

THE EFFECT OF SIZE AND SWIMMING SPEED ON LOCOMOTOR KINEMATICS OF RAINBOW TROUT

By P. W. WEBB, P. T. KOSTECKI

*School of Natural Resources, The University of Michigan, Ann Arbor,
MI 48109, U.S.A.*

AND E. DON STEVENS

*Department of Biological Sciences, University of Guelph, Guelph, Ontario
N1G 2W1, Canada*

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SUMMARY

1. During swimming at constant speed the frequency (f), amplitude (a) and depth (d) of the tail trailing edge, and the length of the propulsive wave (λ) were measured for rainbow trout ranging in total length (L) from 5.5 to 56.0 cm. Fish were tested in a water flume using increasing velocity tests to sample a range of swimming speeds, V .

2. λ was independent of V and related to size by:

$$\lambda = 1.43L^{0.83}$$

so that wavelength was relatively larger in smaller fish.

3. f was related to L and V according to:

$$f = 3.19L^{-1/3} + 1.29V/L.$$

4. a was independent of V but was relatively smaller in larger fish:

$$a = 0.36L^{0.74}.$$

5. d was also independent of V but relatively larger in larger fish:

$$d = 0.18L^{1.05}.$$

6. Thrust power (= drag power) calculated using Lighthill's small amplitude bulk momentum model was two to three times the theoretical minimum of a flat plate of equivalent length and area moving parallel to the flow with a presumed turbulent boundary layer.

7. Froude efficiency increased with swimming speed, and it is shown that this is the usual relationship for fish studied so far. Froude efficiency was essentially independent of size at the critical swimming speed.

8. Estimated aerobic efficiency increased with size at the critical swimming speed, implying that muscle efficiency also increases with size.

INTRODUCTION

The way animals move and how these movements vary with size have long been of interest to biologists (see Pedley, 1977). For fish, observations on the effect of size on

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swimming kinematics have been limited almost exclusively to relationships between tail-beat frequency, swimming speed and length (Bainbridge, 1958; Hunter & Zweifel, 1971). Excellent data on rates of oxygen consumption with speed and size are also available for sockeye salmon, *Oncorhynchus nerka* (Brett & Glass, 1973) and these data have been widely used with various assumptions to deduce other kinematic scaling relationships (see Webb, 1975, 1977; Wu, 1977). Not surprisingly, the paucity of data and indirect methods have resulted in conflicting hypotheses concerning scaling of swimming kinematics and efficiency.

Our purpose is to evaluate scaling of kinematics in constant speed swimming. Observations were made of frequency, amplitude and depth of the tail trailing edge, and the propulsive wavelength of rainbow trout (*Salmo gairdneri*, Richardson) spanning an order of magnitude of length, during increasing velocity tests on fish swimming in flumes.

MATERIALS AND METHODS

Rainbow trout (*Salmo gairdneri*, Richardson), ranging in total length from 5.5–56.0 cm, were obtained from University of Guelph stocks that had been held for several weeks at 11–15 °C. The experimental temperature was 14.9 ± 0.2 °C ($\bar{X} \pm 2$ s.e.; $N = 12$).

We recorded swimming movements of fish using two flow-through chambers suspended in the centre of a water treadmill designed for humans and seals. The usable portion of the treadmill was 5 m long, 2 m wide and 2 m deep. Water speed could be varied from 0–2 m s⁻¹ with a 50 horsepower hydraulic motor. Chambers were constructed from clear Plexiglass. They had large floating lids to eliminate visual distortion of the fish due to surface waves. A 45° mirror permitted simultaneous observation of dorsal and side aspects of the fish as viewed from above. Grids delineated upstream and downstream ends of the chambers, the downstream grid being electrified (5 V a.c.) as needed to train fish to swim, or to encourage continued swimming as they approached exhaustion. Fish larger than 15 cm in length were exercised in a chamber 74 cm long, 31 cm deep and 31 cm wide. Smaller fish swam in a chamber 22.5 cm long, 12 cm deep and 14 cm wide. No blocking corrections were required.

We measured water velocities and flow profiles outside the boundary layer using Ott meters with 2- or 5-cm diameter propellers. Water velocity did not vary significantly within the chambers, probably because they were not watertight and fluid (and energy) could be exchanged with the main flow in the flume. The rectilinear path of neutrally buoyant particles showed no large-scale turbulence in the observation chambers. The intensity of micro-turbulence was not measured, but was presumed to be above thresholds for boundary layer flow transition (Schlichting, 1968).

Individual fish were placed in the observation chambers and swam at a low speed for 1 h. Then the water velocity was incremented every 10 min until the fish could no longer be induced to swim off the downstream grid. The speed increments varied among fish but were intended to achieve six to eight velocity increments prior to exhaustion. 10-min critical swimming speeds were calculated from the time to exhaustion, the speed before the final increment, and the speed at which exhaustion occurred (Brett, 1964). Extensive acclimation and post-handling recovery of fish w

Not possible, but our objective was the measurement of kinematic variables during swimming. Therefore, critical swimming speeds provide internal reference points for this study, but should not be compared with physiological performance limits from other studies (e.g. Fry & Cox, 1970; Farlinger & Beamish, 1977).

Body and caudal fin movements were recorded on 16 mm movie film (measured framing rate 60.9 Hz) at each swimming speed. We analysed films frame-by-frame to measure the length of the propulsive wave, tail-beat frequency and trailing edge amplitude and depth.

Propulsive wavelength can be measured using many techniques, employing one of two approaches based on; (a) the rate of backward displacement of body wave crests and (b) body wave geometry. The former method, used originally by Bainbridge (1963), calculates wave velocity, c , from which the wavelength can be obtained by dividing c by the tail-beat frequency. The geometric method, used by Webb (1971a), examines the waveform of the body relative to the axis of progression and measures the wavelength directly.

