

## Hydrodynamics of suction feeding of fish in motion

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(Received 16 July 1979, Accepted 11 September 1979)

Forward motion was shown to increase the efficiency of suction feeding by causing the ingested volume to be predominantly in front of the fish, instead of being a sphere centred on the fish mouth. This increases the distance from which a prey, located in front of the predator, can be ingested by suction.

A general hydrodynamic model of the external effects of the suction process is presented, showing that this is dependent upon a single non-dimensional parameter, the ratio of a characteristic mouth dimension, divided by the forward swimming speed and the suction time. Data for large-mouth bass, *Micropterus salmoides* show that the observed average forward velocity while feeding, of 3.1 body length/s, serves to increase the ingestion range by more than 60% over suction while not moving.

### I. INTRODUCTION

Many teleost fishes feed by means of a sudden enlargement of the buccal and opercular cavities, producing a suction force (Nikolsky, 1963; Alexander, 1967). This suction causes a certain volume to be engulfed and prey capture will take place only if the prey (or at least its centre of gravity) is within this volume. Alexander's (1967) model assumes that the water flow towards the mouth is equal from all directions. This model is applicable mainly to feeding while the fish is motionless. Observations by Nyberg (1971) show that the water swallowed originates mainly in the volume in front of the fish's mouth when the fish is moving while feeding. The present paper describes a quantitative hydrodynamical model for suction feeding while the fish is in motion. Forward motion is shown to increase considerably the range over which food is ingested for a given mouth size and opening rate.

### II. THE THEORETICAL MODEL

Suction feeding can be modelled as a hydrodynamic sink (Milne-Thomson, 1968), i.e. a point in space in which fluid is being withdrawn from the ambient surroundings. Essentially, this is the basis for Alexander's (1967, 1969) model of suction feeding. This model, which predicts equal intake from all directions, describes stationary feeding (i.e. when the fish is not moving while feeding) (Alexander, loc. cit.; Elshoud-Oldenhave & Osse, 1976). However, the symmetry required by this model breaks down when the predator is moving while the feeding process takes place and fluid is ingested preferentially from the forward direction (Nyberg, 1971). This enables more efficient feeding as the volume of water in which the prey has to be located is distended in the forward direction.

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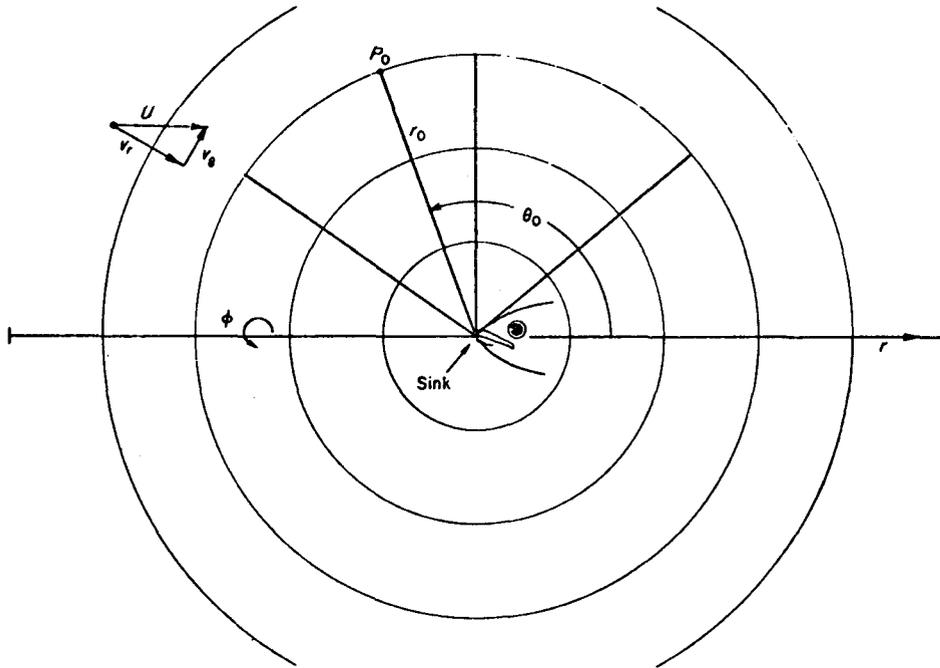


FIG. 1. Definition of the spherical coordinate system moving with the fish.  $r_0$  and  $\theta_0$  are the coordinates of point  $P_0$  and  $v_r, v_\theta$  are the radial and tangential components of the oncoming velocity (which is equal and opposite to the fish velocity).

