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A STUDY IN JET PROPULSION: AN ANALYSIS OF THE MOTION OF THE SQUID, *LOLIGO VULGARIS*

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INTRODUCTION

Squids and other cephalopods have evolved a remarkably effective form of locomotion by jet propulsion. The high-velocity jet is produced by contraction of the mantle muscles so as to expel water from the respiratory mantle cavity through a narrow funnel (Fig. 1). The animal can repeat the process after water has been drawn into the cavity by the expansion of mantle musculature and may produce a number of jet pulses in quick succession. Experimental studies on the squid *Loligo vulgaris* Lam. and other cephalopods have been conducted by Trueman & Packard (1968) and Packard (1969). A theoretical study has been carried out by Siekmann (1963) but he considered a cephalopod as a rigid body of constant mass propelled by a continuous and regularly pulsating jet with a continuous flow of water replenishing the mantle cavity.

The purpose of this paper is to outline an analytical approach to the study of cephalopod locomotion, resulting from one contraction of the muscular mantle producing a single jet of water. The theory and method of analysis is described and results for a simplified model are compared with the results of the experimental studies.

Notation

A	frontal area of body
a	area of funnel outlet
C	drag coefficient
C_d	coefficient of discharge
d_0	internal diameter of empty sphere (or cylinder)
F	component of gravity force acting in direction of thrust
G	modulus of rigidity
m	instantaneous mass of body and contents
m_b	mass of body
m_c	total mass of water expelled from mantle cavity
m_0	initial mass of body and contents
P	pressure inside cavity
q	velocity of jet relative to body
t	time
t_0	thickness of empty sphere (or cylinder)

U	instantaneous velocity of body
U_0	initial velocity of body
ΔU	change in velocity
V	instantaneous volume of fluid in container
V_b	volume of body tissue contained within the mantle musculature
V_0	volume of fluid in the fully contracted container
w	weight of mantle muscle
ρ	density of fluid
ρ_m	density of muscle

General principles

The motion of a jet-propelled body travelling through a fluid medium is governed by the equation of motion which, in the direction of thrust, is

$$F + \tfrac{1}{2}C\rho A U^2 + m\frac{dU}{dt} + q\frac{dm}{dt} = 0. \quad (1)$$

The derivation of this equation allows for the fact that the total mass of the body and its contents decreases as fluid is ejected.

The four terms of this equation are, respectively, the forces associated with gravity, drag, acceleration and jet thrust.

Gravity forces

The resultant of body weight acting vertically downwards and buoyancy force acting vertically upwards will have a component F in the direction of thrust. If the body and fluid have equal density, or if the thrust is horizontal, the gravity force F will of course be zero.

Drag

The drag force will depend upon the density (ρ) of the fluid, the frontal area (A) which probably decreases as the creature discharges the contents of its mantle cavity, the velocity (U) of the body and upon the drag coefficient (C). The latter depends upon the instantaneous shape of the body and the nature of the fluid flow around it, which in turn is a function of the velocity U.

Inertia forces

The third term of equation (1) is familiar from Newton's Second Law of Motion, from which the whole equation may be derived (Hunsaker & Rightmire, 1947). This term depends upon the total mass of the body together with the mass of the fluid at an instant in the mantle cavity and upon the instantaneous acceleration (du/dt) of the body.

Jet thrust

The jet thrust developed by the jet of water is given by the product of jet velocity (q) and the rate of mass flow (dm/dt) through the funnel. We shall show later that it can also be determined from the shape and size of the funnel together with a knowledge of either the jet velocity of the fluid pressure inside the mantle cavity or the shape and properties of the mantle material.

