

The forces exerted by aquatic suction feeders on their prey

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Successful prey capture by aquatic suction feeders depends on the ability of the predator to generate a flow of water external to the mouth that overcomes any movements and forces that the prey uses to resist the suction flow. Elucidating the nature and magnitude of these forces is a key to understanding what limits suction feeding performance. We identify three potential forces produced by the suction flow field: drag, acceleration reaction and the fluid pressure gradient. Using a mathematical model parametrized with empirical data from feeding bluegill, *Lepomis macrochirus*, we explore the relative magnitude of these forces under three encounter scenarios with a 5 mm diameter, spherical prey: an immobile mid-water prey; a similar prey that executes an escape response; and a prey item that grips a substratum. Contrary to the almost exclusive emphasis on drag in the suction feeding literature, it made a minor contribution to the total forces in all three cases. In all three scenarios, the pressure gradient is the largest of the three forces. These results are important because previous researchers have emphasized drag and have not explicitly recognized a role for the pressure gradient force in suction feeding. The simulations suggest previously unrecognized mechanisms that suction feeders can use to enhance the forces that they exert, by increasing the steepness of the pressure gradient that the prey item is exposed to. This can be accomplished either by increasing the rate of increase in fluid velocity or by restricting the size of the mouth aperture, which creates a steeper spatial gradient in pressure.

Keywords: suction feeding; fish feeding; fluid mechanics; prey capture strategy; fish feeding performance

1. INTRODUCTION

Suction feeding is the most widely used method of prey capture among aquatic feeding vertebrates (Ferry-Graham & Lauder 2001). The prey is transported into the oral cavity by a flow of water external to the mouth that is generated by the predator. While the musculoskeletal mechanisms used to generate this flow and the spatial and temporal patterns of water movement are well studied (Van Leeuwen 1984; De Visser & Barel 1998; Day *et al.* 2005), the nature of the interaction of this flow with the prey has received less attention (Lauder & Clark 1984; de Jong *et al.* 1987; Drost *et al.* 1988; Van Wassenbergh *et al.* 2006a). This represents a significant gap in our understanding of suction feeding, because all of the forces exerted on the prey are mediated by the flow of water generated by the suction feeder and hence success of the feeding attempt is rooted in this interaction.

The purpose of the present paper is to identify these forces and evaluate their relative magnitude under

conditions that are common in aquatic predator–prey interactions. We focus on three forces that can be exerted on a prey item by the water motion generated by the suction feeder: drag, acceleration reaction and the pressure gradient force. The velocity of fluid moving relative to the prey item will generate a drag force. A fluid velocity increasing through time, as characterizes suction feeding (Day *et al.* 2005), will also generate an acceleration reaction. Finally, because fluid velocity will vary both in space, being higher at the mouth aperture and decreasing with distance from the mouth, and in time, the pressure in front of the mouth will also vary spatially. A pressure gradient exists with the lowest pressures at or inside the mouth and increasing away from the predator. This pressure gradient creates a force that moves the prey towards the mouth.

Which of these is the most potent force to act on the prey during its encounter with a suction feeder? Is the answer to this question affected by whether the prey is free moving in open water or gripping the substratum, both commonly encountered scenarios for feeding fishes? The answer to these questions may shed light on how suction feeding predators can best enhance the

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List of symbols.

m	mass of the prey
F	net force acting on prey
F_d	force due to drag
F_{pg}	force due to pressure gradient of fluid field
F_{ar}	force due to acceleration reaction
F_{sw}	force due to swimming or escape response of the prey
G	gape
x	absolute position
x_p	x position of the prey in the absolute reference frame
x'	distance in front of the mouth aperture (relative to the fish)
x'^*	scaled distance in front of mouth, equal to x'/G
C_d	drag coefficient
A_f	frontal area of an object
FS	fluid speed in the absolute frame of reference
FS _p	fluid speed at the location of the prey
PS	speed of the prey
PA	acceleration of prey
FA	total acceleration of the fluid at the location of the prey
d	diameter of the prey
V	volume of the prey
L_x	effective length of prey in the x -direction

forces exerted on their prey and what modifications to strike behaviour might be effective under different predator-prey encounters. Identifying these forces and their importance will help researchers to develop more realistic models of the predator-prey interaction.

We apply a model of the suction feeding flow interaction with the prey item and calculate the relative magnitudes of these three forces under three scenarios that characterize a range of conditions which occur during suction feeding events: a prey item that is neutrally buoyant and freely suspended in the water; a mid-water prey that executes an escape response during the attack, exerting a force that is counter to the suction-induced forces; and, finally, a prey item that is clinging to the substratum. In this case, the prey body does not move and the suction flow washes over it. Using data from our previous research, we fit our model with physical dimensions and fluid velocities that would be typical of a 15 cm feeding bluegill, *Lepomis macrochirus*, and we ask what the relative magnitude of the three forces experienced by a 5 mm diameter, spherical prey will be in each of the three scenarios. From the results of these calculations, we identify the pressure gradient force as the dominant component of the total force in suction feeding encounters and we explore ways in which this force may be enhanced by suction feeders, either by behavioural modifications or by evolutionary changes to the feeding mechanism.