Each method has advantages and disadvantages. The important kinematic parameter for the calculation of thrust and power is the wave velocity, so that the direct measurement of c is desirable. However, inaccuracies can be high in determining the exact location of wave crests. Direct measurement of wavelengths has the advantage of greater accuracy, especially when the mirror images of fish centre-lines are superimposed at the start of successive half tail-beats (Fig. 1). A possible disadvantage of this method is that the waveform is less distinct over the anterior part of a fish due to the caudally increasing amplitude, such that complete wavelengths

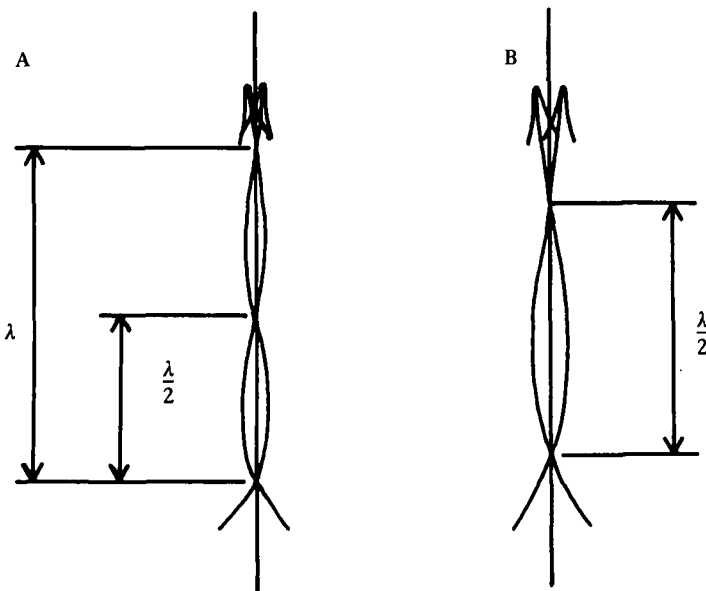


Fig. 1. Tracings of the centre-lines of trout at the start of two successive half-beats of the tail to show how the propulsive wavelength, λ , was measured from fish geometry, and to illustrate the variation in λ with size. (A) a 56-cm trout swimming at 80 cm s^{-1} showing the measurements made for a complete wavelength (λ) and a half wavelength ($\lambda/2$) and (B) a 5.5-cm trout at 60 cm s^{-1} showing the measurement of the half wavelength ($\lambda/2$).

cannot be easily distinguished when λ is large relative to body length. Under these circumstances, the length of a half-wave can be measured and multiplied by two to obtain the total wavelength. However, this may result in errors if λ varies with position along the body. Because of the importance of λ and wave velocity in determining thrust and efficiency these three methods were compared. We are aware that emerging computerized graphical analysis techniques can increase the nominal precision of all these methods, especially direct measurements of c , but do not yield results that are different from these simple methods (P. W. Webb, unpublished observations).

All results were analysed using non-linear regression methods on untransformed data (MINFIT algorithm). Models based on Hunter & Zweifel's (1971) analysis of tail-beat frequencies were used, starting from:

$$Y = \alpha_1 L^{\beta_1} + \alpha_2 L^{\beta_2} V^{\beta_3} . \quad (1)$$

Y is a kinematic variable, L is length (cm) and V is swimming speed (cm s^{-1}). All symbols and units are listed at the end of the paper. Regression coefficients and/or expressions were deleted until a best fit was obtained. The second term on the right did not prove to be significant for most kinematic variables and β_2 and β_3 were never significantly different from -1 and $+1$ respectively. Variance around regression coefficients is given as ± 1 s.e.

Total length (L, cm) and mass (M, g) were measured for fish at the end of each experiment. They were related by:

$$M = 0.071 \pm 0.028L^{2.52 \pm 0.10} \quad (r^2 = 0.99) . \quad (2)$$

RESULTS

Critical swimming speed

The relationship between the 10-min critical swimming speed (V_{crit} , cm s^{-1}), expressed as specific critical swimming speed normalized with length and size, is shown in Fig. 2A. The relationship was described by:

$$V_{\text{crit}}/L = 32.2 \pm 4.8L^{-0.81 \pm 0.07} \quad (r^2 = 0.95) . \quad (3)$$

The decrease in V_{crit}/L with increasing L is typical for fish (Beamish, 1978).

Propulsive wavelength

All methods of measuring the propulsive wavelength (λ , cm) gave values increasing with L but independent of V (Table 1, Fig. 2B). However, specific wavelength (λ/L) decreased with L from about 1 at 5.5 cm to 0.7 for the largest fish. Measurements of wavelength using the various methods were not significantly different (*t*-test; $\alpha = 0.10$) except for the fish 19.8 cm in length. The reason for this exception is not known.

The three methods were not judged equally useful because of the inaccuracies noted in the Methods. It was difficult to define wavecrests with precision. Wavecrests should be defined at the tangent to the body curvature of a line parallel to the axis of progression. The location of this point is more difficult when the specific wavelength is large and body curves have larger radii. As a result, variability in calculations was usually greatest when wavelengths were calculated from wave velocities (Table 1)

