

STUDIES IN ANIMAL LOCOMOTION

VI. THE PROPULSIVE POWERS OF THE DOLPHIN

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(With Three Text-figures)

It is well known that certain aquatic vertebrates (notably dolphins and some of the larger teleostean fishes) are able to travel at surprisingly high speeds. The movements performed by such animals during rectilinear locomotion are all of the same type, for the hind end of the body vibrates rhythmically in a plane at right-angles to the axis of locomotion; the plane of vibration of the dolphin is dorso-ventral, whereas that of a fish is transverse to the long axis of the body. In all cases the orientation of the hind end of the body and of the caudal fin, in particular, is such that during both phases of each vibration the leading surface (relative to the direction of the vibration) is inclined at an angle to its own direction of motion through the water and is directed obliquely backwards relative to the head of the animal (Gray, 1933). The anatomical arrangements of the propulsive muscles of a dolphin appear to be simpler than those of a fish, since the locomotory movements are produced by four bands of musculature connected to the base of the caudal fin by strong tendons; on the ventral side of the vertebral column the two muscle bands extend forward to the region of the diaphragm, whereas the two dorsal bands extend over the whole back of the animal. The weight of the dorsal musculature is approximately twice that of the ventral muscles. The tail is deflected upwards by the contraction of the dorsal muscles and downwards by contraction of the ventral muscles. Reciprocity thus exists between the dorsal and ventral muscle groups, whereas, in a fish, reciprocity of this type is restricted to the right and left musculature of individual segments. Apart from these anatomical differences the propulsive mechanisms of a fish and of a dolphin appear to be of essentially the same type.

It is commonly stated that the streamlined form characteristic of rapidly swimming vertebrates enables them to move through the water with a minimum resistance. Attempts to measure this resistance (Houssay, 1912; Mangan, 1930) have been made on the assumption that when a fish is swimming freely in water it is overcoming a resistance which is equal to that encountered by an inert body of the same size and shape when towed through water at the same speed. The recent work of Richardson (1936) has shown that the towing resistance of an inert fish is not substantially different from that of a model of similar form, but observations of this type do not enable us to decide how closely this value is related to the resistance actually overcome by a free-swimming fish. The problem is of considerable interest,

since a reliable estimate of the "free-swimming" resistance of a large fish or dolphin would indicate whether the mechanism of swimming is or is not substantially more efficient than those, at present, available for the propulsion of a torpedo or airship.

Direct determination of the horse-power of a freely swimming fish or dolphin would involve very great technical difficulties. It is, however, possible to approach the problem from a theoretical point of view and from arguments based on the observation of models.

The velocity of a rapidly moving dolphin has seldom been determined with great accuracy, and no doubt it has often been exaggerated. The following observation made by Mr E. F. Thompson whilst in the Indian Ocean is therefore of interest. A dolphin swimming approximately 30 ft. from the side of the ship passed the ship in the direction of stern to bow in just under 7.0 sec. as timed by a stop-watch; the length of the ship was 136 ft. and its speed was logged at 8½ knots. This dolphin must therefore have been travelling at 20 knots (= 33 ft. per sec.). On many occasions dolphins have been seen to keep abreast of the ship's bows when the vessel was travelling at 15 knots, and so far as could be determined this speed could be maintained for considerable periods.

If the resistance (*R*) overcome during normal locomotion at a speed of 33 ft. per sec. is equal to the towing resistance of a rigid body of the same size and shape, then

$$R = \frac{d\rho AV^2}{g},$$

and the horse-power (H.P.) = $\frac{d\rho AV^3}{550g}$,

where *d* = drag coefficient, ρ = weight of 1 cu. ft. of water, *A* = surface area in sq. ft., *V* = velocity in ft. per sec., *g* = 32. The value of the drag coefficient varies with the velocity and length of the moving body, but for a 4-ft. porpoise travelling at 25 ft. per sec. the appropriate coefficient is about 1.5×10^{-3} , while for a 6-ft. dolphin travelling at 33 ft. per sec. the coefficient is approximately 1.3×10^{-3} .

The surface area of a 4-ft. porpoise (*Phocaena communis*) was found by direct measurement to be very nearly 7 sq. ft., whilst that of a model of a dolphin (*Delphinus delphus*) was 15 sq. ft. Using the equations given above, the towing resistance and requisite horse-power can be calculated; they are recorded in Table I.