If the drag and gravity forces are neglected, equation (1) reduces to

$$m\,dU = -q\,dm \tag{2}$$

or

$$dU = -q\,(dm/m), \tag{3}$$

and if the jet velocity is assumed constant, equation (3) can be integrated to give the following well-known expression (Hunsaker & Rightmire, 1947; Barrère *et al.* 1960) for the increase in velocity (ΔU) which will occur as the total mass decreases from m_0 to m:

$$U = U - U_0\, q = \ln\,(m_0/m). \tag{4}$$

If it is assumed that a squid having a body mass m_b expels the entire contents of its mantle cavity m_c, then equation (4) can be rewritten as

$$\Delta U = q \ln \frac{m_b + m_c}{m_b} = q \ln \left(1 + \frac{m_c}{m_b}\right). \tag{5}$$

This equation (5) gives a simple expression for calculating the increase in velocity resulting from a single jet pulse. However, particular notice should be paid to the assumptions that (i) gravity forces are negligible, (ii) drag forces are negligible, and (iii) jet velocity is constant.

Assumption (i) may not be unreasonable as *Loligo* is only about 4% more dense than sea water; however, hydrodynamic drag forces may be considerable and the jet velocity is unlikely to be constant throughout the pulse.

Determination of jet thrust

The jet velocity influences the equation of motion (1) through its effect on jet thrust and this important term of the equation may now be examined in more detail. Jet thrust depends upon both jet velocity and rate of mass flow from the funnel but the latter can be regarded as the product of the jet velocity, the funnel outlet area and the fluid density. Losses which occur at an outlet may be taken into account by introducing a coefficient of discharge (C_d) which is less than unity. The mass-flow rate can then be written as

$$dm/dt = C_d \rho a q \tag{6}$$

and the jet thrust

$$q(dm/dt) = C_d \rho a q^2. \tag{7}$$

The jet thrust can thus be readily calculated provided the instantaneous jet velocity is known. Unfortunately the instantaneous jet velocity is not easy to measure directly, so that it is worth while considering the relationship between jet velocity and mantle pressure. This relationship can be determined if the nature of the flow through the funnel is known. For example, if friction is negligible the Bernoulli equation (Hunsaker & Rightmire, 1947) gives the jet velocity as

$$q = \sqrt{(2P/\rho)}, \tag{8}$$

where P is the pressure in the mantle cavity.

The equation (7) for jet thrust then becomes

$$q\,(dm/dt) = 2C_d a P. \tag{9}$$

Thus both jet velocity and jet thrust can be calculated if the instantaneous pressure in the mantle cavity can be determined, either experimentally as by Trueman & Packard (1965) or by some other means.

Simple model

It should be possible to calculate the instantaneous pressure in the mantle cavity if sufficient is known about the anatomy of the mantle, the mechanical properties of the mantle material and its response to stimulation. Not all of this information is readily available but the method of calculation can be illustrated by considering a simplified model. For this purpose we shall assume that the mantle is a hollow sphere of uniform wall thickness and rubber-like properties.

According to the simplified statistical theory of rubber-like elasticity (Johnson & Soden, 1966; Treloar, 1958) the pressure inside such a thin-walled container is related to the volume by the equation

$$P = \frac{4Gt_0}{d_0}\left(\frac{V_0}{V}\right)^{\frac{1}{3}}\left[1-\left(\frac{V_0}{V}\right)^2\right], \tag{10}$$

where G is the modulus of rigidity for the material.

In our simplified model we shall assume that the rigidity of the distended mantle increases instantaneously in response to stimulation and that the modulus of rigidity then remains constant until the mantle has discharged all of its liquid contents.

The rate at which the volume of the container decreases equals the rate at which fluid flows through the outlet, hence

$$\frac{dV}{dt} = -C_d aq. \tag{11}$$

Combining equations (11), (8) and (10),

$$\frac{dV}{dt} = -C_d a\sqrt{\left(\frac{8Gt_0}{\rho d_0}\left(\frac{V_0}{V}\right)^{\frac{1}{3}}\left[1-\left(\frac{V_0}{V}\right)^2\right]\right)}. \tag{12}$$

The differential equation (12) can be integrated numerically to show how the mantle cavity volume varies with time. Substituting the resulting values into equation (10) will then give the variation of mantle pressure with time. The instantaneous jet velocity and jet thrust may be determined by putting these values of mantle pressure back into equations (8) and (9).