2. METHODS AND RESULTS

A mathematical model was adopted for this study. If the velocity field in front of the mouth is known for all times during the strike, then all the components of force that act on a prey may be calculated or estimated for

the duration of the strike. The sum of these component forces is the net force acting on the prey, from which we calculate the resultant kinematics, velocity and position, as a function of time. Additionally, comparison of the magnitudes of the component forces lends insights into the fundamental mechanisms of force generation. All calculations are based on a coordinate system rooted at the mouth aperture with the positive x -direction pointing caudally. As a result, positions in front of the predator are negative and all accelerations and forces are positive when acting towards the predator mouth.

The input to the model consists of the prescription of a fluid flow field generated by the predator and the properties and initial position of the prey. We have shown previously that the pattern of fluid speed in front of a feeding fish is a function of the magnitude of fluid speed at the mouth, FS_{mouth}, and of the gape of the fish, G . Based on this relationship for bluegill (Day *et al.* 2005), the fluid speed in front of the mouth may be represented by the following relationship:

$$FS(x'^*) = FS_{\text{mouth}}(0.098x'^{*4} - 0.70x'^{*3} + 1.86x'^{*2} - 2.19x'^{*} + 1), \quad (2.1)$$

where x' is the distance in front of the mouth aperture and x'^* is the distance x' normalized to the instantaneous gape of the fish, G . The flow field for each strike is prescribed by specifying G , and fluid speed at the mouth, FS_{mouth}, as a function of time. For these cases presented here, G was held constant throughout the strike. Additional studies are planned that incorporate more complete modelling of the dynamics of the fish strike.

Based on this distribution of fluid speed and position and properties of the prey, the generated forces are calculated according to the following relations. An assumption of this model is that the fluid flow field is not affected by the presence of the prey. This is particularly valid for small free objects, but less true for large fixed prey. The calculation of forces as a function of time is accomplished numerically with approximately 1000 time-steps per suction feeding event.

2.1. Drag

The force due to drag, F_d , is estimated by using the following relationship:

$$F_d = \frac{1}{2} C_d A_f |FS_p - PS_p| (FS - PS), \quad (2.2)$$

where C_d is an empirically determined drag coefficient, A_f is the frontal area of the prey and $(FS_p - PS)$ is the relative speed of the fluid at the location of the prey, FS_p, and of the prey, PS. In these calculations, we assumed a spherical prey, for which the drag coefficient is well documented over a wide range of Reynolds numbers (Fox & McDonald 1992).

2.2. Pressure gradient

Owing to both the temporal and the spatial gradients of velocity in the flow, spatial gradients of pressure exist. At each time-step, the pressure gradient, dp/dx , is

calculated at the location of the prey according to equation (2.3), which is a form of the conservation of x -component of momentum (White 1979) arrived at by assuming that along the centreline of the fish the fluid moves only in the x -direction, that gravity acts normal to the centreline, and neglecting the effects of viscosity. The exclusion of viscous forces in the calculation of the pressure gradient is justified by the fact that spatial gradients of the velocity normal to the direction of flow are very small along the centreline of the fish (Day *et al.* 2005),

$$\frac{dp}{dx} = -\rho \left(\frac{\partial u}{\partial t} + u \frac{\partial u}{\partial x} \right). \quad (2.3)$$

The force resulting from the spatial pressure gradient, F_{pg} , may be calculated by integrating the pressure over the surface of the prey. A first-order approximation of this x -component of this force is calculated according to the following equation:

$$F_{pg} = - \frac{dp}{dx} L_x A_f. \quad (2.4)$$

The right-hand side of equation (2.4) corresponds to the first term of a Taylor series expansion of the integrated pressure acting on the surface of the object. A_f is the frontal area of the prey and L_x is the effective dimension of the prey in the x -direction, the latter of which is shape dependent. This is based on an infinitely small prey, but inclusion of higher-order terms has no effect on the results presented here.

2.3. Acceleration reaction

The usual form of acceleration reaction (Denny 1988; Vogel 1994) can be rearranged to the following form when both the prey and the fluid are moving:

$$F_{ar} = -C_{am} V \rho_{H_2O} (PA - FA), \quad (2.5)$$

where F_{ar} is the additional force felt by the reaction of fluid accelerating around the object, C_{am} is the coefficient of added mass, which is an empirically determined shape-dependent coefficient equal to approximately 0.5 for a sphere (Batchelor 1967), V is the volume of the prey, ρ is the density of water and the quantity $(PA - FA)$ is the relative acceleration of the prey, PA , and the surrounding fluid, FA . We emphasize that in the literature the term 'acceleration reaction' is used to mean different things, as illustrated by the canonical case of a stationary object and uniformly accelerating flow. The definition of acceleration reaction used by Denny (1988), which includes the virtual buoyancy, is different from the definition of Batchelor (1967), which accounts for virtual buoyancy in a separate term from the acceleration reaction. In the formulation presented here, the virtual buoyancy need not be included as an additional explicit term because it is exactly accounted for by inclusion of the pressure gradient force.

2.4. Swimming

Steady or accelerative swimming is the result of a force that can be treated as either the prey acting on the fluid or the fluid acting on the prey. The escape response is

included in this model as an additional force, referred to as the swim force, F_{sw} , which is applied to the prey and acts away from the predator. The magnitude and temporal pattern of this force are parametrized based on the available data.

