THE LIFT PRODUCED BY THE HETEROCERCAL TAILS OF SELACHII

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INTRODUCTION

Selachians have no swimbladders, and are denser than the water in which they live. When swimming horizontally, they must therefore exert a force against gravity. It is generally accepted that in the case of the sharks and dogfish upward forces are generated by the passage of the pectoral fins through the water at a positive angle of attack, and by the action of the heterocercal tail. Harris (1936, 1938) demonstrated the lift produced by the pectoral fins in wind-tunnel experiments with a cast of *Mustelus*. The lift produced by the heterocercal tail has been demonstrated qualitatively in experiments with models by Grove & Newell (1936) and by Affleck (1950).

This paper reports experiments in which actual tails, not models, were used. The lift produced by them at various speeds of transverse movement was determined. The results are used in a quantitative discussion of the equilibrium of sharks swimming horizontally.

MATERIALS AND METHODS

The tails of two lesser spotted dogfish, *Scyliorhinus canicula* (L.), and one tope, *Galeorhinus galeus* (L.), were used in the experiments. The dogfish were 64 and 65 cm. long and weighed 877 and 863 g., respectively. Only the tail of the tope was received, but it was estimated from its dimensions (see Fig. 1) that the fish from which it came must have been about 95 cm. long and have weighed roughly 3.5 kg. The estimate of length is based on photographs of tope in angling magazines, and that of weight on Magnan's (1929) table giving the weights of tope of various lengths. The dogfish had been deep-frozen for an unknown period before the experiments, but the tope tail had not been frozen when it was received. The tope was caught in the evening, and the tail was used in an experiment on the following day. The tail was then deep-frozen for 7 weeks, thawed, and the experiment was repeated to determine the effect of freezing. This gave an indication of the reliability of the results of the experiments on dogfish.

No attempt was made to imitate the reciprocating motion of the tail in swimming, as the variations of speed of the tail during a cycle could be expected to result in cyclical changes in the forces acting on the tail. Instead, the tail was moved at constant speed during each observation. Constant forces are easier to measure than oscillating ones.

The apparatus is shown in Fig. 2. The moving parts are supported by a framework of 1/4 in. angle iron which is not illustrated. $AB$ is a brass rod of diameter 1 in. Near its upper end, it runs through the centre of a small kymograph drum, $C$, which is
firmly attached to it. It is suspended from a ball race at $A$, and passes through another bearing below the drum. The rod and drum are thus held vertical, but can rotate freely.

A cord is attached to the drum, wrapped several times round it, passed over the pulley $D$ and attached to the pan $E$. $AB$ can be made to rotate by putting weights in this pan. It makes two revolutions as the pan falls from just below the pulley to the

Fig. 1. Lateral views of the tope tail (above) and one of the dogfish tails used in the experiments. They have been skinned to reveal the radial muscles (black), the longitudinal swimming muscles (hatched) and the fin rays (stippled). The points $\times$ are explained in the text.

Fig. 2. The apparatus. This figure is explained in the text.
Lift produced by the heterocercal tails of Selachii

floor. The direction of rotation can be reversed by winding the cord round the drum in the opposite direction. A jockey (not shown) between C and D serves to align the cord with the pulley.

B is at the centre of a rectangular tank of horizontal dimensions 75 and 90 cm. containing water to a depth of 35 cm. An aluminium bar FG is attached to AB at B by a horizontal pivot which allows it to swing freely through angles of about 45° on either side of the horizontal, but which allows very little lateral play. A hole is bored through the bar at G so that weights (nuts and washers) can be bolted to it. Two sharpened prongs of 3/16 in. diameter brass project 9 cm. beyond the bar at F. They lie side by side, and their axes are 1.5 cm. apart.

The tail is impaled upside-down on these prongs, with the prongs parallel to and on either side of the vertebral column. In impaling the tail, its sagittal plane is kept as nearly vertical as possible. The whole free length of each prong is embedded in the tail. In most experiments, the tail was cut off 6 cm. anterior to the base of the hypo-caudal lobe, and the prongs thus reached 3 cm. posterior to the anterior end of this lobe. In the case of one of the dogfish, however, an experiment was first carried out with the cut 9 cm. anterior to the base of the lobe, and the prongs only reaching the transverse plane of the anterior end of the lobe.