Determination of squid motion

Using the information derived from the above and from the equilibrium equation (1) it is possible to calculate the instantaneous velocity of the squid. This is achieved by inserting the instantaneous values of mass and thrust calculated as above into equation (1) and solving the resulting differential equation.

Some additional information is needed or assumptions have to be made about the gravity forces and drag coefficient. The frontal area was calculated from the contained volume (V) assuming that the body of a squid would be incompressible. This area could alternatively be determined from the frontal area of the head. The total instantaneous mass of the squid and mantle contents can be derived from

$$m = m_b+(V-V_b)\,\rho, \tag{13}$$

where m_b is the total mass of the squid's body and V_b is the volume of the viscera contained within the mantle musculature (Fig. 1). When the instantaneous velocity is known the instantaneous position of the squid can be found by integrating once again.

Using this approach it should thus be possible to derive a great deal of information about mantle pressure, jet velocity, jet thrust and squid velocity.

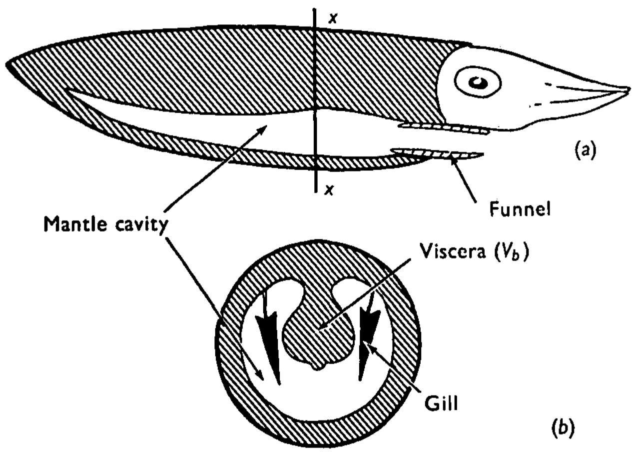

Fig. 1. Diagrams of *Loligo* in (*a*) sagittal section, behind the head, and (*b*) transverse section (line *x–x* in (*a*), showing extent of mantle cavity, viscera and mantle muscles (hatched).

COMPARISON OF THEORETICAL AND EXPERIMENTAL VALUES OF JET THRUST

Some calculations have been carried out using the simplified model and taking, as far as possible, proportions and properties relating to those of a 350 g adult *Loligo vulgaris*. The volume of sea water expelled from the mantle cavity was taken as 200 ml (Trueman & Packard, 1968). Dimensions of the animal with the mantle contracted are not available but the volume contained within the fully contracted mantle was taken as 160 ml, which corresponds to a sphere of approximately 7 cm diameter and gives a change in volume consistent with the 30% reduction in body width recorded by Packard (1969). The space within the fully contracted mantle musculature was assumed to be occupied almost completely by the tissues of the squid's body.

Treating the mantle as a hollow rubber-like sphere requires that we should know the rigidity of the contracted tissue. The value of $4Gt_0/d_0$ was taken as 490 g/cm^2 as this gives a maximum mantle pressure of approximately 300 g/cm^2 as was recorded by Trueman & Packard (1968). In addition to the details of the pressure pulse and volume of fluid discharged, these authors also measured the area of the funnel outlet. The funnel area for the 350 g freshly dead squid was 1·5 cm^2; no information was available on losses in the funnel so the value of the discharge coefficient C_d has been assumed to lie in the range 0·6–1·0. Together with the assumptions implicit in the model this data was sufficient to enable the theoretical pressure, jet velocity and thrust pulses to be calculated.

Two theoretical pressure pulses shown in Fig. 2(*a*) both predict the same maximum pressure of 300 g/cm^2 because the rigidity of the mantle was assumed to be the same. The duration of the pressure pulses differ because of the different values of discharge coefficient assumed. In the case where losses at the funnel were assumed negligible

(C_d = 1) the pulse duration was 0·23 sec compared with the experimental duration of 0·18 sec (Trueman & Packard, 1968). The theoretical value could be reduced to equal the experimental one if it was assumed that the mantle pressure caused the funnel outlet to dilate slightly.

