

EFFECTS OF PARTIAL CAUDAL-FIN AMPUTATION
ON THE KINEMATICS AND METABOLIC RATE OF
UNDERYEARLING SOCKEYE SALMON
(*ONCORHYNCHUS NERKA*) AT STEADY
SWIMMING SPEEDS

By P. W. WEBB*

Fisheries Research Board of Canada, Pacific Biological Station, Nanaimo, B.C.

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INTRODUCTION

Breder (1926) and Gray (1968) have noted that caudal-fin amputation in fish swimming in the carangiform mode does not markedly impair steady, or sustained swimming performance. The effects of amputation are explained in terms of redistribution of thrust-related hydrodynamic loading over the remaining portion of the tail and the body. This would change the loading on the muscle system, which is expected to affect the efficiency of muscular activity (Hill, 1950). A change in muscle efficiency implies an alteration in the amount of metabolically available energy transmitted to the mechanical caudal-propeller system, and consequently a change in metabolic energy expenditure or thrust/drag relations.

Recently, interest in fish propulsive mechanics has again increased with revision or new models of the locomotor system being formulated (Lighthill, 1969, 1970, 1971; Wu, 1971*a, b, c*; Weihs, 1972, 1973). Of particular interest is the hydro-mechanical model proposed in Lighthill (1969), a simplified form of that developed in detail by Lighthill (1960, 1970, 1971), but which can be expressed in a form of immediate predictive value to a wide range of biological situations.

However, this model implies that amputation of the caudal fin would greatly reduce thrust generated, and consequently decreased swimming speed would be expected at all levels of activity.

A boundary-layer thinning hypothesis has been advanced by Dr Q. Bone (in Lighthill, 1971) which considers the effect of locomotory movements on drag, particularly at the caudal fin where lateral movements are greatest (Bainbridge, 1963). This hypothesis could explain the apparent discrepancy of reduced thrust without reduced steady speeds by reduced drag following caudal-fin amputation.

This paper therefore seeks to use caudal-fin amputation as a tool to examine drag and thrust energetic relations for a swimming fish. Lighthill's (1969) model is used to analyse thrust mechanics. Conventional equations are used to describe drag. These are developed for a simplified drag distribution between the body and caudal fin as suggested by the boundary-layer thinning hypothesis.

* Present Address: School of Natural Resources, University of Michigan, Ann Arbor, Michigan 48104, U.S.A.

5 cm

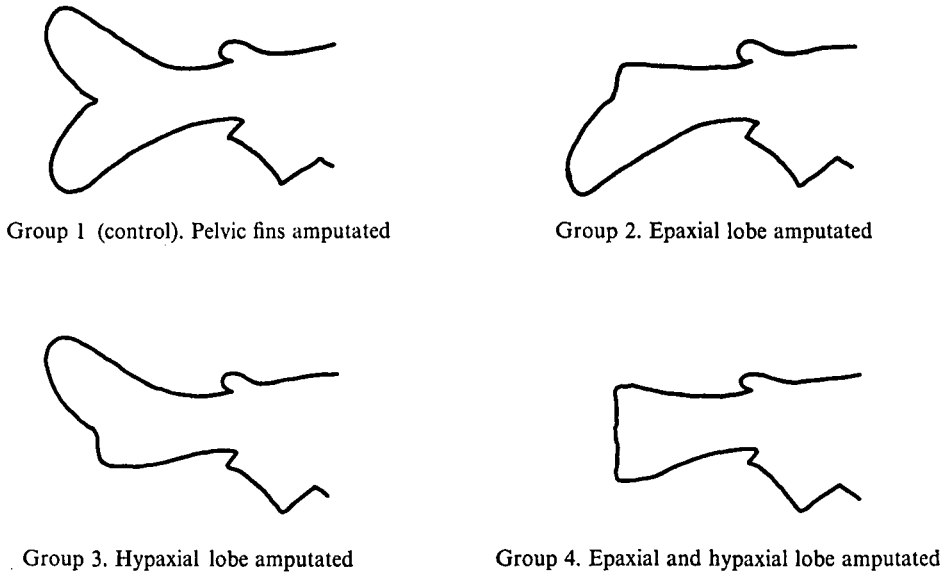


Fig. 1. Diagrammatic representation of the posterior portions of the body following caudal-fin surgery in the four groups of sockeye salmon.