The acceleration of the prey, PA , is found from $PA = F/m$, where F , the net force acting on the prey, is the sum of the component forces, $F = F_d + F_{pg} + F_{ar} + F_{sw}$, and m is the mass of the prey. Knowing the current prey position, x_p , speed, PS , and the calculated acceleration, PA , the position and speed of the prey at the next time-step are calculated based on a first-order forward differencing scheme.

The model is parametrized for conditions representing an adult bluegill. The prescribed velocity field and prey properties are the same for all of the three cases. FS_{mouth} is initially 0 and reaches a maximum value of 2 m s^{-1} after 30 ms. The shape of FS_{mouth} as a function of time is based on the form of eqn (11) from Muller *et al.* (1982), with a shape factor, α , equal to 2. Gape, G , is a constant 15 mm, and the initial position of the prey, $x_p(0)$, is 15 mm. The prey is a sphere of 5 mm diameter, d , and has a density of 1000 kg m^{-3} , equal to the surrounding water. Geometrical considerations show that for the spherical prey used in the current simulations, A_f is equal to $\pi/4 d^2$ and L_x is $2/3 d$. Thus, $A_f L_x$ is equal to the volume of the sphere. It was assumed that the presence of the prey did not influence the flow.

In Case I, the prey is freely suspended in the water column. The forces acting on the prey and the resultant position of the prey are both shown in figure 1. The prey moves towards the mouth, forces increase as the distance to the mouth decreases, and as a result the acceleration and the speed of the prey also increase as it moves towards the mouth. At a time of approximately 50 ms, the prey is ingested. The model shows that the prey moves as though it is a particle of fluid, always having the exact speed of the surrounding water. As a result, the relative speed and the acceleration of the prey and the surrounding fluid is zero, so that drag and acceleration reaction are exactly zero. For a neutrally buoyant prey, the resultant force is entirely the consequence of the pressure gradient of the fluid field. Prey with densities greater than the surrounding fluid tend to lag behind the motion of the fluid, and prey less dense than the surrounding fluid will accelerate towards the mouth faster than the surrounding water.

Case II has mostly the same conditions as the free prey case, but in addition to the flow-generated forces, the prey initiates an escape response. The inclusion of this escape response is modelled by an additional force, F_{sw} , applied to the prey, which acts directly away from the fish. A typical acceleration from a maximal effort escape response of a fish of this length is 19 m s^{-2} (2 gs; Domenici & Blake 1997; Wakeling *et al.* 1999). This is related to force based on the mass of the prey. For our simulations, the swim force increased from 0 at the onset of the strike to a maximum value corresponding to 19 m s^{-2} , 100 ms later. If the predator does not move towards the prey, swim force easily overcomes the suction forces and the prey escapes. If a moderate ram speed (greater than 0.6 m s^{-1}) of the predator is

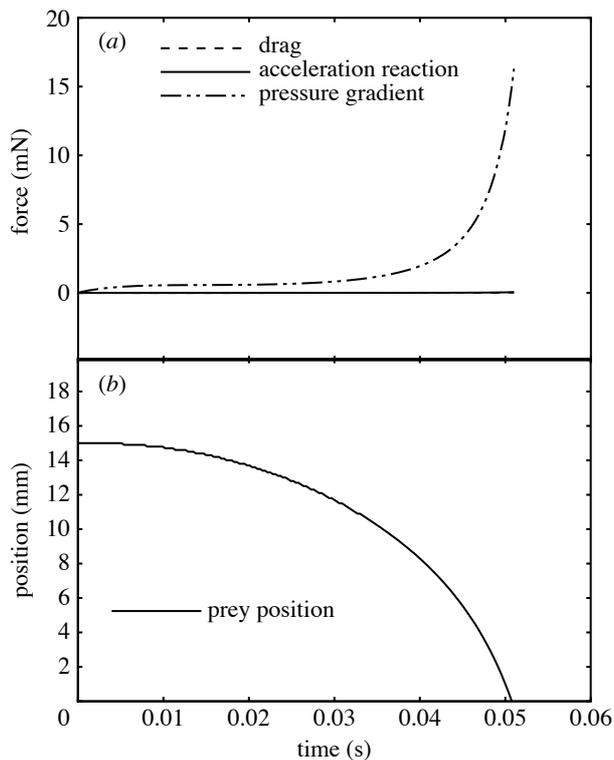


Figure 1. Free prey suspended in the water column (Case I) captured by a feeding fish. The predator mouth is a constant 15 mm diameter and the fluid speed at the mouth is time varying, reaching a maximum of 2 m s^{-1} at 30 ms. Prey diameter is 5 mm and the density is the same as the surrounding water, 1000 g cm^{-3} . (a) The magnitude of the component forces acting on the prey is shown as a function of time. In this case, the prey moves as though it is a particle of water (b), having no relative motion to the surrounding water and therefore no acceleration reaction or drag forces. All of the forces acting on the prey are the result of the pressure gradients in the flow field. The magnitude of the resultant force increases dramatically as a function of time as a result of the prey being located closer to the mouth. The trajectory of a particle of water originating at the prey location obtained by integrating the fluid velocity is identical to the prey trajectory shown in (b).

invoked, it is able to locate its mouth near enough to the prey that the suction forces overcome the swim force and the prey is ingested. The initial escape and subsequent capture are evident in the plot of prey position shown in figure 2b. The total distance travelled by the prey is small and in this case, it actually moves away from the predator. All of the closure of the distance between the predator and the prey is the result of the fish swimming towards the prey. The resultant forces are still dominated by the pressure gradient force (60% of total), but drag and acceleration reaction play an appreciable role, with acceleration reaction contributing approximately 20% and drag contributing 15% of the total force.