Table I

Species	Total wt. lb.	Length ft.	Surface area sq. ft.	Speed ft. per sec.	Drag coeff.	Towing resistance lb.	H.P.	Wt. of muscles lb.	H.P. per lb. of muscle
Porpoise	53	4	7	25	1.5×10^{-3}	16	0.6	9	0.067
Dolphin	200	6	15	33	1.3×10^{-3}	42.5	2.6	(35)	0.074

Reliable estimates of the horse-power of mammalian muscle have been obtained in the case of man and of the dog. Henderson and Haggard (1925) showed that the output of very highly trained oarsmen was approximately 0.5 H.P. per man. If we

assume a conservative estimate of the weight of muscle employed, namely 50 lb., the available horse-power per lb. of muscle is 0.01, a figure which is substantially the same as that obtained by Dill, Edwards and Talbot (1932) for the dog. If, therefore, the output of cetacean muscle is of the same order as that of other mammals the 4-ft. porpoise would require 60 lb. of muscle, and the 6-ft. dolphin would require 260 lb. Both of these figures are clearly fantastic; in fact, the total weight of the propulsive muscles of the porpoise was found to be 9 lb. and that of the dolphin was estimated to be 30-40 lb.¹ In order, therefore, to endow the cetaceans with their estimated horse-power we must assume that their muscles are approximately seven times more powerful than those of other mammals, in which case the ability of these animals to dissipate heat and to supply oxygen and nutritive substances to the active muscles must be very remarkable.

Before accepting an abnormally high horse-power for cetacean muscle, it is reasonable to reconsider the validity of the figure which has been accepted for the drag coefficient of the actively moving animal. The resistance per square foot of surface area will vary with the nature of the flow of water over the surface of the animal, and this, in turn, depends upon the size and velocity of the organism. So long as the product of the velocity and the length of a smooth rigid body does not exceed a critical value the flow past the surface may be expected to be of the laminar type and free from turbulence; if the critical value be exceeded the flow past the posterior end of the body becomes turbulent. The transition from laminar to turbulent flow sets in when the Reynolds' number² exceeds a value of 5×10^5 (see Ewald, Pöschl and Prandtl, 1930, p. 319).

Until the transitional value for Reynolds' number is exceeded, the value of the drag coefficient falls continuously for increasing speeds, but once the transitional point has been passed the additional resistance, introduced by the formation of eddies, leads to a marked rise in the value of the coefficient. Table II shows, for the

Table II

Reynolds' No.	Drag coefficient	
	Laminar flow	Turbulent flow
10^5	2.1×10^{-3}	—
2×10^5	$1.5 \times$	—
3×10^5	$1.2 \times$	—
4×10^5	$1.0 \times$	—
5×10^5	$0.9 \times$	1.0×10^{-3}
10^6	$0.7 \times$	$1.5 \times$
2×10^6	$0.5 \times$	$1.6 \times$
4×10^6	$0.3 \times$	$1.56 \times$
8×10^6	$0.2 \times$	$1.4 \times$
10^7	$0.2 \times$	$1.3 \times$
2×10^7	$0.15 \times$	$1.25 \times$

¹ The actual weight of the muscles of a dolphin (5 ft. 8 in. long) has since been found to be 33 lb. For this and other useful data I am indebted to Dr Frazer, British Museum (Nat. Hist.).

² Reynolds' No. = $\frac{Vl}{\nu}$, where V = velocity, l = length and ν = kinetic viscosity of water.

sake of convenience, the drag coefficient for laminar flow and for the transitional change to turbulent flow for various values of Reynolds' number.