In order to describe this process mathematically we define a spherical coordinate system attached to the centre of the predator's mouth, which will serve as the sink point (Fig. 1). Thus, any motion of the fish as a whole will be described by a velocity,  $U$ , of the surrounding fluid. This velocity can be constant, or time dependent (acceleration) and is in a direction opposite to the movement of the fish's centre of mass. We assume that the direction of motion of the fish is constant, i.e. it is swimming in a straight line while feeding takes place. This limitation could easily be relaxed but as most suction feeding takes place in less than one-tenth of a second, it is probably a realistic assumption.

The velocity field induced in an incompressible fluid (water) by a point sink is (Milne-Thomson, 1968):

$$v_r = -\frac{Q}{4\pi r^2}; v_\theta, v_\phi = 0 \tag{1}$$

where  $v_r$  is the radial component (the minus sign indicates inward flow),  $r$  is the distance from the sink,  $Q$  is the rate of mass intake, and  $\theta$  and  $\phi$  are defined in Fig. 1. As mentioned above, any forward speed of the fish is translated into water motion, so that the velocity components due to this motion are, from Fig. 1 (assuming axial symmetry):

$$V_r = U \cos \theta; v_\theta = -U \sin \theta \tag{2}$$

and the total velocity at each point is obtained by superposition of the two fields:

$$v_r = U(\cos \theta - \frac{Q}{4\pi U r^2}) \tag{3a}$$

$$v_\theta = -U \sin \theta. \tag{3b}$$

We now calculate the time,  $T$ , it takes for the mouth cavity to fill. This is obtained from:

$$N = \int_0^T Q dt \quad (4)$$

where  $N$  is the change in mouth volume obtained by the feeding action. For the cases observed (Alexander, 1969; Nyberg, 1971) the rate of water intake  $Q$  is essentially constant. This enables a simple solution to the integral equation (4), so that:

$$T = N/Q. \quad (5)$$

The trajectories of different points in the water mass are now calculated by integrating the velocities. This is done numerically by defining a starting point  $P_0(r_0, \theta_0)$  at which the particle considered is positioned when the suction process starts, i.e.,  $t=0$ . The velocity induced by point  $P_0$  is then found by equation (3). Taking a very short time interval,  $\Delta t$ , the position  $P_1(r_1, \theta_1)$  of the particle initially at  $P$  is obtained by:

$$r_1 = r_0 + (v_r)_0 \Delta t \quad (6a)$$

$$\theta_1 = \theta_0 + (v_\theta)_0 \Delta t. \quad (6b)$$

This step is repeated a large number of times so that the trajectory of particles originating at each point is found. The calculation for a given initial point was terminated when the trajectory approached within a very small distance from the origin, which indicates ingestion. At the origin  $r=0$  the radial velocity becomes infinite, which causes numerical difficulties, so that a very small distance ( $10^{-5}$  cm) was chosen, after checks for accuracy. The computation was also terminated for a given point when a comparison of the coordinates at two successive time-steps during the interactive process showed the distance from the origin increasing, i.e. the particle was moving away from the sink. This indicates that the particle would not be ingested.

The calculations were carried out on a Tektronix mini-computer. Various initial points  $P_0$  were selected for given values of  $Q$  and  $U$  and their trajectories calculated after the suction process began. The time step was chosen as  $\Delta t = 0.0001$  [s], after testing to see that further reducing the time step did no longer noticeably affect results. When a particle reached a point within the minimum radius  $r_m = 10^{-5}$  [cm] mentioned before, the initial coordinates and the time elapsed was recorded. A map of initial positions for particles finally ingested, and the time it takes for them to reach the sink was obtained.