MATERIALS AND METHODS

Fish

Forty yearling cultured sockeye salmon (*Oncorhynchus nerka*) were selected for uniform size from a stock acclimated to 15 °C. The fish were assigned to one of four groups by means of a random number process. Each fish was lightly anaesthetised with MS 222 and various portions of the caudal-fin lobes were amputated (Fig. 1):

Group 1: control, pelvic fins amputated, caudal fin intact.

Group 2: epaxial caudal-fin lobe amputated.

Group 3: hypaxial caudal-fin lobe amputated.

Group 4: epaxial and hypaxial caudal-fin lobes amputated.

Pelvic fins were intact in groups 2 to 4. Epaxial or hypaxial caudal-fin lobes were amputated in groups 2 and 3 in case there was a mechanical difference in subsequent swimming patterns. Amputation of fin lobes was not complete, only fin rays being removed. In group 4 a flexible but short section of the caudal-fin was retained contiguous with the caudal peduncle. In this way it was hoped to avoid the effects of complete amputation on kinematics demonstrated by Gray (1933*c*) for the whiting.

Following the operation, each group of fish was held in separate 197-l tanks for 2 weeks. Tanks were flushed continuously at 60 l/hr. Temperature was controlled at 15.0 ± 0.5 °C, and dissolved oxygen levels were maintained close to air saturation. Fish were fed to excess once a day on Abernathy pellets.

Water was circulated in the tank at a mean velocity of approximately 20 cm/sec. Fish swam continuously against this current.

Experimental procedure

Individual fish were starved for 2 days, lightly anaesthetised, and introduced to the fish chamber of a water-tunnel respirometer (Brett, 1964). The water velocity was set at 15 cm/sec, and fish were trained to swim steadily by means of an electrified grid downstream of the fish chamber. The respirometer was continuously flushed with air-saturated water, maintaining dissolved oxygen levels close to air saturation (10 mg O₂/l). Temperature was controlled at 15.0 ± 0.2 °C at all times.

The following day, and never less than 16 h after placing the fish in the respirometer, swimming performance and oxygen consumption were measured in an increasing-velocity test (Brett, 1964), with speed increments of 7.5 cm/sec every 45 min. The time to exhaustion after the last velocity increment was recorded in order to calculate the 45 min critical swimming speed, 45 min U_{crit} (Brett, 1964). No speed corrections for blocking of the chamber profile were applied, as the fish never occupied more than 7% of the cross-sectional area.

At each swimming speed, tail beat frequency, trailing-edge amplitude and propulsive wavelength were measured. Frequency was measured by timing 50 tail-beat cycles every 5 min, with the fish swimming steadily near the chamber centre. Amplitude was measured photographically during the same or similar swimming periods, lateral and dorsal views being recorded with the aid of a 45° mirror above the fish chamber. In most cases time exposures of 0.25–0.5 sec were used in still photographs. The resulting photographs showed the limits of lateral body movements for several tail-beat cycles. These limits were clearly defined because the velocity of lateral movements is momentarily zero at positions of maximum amplitude (Gray, 1933*a*, *b*, *c*). These photographs were supplemented by cine-film records, recorded at 54 frames/sec.

Wavelength was measured from photographs taken at $\frac{1}{30}$ th or $\frac{1}{60}$ th sec, and from cine-film records.

Records were obtained for fish swimming in a cylindrical chamber. Corrections were applied for spherical aberration. These were minimal because fish tend to swim near the chamber centre.

Data obtained from the two photographic methods gave the same results. Consequently, pooled data were used in analysis.

Oxygen consumption was calculated from the decrease in dissolved oxygen tension after cutting off the water flow through the respirometer. Oxygen tensions were measured by a Mackereth macro-electrode (Mackereth, 1964), and continuously recorded on a pen recorder. Measurements were commenced at the 15th min following a velocity increment, ensuring that fish had settled down at each swimming speed (Webb, 1971*b*). When the dissolved oxygen tension fell to 85% air saturation, water was again flushed through the respirometer, rapidly returning oxygen levels close to 100% air saturation. Metabolic rates were computed in mg O₂/kg h.

Experiments were performed in the spring.

