J. exp. Biol. (1980), 85, 337–342
With 4 figures
Printed in Great Britain

THE MECHANICS OF LABRIFORM LOCOMOTION

II. AN ANALYSIS OF THE RECOVERY STROKE AND THE OVERALL FIN-BEAT CYCLE PROPULSIVE EFFICIENCY IN THE ANGELFISH

BY R. W. BLAKE*
Department of Zoology, University of Cambridge

(*Received* 31 *August* 1979)

It is likely that the 'undulatory propulsors' employed by many fish are capable of producing a usefully directed thrust force over most of the tail-beat cycle. In contrast, fish which employ the 'paddling pectoral fin propulsor' only produce thrust during the power stroke phase of their fin-beat cycle, after which a recovery stroke occurs, when little usefully directed thrust force is produced. However, in order to gain a complete understanding of the mechanics of the paddling propulsor it is necessary to investigate the recovery stroke fully.

The basic movements performed by the pectoral fins during the recovery stroke have been qualitatively described and schematically illustrated (Blake, 1979). The present analysis is based on kinematic information derived from one representative stroke, taken from the same steady swimming sequence (forward velocity, $V = 0{\cdot}04\ \mathrm{ms}^{-1}$) selected for the power stroke analysis (Blake, 1979).

The leading edge of the right side pectoral fin moved from a positional angle (γ', the angle between the projection of the leading edge of the fin on to the horizontal plane) of about 7–107° in a time (t_r, the recovery stroke duration time) of 0·1 s. The angular velocity (Ω, the angular velocity of the fin projected on to the horizontal plane) during the stroke is shown in Fig. 1.

We recognize four blade-elements ($e'1$–$e'4$); the values for the lengths (l'), mid-points (r') and masses (m_e') of which are the same as those for l, r and m_e respectively, used in analysis of the power-stroke (Blake, 1979).

The components of velocity perpendicular to the major axis of the fin, v_p', and parallel to the major axis, v_s' are given by:

$$v_p' = \Omega r' + V\sin\gamma', \tag{1}$$

$$v_s' = V\cos\gamma'. \tag{2}$$

The values of v_p' and v_s' are plotted against time in Fig. 2.

The spanwise (dF_s) force on the fin is given by:

$$dF_s = 1/2\rho v_s'^2 A_{r(t)} C_s, \tag{3}$$

* Present address: Department of Zoology, University of British Columbia, Wesbrook Mall, Vancouver, VT6 1W5, Canada.