Fig. 2(*b*) shows the two theoretical thrust curves. As would be expected from equation (9) their duration is the same as the corresponding pressure pulses; however, in this case it is the curve which assumes the higher funnel losses (C_d = 0·6) that corresponds more closely with the maximum experimental thrust (Table 1). The curve for C_d = 1 gives a maximum thrust which is much higher than the experimental one.

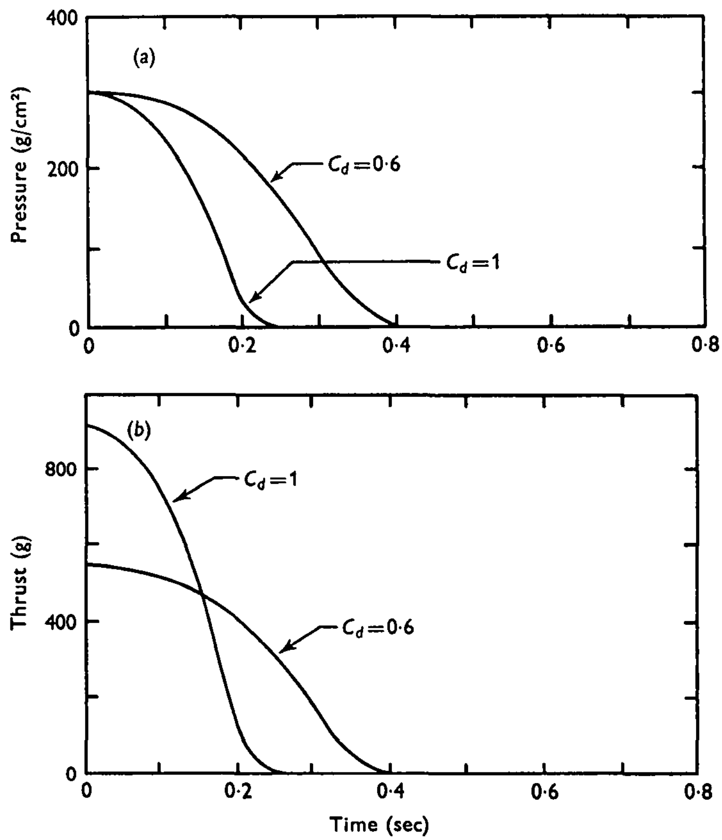

Fig. 2*a* and *b*. For legend see facing page.

The agreement is reasonably good considering the many possible sources of discrepancy introduced by the simplified model such as the assumptions that the material is rubber-like, that the response to stimulation is instantaneous, that the mantle is spherical and that the funnel behaves like a simple rigid orifice. However, these assumptions may not be as extravagant as they seem at first sight; for instance, many tissues, including contracted muscle, show rubber-like properties (King & Lawton, 1950).

The accuracy of the experimental results is also open to criticism. For example, the characteristics of the pressure transducer appear to be unsuitable for the particular