Morphometrics

At the end of an experiment, fish were blotted on a moist cloth to remove excess water, and weighed to the nearest 0.01 g. Total length was recorded, both at the end

Table 1. *Physical characteristics of the four groups of sockeye salmon used to evaluate affects of partial and complete caudal-fin-lobe amputation*

	Group 1 Control, pelvic fins amputated	Group 2 Epaxial lobe amputated	Group 3 Hypaxial lobe amputated	Group 4 Epaxial and hypaxial amputated
Length before amputation, cm (mean - 2 S.E.)	20.4 ± 0.7	19.9 ± 1.0	20.5 ± 0.8	20.5 ± 0.8
Mass, g.	63.13 ± 6.31	56.90 ± 5.33	62.06 ± 6.33	60.15 ± 6.03
Caudal fin wetted surface area, cm ²	18.0 ± 1.7	11.6 ± 0.8	11.8 ± 0.9	6.7 ± 0.6
Trailing-edge depth, cm	4.0 ± 0.3	3.1 ± 0.2	3.2 ± 0.5	2.1 ± 0.1
β	0.85	0.84	0.84	1.00
Trailing-edge virtual mass, g cm ⁻¹	10.7	6.3	6.8	3.5
No. fish	9	6	6	9

of an experiment and at the time of operation. Caudal-fin trailing-edge depth was measured. The outline of the caudal-fin, including the expanding portion of the caudal peduncle, was drawn on paper, and the area was measured by means of a planimeter. These measurements are included in Table 1, together with values for some derived parameters discussed below.

SYMBOLS

A	caudal-fin trailing-edge amplitude, cm
C	total drag coefficient
C_B	body drag coefficient
C_T	caudal-fin drag coefficient
d_T	caudal-fin trailing-edge depth
E	total power generated by locomotory movements, ergs/sec
E_D	power required to overcome total drag, ergs/sec
E_{DB}	power required to overcome body drag, ergs/sec
E_{DT}	power required to overcome caudal-fin drag, ergs/sec
E_K	power lost as kinetic energy, ergs/sec
E_T	thrust power, ergs/sec
f	caudal-fin beat frequency, sec
L	total length of fish, cm
m_T	trailing-edge virtual mass, g/cm
R_L	Reynolds number, based on L
S	total wetted surface area, cm ²
S_B	wetted surface area of body, cm ²
S_T	wetted surface area of caudal-fin, cm ²
U	swimming speed, cm/sec
U_{crit}	45 min critical swimming speed, cm/sec
V	backward velocity of propulsive wave, cm/sec

w	$W(V-U)/V$, cm/sec
W	lateral velocity of trailing edge, cm/sec
W_R	resultant velocity of trailing edge, cm/sec
$k, m, n,$ p, q	} constants
β	
θ	rotational component for caudal-fin motions. Note $\cos \theta$ is equal to Lighthill's (1971) $\partial a/\partial x$
λ_B	length of propulsive wave, cm
ν	kinematic viscosity of water, stokes
π	3.14
ρ	density of water, g/cm ³

RESULTS

Swimming mode

The swimming movements of fish in groups 1 to 3 were typical of fish swimming in the sub-carangiform mode (Breder, 1926; Bainbridge, 1963; Gray, 1933c; Webb, 1971a). Amplitude increased over the posterior half of the body to reach maximum values over the posterior third of the caudal fin. Group 4 was intermediate between this type of motion and that described by Gray (1933c) for the whiting following complete caudal-fin amputation. Thus amplitude tended to continue increasing posteriorly to some extent, with the tail somewhat splayed outwards. Therefore, the portion of flexible caudal fin left intact was not sufficient to permit completely normal locomotory movements. λ_B was similar in all groups. Expressed as specific wavelengths, λ_B/L , values were 1.02, 1.00, 0.95 and 1.03 for groups 1-4 respectively.

Critical swimming speed

Partial caudal-fin lobe amputation had a relatively small effect on critical swimming speed, supporting observations by Breder (1926) and Gray (1933c). Values were 61.6 ± 2.7 , 59.5 ± 3.9 , 57.4 ± 6.0 and 51.8 ± 7.3 (cm/sec, mean ± 2 S.E.) for groups 1-4 respectively. U_{crit} was just significantly lower for group 4 compared with the control group 1 (Student's 't' test, $P > 0.05$). Values for U_{crit} were lower than those reported elsewhere for this species (Brett & Glass, 1973), but reflect normal seasonal variance.