### III. RESULTS AND DISCUSSION

We can distinguish three cases: (i) initial positions where particles never reach the sink as they are swept away faster than being pulled towards the mouth. This case does not exist for the stationary suction feeder, (ii) particles which end up at the origin, but the time it takes them to get there is longer than the time,  $T$ , it takes to fill the mouth cavity so that they are not included, and (iii) particles that arrive at the mouth opening in times less than  $T$ , and are ingested.

We first examine category (i) which describes the region from which prey particles will always escape. This can be found by inspection of equation (3a). For a particle to escape the radial velocity has to be positive at some point of its trajectory. This condition is written as:

$$\cos \theta \geq \frac{Q}{4\pi Ur^2}$$

defining a new parameter  $K$  as:

$$K = \frac{Q}{4\pi U}$$

the escape condition becomes:

$$\cos \theta \geq \frac{K}{r^2} \tag{7}$$

which gives, for known  $Q$  and  $U$ , a relation between distance and angle for escaping particles. Equation (7) indicates that the 'escape' zone includes only points to the rear of the sink. Particles which are in such positions when suction starts are never ingested. This region includes the area to the left of the broken lines in Fig. 2 each of which stands for a different value of  $K$ , which is a measure of the ratio of mouth cavity opening rate to forward swimming speed. For a given fish (with known opercular and buccal volume change rate) increasing  $K$  stands for decreasing forward velocity while feeding.  $K \rightarrow \infty$  is the case of a non-moving fish described by Alexander (1967, 1969).

The broken lines on Fig. 2 are the limits of the initial escape zone. Prey anywhere in this zone (which is defined by  $\cos \theta_0 \geq \frac{K}{r_0^2}$ ) will never move towards the sink and never be in any danger of ingestion. The full lines indicate the actual limits of the region which can be ingested. The volume between the dotted and full lines for any given  $K$  define a region where prey is initially attracted to the mouth by suction, but at some intermediate time

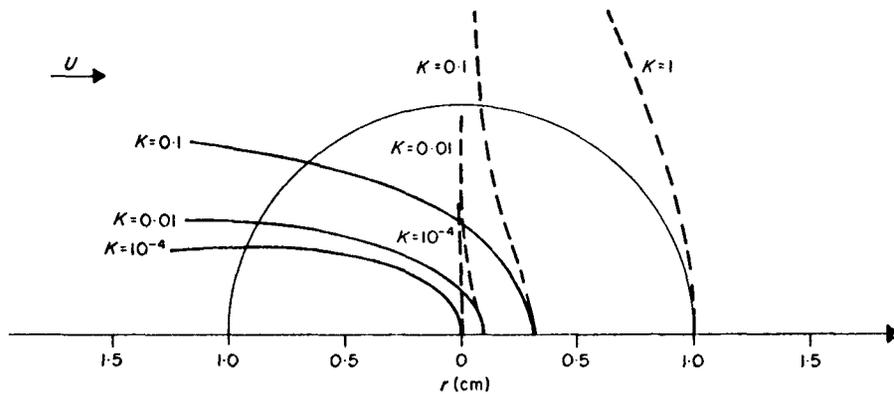


FIG. 2. Limits of capture area for various values of the capture parameter  $K$ . The broken lines indicate the limits of the escape zone defined in equation (7). Points in the area between the solid and the broken line for a given value of  $K$  initially approach the sink but finally escape. Only points to the right of the full lines are ingested. The unit circle is also given for orientation purposes.

is swept off. This change takes place when the particle moves beyond the broken line, at any time during its trajectory.