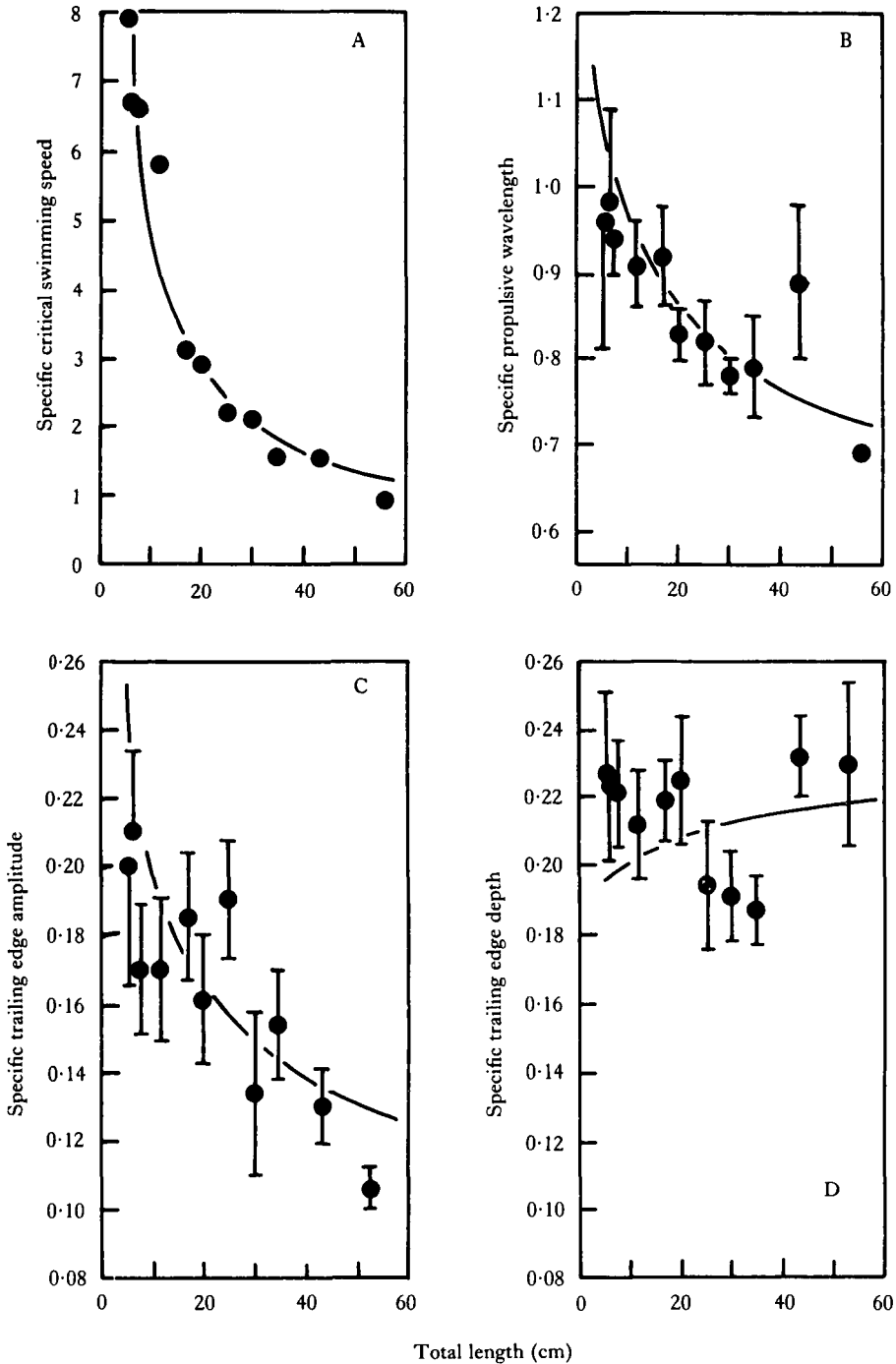


Fig. 2. Relationships between total length of rainbow trout and (A) length specific 10-min critical swimming speed; (B) length specific propulsive wavelength, λ/L (calculated by multiplying measured half wavelengths by 2; see text); (C) length specific trailing edge amplitude, a/L , and (D) length specific trailing edge depth, d/L . Vertical bars are ± 2 s.e. averaged over the range of swimming speeds tested as wavelength, trailing edge amplitude and trailing edge depth were not speed dependent. The solid lines were calculated from the equations given in the text.

Table 1. Results of measurements of the length of the propulsive wave (λ) of swimming trout

Total length of fish (cm)	Wavelength (λ) measured from body wave geometry		Wavelength (λ) measured from wave velocity, c and tail-beat frequency, f : $\lambda = c/f$ (cm)
	Wavelength of a complete wave (cm)	Wavelength calculated as twice the half wavelength (cm)	
5.5	-	5.3 \pm 0.8	6.0 \pm 1.4
6.4	-	6.3 \pm 0.7	5.7 \pm 1.4
7.7	-	7.2 \pm 0.3	6.5 \pm 0.6
11.6	-	10.6 \pm 0.6	11.2 \pm 1.6
17.0	-	15.6 \pm 1.0	17.3 \pm 1.9
19.8	17.8 \pm 0.2*	16.4 \pm 0.5*	22.7 \pm 3.1*
24.9	20.9 \pm 1.1	20.5 \pm 1.3	21.4 \pm 0.9
29.8	22.9 \pm 0.6	23.3 \pm 0.6	26.2 \pm 3.2
34.2	27.4 \pm 1.5	27.3 \pm 2.0	29.8 \pm 3.0
43.3	36.2 \pm 3.4	38.6 \pm 4.0	40.8 \pm 4.4
56.0	40.2	38.8	43.1

* Indicates significantly different means ($\alpha = 0.10$). Data are the mean values ± 2 s.e.

Variability also showed some scale dependence. For example, 95 % confidence limits around mean wavelengths of the two smallest fish were ± 24 % of the mean based on c , compared to ± 13 % for the method based on body half wavelengths. For the 34.2-cm and 43.3-cm fish these values were ± 10 % based on c and ± 9 % based on the half wavelength. Videler & Wardle (1978) and Webb & Keyes (1982) effectively used c to determine wavelength for large fish, ≥ 1 m in total length. Batty (1981) also used this method for larvae. In these cases, the body is thrown into relatively tight curves when the present observations show that the method is most accurate.

Measurements of half wavelengths and complete wavelengths were considered most accurate and gave similar values. Therefore, wavelength did not vary along the body length. In contrast (Batty, 1981) has shown that wavelength of larvae does vary along the body. Complete data for trout were obtained for half wavelengths (Fig. 2B), and these were used to calculate the relationship between total wavelength, λ , and length as:

$$\lambda = 1.43 \pm 0.34L^{0.83 \pm 0.07} \quad (r^2 = 0.83) \quad (4)$$

Tail-beat amplitude

Tail-beat amplitude (a , cm) was not significantly related to swimming speed, but did vary with length such that the specific amplitude (a/L) was smaller in larger fish (Fig. 2C). The best fit regression equation relating a and L was:

$$a = 0.36 \pm 0.05L^{0.74 \pm 0.04} \quad (r^2 = 0.85) \quad (5)$$

Thus absolute amplitude increased with size but relative amplitude (Fig. 2C) decreased with increasing size. Thus a/L is 0.24 for a 5-cm fish and 0.13 for a 50-cm fish. This result contrasts with that of Hunter & Zweifel (1971) who considered a/L was independent of size, taking a value of 0.21 for several teleost species, including

rainbow trout. However, Bainbridge's (1958) data used by Hunter & Zweifel actually suggests a/L declines with increasing L (see Webb, 1975, 1977). Interspecific differences in a/L with size are suggested, but the reason for such possible variation is not known.

Trailing edge depth

Trailing edge depth (d , cm) was quite variable (Fig. 2D). However, d was not significantly related to speed, but a significant relationship was obtained for length dependence:

$$d = 0.18 \pm 0.2L^{1.05 \pm 0.03} \quad (r^2 = 0.95). \quad (6)$$

Thus, both trailing edge depth and specific trailing edge depth (d/L) increased slightly with size. For example d/L was 0.20 for a 5-cm fish and 0.22 for a 50-cm fish.