Tail-beat frequency, f , and amplitude, A

Webb (1971a) has demonstrated the utility of expressing kinematics and performance levels in relation to mechanical scope in order to compare kinematic changes following experimental manipulation of the locomotor system. Mechanical scope was defined as the difference between the product $f \times A$ at zero speed and at U_{crit} , providing λ_B was unchanged. More simply, levels of mechanical scope could be expressed as a percentage of U_{crit} , as $\% U_{crit}$. Analytical use of such mechanical scope makes the assumption that fish are exercised to a physiological limit at U_{crit} , as demonstrated by fatigue of the fish and failure to swim. This transformation of activity levels to $\% U_{crit}$ will be used here to facilitate discussion. Original data are given in Table 2.

The relationship between f and $\% U_{crit}$ was the same for each group of fish (Fig. 2).

Table 2. Data for tail-beat frequency, f , trailing-edge amplitude, A , and their product measured for the four groups of fish at various swimming speeds U

Values for mechanical scope as % U_{crit} are also shown.

U (cm/sec)	% U_{crit}	$f(\bar{X} \pm 2 \text{ S.E.})/\text{sec.}$	$A(\bar{X} \pm 2 \text{ S.E.})$ (cm)	$f \times A$ (cm/sec)
Group 1				
15.0	24	2.2 ± 0.2	3.0 ± 0.5	6.6
22.5	37	2.6 ± 0.2	3.0 ± 0.4	7.8
30.0	49	3.0 ± 0.1	3.3 ± 0.2	9.9
37.5	61	3.3 ± 0.1	3.5 ± 0.2	11.6
45.0	73	3.6 ± 0.2	3.7 ± 0.4	13.3
52.5	85	4.5 ± 0.1	3.7 ± 0.2	16.7
60.0	97	4.8 ± 0.1	3.6 ± 0.2	17.3
67.5	110	5.0	2.6	19.0
75.0	122	5.4	3.8	20.5
Group 2				
15.0	25	2.5 ± 0.4	2.6 ± 0.6	6.5
22.5	38	2.8 ± 0.3	2.6 ± 0.6	7.3
30.0	50	3.0 ± 0.2	3.0 ± 0.3	9.0
37.5	63	3.5 ± 0.1	3.1 ± 0.2	10.9
45.0	76	4.2 ± 0.3	3.3 ± 0.4	13.9
52.5	89	4.8 ± 0.3	3.5 ± 0.3	16.8
60.0	101	4.9 ± 0.2	3.6 ± 0.2	17.6
67.5	113	5.4	3.7	20.0
Group 3				
15.0	26	2.4 ± 0.5	2.4 ± 0.5	5.8
22.5	39	2.7 ± 0.4	3.0 ± 0.5	8.1
30.0	52	3.3 ± 0.4	3.3 ± 0.3	10.9
37.5	65	3.7 ± 0.5	3.1 ± 0.3	11.5
45.0	79	4.5 ± 0.3	3.3 ± 0.2	14.9
52.5	91	4.8 ± 0.4	3.6 ± 0.2	17.3
60.0	105	5.0	3.8	19.0
67.5	118	5.3	3.8	20.1
Group 4				
15.0	29	2.5 ± 0.3	3.0 ± 0.2	7.5
22.5	43	2.7 ± 0.2	3.3 ± 0.2	8.9
30.0	58	3.3 ± 0.3	3.5 ± 0.2	11.6
37.5	72	3.8 ± 0.3	3.3 ± 0.2	12.5
45.0	87	4.7 ± 0.6	3.5 ± 0.3	16.5
52.5	101	4.9 ± 0.4	3.7 ± 0.3	18.1
60.0	116	5.3 ± 0.3	3.8 ± 0.3	20.1

It was curved slightly at lower % U_{crit} (and hence low U) as demonstrated for several other species swimming in the sub-carangiform mode (Bainbridge, 1958; Webb, 1971a). This curvature was associated with compensatory changes in A , such that A increased with speed to reach maximum values as U_{crit} approached. This trend is shown for the present fish in Fig. 2.

Where both f and A vary with swimming speed their product $f \times A$ appears to be linearly related with U or % U_{crit} (Webb, 1971a). This was confirmed for the sockeye salmon used in the present experiments (Fig. 2).