So long as a 6-ft. dolphin is travelling at speeds higher than 1 ft. per sec., the flow has been assumed to be turbulent, and the Reynolds' number for a 6-ft. dolphin travelling at 33 ft. per sec. is of the order of 1.6×10^7 ; in calculating the resistance of the animal the drag coefficient (1.3×10^{-3}) characteristic of turbulent flow has therefore been used.¹ If, on the other hand, the flow past the body were laminar and free from turbulence, the resistance would be very much smaller, for d would become 0.15×10^{-3} . Under such circumstances the resistance of the dolphin would fall to 4.9 lb. and the horse-power to 0.3. This output of work could be maintained by 30 lb. of typical mammalian muscle—a figure in good agreement with the actual weight of muscle present. Similarly the drag coefficient for laminar flow past a porpoise 4 ft. long and travelling at 25 ft. per sec. would be 2.3×10^{-4} ; the resistance would be 2.0 lb. and the calculated horse-power 0.09. This is equivalent to 9 lb. of typical mammalian muscle and happens to be the exact weight of the muscles of the porpoise itself. In view of these results, it is of interest to consider how far the flow over the surface of the body of an actively swimming fish or dolphin is determined by conditions which tend to eliminate the turbulence characteristic of the flow past a rigid body of similar form.

The nature of the movements executed by a fish or a dolphin are known with considerable accuracy, and their propulsive effect has been considered elsewhere (Gray, 1933). For the purpose of the present discussion, however, it is necessary to know in detail the type of flow which these movements generate in the surrounding water. Comparatively little information is available concerning the flow set up by vibrating systems immersed in a fluid (see Richardson, 1936), and so far it has proved impracticable to record the flow of water past the body of a living fish swimming freely in water. The present series of observations have therefore been made on models, composed of flexible rubber, whose movements were made to conform with those of a variety of fish. This was effected by inserting into the dorsal surface of the model (12–15 in. in length) a series of rigid rods which were capable of performing simple harmonic movements in a plane at right-angles to the long axis of the model. The amplitude of movement of each rod and the phase difference between itself and its neighbours were adjusted to conform with cinematograph records of an actively swimming fish of the same length as the model. The rods actuating the model were driven by a single shaft, so that the frequency of movement could readily be adjusted to any value. The model was half submerged in a large tank of water, and the movement of the water past the body of the model was detected by photographing the movement of particles lying at or near the surface of the water. By means of cinematograph pictures it was possible to obtain a tolerably complete picture of the flow past the model.

¹ In calculating the oxygen requirements of a blue whale (27 m. in length) travelling at 10 knots, Krogh (1934) accepts an estimate of the horse-power of 46.8. This appears to be based on a drag coefficient characteristic of turbulent flow: if the flow were laminar the oxygen requirements would obviously be very much less than those calculated by Krogh. It is unlikely that the flow past the body of a large whale is entirely free from turbulence, but it may well involve very much less than that past a rigid body.

In a normal fish the amplitude of the muscular waves increases as the waves pass backwards (Gray, 1933), but, for the moment, it is convenient to consider the movement of particles in the neighbourhood of a wave whose velocity and form remain constant. It is possible to summarise the flow of particles lying in the neighbourhood of such a wave as follows: (1) The direction and velocity (relative to the ground) of a particle depends upon its position relative to the crest (Fig. 1) of the wave and upon the velocity with which the wave is travelling relative to the ground. (2) A particle lying in the median plane of a wave trough (*e.g.* a particle situated on one of the lines gg_1 , cc_1 , jj_1 in Fig. 1) travels in the same direction as the wave but at a velocity which is always less than that of the wave itself and which decreases the farther the particle lies from the surface of the fish (Fig. 1, cc_1). (3) Particles lying in a transverse plane which cuts a leading surface of the body travel obliquely outwards from the longitudinal axis of the body, as can be seen from the direction of the arrows along the regions fg , bc , hj , de in Fig. 1, these regions each being leading surfaces of waves. (4) Particles lying in planes which cut trailing surfaces flow obliquely inwards as in Fig. 1, ab , gh , cd , jk . (5) Particles at positions near the outer crests of the waves flow in a direction opposite to that of the waves as in Fig. 1, b , h , d . Since the posterior¹ velocity of the particles relative to the ground is always less than that of the waves themselves, an individual particle is constantly changing its position relative to the crest of the wave; it is, in fact, constantly being overtaken by successive waves. This is illustrated in Fig. 2. The whole flow is determined by the fact that the leading surfaces of a wave are displacing water, while the trailing surfaces are acting as centres towards which water flows (see Fig. 1). In so far as water is prevented from flowing across the body of the fish the water displaced at a leading surface flows towards a trailing surface, lying posteriorly to itself. The leading surfaces represent regions of high pressure and the trailing surfaces represent regions of low pressure. As these regions pass towards the hind end of the fish, water is constantly moved backwards relative to the ground (Fig. 2), thereby giving a forward thrust to the body. These observations have been checked against the movement of particles lying in the vicinity of a slowly moving eel, and

¹ The propulsive waves travel over the body of a fish from the anterior to the posterior end of the body. The term "posterior" as used in respect of the model is therefore employed to denote the end of the model towards which the waves are travelling.