The prey is attached rigidly to the substrate in Case III. The acceleration and velocity of the prey are equal to zero and position remains constant, as shown in figure 3. In this simulation, the distance between the predator mouth and the prey remains a constant 15 mm, because the predator is not using ram and is not protruding its mouth. The largest force is due to the pressure gradient, followed by the acceleration reaction

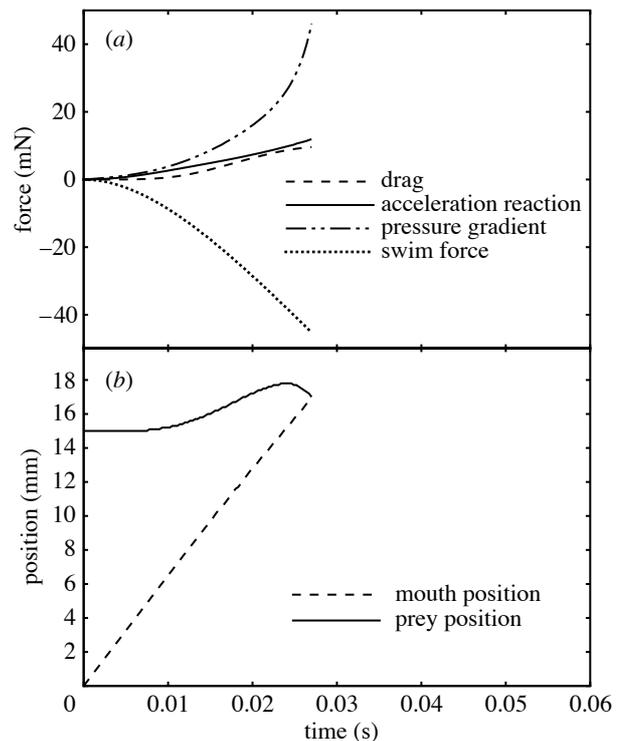


Figure 2. Prey executing an escape response (Case II). In this scenario, the prey initiates an escape response beginning at $t=0$ and is able to move away from the predator during the first portion of the strike (solid line in b). All other conditions are identical to Case I (figure 1). If the predator was not moving towards the prey, the prey would be able to escape, but forward motion of the predator (dashed line in b) locates the predator mouth near enough to the prey that the suction forces overcome the escape response and the prey is eventually drawn towards and into the mouth. Pressure gradient still dominates the generated force, although both drag and acceleration reaction each contribute as much as 15% of the total force on the prey. As was true for Case I, the magnitude of forces increases as the distance to prey decreases.

(approx. 50% of pressure gradient force) and drag (approx. 32% of pressure gradient force). There is also a distinct difference in the timing of the forces, in which acceleration reaction and pressure gradient peak in about a third of the time required for drag to reach its peak.

Whereas drag depends only on the magnitude of relative flow speed, acceleration reaction and pressure gradient forces depend on the spatial pattern of the flow. The effect of two manipulations of this flow field was explored by numerical experiments using the model for the rigidly attached prey Case III. In the first manipulation, all parameters are the same as in Case III, but the time to peak fluid speed (TTPFS) was varied. The drag force, which is strictly a function of the relative speed, was constant, but the forces due to acceleration reaction and pressure gradient increase as a function of lower TTPFS, which correlates with higher temporal accelerations (figure 4). Compared with the nominal case, where the peak fluid speed occurred at 30 ms, the forces generated with TTPFS=15 ms are approximately twice as large. This is true at all locations in front of the fish.