Oxygen consumption

The data for oxygen consumption at various swimming speeds were best expressed as least-squares linear regression equations relating the logarithm of oxygen con-

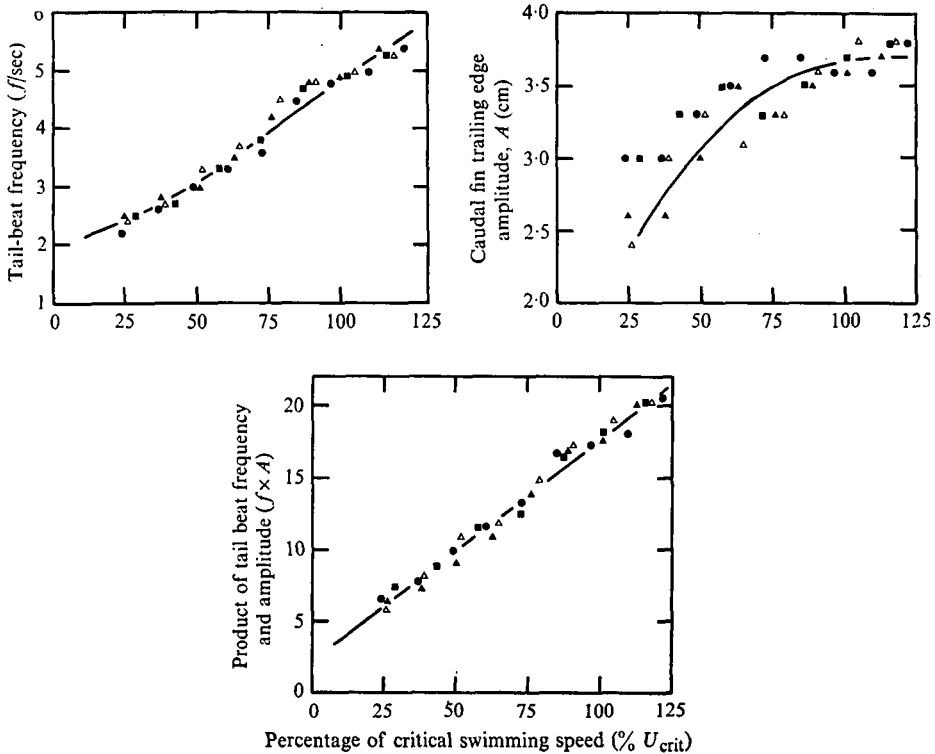


Fig. 2. The relationships of tail-beat frequency, f , trailing-edge amplitude, A , and their product, $f \times A$, with mechanical scope for activity expressed as % U_{crit} . Key; group 1, solid circles; group 2, solid triangles; group 3, open triangles; group 4, solid squares.

Table 3. Least-squares regression equations relating log. oxygen consumption (Y mg O_2 kg h) to swimming speed (U cm/sec), and standard and active metabolic rates for the four groups of fish

	Group 1	Group 2	Group 3	Group 4
Least-squares regression equations, Log Y	$1.907 + 0.0141U$	$1.864 + 0.0154U$	$1.901 + 0.0152U$	$1.875 + 0.0185U$
Standard metabolic rate mg O_2 /Kg h ($Y \pm 2$ s.e.)	81 ± 18	73 ± 14	80 ± 17	75 ± 11
Active metabolic rate mg O_2 /Kg h ($Y \pm 2$ s.e.)	595 ± 103	607 ± 70	590 ± 60	680 ± 75

sumption to U (Brett, 1964; Brett & Glass, 1973). Only the equations are presented here (Table 3). Standard and active metabolic rates were calculated as described by Brett (1964).

There was no significant difference in standard or active metabolic rates within the four groups of fish tested (Students 't'), although the active rate was somewhat higher for group 4 fish (Table 3). Both active and standard rates were typical for the species for equivalent activity levels (Brett & Glass, 1973).

Data for oxygen consumption shows that caudal-fin amputation affected neither standard nor active metabolic rates, and metabolic scope was comparable for four groups.

DISCUSSION

Metabolic rates and metabolic scope were not affected by amputation. Consequently, the metabolic power made available to the muscular system will be the same in each of the four groups of fish at a given level of activity, expressed as % U_{crit} . The contribution made by anaerobic metabolism is neglected. However, as discussed by Webb (1971*b*) this contribution is expected to be small in comparison with that from aerobic metabolism. Furthermore, there is no reason to expect different anaerobic contributions to the energy budget of fish in the different groups, because all fish were equally exhausted at the end of an experiment.

It should be noted that there is no intention to consider the level of activity at U_{crit} as the maximum physiologically permissible level. It is a level designated as the maximum level of activity which fish would be able to maintain for a period of 45 min. Clearly other and higher maxima would be permissible at higher speeds and *vice versa* (Bainbridge, 1958).