Tail-beat frequency

Tail-beat frequency (f , Hz) is the most studied kinematic variable, and has been shown to increase linearly with speed in all species studied to date. The same was found for trout (Fig. 3). The best-fit regression equation for the rainbow trout in these experiments was:

$$f = 7.9 \pm 0.56L^{-0.59 \pm 0.02} + 1.15 \pm 0.02V/L \quad (r^2 = 0.99). \quad (7)$$

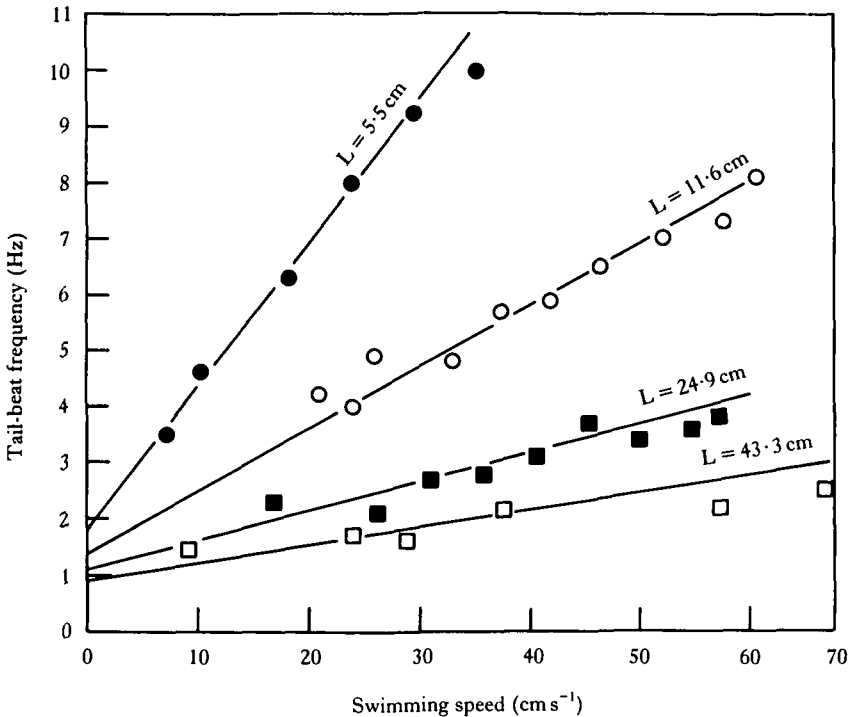


Fig. 3. Examples of relationships between tail-beat frequency and swimming speed for rainbow trout spanning the size range used in experiments. Solid lines were calculated from equation 10.

Hunter & Zweifel (1971), using Bainbridge's (1958) data for the same species obtained:

$$f = 1.26L^{-0.12} + 0.71V/L^{0.76}, \quad (8)$$

which they called their Case I model. However, after reviewing results from seven species of teleost fish, Hunter & Zweifel concluded that the intercept value of f at zero speed was generally proportional to $L^{-1/3}$. They therefore suggested a Case II model:

$$f = 2.0L^{-1/3} + 1.56V/L. \quad (9)$$

The present experiments recast in the Case II form of equation 9 gave;

$$f = 3.19 \pm 0.19L^{-1/3} + 1.29 \pm 0.03V/L \quad (r^2 = 0.99). \quad (10)$$

Tail-beat frequencies calculated from equations 5 and 8 are similar. Hunter & Zweifel's Case II model is not rejected, and equation 8 is considered the best description of the present data.

DISCUSSION

The kinematic variables tail-beat frequency, amplitude and depth together with propulsive wavelength largely determine the thrust and Froude efficiency of swimming fish. These experiments show how they vary with fish total length and swimming speed for a sub-carangiform swimmer, up to a 10-min critical swimming speed. They therefore permit evaluation of the magnitude of thrust forces for a swimming fish over a range of sizes and speeds, and the evaluation of some general features of locomotor mechanics that are subject to disagreement.

Power requirements

The thrust power required to overcome the drag of a swimming fish can be calculated using a variety of hydromechanical models (see Lighthill, 1975; Webb, 1975; Wu, 1977). Lighthill's models have proved easiest for biologists to apply to fish. Since details of such application have been described several times (e.g. Lighthill, 1975; Webb, 1975; Alexander & Goldspink, 1977; Wardle & Reid, 1977; Videler & Wardle, 1978) only the immediately relevant components are given here.

We use Lighthill's (1970) small amplitude bulk momentum model, as the large amplitude variation does not substantially influence results (Lighthill, 1971; Webb, 1977). The mean rate of working, (P_{TOT} , erg s⁻¹) of a fish during periodic swimming at constant speed is determined by:

$$P_{TOT} = m\omega WV, \quad (11)$$

where m (g cm⁻¹) is the added mass per unit length, W (cm s⁻¹), the lateral velocity of the tail and ω (cm s⁻¹) the speed given to the water.

Kinetic energy associated with acceleration of water with virtual mass m to ω is lost to the fish at a rate P_{KE} (erg s⁻¹).

$$P_{KE} = \frac{1}{2}m\omega^2V, \quad (12)$$

so that thrust power, P_T , (erg s⁻¹) is:

$$P_T = P_{TOT} - P_{KE}. \quad (13)$$

The virtual mass of water, m , per unit length is:

$$m = \rho \pi d^2 / 4, \quad (14)$$

where d is given in equation 6 and $\rho(1.0 \text{ g cm}^{-3})$ is the density of water.

W is the lateral velocity of the trailing edge. The appropriate root mean square value (Webb, 1971a; Alexander, 1977) is:

$$W = \pi f a / \sqrt{2}, \quad (15)$$

where f and a are given in equations 10 and 5 respectively.

The velocity given to the water discharged at the trailing edge, w , depends on W and the wave velocity c (cm s^{-1}) relative to speed, V (cm s^{-1}),

$$w = W(c - V)/c \quad (16)$$

and

$$c = f\lambda, \quad (17)$$

with λ obtained from equation 4 and f from equation 10.

The Froude efficiency, η_F of converting P_{TOT} to useful work, P_T is:

$$\eta_F = P_T / P_{\text{TOT}} \quad (18A)$$

or

$$\eta_F = \frac{c + V}{2c}. \quad (18B)$$

Equations 11 to 18 were used to calculate thrust power (= drag power) and Froude efficiency for fish of various lengths, swimming at various speeds. Size relationships were evaluated for the 10-min critical swimming speed. Such references are regularly used in discussing scaling problems (see Heglund, Taylor & McMahon, 1974; Webb, 1975, 1977; Wu, 1977) because they are believed to represent a physiologically similar speed for all sizes. For fish, the critical swimming speed in increasing velocity tests estimates the transition from primarily aerobic metabolism to anaerobic metabolism.