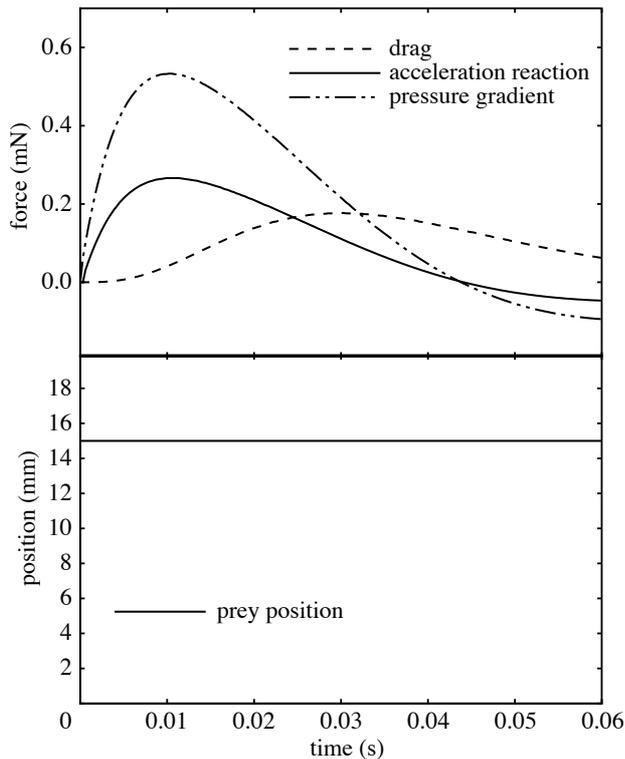


Figure 3. Prey attached rigidly to the substratum (Case III). The position of the 5 mm spherical prey remains a constant 15 mm from the mouth owing to its rigid attachment. The mouth of the predator is a constant 15 mm diameter and maximum fluid speed of 2 m s^{-1} is achieved at 30 ms. During the initial portion of the strike when total force is at its highest, forces due to the pressure gradient constitute approximately 67% of the total force and the remainder is generated by the acceleration reaction. Just before the time of peak gape and fluid speed, the pressure gradient and acceleration reaction forces decrease and the drag force is at its strongest. The total force is smaller at this time because the magnitude of peak drag force is only 30% of the peak pressure gradient force. Pressure gradient and acceleration reaction forces are highest during the period of acceleration of drag at the time of peak fluid speed. Forces are an order of magnitude lower than in Cases I or II and trend back towards zero at the end of the strike because the relative position of the mouth and prey is large (one mouth diameter) throughout the strike.

In the second manipulation, the prey was located at the aperture and the size of the mouth aperture was varied. As is expected, all components of force are much higher than for Case III, owing to the closer proximity to the mouth. Three cases of varying gape, 7.5, 15 and 30 mm, were run with the prey located at this position (figure 5). All forces reach a maximum near the time of peak fluid speed, 30 ms. The magnitude of the drag force is the same for all mouth sizes, although the magnitudes of acceleration reaction and pressure gradient forces are a function of the mouth aperture, with the peak forces being largest for the case with the smallest aperture (figure 5).

2.5. Effects of prey size

The effect of prey size on the forces experienced in the restrained prey scenario, Case III, was explored by varying the prey from 0.5 mm diameter to 10 mm.

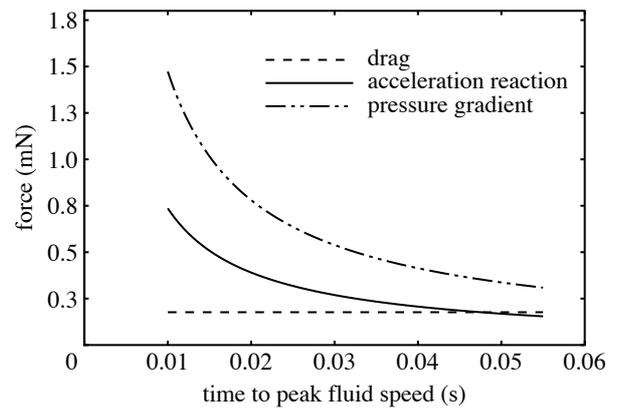


Figure 4. Magnitude of the component forces due to drag, acceleration reaction and the pressure gradient as a function of the TTPFS. The prey is located as a fixed position 15 mm away from the mouth and maximum fluid speed is held constant at 2 m s^{-1} . When a feeding fish achieves this same maximum velocity in a shorter period of time, the acceleration reaction and pressure gradient forces increase dramatically. The drag force, which is strictly a function of the relative velocity of the fluid and the prey, is not affected.

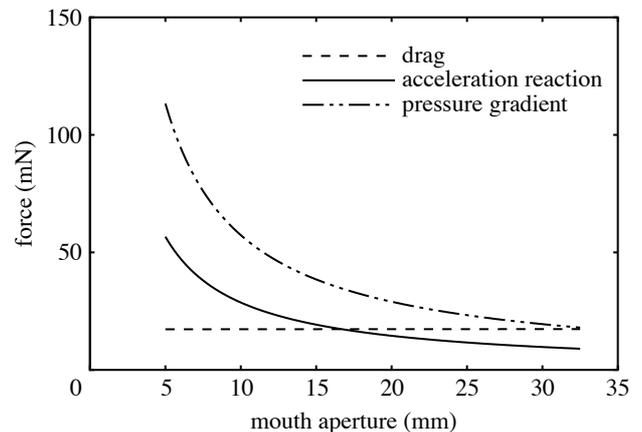


Figure 5. Variation in the mouth aperture causes a change in forces exerted on a fixed prey located at the mouth aperture. Decreasing the size of the mouth aperture, while maintaining the same fluid speed at the mouth, increases the pressure gradient force and acceleration reaction as a result of the increased magnitude of the spatial derivatives of velocity and pressure, while drag remains constant.

The same attributes of the predator and water flow pattern were used in these calculations as done previously. All forces increased with prey size, but the peak pressure gradient force was always about two times the peak acceleration reaction force. However, the ratio of peak pressure gradient force to peak drag force varied as a function of prey size (figure 6), dropping below 1.0 for prey smaller than 15% of gape width. For prey larger than 15% of gape diameter, pressure gradient force was larger than peak drag force and an increasingly larger fraction of the total force.