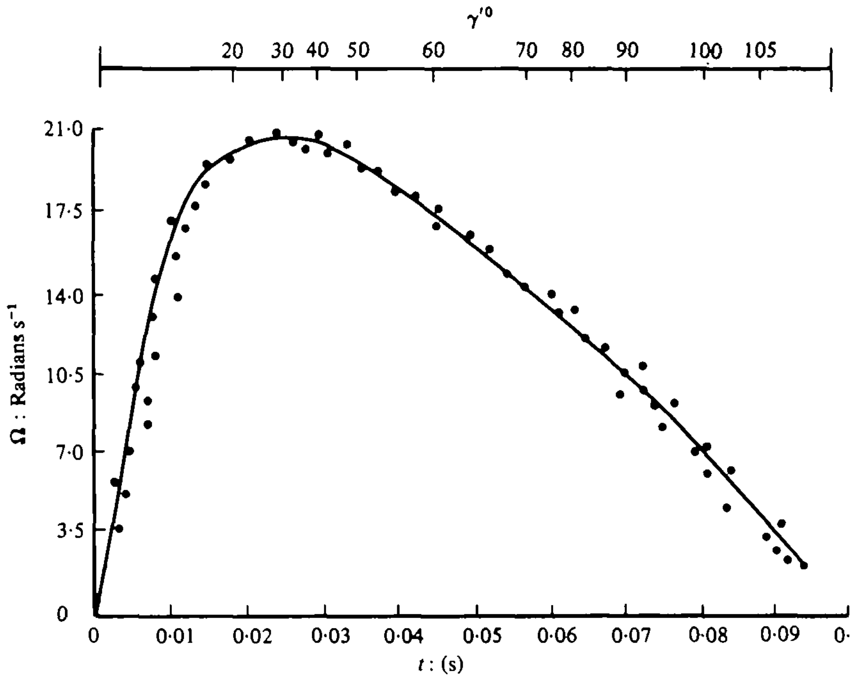

Fig. 1. The angular velocity of the fin plotted against time.

where $A_{r(t)}$ is the total wetted area of the fin during the recovery stroke and C_s is a frictional drag coefficient, the value of which depends on the fin's boundary layer flow regime. For laminar boundary layers over flat plates the frictional drag coefficient can be calculated from Blasius's equation:

$$C_s = 1\cdot33 R_s^{-0\cdot5}, \tag{4}$$

where R_s is a Reynolds Number, which is defined on the basis of the length of the fin (R) and the component of velocity which is parallel to the fin's major axis, so:

$$C_s = 1\cdot33(R\, V\cos\gamma'/\nu)^{-0\cdot5}, \tag{5}$$

where ν is the kinematic viscosity of the water.

The chordwise component of force (dF_c) for an element is given by:

$$dF_c = \tfrac{1}{2}\rho(v'_p\cos\beta)^2 A_{r(e)}\, C_c, \tag{6}$$

where $A_{r(e)}$ is the total wetted area of an element, β is the geometrical angle of attack (defined as the angle between the local chord and the horizontal, mean values of β over the stroke = 8·5°, 5·1°, 4·7° and 1·5° for elements $e'1$–$e'4$ respectively) and C_c is a frictional drag coefficient. Values of C_c have been calculated from Blasius's equation; using a Reynolds Number (R_c) based on the chord (c': measured at r') and the chordwise velocity component ($v'_p\cos\beta$):