Actual measurements of all the parameters required for equations (3-5) were found for only one case, that of large-mouth bass, *Micropterus salmoides* (Nyberg, 1971). These are now used to calculate the shape of the feeding volume of this species. The data used is from Nyberg (1971: fig. 3 and data for bass number 4). This was 14 cm long and moving at an average speed of 3.1 body-lengths/s, i.e. at a speed of  $\approx 43$  cm/s. The mouth volume change is 5.2 cm<sup>3</sup>, this occurring with  $T = 0.02$  s. The rate of intake is therefore  $Q = 250$  cm<sup>3</sup> s<sup>-1</sup> and:

$$K = \frac{250}{4 \times \pi \times 43} = 0.46 \text{ cm}^2 \tag{8}$$

to two significant figures. Figure 3 shows the volume of water taken in during the feeding process. The centre of mass of the prey has to be within this volume to be caught. The sphere of equal volume appears on this figure as a broken line for comparison, showing the increase in forward feeding range due to the forward motion of the fish. The radius of the sphere mentioned, which indicates the volume ingested by a non-moving fish, is 1.07 cm while the maximum forward dimension of the feeding volume is  $\approx 1.73$  cm, i.e. the maximum capture distance is increased by over 60% in this case.

The volume indicated in Fig. 3 was found by searching for the points which would be captured by the source within time  $T = 0.02$  s, starting from initial positions in various directions. This calculation has to be corrected slightly for the effect of the bass head, which defines a region of no intake (shaded area in Fig. 3). This displaced volume is obtained by:

$$N_{\text{head}} = \int_{-\phi_h}^{\phi_h} \int_{-\theta_h}^{\theta_h} \int_0^{R_h} r^2 \sin\theta dr d\theta d\phi \tag{9}$$

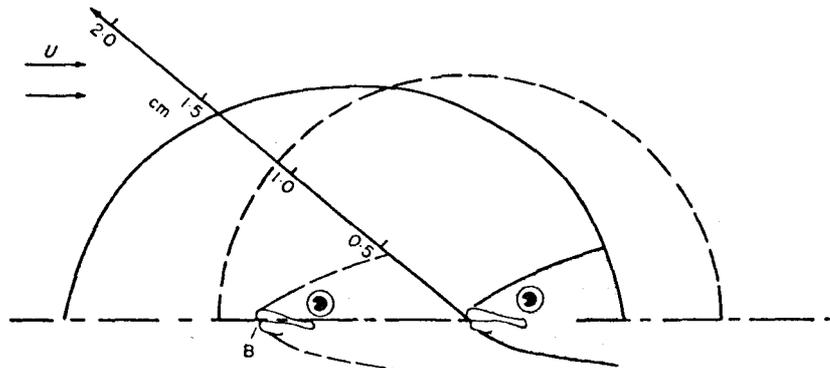


FIG. 3. The capture area (full line) of a large-mouth bass described by Nyberg (1971), the broken circle indicates the ingested volume of a stationary fish. Point B indicates the fish's position at the end of the suction process.

where  $R_h$  is the radius of the shaded volume and  $\theta_h$ ,  $\phi_h$  are the angular half-depth, and half-width of the head. The radius is essentially constant over the included head area  $0.65 < R_h < 0.68$  cm, and with  $\theta_h \approx 30^\circ$  and  $\phi_h \approx 15^\circ$  (Trautman, 1957) gives a volume  $N_h \approx 0.05$  cm<sup>3</sup>, which is less than 1% of the total volume engulfed. Including this negligible correction moves the most forward point by 0.015 cm outwards, and can therefore not be shown clearly on Fig. 3.

The accuracy of the calculations above was checked by means of a numerical integration of the contour of the body of revolution in Fig. 3. A 16-point Simpson's rule integration gave a total volume of 5.185 cm<sup>3</sup>, i.e. an error of less than 0.3%.