3. DISCUSSION

The fluid pressure gradient is the dominant component of the forces that suction feeders exert on their prey. In the three scenarios that we explored, the pressure

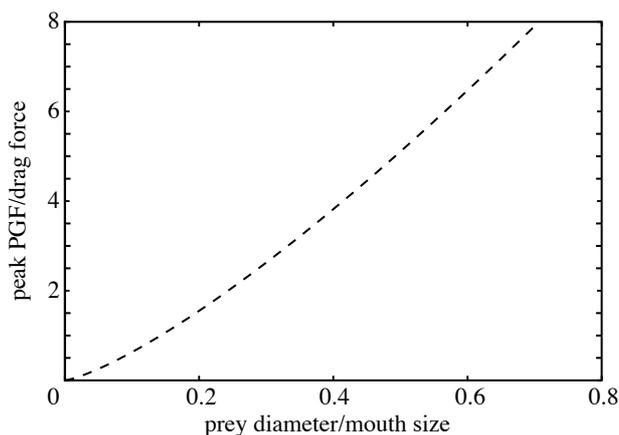


Figure 6. Illustration of the effect of prey size on the relative magnitude of the peak pressure gradient force (PGF) and the peak drag force. At prey size above approximately 0.2 of the mouth diameter, the pressure gradient force is larger than drag, whereas below 0.2, drag is larger than the PGF. All calculations were done with the same mouth diameter, 15 mm, and flow field and using the fixed-prey case (Case III).

gradient force was either the only force exerted by the suction feeder on the prey (Case I) or the largest force (Cases II and III). Surprisingly, with free-moving prey, drag was either negligible or non-existent. Even in the fixed-prey case, drag was only approximately 20% of the combined pressure gradient and acceleration reaction forces. These results may help reverse a widely held notion that drag is typically the most important force in this predator-prey interaction (Norton & Brainerd 1993; Ferry-Graham & Wainwright 2002; Van Wassenbergh *et al.* 2006*a,b*). Clearly, attempts to estimate the forces experienced by the prey of suction feeders must account for all three forces.

A second notable result of our study is that the relative magnitude of the component forces is markedly affected by whether the prey item is mid-water or attached to a holdfast, and whether the prey can execute an escape response. Drag and acceleration reaction are non-existent if the prey item is neutrally buoyant and moves as a particle of water; but these forces become substantial if the prey is fixed to a substratum and the suction flow moves around it. Since the vast majority of prey are likely to have some capacity for escape or will resist capture by clinging to a holdfast, it is likely that an important role for drag and, especially, acceleration reaction will characterize most natural suction feeding encounters.

Finally, the significance of the fluid pressure gradient force in these simulations suggests previously unrecognized mechanisms available to fishes, which could be used to enhance the forces that they exert on the prey. Either temporal or spatial manipulations that increase the steepness of the pressure gradient will increase the force experienced by the prey item. This can be accomplished temporally by increasing the rate at which peak flow velocity is achieved, by increasing the rate of expansion of the buccal cavity (figure 4), or spatially, by decreasing the size of the mouth aperture. A smaller mouth opening will reduce the spatial scale of the flow pattern, such that fluid velocity declines more rapidly with distance away from

the mouth. This decreases the magnitude of forces far from the mouth, but drastically increases the imparted forces near the mouth (figure 5). Even when maintaining a constant value of peak fluid velocity at the mouth aperture, the forces exerted on the prey can be elevated either by increasing the rate at which this velocity is achieved or by reducing the size of the mouth aperture. Both these manipulations were investigated with the parametric model, and in both cases the force due to the pressure gradient increases markedly, as does the acceleration reaction, but peak drag remains constant because the peak flow velocity is unchanged.

3.1. The nature of the suction feeding interaction

Suction feeding does not involve direct physical contact between the predator and the prey. Instead, the predator manipulates the relatively dense and viscous aquatic medium by expanding the buccal cavity, thereby generating a flow of water directed into the mouth. Prey capture is accomplished by positioning this short-lived flow so that the prey item is drawn into the mouth. Success of a feeding attempt depends on the ability of the predator to appropriately time the burst of flow so that it contains the prey item, and on the strength of this flow to overcome any resistive forces exerted by the prey item.

Although drag and acceleration reaction are the most commonly recognized and discussed forces acting on the prey of suction feeders (Norton & Brainerd 1993; Ferry-Graham & Wainwright 2002; Van Wassenbergh *et al.* 2006*a,b*), the pressure gradient force was the largest force in the three scenarios that we explored. The dominance of the pressure gradient is severe when the prey are neutrally buoyant bodies (figure 2). Under these conditions, there is no movement of the fluid relative to the prey and therefore no drag or acceleration reaction; so the only force acting on the prey item is the pressure gradient force.