Examples of relationships between thrust power, calculated using equations 11 to 17 are given in Fig. 4 showing the usual increase in power requirements with speed. Such results are commonly compared with the drag required to overcome some rigid-body reference of equal length and area. For a flat plate, moving parallel to the flow, the reference drag power is;

$$P_{\text{Dref}} = \frac{1}{2} \rho A V^3 C_{\text{Dref}}, \quad (19)$$

where C_{Dref} is the drag coefficient. The boundary layer flow is expected to be turbulent in these experiments when;

$$C_{\text{Dref}} = 0.072 R_e^{-0.2} \quad (20)$$

and R_e = Reynolds number:

$$R_e = LV/\nu \quad (21)$$

and ν = kinematic viscosity (0.01 St).

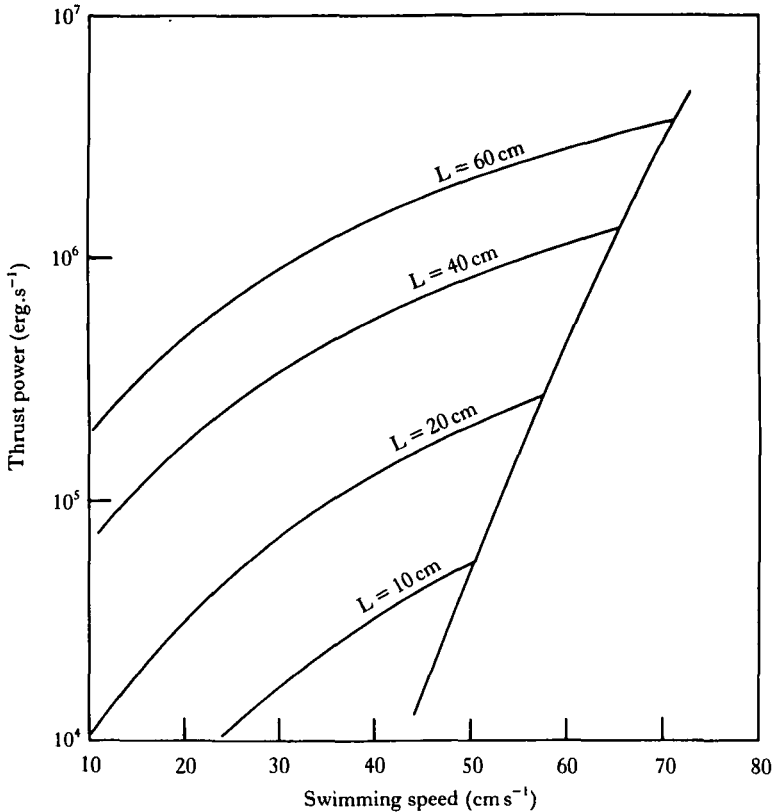


Fig. 4. Relationships between thrust power, calculated using equations 11 to 17, and swimming speed for selected trout lengths, up to the 10-min V_{crit} .

For rainbow trout, area A (cm^2) is related to length by (Webb, 1976):

$$A = 0.28L^{2.11} \quad (22)$$

Ratios of P_T/P_{Dref} varied from 3.6 for 5-cm fish to 2.4 for 50-cm fish at their critical swimming speeds, when swimming drag is usually found to be two to five times such theoretical reference drag values (Webb, 1975; Alexander, 1977; Videler, 1981).

Differences between flexing bodies and non-flexing references, and the consequences of size, are best evaluated by calculating drag (= thrust) coefficients. These can be obtained by replacing P_{Dref} with P_T in equation 19 and rearranging to calculate a value of C_D based on calculations of thrust power. Examples are shown in Fig. 5. This shows quite different relationships for drag and scale for flexing *versus* non-flexing bodies; (a) drag coefficients are greater than for the reference, as expected from power requirements; (b) C_D declines more rapidly with Re for the fish and (c) C_D-Re relationships are displaced with respect to size so that larger fish have higher drag coefficients at a given Reynolds number. Wu & Yates (1978) have gathered data from several sources which show the same phenomena.

The increase in drag of flexing bodies compared to rigid bodies is not surprising, as noted above. Lateral undulations modify flow and the magnitude of drag coefficients because of boundary layer effects, called 'boundary layer thinning' (Lighthill, 1971)

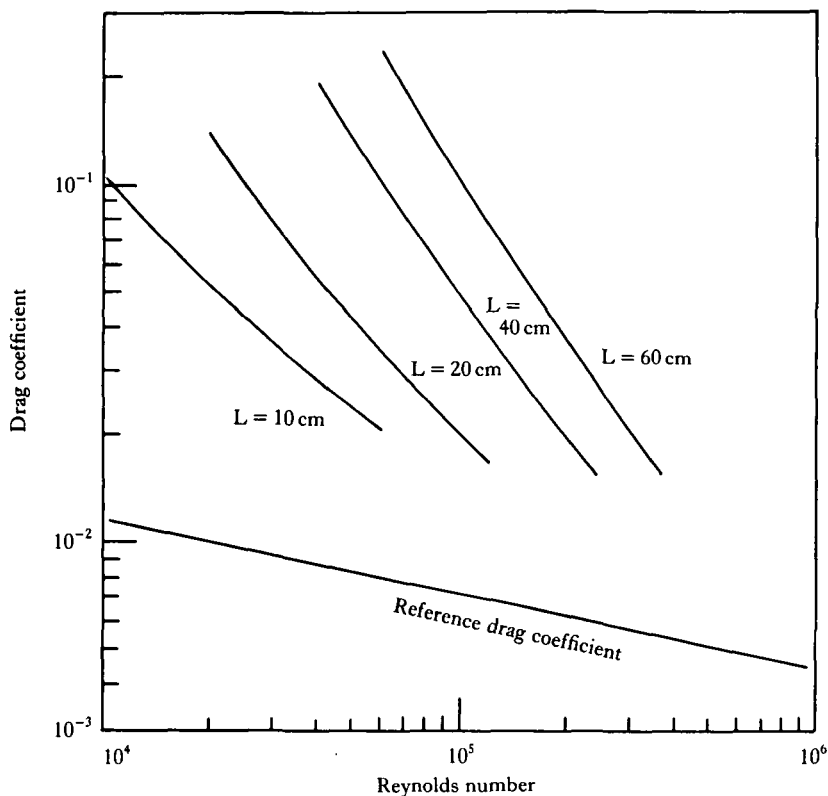


Fig. 5. Relationships between the drag coefficient (calculated from thrust power) and Reynolds number for selected trout lengths. The reference relationship is shown for a flat plate parallel to the flow, with a turbulent boundary layer flow.

together with increased resultant water velocities due to lateral movements. Furthermore, form drag may be increased because the body is thrown into large amplitude waves (D. Weihs, personal communication). In addition, as swimming speed increases, the difference between wave speed and swimming speed decreases (see below) so that any drag component due to the waveform could be more strongly speed dependent than frictional drag (D. Weihs, personal communication). Drag components related to the waveform might explain the difference in slopes between C_D and C_{Dref} shown in Fig. 5.