$$C_c = 1\cdot33(c(v'_p\cos\beta)/\nu)^{-0\cdot5}. \tag{7}$$

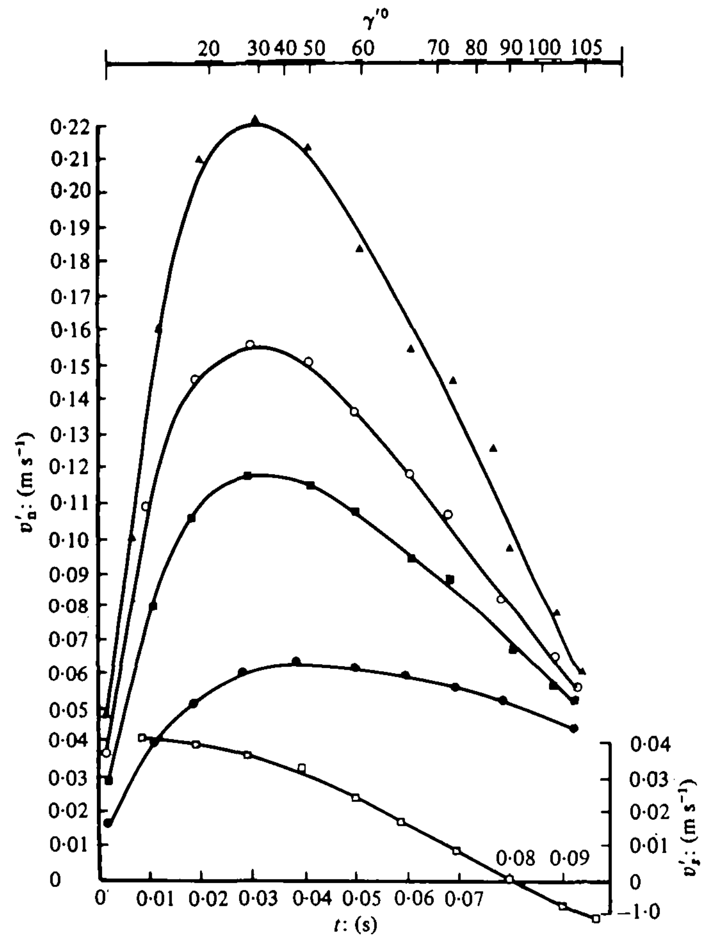

Fig. 2. The component of velocity perpendicular (v'_p) to the major axis of the fin (●, $e'1$; ■, $e'2$; ○, $e'3$ and ▲, $e'4$) and the spanwise velocity component (v'_s, □) plotted against time.

The force acting normal to the surface of an element (dF_n) can be calculated from:

$$dF_n = \tfrac{1}{2}\rho v_p'^2 A_{r(e)} C_n, \tag{8}$$

where C_n is a normal force coefficient, which depends on the angle of attack of the elements Fig. 6, Curve B of Blake, 1979).

A drag force acts in the direction of the body (dF_d), which is given by:

$$dF_d = \int_{r'=0}^{R} (dF_s \cos\gamma' + dF_c \cos\beta \sin\gamma' + dF_n \sin\beta \sin\gamma')\, dr, \tag{9}$$

and is plotted against time in Fig. 3.

The impulse of this drag force (P_r) is

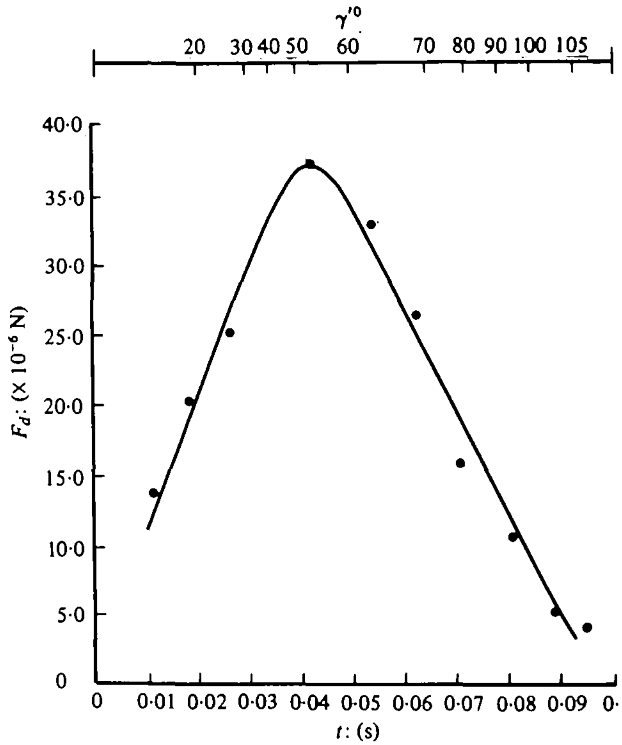

Fig. 3. The total drag force acting in the direction of the body plotted against time.

$$P_r = \int_0^{t_r} dF_d dt \tag{10}$$

$$= \int_{r'=0}^{R} \int_0^{t_r} (dF_s \cos\gamma' + dF_c \cos\beta \sin\gamma' + dF_n \sin\beta \sin\gamma')\, dt, \tag{11}$$

and amounts to about $1{\cdot}8 \times 10^{-6}$ N s.

The power required to overcome the drag force acting in the direction of the body (dW_d) is given by:

$$dW_d = \int_{r'=0}^{R} (dF_s v_s' \cos\gamma' + dF_c v_p' \cos\beta \sin\gamma' + dF_n v_p' \sin\gamma' \sin\beta)\, dr, \tag{12}$$

and is plotted against time in Fig. 4.