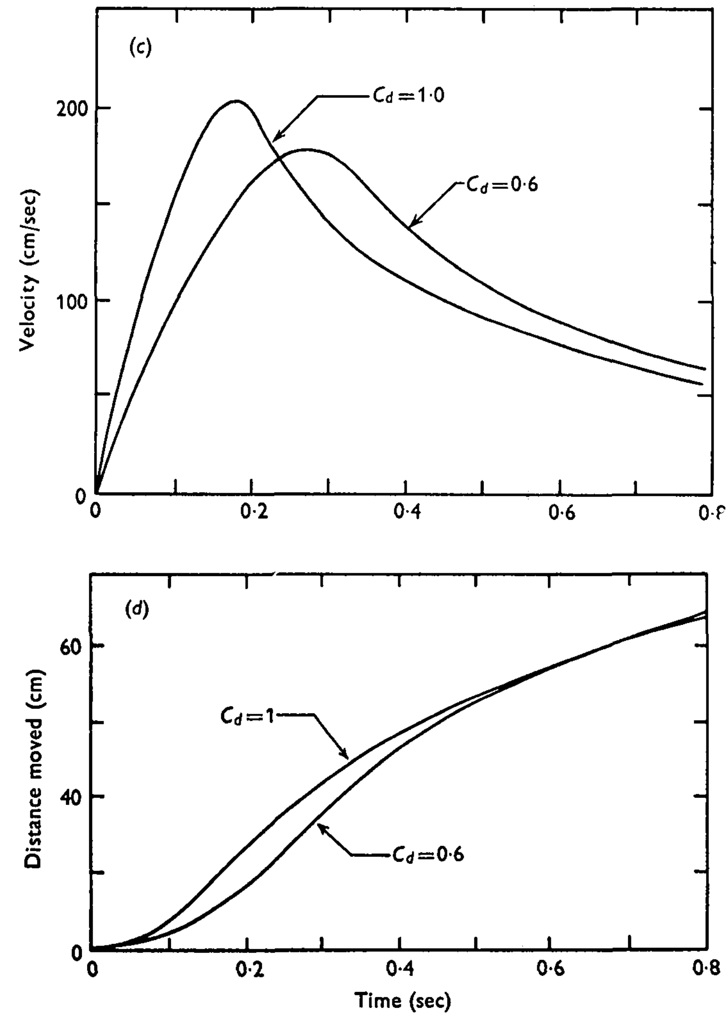

Fig. 2. Graphs showing theoretical relationship between time and (*a*) mantle cavity pressure, (*b*) jet thrust, (*c*) velocity, (*d*) distance moved for two values of the coefficient of discharge of the funnel (C_d).

Table 1. *Theoretical and experimental values of maximum jet thrust and pulse duration in* Loligo vulgaris

(Experimental data from Trueman & Packard (1968).)

	Weight of squid (g)	Funnel area (cm^2)	C_d	Maximum pressure (g/cm^2)	Mantle volume (cc)	Pulse duration (sec)	Maximum thrust (g)
Theoretical	350	1·5	1·0	300	200	0·23	900
	350	1·5	0·6	300	200	0·39	550
Experimental	350	1·5	—	300	200	0·18	—
	400	—	—	330*	—	—	560*

* Maximum values, different pulses.

purpose for which they were applied and the curved trace produced by the pen recorder makes the comparison of pulse shapes difficult. Certain anomalies also arise in the experimental results. A raised pressure is observed in the funnel whilst the mantle pressure is zero and a jet thrust is still evident after the mantle pressure has fallen to zero. The latter, together with the appearance of the thrust pulse (Trueman & Packard, 1968, fig. 5), suggests a certain amount of elasticity in the nylon thread used to record the thrust and in the tissue between the mantle and the point at which the line was attached. Problems in aligning the restraining line with the direction of thrust were also reported. Misalignment would cause experimental values to be lower than the actual ones.

COMPARISON OF THEORETICAL AND EXPERIMENTAL VELOCITIES

The theoretical velocities and change in position of the simplified model produced by single jet pulses was calculated from equation (1) by the method described previously. It was assumed that the drag coefficient remained constant at an arbitrary value (0·47) regardless of the squid velocity. This value is the drag coefficient for a sphere with Reynolds number in the range 10^3–10^5 (Hunsaker & Rightmire, 1947). The density of the squid was assumed to be equal to that of sea water. This last assumption eliminated gravity effects and hence the need to consider the direction of motion.

Table 2. *Theoretical and experimental values of the velocity of jet swimming of* Loligo vulgaris

(Experimental data from Packard (1969).)

	Weight (g)	Coefficient of discharge	Maximum velocity (cm/sec)	Time to reach maximum velocity (sec)
Theoretical	350	1·0	206	0·175
	350	0·6	180	0·280
Experimental	100*	—	210	0·085–0·125
	240†	—	176	0·200

* Backward escape. † Forward attack.