The displacement of C_D - Re curves with size might also relate to waveforms of the fish. Lighthill (1970) suggested that viscous forces developing with time could influence thrust and efficiency in fish with small specific wavelengths. Such effects would appear as increased drag coefficients of fish with smaller specific wavelengths (i.e. larger fish) at a given Reynolds number, as observed here and by Wu & Yates (1978). Unfortunately, all these hypotheses remain conjectural, and the probability for rigorous test seems improbable in the foreseeable future.

Froude efficiency

Froude efficiencies were calculated using equation 18. Efficiency increased with

swimming speed at all lengths (Fig. 6) but was only slightly length dependent at the critical swimming speed (Fig. 7). Wu (1977) believed this would be the situation for fish. In contrast Webb (1977) assumed muscle efficiency was size independent and used Brett's data on metabolic rate (Brett & Glass, 1973) to argue that Froude efficiency would be scale dependent at the critical swimming speed (see below). The present data on trout clearly confirm Wu.

Webb (1971*b*) also concluded that Froude efficiency would normally increase with speed, reaching maximum values at higher speeds as observed here. His conclusions were based on the form of the relationships between tail-beat frequency, propulsive wavelength and swimming speed. The appropriate form of this relationship between Froude efficiency and swimming speed can be determined from equation 18B, in terms of c and V . Then, η_F depends on the relationship between f and V since λ is independent of V . For a given fish, equations 7 to 10 reduce to;

$$f \propto \alpha + \beta V. \quad (23)$$

The same equation form has been described for all fish studied to date (see for example Bainbridge, 1958; Hunter & Zweifel, 1971; Webb, 1971*a*, 1975; Videler & Wardle, 1978; Wu & Yates, 1978 and others). Studies particularly by Bainbridge (1958) have extended V to sprint speeds, so that generalizations are possible for a large number of species swimming in the subcarangiform mode and over a large swimming speed range.

Then, from equation 23, it follows that when α is positive and as V becomes small, f tends towards α , and as V approaches zero, c ($= f\lambda$) becomes much larger than V . Since η_F is given by $(c+V)/2c$ it follows that η_F tends towards a theoretically derived minimum value of 0.5, as shown by Lighthill (1975). Alternatively, as V becomes large, f tends towards βV , as the importance of α declines. At lower aerobic speeds, α has a large influence on the magnitude of f and c , but this declines rapidly at higher

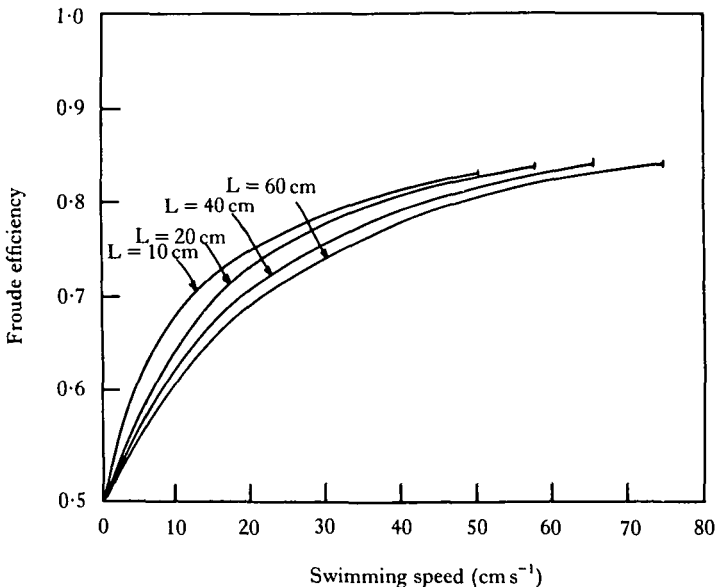


Fig. 6. Relationships between Froude efficiency and swimming speed for trout of four lengths.

peeds. Thus, as V increases, so does V/c and hence η_F , which reaches high values at intermediate speeds and approaches unity at maximum sprint speeds (Webb, 1971a). It therefore follows that whenever α is positive, and λ independent of speed, then η_F is speed dependent, increasing with speed. However, when α is negative, then η_F decreases with increasing speed.

We know of only two situations where α is negative; Pacific sardine, *Sardinops sagas* (Hunter & Zweifel, 1971) and Alaskan stocks of coho salmon, *Oncorhynchus kisutch* (Besner & Smith, 1983). The Pacific sardine was tested in groups while other species have been tested as individuals. This difference raises unanswered questions of the influence of schooling on kinematics.

Besner & Smith (1983) found α was negative for an Alaskan stock of coho but positive for a stock from Toutle River in Washington. They recognized that the