The mean power required ($\bar{W}_d$) is:

$$\bar{W}_d = \frac{1}{t_r} \int_0^{t_r} dW_d dt. \tag{13}$$

W_d is calculated to be about $3{\cdot}6 \times 10^{-6}$ W.

The total amount of energy dissipated during the recovery stroke on overcoming the drag force acting in the body direction (E_d') is given by:

$$E_d' = \int_0^{t_r} (dF_s v_s' \cos\gamma' + dF_c v_p' \cos\beta \sin\gamma' + dF_n v_p' \sin\beta \sin\gamma')\, dt, \tag{14}$$

and amounts to approximately $3{\cdot}6 \times 10^{-7}$ J.

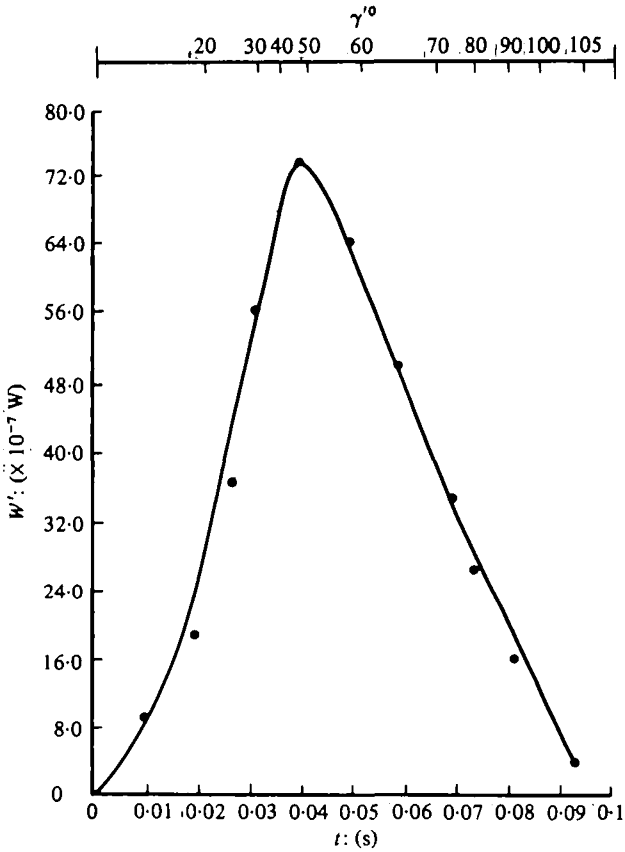

Fig. 4. The power required to overcome the drag force in the direction of the body plotted against time.

The mean amount of energy required to move the mass of the fin during the stroke ($\bar{E}'_{f(\mathrm{tot})}$) is calculated as previously described (Blake, 1979). Here, however, the analysis is simplified by only considering the component of velocity that acts in a direction that is perpendicular to the fin's major axis:

$$\bar{E}'_{f(\mathrm{tot})} = \sum_{e'=1}^{e'=4} \tfrac{1}{2} m'_e \overline{(\dot{\Omega} r' + V \sin \gamma')^2}/N_e, \tag{15}$$

(where N_e is the total number of elements); $\bar{E}'_{f(\mathrm{tot})}$ amounts to about $3{\cdot}0 \times 10^{-7}$ J.

Combining the results from this study with those for the power-stroke (Blake, 1979), a final value of the fin-beat cycle propulsive efficiency (η_c) can be written:

$$\eta_c = E_0/2(E_{(\mathrm{tot})} + E_{\alpha(\mathrm{tot})} + \bar{E}_{f(\mathrm{tot})} + E'_d + \bar{E}'_{f(\mathrm{tot})}), \tag{16}$$

$\eta_c = 0{\cdot}16$.