Our escaping prey easily generated large enough swim force to overcome suction produced by an immobile predator, but with the addition of a moderate ram velocity, the predator was able to get close enough to the prey item that the pressure gradient force overcame the escape force (figure 2). Even in this simulation, pressure gradient was a much larger force than either drag or acceleration reaction. When the prey was fixed to a substratum, pressure gradient was the largest of the forces experienced, but acceleration reaction force and drag were approximately 50 and 30% of pressure gradient force, respectively, with acceleration reaction and pressure gradient force peaking over 20 ms prior to peak drag force (figure 3). Forces experienced by a fixed prey could also potentially be affected by the presence of the substratum, which can be expected to alter the water flow in such a way as to increase the spatial pattern of velocity (Nauwerlaerts *et al.* in press).

The pressure gradient force that we are describing (i) is present everywhere within the fluid field, (ii) is the result of the spatial variation and temporal acceleration of the fluid speed, and (iii) exists even in the absence of the prey (Fleagle & Businger 1980). However, it is not

the only potential pressure gradient that could arise in a suction feeding event. The drag force on a submerged surface is often decomposed into two components: pressure drag, also known as form drag, and viscous drag (Denny 1993; Vogel 1994). The form drag is due to varying pressure acting on the surface of the object; this pressure variation being a result of the presence of the object. The distinction between form drag and pressure gradient can be clarified in the case of a uniform flow. In a uniform flow, the pressure gradient in the direction of flow may be negligible, yet an object held fixed against the flow will alter the flow around it and generate pressure gradients on its surface. A neutrally buoyant object moving along with this uniform flow does not alter the flow and, thus, does not experience a pressure gradient along its surface. The net imbalance of surface pressure, if present, is accounted for in the drag force and is not what we are referring to as the pressure gradient force.

There has been some confusion in the literature concerning what forces a suction feeder's prey experiences. When identifying these forces, some workers have only explicitly identified drag as a force that moves the prey (e.g. Van Wassenbergh *et al.* 2006a), while others also included acceleration reaction (Norton & Brainerd 1993; Wainwright *et al.* 2001). Our calculations indicate that pressure gradient and acceleration reaction are the dominant forces under most parameter combinations, indicating that the previous emphasis on drag was significantly misplaced.

Some authors have explicitly modelled the prey as a 'particle of water' that is neutrally buoyant and of infinitesimally small size (Van Leeuwen & Muller 1984; Drost *et al.* 1988; Van Wassenbergh *et al.* 2006b). With this approach, prey motion can be calculated directly by integrating the velocity field. While we question how frequently natural prey items are infinitesimally small and lack any capacity for escape, our calculations indicate that even relatively large prey that can employ an escape response primarily experience the pressure gradient force. Calculations of prey movement in reference to the fluid velocity (e.g. Drost *et al.* 1988) do allow realistic evaluation of the times and velocities involved in successful prey capture or escapes by prey. However, this approach can only be used with free-moving prey and does not work in cases where the prey is attached to a substratum. In the attached case, the suction feeder must exert enough force on the prey to overcome the strength of the holdfast, so force should be the focus of the analysis.

The simulations reported in Cases I–III of this paper were initially all done with a single mouth size, prey size and flow profile. While the values used were informed by our experimental work with bluegill (Day *et al.* 2005; Higham *et al.* 2006), the generality of some of our conclusions will be affected by changes in these parameters. As prey became smaller, the relative magnitude of drag and pressure changed, and the drag became the higher of the two for attached prey that were less than 15% of the mouth diameter. As prey size increased above this ratio, the pressure gradient force steadily increased relative to the drag (figure 6).

3.2. Implications for suction feeding performance

Given that the fluid pressure gradient appears to be the major force exerted on prey by suction feeders, what strategies are available to the predator for enhancing this force? We emphasize two general options that are available to the predator, both involving the manipulation of the magnitude of the pressure gradient. Any change which results in an increase in the slope of the fluid pressure gradient will result in higher pressure forces. Interestingly, these changes in the gradient can be effected either temporally or spatially. As compared to a fish with a certain peak fluid speed at the mouth aperture, a predator that more quickly achieves that flow velocity will exert higher pressure forces on the prey item (figure 4). In this case, the acceleration reaction force will also increase, but drag will be unaffected because the peak fluid velocity is unchanged.

The pressure gradient can also be spatially compressed by manipulating the size of the mouth aperture. It has been shown that the spatial pattern of fluid flow in front of a suction feeder's circular mouth scales isometrically with the diameter of the mouth (Day *et al.* 2005). A smaller mouth diameter, coupled with no change in peak fluid velocity, will result in a more rapid drop-off in fluid velocity and pressure with increasing distance from the mouth. As a result of this increase in the slope of the pressure gradient, the force due to the pressure gradient will be higher, as will the acceleration reaction force (figure 5). But again, the drag experienced by a prey item at the mouth aperture will be unaffected by these changes because peak fluid velocity is unchanged.

This latter result may provide some insight into the frequently observed tendency for species that rely most heavily on suction to capture prey to have a relatively small mouth in comparison to taxa that employ considerable swimming to overtake their prey (Norton 1991; Carroll *et al.* 2004; Higham *et al.* 2006). While a larger mouth aperture will allow a larger spatial region to be influenced by the suction flow, a smaller aperture will result in higher forces exerted on the prey item, even in the absence of increased flow velocity.