Fig. 1. Figure showing the direction of flow (relative to fixed axes) of particles in the neighbourhood of a series of waves of constant form passing over the body of a model fish in the direction of the large arrow. Leading surfaces are shown at fg , bc , hj , de . Trailing surfaces are shown at ab , gh , cd , jk . The relative velocities of particles lying in the plane of a wave crest are shown at the level hcc_1 : the length and direction of the arrows at this level indicate the velocity and direction of movement of the particles.

Fig. 2. Figure showing the movement of a particle relative to a wave and to fixed axes respectively as a wave of constant form advances in the direction of the large arrow from A_1 to A_{111} . The particle (originally situated at position 1 near the leading edge of the wave) travels backwards relative to the wave along the line —. When the crest of the wave has reached A_{111} the particle is situated (relative to the wave) at the posterior edge of the wave (position 9). The motion of the particle relative to fixed axes is shown by the dotted line; the points marked on this line correspond with those showing the movement of the particle relative to the wave. The dotted wave indicates the position of the wave when the particle has reached position 5. The figures along the line A_1 – A_{111} indicate the position of the wave crest for each of the positions marked on the track of the particle.

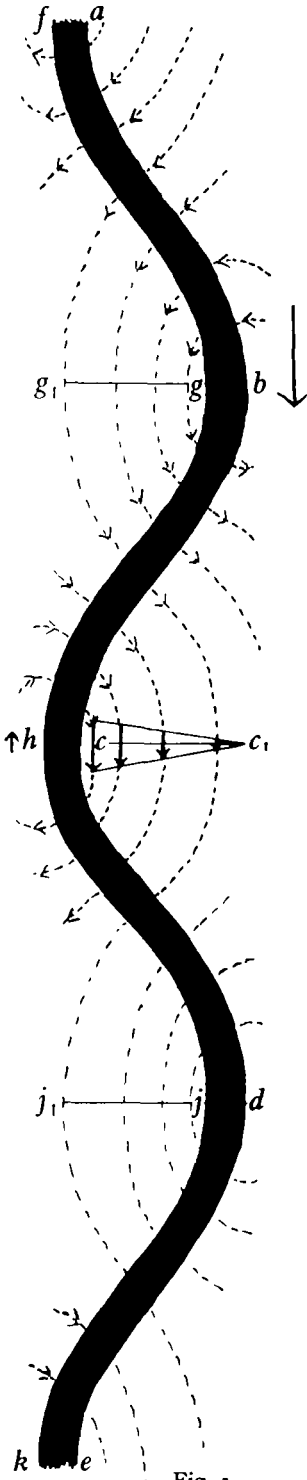


Fig. 1.

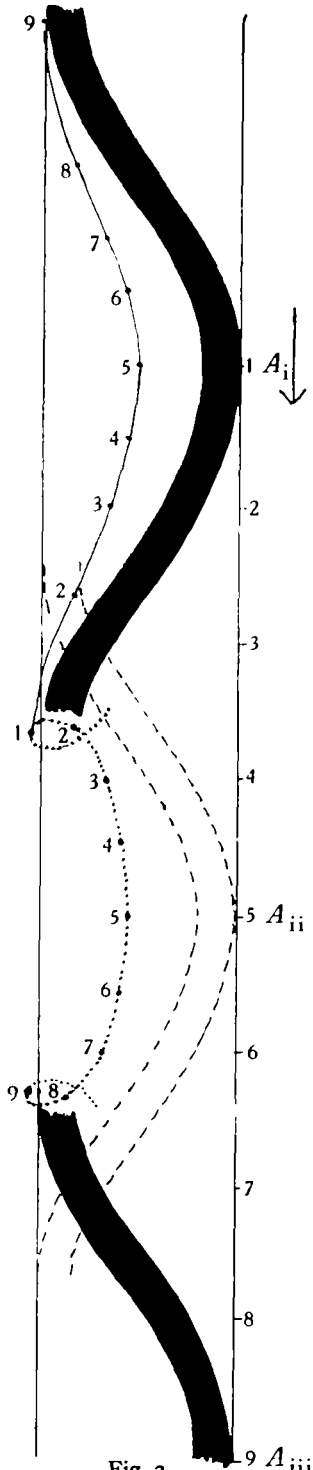


Fig. 2.