Packard (1969) has used stroboscopic and cinephotography to record the motion of squids at various stages of their development. A comparison of his results for adult squids with the theoretical results for the model shows reasonably good agreement (Table 2).

Fig. 2(*c*) shows theoretical velocity curves for two coefficients of discharge, and in Fig. 3 one of the theoretical curves is superimposed upon Packard's experimental results. The shapes of the curves appear to be similar.

The effect of drag will be to reduce the maximum velocity and cause the peak to occur earlier. The reason for the shorter time to reach peak velocity can be understood if the forces acting on the body are examined (Fig. 4). In the absence of drag and gravity forces the body would continue to accelerate until the jet thrust fell to zero. If drag forces are present as in Fig. 4 the body ceases to accelerate as soon as the drag forces equal the jet thrust. The jet thrust will fall off as the mantle pressure decreases, but meanwhile the drag forces increase rapidly as the squid velocity increases, with the result that the drag forces exceed the thrust forces and cause retardation before the pressure pulse is complete. Note, however, that if the fall in pressure at the end of the pulse is very rapid the effect of drag on the time to peak velocity will be small. In the case considered in Fig. 4 the decrease in the time to peak velocity due to drag is approximately 25%.

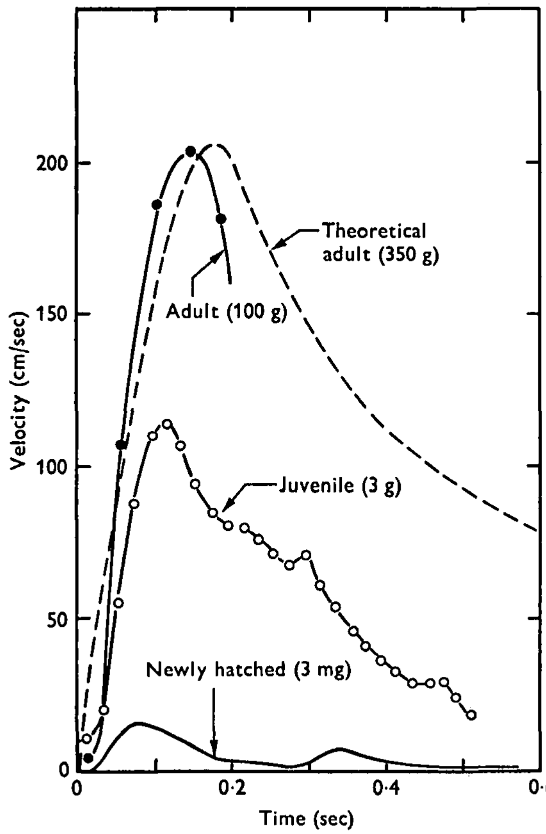

Fig. 3. Theoretical and experimental squid velocity. Instantaneous velocity curves for *Loligo vulgaris* of different weight (Packard, 1969) compared with a theoretical curve (broken line) for a 350 g squid.

It is interesting to compare the two theoretical cases considered and to note that the case in which the funnel losses are lowest ($C_d = 1$) and the instantaneous velocity highest does not give the greatest distance of travel after say 0·8 sec (Fig. 2(*d*)). This is presumably due to the combined effects of shorter pulse duration and higher velocity leading to higher drag losses.

DISCUSSION

This analytical approach to the study of jet propulsion in *Loligo* enables values of mantle pressure, jet velocity, jet thrust, body acceleration, velocity and change of position to be calculated from basic information on the shape and material properties of the animal. All of the results are presented as instantaneous values so that the variation with time may be studied and theoretical values of such factors as pressure pulse duration or the time for the body to reach maximum velocity can be investigated.