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REFERENCES

- Batchelor, G. K. 1967 *An introduction to fluid mechanics*. Cambridge, UK: Cambridge University Press.
- Carroll, A. M., Wainwright, P. C., Huskey, S. H., Collar, D. C. & Turingan, R. G. 2004 Morphology predicts suction feeding performance in centrarchid fishes. *J. Exp. Biol.* **207**, 3873–3881. (doi:10.1242/jeb.01227)
- Day, S. W., Higham, T. E., Cheer, A. Y. & Wainwright, P. C. 2005 Spatial and temporal flow patterns during suction feeding of bluegill sunfish (*Lepomis macrochirus*) by particle image velocimetry. *J. Exp. Biol.* **208**, 2661–2671. (doi:10.1242/jeb.01708)

- de Jong, M. C., Sparenberg, J. A. & de Vries, J. 1987 Some aspects of the hydrodynamics of suction feeding of fish. *Fluid Dyn. Res.* **2**, 87–112. (doi:10.1016/0169-5983(87)90021-9)
- De Visser, J. & Barel, C. D. N. 1998 The expansion apparatus in fish heads, a 3-D kinetic deduction. *Neth. J. Zool.* **48**, 361–395.
- Denny, M. W. 1988 *Biology and the mechanics of the wave-swept environment*. Princeton, NJ: Princeton University Press.
- Denny, M. W. 1993 *Air and water: the biology and physics of life's media*. Princeton, NJ: Princeton University Press.
- Domenici, P. & Blake, R. W. 1997 The kinematics and performance of fast-start swimming. *J. Exp. Biol.* **200**, 1165–1178.
- Drost, M. R., Osse, J. W. M. & Muller, M. 1988 Prey capture by fish larvae, water flow patterns and the effect of escape movements of prey. *Neth. J. Zool.* **38**, 23–45.
- Ferry-Graham, L. A. & Lauder, G. V. 2001 Aquatic prey capture in ray-finned fishes: a century of progress and new directions. *J. Morphol.* **248**, 99–119. (doi:10.1002/jmor.1023)
- Ferry-Graham, L. A. & Wainwright, P. C. 2002 Evaluating suction feeding performance in fishes: implications for evolutionary diversification. In *Biomechanics in evolution* (ed. V. L. Bels), pp. 101–116. Oxford, UK: BIOS.
- Fleagle, R. G. & Businger, J. A. 1980 *An introduction to atmospheric physics*. International Geophysics Series. New York, NY: Academic Press.
- Fox, R. W. & McDonald, A. T. 1992 *Introduction to fluid mechanics*. New York, NY: Wiley.
- Higham, T. E., Day, S. W. & Wainwright, P. C. 2006 Multidimensional analysis of suction feeding performance in fishes: fluid speed, acceleration, strike accuracy and the ingested volume of water. *J. Exp. Biol.* **209**, 2713–2725. (doi:10.1242/jeb.02315)
- Lauder, G. V. & Clark, B. D. 1984 Water flow patterns during prey capture by teleost fishes. *J. Exp. Biol.* **113**, 143–150.
- 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. (doi:10.1016/0022-5193(82)90287-9)
- Nauwerlaerts, S., Wilga, C., Sanford, C. & Lauder, G. In press. Hydrodynamics of prey capture in sharks: effects of substrate. *J. R. Soc. Interface*.
- Norton, S. F. 1991 Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics. *Ecology* **72**, 1807–1819. (doi:10.2307/1940980)
- Norton, S. F. & Brainerd, E. L. 1993 Convergence in the feeding mechanics of ecomorphologically similar species in the Centrarchidae and Cichlidae. *J. Exp. Biol.* **176**, 11–29.
- Van Leeuwen, J. L. 1984 A quantitative study of flow in prey capture by rainbow trout, with general consideration of the actinopterygian feeding mechanism. *Trans. Zool. Soc., Lond.* **37**, 171–227.
- Van Leeuwen, J. L. & Muller, M. 1984 Optimum sucking techniques for predatory fish. *Trans. Zool. Soc., Lond.* **37**, 137–169.
- Van Wassenbergh, S., Aerts, P. & Herrel, A. 2006a Scaling of suction feeding performance in the catfish *Clarias gariepinus*. *Physiol. Biochem. Zool.* **79**, 43–56. (doi:10.1086/498188)
- Van Wassenbergh, S., Aerts, P. & Herrel, A. 2006b Hydrodynamic modeling of aquatic suction performance and intra-oral pressures: limitations for comparative studies. *J. R. Soc. Interface* **3**, 507–514. (doi:10.1098/rsif.2005.0110)
- Vogel, S. 1994 *Life in moving fluids*. Princeton, NJ: Princeton University Press.
- Wainwright, P. C., Ferry-Graham, L. A., Waltzek, T. B., Carroll, A. M., Hulsey, C. D. & Grubich, J. R. 2001 Evaluating the use of ram and suction during prey capture by cichlid fishes. *J. Exp. Biol.* **204**, 3039–3051.
- Wakeling, J. M., Kemp, K. M. & Johnston, I. A. 1999 Biomechanics of fast-starts during ontogeny in the common carp, *Cyprinus carpio*. *J. Exp. Biol.* **202**, 3057–3067.
- White, F. M. 1979 *Fluid mechanics*. New York, NY: McGraw-Hill.