (1982: pp. 76–77) explicitly rejected the notion that the gill apparatus within the mouth could be responsible for the large differential pressures measured between the buccal and opercular cavities. They state (Muller *et al.* 1982: bottom of p. 76): 'It is in our view inconceivable that such a wide range of resistance can be achieved in the gills.' I have suggested otherwise (1980*b*) and proposed that the gill apparatus forms a dynamic resistance to flow that entirely explains the differences in pressure recorded within the mouth.

Muller *et al.* (1985: p. 390) now suggest that their model does not necessarily predict a causal relationship between opercular movement and negative buccal pressure, but their previous papers in which the details of the model are presented contradict this (see Muller *et al.* 1980: p. 930; Osse & Muller, 1980: p. 349; Muller *et al.* 1982: p. 51; Osse, 1969: p. 368).

Experimental tests

In my 1983 paper, three tests of these two views of the role of the operculum and gill apparatus were provided. These tests were simple experimental manipulations designed to decide clearly between the alternative hypotheses. For example, in order to determine if the operculum contributed to generating negative pressure in the mouth cavity, I cut the thin tendon of the major muscle that abducts the operculum. Control measurements of pressure were made prior to surgery and compared to the experimental treatment. In a second test, I removed about 1 cm² of the posterior opercular margin, establishing a connection between the opercular cavity and the outside. No biomechanical linkages were disrupted by this procedure.

In order to test the possible role of the gill apparatus in causing the large pressure differential between the buccal and opercular cavities, I made control recordings of both pressures *simultaneously* during feeding, and then placed small spacers between the gill bars of the same fish. The spacers were designed to open a pathway for water flow between the buccal and opercular cavities. If the gill bars are acting as a resistance, then the pressure differential should sharply decrease after the spacers are put in place. Furthermore, subsequent removal of the spacers should restore the pressure differential. This is in fact exactly what happened in all fish studied.

Muller *et al.* (1985: pp. 391–392) do not accept the evidence provided by these experiments. Some of their objections appear to stem from a general lack of confidence in experimental biology, as they object to my use of surgical intervention

as an experimental treatment. In contrast to their suggestions, each test did indeed only modify one parameter. In addition, experimental manipulations of this kind are common in vertebrate functional morphology precisely because of the power of direct experimental intervention to decide between alternative explanations (e.g. Gans & Gorniak, 1982: wiring the hyoid of *Bufo* to the sternum; Jenkins, 1974: removing the clavicles from rats; Liem, 1970: cutting tendons and ligaments in the fish feeding mechanism; Webb, 1971: suturing extra drag loads to the dorsum of fishes; Webb, 1973: removing various pieces of the trout caudal fin).

Muller *et al.* (1985) have also seriously misunderstood the nature of the statistical analyses used. It is simply not true, as these authors claim, that control opercular pressures were more negative than buccal pressures as an examination of the figures will show. Furthermore, the entire experimental design was paired, so that individual differences would be taken into account. Individual fishes are indeed significantly different from one another, a fact surprising to Muller *et al.* (1985), but now well documented for many functional aspects of lower vertebrate feeding patterns (Shaffer & Lauder, 1985*a,b*; Wainwright & Lauder, 1986). This is exactly the reason why I replicated each test on three individuals and tested for differences between control and treatment recordings *within* individuals. In each case, all three individuals produced identical results.

Throughout their paper, Muller *et al.* (1985) suggest that I have modelled the process of suction as a steady-state process based on pressure recordings alone. This is not true, as noted in the Summary of Lauder (1983), 'Inertial effects and accelerational flows are key aspects of high-speed suction feeding' (p. 1), and again at the bottom of page 1 and on pages 10 and 12.

Muller *et al.* (1985) criticize the accuracy of my pressure measurements, despite the fact that they were made with catheter-tipped transducers that have a frequency response of over 10 kHz. I have found absolutely no significant differences between pressure traces recorded with the catheter tip located directly adjacent to the mouth cavity and when the transducer is located 1–2 cm from the mouth cavity. Remarkably, Osse & Muller (1980: p. 339) published pressure traces of *Amia* feeding obtained with a Statham transducer (maximum frequency response of about 100 Hz) to which they then connected a 60-cm long, narrow, fluid-filled catheter.