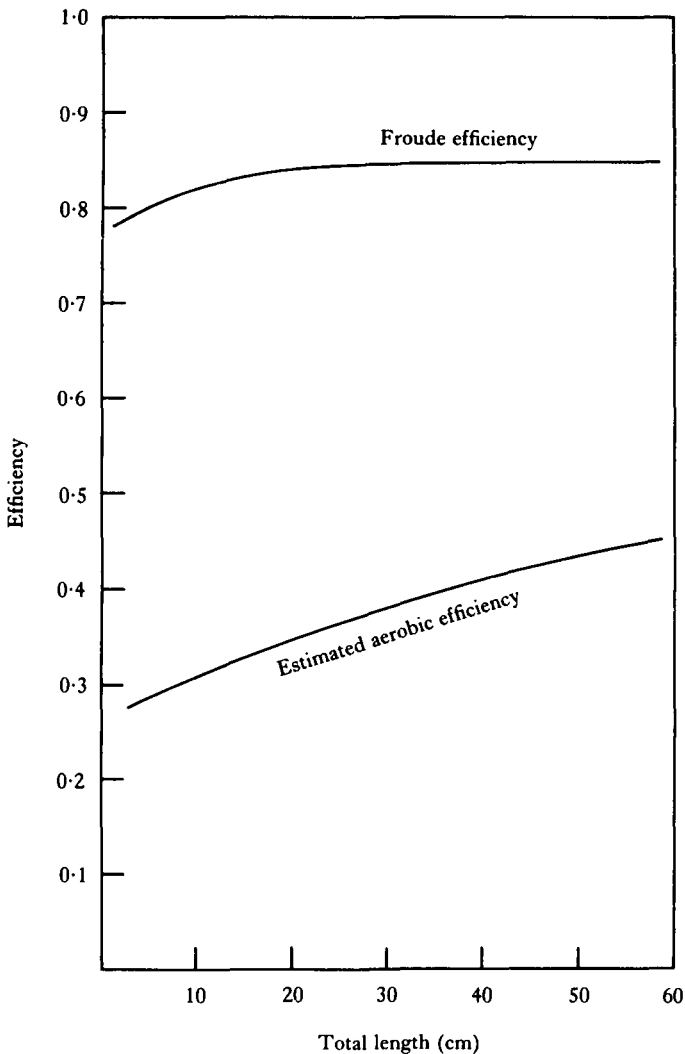


Fig. 7. Relationships between Froude efficiency and estimated aerobic efficiency as a function of length for salmonids at the 10-min V_{crit} measured here.

swimming efficiency of the Alaskan stock decreased as speed increased, which they suggested would maximize efficiency at low speeds used in longer migrations.

Videler & Wardle (1978) have also suggested that Froude efficiency declines with increasing speed. Videler & Wardle assumed that thrust was proportional to the difference between c and V so that $c - V$ was also proportional to drag. They recognize that their assumption led to a rough estimate. Wu (1977) showed that the thrust force could be most simply related to kinematics according to;

$$\text{Thrust force} \propto mf^2a^2 \left(\frac{c - V}{c} \right) \quad (24)$$

so that the attractive simplification of relating thrust to $c - V$ neglects other major influences of the wave parameters on thrust, and must be rejected (J. J. Videler, personal communication).

It is essential to realize that the general relationships between efficiency and speed can only be observed when caudal propulsion is examined over a wide range of speeds, especially at low speeds. Videler & Wardle (1978) used methods exploiting conditioned behaviour of fish racing towards food. This technique does not appear to give data on caudal swimming at low speeds. However, Videler & Wardle (1978) still showed their results for cod swimming at their steady speeds (four datum points in their Table 1) were comparable to Bainbridge's (1958) data on trout and gave:

$$f = 0.32 + 1.44V/L \quad (r^2 = 0.95) . \quad (25)$$

Sequences in which cod accelerated were not included because the added thrust to accelerate modified kinematics compared to swimming at constant speed (Videler & Wardle, 1978). Comparing equations 23 and 25 shows α is positive and η_F must also increase with speed for this species too. Thus the different conclusions between Videler & Wardle (1978) and other studies appears to be due to differences in methods.

The conclusion that efficiency increases with speed is important to the evolutionary ecology of animals. Heinrich (1977), in discussing reasons for endothermy, has argued that selection should favour animals maximizing rates of performance at energy bottlenecks important to survival and reproduction. In terms of periodic swimming, high sprint speeds are important in predator avoidance. For salmonids, higher cruising speeds are also important in upstream migrations for reproduction (Brett & Groves, 1978). Then higher Froude efficiencies at higher speeds would contribute to maximizing performance where this is most important. Furthermore, it is well known that fish shift to non-caudal propulsion at very low speeds (e.g. Webb, 1971a; Brett & Sutherland, 1965; J. J. Videler, 1981 and personal communication). The non-caudal propulsors achieve higher Froude efficiency at these very low speeds (see review by Webb, 1984). Thus the decrease in Froude efficiency with decreasing speed helps to explain the need for alternative locomotor systems for low-speed swimming.

The observation on Alaskan coho salmon, however, remains an exception, but Besner & Smith (1983) suggest that the reasons for this remain energetic considerations. Thus under most situations Froude efficiency increasing with speed would be expected, for the reasons given above, but occasionally other circumstances may be more important, as is apparently the case for Alaskan coho salmon.

Overall efficiency

An estimate can be made of the aerobic efficiency of converting metabolic energy to useful work, using data for rates of oxygen consumption for sockeye salmon (Brett & Glass, 1973); such interspecific calculations are, of course, imprecise and hence the estimates must be very approximate. Nevertheless, the calculation should illustrate the form of the scaling relationship. For sockeye salmon at 15 °C.

$$Q_s = 77 \cdot 4L^{2.656} \quad (26)$$

$$Q_{act} = 270 \cdot 8L^{3.022} \quad (27)$$

$$VC = 13 \cdot 46L^{0.6345}, \quad (28)$$

where Q_s = standard metabolic rate (ergs^{-1}), at zero speed, Q_{act} = metabolic rate (ergs^{-1}) at VC for sockeye salmon and VC = 60-min critical swimming speed for sockeye salmon (cm s^{-1}).

From equations 26 to 28, rates of oxygen consumption were calculated at the 10-min critical swimming speeds measured here (equation 3). This was done as follows; Q_s at zero speed and Q_{act} at VC were used to calculate the relationship between oxygen consumption and swimming speed for sockeye salmon ($Q_{\text{consumption}} \propto ae^{bV}$). The equation was then used to obtain Q_s and Q_{act} at V_{crit} from equation 3 for the rainbow trout used here. Then, the energy used in swimming by trout was calculated from the difference between the metabolic rates at zero speed and at the trout 10-min critical swimming speed. 1 mgO_2 is equivalent to 14–22 J (Webb, 1975; Priede & Holliday, 1980); the lower conservative value was used here. Results of calculations of aerobic power are shown in Fig. 8, and compared with thrust power obtained from equations 11 to 17. These were used to calculate aerobic efficiencies (thrust power/metabolic power) shown in Fig. 7. These estimated aerobic efficiency values range from 0.29–0.46 for 5- and 50-cm fish respectively; a maximum value of the order of 0.25 would be reasonable, but in view of the interspecific comparison, and use of a conservative oxygen energy equivalent, the results are of the right order.