The impulse of the drag force acting in the direction of the body of the Angelfish during the recovery stroke is about 1/20th of that associated with the hydrodynamic thrust force generated during the power stroke. The mean power associated with it is approximately one fifteenth of that required to produce the thrust force of the power stroke phase. The overall efficiency ($\eta_c = 0{\cdot}16$) is about 11% less than the value calculated for the power stroke phase only ($\eta'' = 0{\cdot}18$; Blake, 1979). Comparable information on other animals employing the paddling propulsor is lacking, so comparisons can not be made at this stage.

Lighthill (1969, 1970) draws a distinction (applicable to animals swimming in the undulatory mode at high Reynolds Numbers) between those animals swimming with a high Froude efficiency ($\eta > 0{\cdot}5$) and those which swim with a low Froude efficiency ($\eta < 0{\cdot}5$). Lighthill's analytical studies indicate that it is probable that fusiform fish swimming in the carangiform modes operate over most of their range of swimming speeds at levels of Froude efficiency similar to those expected of well designed screw propellers ($\eta > 0{\cdot}75$).

Webb (1971) estimated the propulsive efficiency of trout (*Salmo gairdeneri*) from respirometric data and compared the values he obtained with those predicted on the basis of Lighthill's reactive models. Good agreement was found at preferred cruising and high swimming speeds (where inertial effects dominate and the models designed to apply), with $\eta > 0{\cdot}7$.

Using a very effective method of wake visualization, McCutchen (1975) calculated the Froude propulsive efficiency of a Zebra Danio (*Brachydanio rerio*, length = 3·15 cm) during steady swimming and in the 'push and coast' mode. Values of about 0·8 were obtained during steady swimming over a range of speeds. However, an upper limit of 0·56 was calculated for the 'push and coast' mode.

It is likely that the pectoral fin propulsor studied here operates at a Froude efficiency ($\eta_c = 0{\cdot}15 - 0{\cdot}3$) that is lower than values typical of fish swimming in the carangiform modes at their preferred cruising speeds. Webb (1975) estimates the propulsive efficiency of *Cymatogaster aggregata* (length = 14·3 cm, velocity = 55 cm s^{-1}) to be between 0·6 and 0·65; showing that the lift-based mechanism of pectoral fin propulsion operates at a higher level of propulsive efficiency than the drag-based one studied here.

However, the efficiency of the 'undulatory body and caudal fin' modes of swimming fall off rapidly as swimming speeds decrease. At low forward speeds the paddling propulsor becomes more efficient than the undulatory mechanism (Blake, 1979) and it is probable that many fusiform fish switch over from the undulatory mode of swimming to a pectoral fin propulsion system when this happens.

I am grateful to Dr K. E. Machin, Professor Sir James Lighthill and Mr C. P. Ellington for their interest in this work. I would like to thank Mr G. G. Runnalls for help with Photography and the N.E.R.C. for financial support.

REFERENCES

BLAKE, R. W. (1979). The mechanics of labriform locomotion. I. Labriform locomotion in the Angelfish (*Pterophyllum eimekei*): an analysis of the power stroke. *J. exp. Biol.* **82**, 255–271.

LIGHTHILL, M. J. (1969). Hydrodynamics of aquatic animal propulsion. *A. Rev. Fluid Mech.* **9**, 305–317.

LIGHTHILL, M. J. (1970). Aquatic animal propulsion of high hydrodynamic efficiency. *J. Fluid Mech.* **44**, 265–301.

MCCUTCHEN, C. W. (1977). Froude propulsive efficiency of a small fish measured by wake visualization. In *Scale Effects in Animal Locomotion* (ed. T. J. Pedley), pp. 339–363. London, New York, San Francisco: Academic Press.

WEBB, P. W. (1971). The swimming energetics of trout. II. Oxygen consumption and swimming efficiency. *J. exp. Biol.* **55**, 521–540.

WEBB, P. W. (1975). Efficiency of pectoral-fin propulsion of *Cymatogaster aggregata*. In *Swimming and Flying in Nature* vol. II (ed. T. Y. T. Wu, C. J. Brokaw, C. Brennen), pp. 573–583.