Finally, it is important to emphasize that the model of Muller *et al.* (1982) fails to predict accurately pressure traces obtained experimentally from feeding fishes. The waveforms predicted by their model simply do not match those recorded from feeding fishes. Their model does indeed predict that the pressure within the mouth will drop and then return to ambient, but surely this is no advance as the decrease in intraoral pressure during feeding has been known for 40 years (Tchernavin, 1948).

I invite Muller *et al.* simply to replicate my simultaneous measurements of buccal and opercular pressures in a variety of fishes (using a technique of their choosing), to provide scatterplots with about 20 points, and to document for themselves the large variation that exists between individuals. As I noted previously (Lauder, 1983) fishes that have relatively slow attack velocities (such as *Lepomis* and *Pterois*) are predicted to have large differential pressures between the buccal and opercular cavities. On

the other hand, fishes such as *Amia*, *Salmo* and *Micropterus* with higher attack velocities should have greatly reduced pressure differentials between the buccal and opercular cavities. These predictions should be easy for Muller *et al.* to test.

Additional evidence

Since the publication of my 1983 paper, several additional investigations have provided direct evidence against the proposals of Muller *et al.* (1982) on the function of the feeding apparatus during suction feeding. First, as predicted, the gill resistance has been shown to be time dependent. While the *existence* of a gill resistance that is causally related to the differential pressures within the mouth cavity was demonstrated by the insertion of spacers (Lauder, 1983), the time course of the gill resistance was then unknown. Lauder (1985a) and Lauder, Wainwright & Findeis (1986) have directly transduced the distance between adjacent gill bars during feeding. These traces clearly show that as the mouth is opened, the gill bars are *adducted*, forming a high resistance to flow. Near peak gape the gill bars begin moving apart, allowing water to flow into the opercular cavity. These gill bar movements were recorded *simultaneously* with mouth pressures and electrical activity in four cranial muscles, allowing a complete description of the determinants of buccal pressure changes.

Second, extensive comparative analyses of aquatic feeding in salamanders have been completed (Lauder & Shaffer, 1985; Shaffer & Lauder, 1985a,b; also see Lauder 1985a,b). These studies are relevant to our understanding of suction feeding dynamics because salamanders lack an operculum, and have the posterior margin of the mouth cavity delimited by the gill apparatus with its interlocking rakers. Salamanders thus permit a *comparative test* of the alternative views of the function of the gill apparatus. These experiments clearly showed that, despite lacking an operculum, suction feeding proceeds normally and that the gill bars adduct to prevent water influx from the back of the mouth cavity. Direct transduction of gill bar motion showed an identical pattern to that seen in ray-finned fishes, extending the generality of the model proposed earlier (Lauder, 1980a,b, 1983), and emphasizing the key role of a dynamic gill resistance in lower vertebrate feeding mechanisms.

Conclusion

The model of aquatic feeding proposed by Muller *et al.* (1982) is unsatisfactory from several perspectives. (1) The model fails to achieve even the most basic goal of predicting accurately the pressures generated by feeding fishes. (2) The assumptions of the model have been shown to be invalid, especially those concerning the function of the gill apparatus and operculum. (3) The model is limited in generality, extremely complex, and requires numerous experimental measurements of a single feeding before the pressures can be estimated for that feeding. This restricts the applicability of the model and its heuristic value.

It is of interest to note that Muller *et al.* have themselves neither outlined the tests that *could* be done to refute their model, nor have they provided the appropriate

experimental data that would allow others to evaluate more completely the usefulness of their model.

The bases of a modern scientific research programme are (1) the testing of hypotheses and (2) the replication of experimental results. Muller *et al.* (1982, 1985) show no evidence that they are willing to replicate my experiments (which I certainly invite them to do), nor do they provide avenues by which other investigators can test their model. If we are to advance our understanding of the diversity of animal design, it is crucial not to attempt to forestall progress with *ad hoc* arguments designed to buttress favoured hypotheses, but rather to provide explicit tests and succinct predictive models of animal function.

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