When the tail is in place weights are bolted to FG at G so that the bar is balanced about the pivot at B. A further weight is then bolted on at G. The following procedure is then used to determine the speed of movement of the tail about the axis AB at which the moment about B of the downward force produced by the (upside-down) tail equals the moment about B of this further weight, and the tail swings neither up nor down.

The drum is turned so that the pan E is raised to a position just below the pulley D. FG is held horizontal. A weight is placed in E. FG is then released. It accelerates, and very rapidly reaches a constant speed (in the experiments with the fresh tope tail, the first revolution was on average only 5% slower than the second). The angle which FG makes with the horizontal as it rotates is observed. It is necessary to use the mirror H for this purpose, as the tank is not transparent. If the tail rises as it rotates, the moment about the pivot at B of the force produced by it is less than the moment due to the load at G. If the tail sinks, the moment of the force produced by it is greater than that due to the load at G.

Several observations are made, using different weights in E, to find the weight for which FG is still horizontal when E reaches the floor. This cannot be done very precisely: the minimum weight for which the tail was observed to sink was on average 45% greater than the maximum weight for which it was observed to rise. The determinations of weight required in E are thus subject to substantial error. The corresponding error in the values for speed is rather smaller, as speed does not increase in proportion to weight in E.

When the weight required in E has been determined, the speed of rotation achieved by the apparatus with this weight in E is measured. In the experiment on the fresh tope tail, the second revolution after the release of FG was timed. In the other experiments the revolution starting after completion of half a revolution was timed. The initial period of acceleration was thus excluded from the timed revolution in each case.
The determination of the weight required in $E$, and of the corresponding speed, is then repeated with the apparatus rotating in the opposite direction. This is done to detect errors due to asymmetrical mounting of the tail.

Further determinations are then made, with different loads at $G$.

At the end of the experiment the tail is removed from the apparatus. Its outline, cut off transversely at the anterior end of the base of the hypocaudal lobe, is traced on cardboard and cut out. The centre of gravity of this piece of cardboard is found. The point on the tail corresponding to this centre of gravity is assumed in the calculation of results to be the centre of pressure for vertical forces of the tail. It is marked $\times$ on the tails in Fig. 1.

The periods of revolution are used to calculate the linear speeds of transverse movement of the point $\times$, which are taken as the speeds of the tail. The corresponding loads at $G$ (corrected to their values in water) are used to calculate the vertical forces produced by the tail, which are assumed to act at $\times$.

The experiments were carried out in fresh water, but the difference in density between fresh water and sea water is too small for this to have affected the results significantly.

The technique is open to two criticisms that cannot fully be answered. First, the lift produced at a given speed in the experiments will not equal the lift produced in swimming at the moments in each stroke when the tail has the same speed, if the mechanical properties of the tail include an appreciable viscous component. No attempt was made to measure viscosity in the tails, but it is believed to be unimportant as the undeformed shape was recovered very rapidly when the tails were released after bending by hand. Secondly, the radial speed of water over the tail was not controlled. The tail must certainly have produced a centrifugal flow of water over itself, but it is not known how the speed of this flow at any transverse speed compared with the longitudinal speeds occurring in life. It seems probable that the transverse speed will be very much more important than the longitudinal speed in determining the lift. The lift produced by a yawed aerofoil is the lift which would be produced by the component of the airflow at right angles to the span, acting alone, when flow is laminar (Mair, 1961). Unfortunately it does not seem to be clear whether this is the case in turbulent flow, and the nature of the flow over shark tails has not been investigated.

RESULTS

Figs. 3 and 4 are graphs of lift against transverse speed, both on logarithmic scales. For each experiment the points lie close to a straight line, except in the cases of dogfish tails at the lowest speeds tried. These lines all have gradients between 1.3 and 1.5. Lift is thus in each case approximately proportional to the 1.4 power of speed.

Deep-freezing had an appreciable effect on the properties of the tope tail. To produce a given lift after freezing the tail had to be moved about 75% faster than before freezing. The dogfish, which had been frozen before they were received, were presumably similarly affected.