they can be applied, also, to the undulatory type of movement seen in active flagella. For present purposes they indicate that undulatory movements of the type seen in actively swimming fish may be expected to set up a type of flow quite distinct from that past a rigid body or past a dead fish towed through water.

When the form and movements of the model are made to approximate in form to those of a whiting or a mackerel the conditions are somewhat different, and it is more difficult to plot the flow with accuracy. It can, however, be seen that particles situated near the surface of the posterior regions of the body are accelerated backwards towards the trailing surface of the caudal fin (Fig. 3). This movement is particularly noticeable in the case of particles lying in the vicinity of the leading surface of the body, for when such particles reach the peduncle of the tail they pass rapidly over the dorsal or ventral surface of the body and are drawn in at the trailing surface of the fin (Fig. 3). It seems clear that the latter surface acts as a centre of low pressure which induces a backward acceleration of all the water lying in the vicinity of the whole of the posterior part of the body.

Probably the only safe conclusion to be drawn from these observations is that the flow of water in the vicinity of a body which is exhibiting undulatory movements of the type performed by a fish or a dolphin when in locomotion, differs substantially from that past a rigid body when being towed through the water, and consequently it is illegitimate to assume that the resistance to movement is the same in both cases. It is, however, tempting to go somewhat farther.

In the case of a rigid body anchored in a stream, the resistance due to turbulent flow is caused by frictional retardation of the flow in the vicinity of the boundary of the body. "If any accelerating or retarding pressure differences exist in the layers of water which adjoin the boundary layer these differences of pressure affect the fluid in the boundary layer also. If the external flow is accelerated by a fall of pressure in the direction of motion the fluid particles which are travelling more slowly in the boundary layer also receive an impulse in the direction of motion, hence all particles continue on their way past the surface of the body" (Ewald, Pöschl and Prandtl, 1930, p. 283). So long as such conditions persist the flow remains laminar and free from turbulence. Owing to the small dimensions of the models described in this paper, it has not been possible to determine by direct observation whether a turbulent flow past the model at rest is replaced by a laminar flow when the model is exhibiting typically propulsive movements, but the evidence suggests that the water in the vicinity of the hind end of the body of a fish or a dolphin is being influenced by such conditions in the external flow as are likely to represent a region or regions of low pressure acting in the direction of motion, and to this extent it seems conceivable that the flow past the surface of an actively moving dolphin is very much less



Fig. 3. Diagrammatic representation of the flow of water induced by the caudal fin of a dolphin or fish.

turbulent than is the case when the inert organism is towed through water at the same speed. In order to test the validity of this conclusion it would be necessary to observe the flow past the body of a much larger model than has so far been available: it would also be necessary to make the observations in an external flow of water whose velocity was approximately that of a free-swimming dolphin.

All fast-swimming fish and dolphins appear to possess a narrow but strong peduncle to the caudal fin, and the latter is expanded to a width approximately equal to the transverse diameter of the widest region of the body. If the suggestions made in this paper are valid, the narrow peduncle and expanded fin seem well adapted for a free flow of water from all the posterior regions of the body surface to the trailing surface of the fin.

SUMMARY

1. If the resistance of an actively swimming dolphin is equal to that of a rigid model towed at the same speed, the muscles must be capable of generating energy at a rate at least seven times greater than that of other types of mammalian muscle.

2. Observation of the flow of particles past the surface of models similar in form to a fish or dolphin shows that rhythmical movements, such as are characteristic of the body and caudal fin of the living animals, exert an accelerating effect on the surrounding water in the direction of the posterior end of the model. An effect of this type may be expected to prevent turbulence in the flow of water past the body.

3. If the flow of water past the body of a dolphin is free from turbulence, the horse-power developed per pound of muscle agrees closely with that of other types of mammalian muscle.

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