Nyberg's statement that particles were not observed flowing forward can now be quantitatively compared by obtaining the volume of fluid swallowed, which was initially at angles  $\theta$  of less than  $90^\circ$ . Again by numerical integration, this is 0.97 cm<sup>3</sup>. Subtracting the volume displaced by the fish head ( $= 0.05$  cm<sup>3</sup>), we see that only  $0.92/5.2 = 18\%$  of the total volume swallowed originates from behind the tip of the fish's nose. This value can be compared to  $\approx 50\%$  originating from the area behind the fish nose in static feeding. In most cases, prey will not be in this region so that a reduction by a factor of 3 in the intake of unwanted volume is achieved. Also, the speeds in the rear zone are lower, so that heavy particles such as the dirt observed by Nyberg would be moved even less, as there is a delay in getting them moving.

Some particle trajectories appear in Fig. 4. These trajectories are obtained by the technique described before, by plotting the instantaneous position at each time step. Here it was assumed that the particles were neutrally buoyant and relatively small (compared to a typical dimension of the problem—the mouth diameter). Bigger, or non neutrally-buoyant prey would be displaced somewhat less in the same time. When a particle is of different density than water, an additional drag force must act on it, to counteract the body force. This drag can

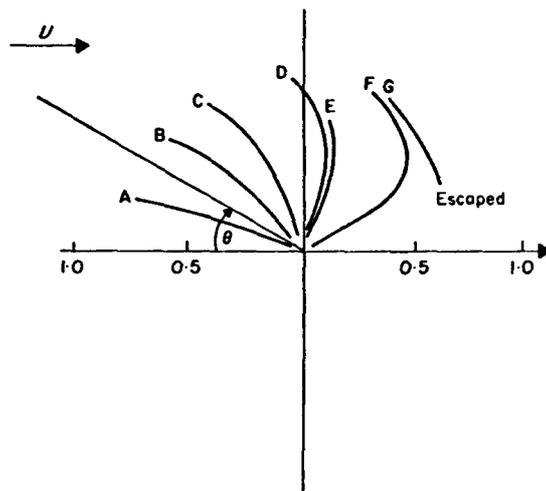


FIG. 4. Particle trajectories for the large mouth bass of Fig. 3.

only be produced by means of a velocity difference between the particle and the surrounding water so that the particle would move a shorter distance in a given time. When prey size is large, different parts of it are moved at different speeds due to the velocity field (3) so that rotation, and similar processes occur at the expense of kinetic energy so that again, the prey moves more slowly.

Heavy particles would also be subject to inertia so that when following a trajectory like *F* (Fig. 4) it would not be able to follow the sharp curvature and might escape. The 'ingestion volume' shown in Fig. 3 is therefore an upper limit, with real feeding distances expected to be somewhat smaller (for both motionless and swimming suction).

It would be of interest to compare the present predictions with further data on various fish species feeding by suction. A more quantitative check would then be possible, testing the influence of the parameter *K* (ratio of rate of mouth volume change to forward swimming speed) by comparing captures by individuals of the same species at different sizes, and swimming speeds. The ratio *K* can be completely non-dimensionalized by dividing by a length parameter (squared). This would probably help collapse experimental data more neatly, especially when data from individuals of greatly varying sizes are compared, thereby generalizing the model. The length-related quantity in *K* is the change in volume of the mouth *N*, which has dimensions of length cubed. The squared length required to non-dimensionalize *K* is therefore  $N^{2/3}$ . The non-dimensional suction number *S* is then:

$$S = \frac{Q}{4\pi UN^{2/3}} \quad (10)$$

and substituting  $Q = N/T$  we obtain:

$$S = \frac{N^{1/3}}{4\pi UT} \quad (11)$$

Defining the characteristic length dimension of the mouth as  $D = N^{1/3}/4\pi$  (related to an average mouth cavity radius) we obtain finally for the nondimensional suction number *S*:

$$S = \frac{D}{UT} \quad (12)$$

The appropriate nondimensional length parameter is then  $r = r/D$ . Figure 5 shows an application of these nondimensional coordinates. The ratio of ingestion distances directly forward to that in the opposite direction, *L* is shown as a function of *S*. When  $S \rightarrow \infty$ , i.e. the case of  $U=0$  (nonmoving predator), this ratio  $L = 1$  as the ingestion distance in all directions is equal. For the large-mouth bass shown in Fig. 3 we have from equation (11):

$$S = \frac{5 \cdot 2^{1/3}}{4 \times \pi \times 43 \cdot 0 \cdot 02} = 0 \cdot 16. \quad (13)$$