It is apparent from Fig. 4 that the results are affected by the position of the prongs in the tail. In the swimming fish, lateral bending of the vertebral column is resisted by the longitudinal swimming muscles, which extend almost to the posterior end of the
Lift produced by the heterocercal tails of Selachii

The lift produced by the heterocercal tails of Selachii column (Fig. 1). The stiffening effect of the active muscles cannot of course be precisely imitated by rigid prongs, but my impression is that the shapes adopted by the tail in the majority of experiments, with the cut 6 cm. anterior to the hypocaudal lobe, were reasonable approximations to the shapes of tails, moving at comparable transverse speeds, of swimming fish. This impression is based on comparison of photographs of tails in the apparatus with photographs of Squalus swimming (Gray, 1933; Wolf, 1960). The results of these experiments are used in the discussion which follows. In the experiment with the cut 9 cm. anterior to the hypocaudal lobe the tail bent unnaturally. At about 80 cm./sec., the posterior half of the tail was almost at right angles to FG, and can have made very little contribution to the lift. Nevertheless, the speed required to produce a given lift was only about 50% greater than with the prongs in the other position.

DISCUSSION

The lift produced by rigid aerofoils and hydrofoils is proportional to the square of their speed. Heterocercal tails are flexible; the vertebral column bends laterally and the angle of attack of the hypocaudal lobe decreases as the speed increases. It is not surprising to find that the lift is proportional only to the 1.4 power of the transverse speed. (After freezing)

Fig. 3. Graphs of lift against transverse speed for the experiments with the tail cut 6 cm. anterior to the hypocaudal lobe.

Fig. 4. Graphs of lift against transverse speed for the same dogfish tail cut 9 cm. (lower line) and 6 cm. anterior to the hypocaudal lobe.
speed. This relationship has been shown to hold for both dogfish and tope over a wide range of speeds, but this range probably does not include the highest speeds attained by the tail in fast swimming.

A discussion of the forces acting on swimming sharks follows. It makes use of the results of the experiments described in this paper.

Consider the equilibrium of a shark swimming horizontally. It is subject to the vertical forces shown in Fig. 5. $W$ is the weight of the fish, $A$ the upthrust due to the weight of water it displaces, $B$ the lift due to the pectoral fins and $C$ the lift due to the heterocercal tail. $a$, $b$, and $c$ will be taken as the distances from the centre of gravity of the lines of action of $A$, $B$ and $C$. The centre of buoyancy is represented as lying anterior to the centre of gravity, as Magnan (1929) found it to do in Scyliorhinus and Squalus. Balancing the vertical forces, we find that

$$A + B + C = W$$

and, balancing the moments about the centre of gravity, we find that

$$Aa + Bb = Cc.$$ 

We will now consider the equilibrium of the dogfish and tope whose tails were used in the experiments. We will estimate the values of the quantities involved in equations (1) and (2).

The dogfish weighed 877 and 863 g.: we will therefore take $W = 870$ g. for dogfish. For the tope, $W = 3500$ g.

The sinking factors of the specimens of Scyliorhinus canicula investigated by Lowndes (1955) averaged 1047. I can find no accurate determinations of the sinking factor of tope in the literature, and will assume that it is the same as that of dogfish (Magnan (1929) gives a value of 1040, but it was obtained by the very inaccurate method of measuring weight and volume, and his value for dogfish is much lower than Lowndes's). We thus have

$$A = 870 \times \frac{1040}{1044} = 831 \text{ g. wt.}$$

for the dogfish and

$$A = 3500 \times \frac{1040}{1047} = 3343 \text{ g. wt.}$$

for the tope.

Magnan (1929) found that the centre of buoyancy of a S. stellaris was 0.12 cm. anterior to the centre of gravity. He does not state the size of the fish for which this value was obtained, but it seems highly probable that it was the 322 g., 47.4 cm.
specimen mentioned frequently elsewhere in his paper. If so, distance \( a \) was 0.25% of the body length. He also found that the centre of buoyancy of a specimen of *Squalus* whose volume was 65 c.c. lay 0.08 cm. anterior to the centre of gravity. This fish must have been about 29 cm. long, so \( a \) was about 0.28% of the body length. Since no other values for \( a \) are available, this value will be used for both dogfish and tope.

Magnan (1929) found that the centres of gravity of a dogfish (*S. canicula*) and a tope lay 36 and 34% of the body length, respectively, from the snout. I estimate from these figures and from measurements on a dogfish and photographs of tope that \( b = 15\% \) of the body length for the former and 13% for the latter, and that \( c = 55\% \) of the body length in both cases. These distances will alter as the body bends in swimming, but it does not seem necessary to allow for this in the present very rough calculation.