In these calculations the shape of the squid has been regarded as spherical for simplicity. It would equally well have been considered as a cylinder of constant length when equation (10) would be replaced by

$$P = \frac{2Gt_0}{d_0}\left[1 - \left(\frac{V_0}{V}\right)^2\right]. \tag{14}$$

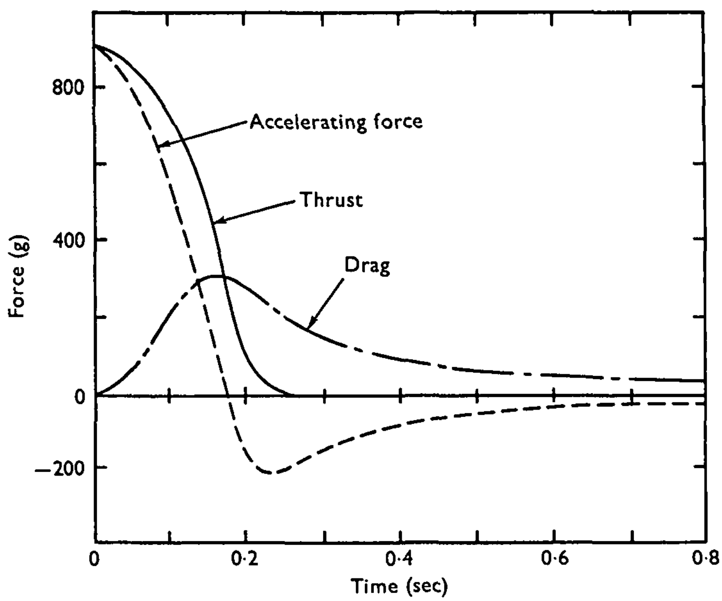

Fig. 4. Graph summarizing the forces acting on the body of a squid resulting from a single jet pulse.

It is interesting to note that for a cylindrical animal having a known mantle muscle weight (w) and known volume (V_0)

$$\frac{t_0}{d_0} = \frac{w}{4V_0\rho_m}, \tag{15}$$

therefore

$$P = \frac{Gw}{2V_0\rho_m}\left[1 - \left(\frac{V_0}{V}\right)^2\right]. \tag{16}$$

Thus for a squid of given volume an increase in muscle weight gives greater pressure and consequently greater jet thrust. Conversely, with a constant weight of mantle muscle, a mantle cavity of larger volume results in lower pressures. This holds regardless of the length-to-diameter ratio of the cephalopod so that the ability to generate jet thrust is not altered by an elongated shape. Such a form may, however, considerably reduce the drag coefficient. This conclusion is drawn on the basis of this analysis for a cylindrical model. Reduction of the length-to-diameter ratio would result in a more nearly spherical animal, but this should not greatly affect the discussion since the equivalent equation to (16) is

$$P = \frac{2}{3}\frac{Gw}{V_0 \rho_m}\left(\frac{V_0}{V}\right)^{\frac{1}{3}}\left[1-\left(\frac{V_0}{V}\right)^2\right]. \tag{17}$$

Both these equations (16, 17) give comparable values for pressure over the probable range of mantle contraction ($V \to V_0$).

Unlike earlier determinations of squid velocity (Trueman & Packard, 1968) calculations discussed here take into account that the animal is moving whilst the jet of water is emitted, that the jet velocity varies with time and that drag forces are present.

Trueman & Packard (1968, table 1) have determined a maximal velocity of 420 cm/sec for a single jet cycle of a 350 g *Loligo vulgaris*. Using equation (5) (which allows for the squid moving backwards as the jet is emitted) and the data from these authors, a velocity of 330 cm/sec is obtained. With the model, which additionally allows for drag and varying jet velocity, a value of 180–206 cm/sec is deduced (Table 2). The latter agrees with the swimming speed observed by Packard (1969).

The performances of other cephalopods, with the exception of *Octopus*, are similar to that of *Loligo* (Trueman & Packard, 1968) and the principles put forward here can be usefully applied to these and other aquatic animals using jet propulsion as a means of locomotion.

SUMMARY

1. A method is presented which allows the jet thrust and motion of a cephalopod to be calculated from basic information on its shape and material properties.

2. A simple model is used to illustrate the technique, and the results are compared with experimental data for *Loligo vulgaris*. Agreement between theoretical and experimental results is shown to be reasonably good.

3. This approach could be applied to other cephalopods and other animals using jet propulsion.

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