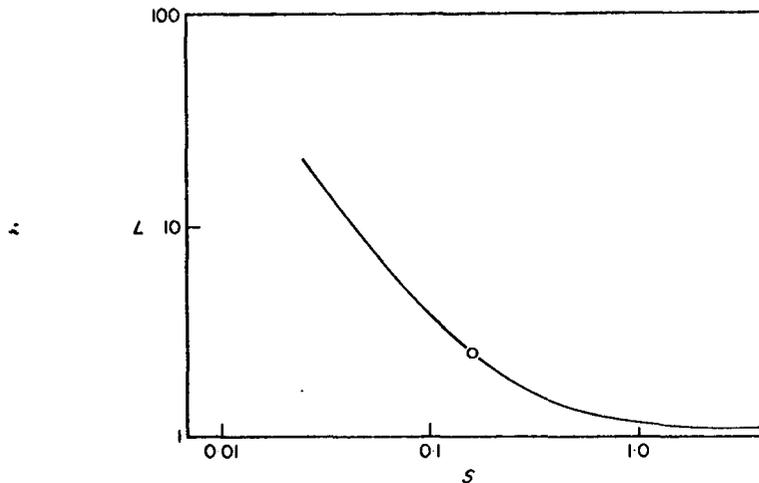


FIG. 5. The ratio of ingestion distance directly forward, and directly behind the fish's mouth  $L$  as a function of the generalized suction number  $S$  (characteristic mouth size divided by forward speed and suction time). The circle shows experimental data for large mouth bass (Nyberg, 1971).

In this case  $L = 2.55$  (Fig. 5). Finally, as the forward speed grows for given suction rate,  $L \rightarrow \infty$  while  $S \rightarrow 0$ . The ratio  $L$  is a measure of the efficiency of directed suction feeding, as prey will usually be in front of the predatory when the feeding starts. Large  $L$  indicates a small proportion of water ingested from behind the head, i.e. the wasted volume is smaller.

The advantage of having Fig. 5 as a function of  $S$  is that otherwise there would be a separate curve for each mouth size  $N$ . We see that forward swimming has no significant influence on the capture distance when  $S > 0.5$ . When  $S$  is smaller, the slope of the curve starts going up more rapidly indicating growing advantage of forward swimming in terms of directed suction. This leads to the conclusion that only rapid swimming is worthwhile for suction feeding as slow swimming does not much increase the forward bias of the capture volume. Also, any further increase in speed just before suction shifts the curve to the left, i.e. to still higher  $L$ . This might explain the observation (Nyberg, 1971) of a last minute increase in velocity of the predator, when hunting mobile, midwater prey (minnows). For the 14 cm large-mouth bass, with a feeding volume of  $5.2 \text{ cm}^3$ ,  $S = 0.5$  is equivalent to a speed of *c.* 14 cm, i.e. one body-length/s. This is just slightly less than the optimum cruising speed (Weihs, 1977). The high swimming speed observed while feeding, which is much more costly energetically, must therefore have a different reason. This is possibly the increased forward capture distance.

An interesting conclusion, from the functional form of the suction number  $S$  is that larger fish (which presumably will have larger mouth cavities) have to move at higher speeds to get the same advantage in suction feeding as smaller predators. Taking equal mouth cavity opening times  $T$ , the required increase in speed grows linearly with fish size (assuming geometric similarity between fish of differing size). Swimming speed, however, grows in less than linear relation to size so that smaller predators will be able to make better, and more efficient use of

suction feeding. This conclusion was also reached by Nyberg (1971) through a different line of arguments, after he observed higher capture rates by suction by the smaller individuals.

This study was made while I was a NRC-NOAA Senior Research Associate. I thank Drs J. R. Hunter and R. Lasker for their hospitality and encouragement.

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