The most important implication of the aerobic efficiencies is that this efficiency increases with length, and this would not be expected to be altered by the assumptions on oxygen consumption. If aerobic efficiency increases with length, then it follows that muscle efficiency must increase with length because Froude efficiency varies little with size at V_{crit} . It is usually assumed that muscle efficiency is scale independent (Hill, 1950 and others; see Heglund, Fedak, Taylor & Cavagna, 1982). However, Heglund *et al.* (1982) concluded muscle efficiency increased with length in mammals, as implied here for fish, and attributed the effect to rates of muscle cross-bridge activity varying with size. Gibbs (1974) also found efficiency increased with decreasing shortening speed in isolated vertebrate muscle. Since tail-beat frequency decreased with increasing size in trout, muscle and aerobic efficiency might be expected to increase with fish size. Further work is required in this area of locomotor mechanics.

Propulsive wavelength

Propulsive wavelength is an important kinematic parameter. Its importance in

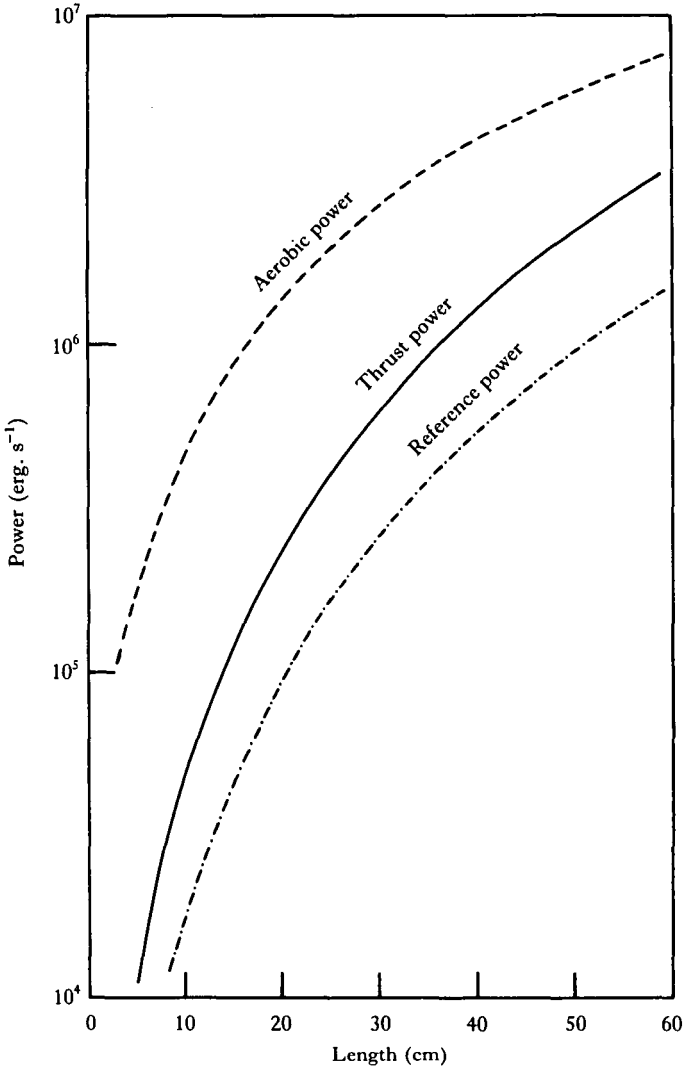


Fig. 8. Summary of the *form* of scaling relationships for swimming power and aerobic metabolic power in salmonids at the 10-min V_{crit} measured here. Swimming power was calculated from kinematic measurements as described here, and data on aerobic power are for sockeye salmon (*Oncorhynchus nerka*) from Brett & Glass (1973).

determining Froude efficiency is clearly illustrated above. In addition, wavelength is a major determinant of swimming mode (Breder, 1926; Lighthill, 1975), influencing among other things the nature and magnitude of lateral recoil forces, and interaction patterns between median fins (Lighthill, 1975, 1977; Wu, 1971). The magnitude of the propulsive wavelength has also received attention because its locomotor role might explain much of the variation in vertebral number with maximum species size and latitude, an aspect of pleomerism (Lindsey, 1975; Spouge & Larkin, 1979).

Wu (1977) suggested λ might vary with $L^{1.13}$, assuming a and d were scale independent and $V \propto L^{0.5}$. Webb (1977) suggested λ would vary with L in a complex fashion

but that λ/L would decrease with increasing size. He assumed V_{crit} , a and d were all scale dependent. The present results show that all kinematic parameters are scale dependent for trout and that $\lambda \propto L^{0.83}$ (equation 4). However, this conclusion is based on relatively large trout and certainly would not apply to larvae. Larvae swim with small λ/L (Hunter, 1972; Batty, 1981) using anguilliform kinematics at small Reynolds numbers, while most juveniles and adults have more carangiform morphologies and swim at large Reynolds numbers.

The biological importance of ontogenetic changes in λ/L in fish such as trout remains to be explored. On the basis of wavelength estimates, it might be argued that the smaller fish should show somewhat more emphasis on cruising compared to larger fish. Small salmonids forage more widely to obtain a relatively larger mass-specific ration, composed of small food items, while larger salmonids utilize larger and more evasive items; larger salmonids are more piscivorous (Scott & Crossman, 1973) when greater body flexibility may facilitate prey capture (Webb & Skadsen, 1980). However, a reduced importance of sustained swimming in larger salmonids seems inconsistent with their long migrations. This is an area where compromises in structure, function and behaviour are suggested that may warrant further study.

SYMBOLS

a	trailing edge amplitude (cm).
A	wetted surface area (cm ²).
c	velocity of propulsive wave (cm s ⁻¹).
C_D	drag (= thrust) coefficient.
$C_{D\text{ref}}$	reference drag coefficient.
d	trailing edge depth (cm).
f	tail-beat frequency (Hz).
L	total length (cm).
M	mass (g).
m	added mass (g cm ⁻¹).
$P_{D\text{ref}}$	reference drag power (erg s ⁻¹).
P_{KE}	rate of kinetic energy loss (erg s ⁻¹).
P_T	thrust power (erg s ⁻¹).
P_{TOT}	total power (erg s ⁻¹).
Q_s	standard metabolic rate (mgO ₂ h ⁻¹).
Q_{act}	active metabolic rate (mgO ₂ h ⁻¹).
Re	Reynolds number.
V	swimming speed (cm s ⁻¹).
V_{crit}	10-min critical swimming speed (cm s ⁻¹).
w	velocity given to water at trailing edge (cm s ⁻¹).
W	lateral velocity of trailing edge (cm s ⁻¹).
α, β, a, b	constants.
η_F	Froude efficiency.
λ	propulsive wavelength (cm).
ρ	density of water (g cm ⁻³).
	kinematic viscosity (St, 1 St = 10 ⁻⁴ m ² s ⁻¹).

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