Substitution of these values in equations (1) and (2) gives \( B = 27 \text{ g.wt.}, C = 12 \text{ g.wt.} \) for the dogfish and \( B = 113 \text{ g.wt.}, C = 44 \text{ g.wt.} \) for the tope. The dogfish tails gave 12 g.wt. lift at transverse speeds of 67 and 74 cm./sec. (1.0 and 1.1 body lengths/sec.) but would probably have given this lift at lower speeds if they had not been frozen. If the effect of freezing was quantitatively similar to the effect on tope, this lift would have been given by fresh tails at about 0.6 body length/sec. The tope tail gave 44 g.wt. lift at 38 cm./sec. or 0.4 body length/sec.

In the experiments, tails moved at constant speed and produced constant lift. In swimming, speed and presumably lift vary cyclically. The mean lift produced and the lift produced at the mean transverse speed by a tail in swimming are not quite the same if lift is proportional to the 1.4 power of speed, but the difference is too small to be important in this calculation. We may therefore conclude that the physical properties of dogfish and tope tails are such as to give the lift required for horizontal swimming when they are moving at a mean transverse speed of about 0.5 body length/sec. This estimate seems unlikely to be wrong by more than a factor of 2.

The swimming speeds corresponding to these transverse tail speeds can be estimated by reference to cinematograph films. Gray's (1933) published sequence shows a 40 cm. *Squalus* swimming 20 cm. and making one cycle of tail movements in 1 sec. The amplitude of transverse movement of the tail is about 10 cm. The mean transverse speed of the tail and the speed of the fish are thus both about 20 cm./sec or 0.5 body length/sec. Another film (Wolf, 1960) includes several sequences showing a 65 cm. *Squalus* swimming horizontally at about 1 length/sec., making about 2 cycles of tail movements/sec. In these sequences the fish is seen from the side, so the amplitude of tail movement cannot be measured, but if it is 0.25 of the length, as in Gray's sequence, the mean transverse speed of the tail is again about equal to the forward speed of the body. If we assumed, in the absence of further information, that these two speeds are about equal in all small sharks (and Bainbridge (1958) has established a similar rule for teleosts, where the forward speed is about 1.5 times the mean transverse speed of the tail) we might conclude that the critical swimming speeds at which the hypocaudal lobes of dogfish and tope, acting passively, would give the lift required by equations 1 and 2 are about 0.5 body length/sec.

Dogfish in aquaria commonly cruise at about this speed. It seems doubtful whether the pectoral fins could produce the required lift \( B \) at speeds much lower than this, but dogfish can certainly swim faster than 0.5 length/sec. When they do so, the hypocaudal lobes would apparently produce more lift than is required for equilibrium.
if they acted passively. The highest recorded speed, relative to body length, for a selachian seems to be Gero’s (1952) record of 13.3 ft./sec. for a 21 lb. *Carcharinus*; according to Bainbridge (1958) this is about 3.9 lengths/sec.

It is probable that the angle of attack of the hypocaudal lobe, and so the lift, can be adjusted by means of the radial muscles of the lobe, though these are not large. They are shown in Fig. 1.

Some pelagic sharks have enormous oily livers, and consequently low sinking factors (Matthews & Parker, 1950; Denton, 1963). These sharks do not require such large hydrodynamic upward forces for equilibrium as do the denser, bottom-living species such as dogfish and tope. One of them, the basking shark, cruises at the very low speed of about 0.15 length/sec. (2 knots; Matthews & Parker, 1950). It has very large pectoral fins as well as a low sinking factor. It would be interesting to investigate the physical properties of the tails of some of these pelagic sharks.

**SUMMARY**

1. The upward forces produced by tails of dogfish and tope, moving transversely through water at various speeds, have been measured.

2. The lift is approximately proportional to the 1.4 power of the transverse speed.

3. The equilibrium of dogfish and tope, swimming horizontally with the whole body horizontal, is discussed quantitatively.

4. It is estimated that in each case the hypocaudal lobe, acting passively, would give more lift than is required for equilibrium, at all swimming speeds greater than about 0.5 length/sec.

5. The lift may be adjusted to the required value by means of the radial muscles of the hypocaudal lobe.

**REFERENCES**


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