Consideration of the kinematic data shows that at a given level of mechanical scope f , A and λ_B are the same for each group. Webb (1971*b*) has pointed out that these parameters not only describe caudal-propeller mechanics, but also propulsive-muscle mechanics because the two parts of the system are morphologically equivalent for fish swimming in sub-carangiform modes. When f , A and λ_B are the same, then so are muscle shortening speed and muscle power output (Hill, 1950). Therefore, at a given % U_{crit} , not only is the metabolic power input to the muscles the same for each group, but so is the muscle power input to the caudal propeller; that is, amputation of various caudal-fin lobes did not affect the power input to the caudal propeller at similar activity levels.

Subsequent discussion of the effects of partial and complete caudal-fin-lobe amputation can therefore be restricted to the mechanics of the caudal propeller system.

The mechanics of sub-carangiform locomotion observed in the present fish are best described by the hydromechanical model proposed by Lighthill (1960, 1969, 1970, 1971). This model considers realistic fish-type body motions, and realistic fish-type body shapes and cross-sections. By comparison of the model's predictions for E_T and E with general equations for drag and metabolic power expenditure, insight can be gained into the drag distribution for swimming fish and biological use of the model.

As with all *hydromechanical* models, inertial forces associated with body movements are emphasised and thrust forces of viscous origin neglected.

The most useful form of the model for a biologist is that whereby the effectiveness of propulsive movements are expressed in terms of bulk momentum and energy as dictated by the kinematics of the caudal-fin trailing-edge. Following Lighthill, the total rate of working, or power generated by the propulsive wave travelling backwards over the body is given by

$$E = m_T w W U, \quad (1)$$

where

$$m_T = \pi \rho \beta (d_T/2)^2. \quad (1A)$$

The value of the shape factor, β , depends on body shape and the arrangement of median fins, in this case the intact caudal-fin lobes. Numerical values from Lighthill (1970) are included in Table 1.

Lateral movements of the trailing-edge are sufficiently close to simple harmonic motion (Gray, 1933*a*) that W may be calculated as the root-mean-square velocity from

$$W = \pi f A / \sqrt{2} \quad (1 B)$$

and
$$w = W[(V - U)/V], \quad (1 C)$$

where
$$V = f \lambda_B. \quad (1 D)$$

The kinetic energy, E_K , of the water with motion w is lost to the wake:

$$E_K = \frac{1}{2} m_T w^2 U / \cos \theta. \quad (2)$$

No measurements were made of θ , and a constant value of $\cos \theta$ of 0.85 will be assumed as calculated by Lighthill (1971) for *Leuciscus* from figures in Bainbridge (1963). Mean values for $\cos \theta$ would certainly have varied between the four groups, more so for group 4 than for groups 1 to 3. However, within the range of θ observed for such fish as *Anguilla* (Gray, 1933*a*), *Merlangus* and other fish photographed by Gray (1933*a, c*) and *Salmo gairdneri* (P. W. Webb, unpublished observations), variations in $\cos \theta$ are relatively small. It will be assumed that such variations are small enough to be neglected.

The thrust power developed, E_T , is found from equations 1 and 2 by difference

$$\begin{aligned} E_T &= E - E_K, \\ E_T &= m_T U (wW - [\frac{1}{2} w^2 / \cos \theta]). \end{aligned} \quad (3)$$

E_T must equal the power required to overcome drag, E_D . Conventionally, E_D is computed from the Newtonian equation

$$E_D = \frac{1}{2} \rho S U^3 C, \quad (4)$$

where C is an empirically fitted drag coefficient in most cases.

Typically
$$C = k / R_L^{0.2}, * \quad (4 A)$$

where
$$R_L = LU / \nu, \quad (4 B)$$

therefore
$$E_D = \frac{1}{2} \rho S U^{2.8} k (L / \nu)^{-0.2}. \quad (5)$$

Equating 3 and 5

$$E_D = E_T,$$

or
$$m_T U (wW - \frac{1}{2} w^2 / \cos \theta) = \frac{1}{2} \rho S U^{2.8} k (L / \nu)^{-0.2}. \quad (6)$$

Considering values at U_{crit} , kinematic parameters were the same in each group, while variations in U_{crit} itself were small. Therefore, differences in $(wW - \frac{1}{2} w^2 / \cos \theta)$

* k will be a fitted non-dimensional number. It is not assumed equal to 0.072, as appropriate for an attached turbulent boundary-layer expected on a flat plate in the fish chamber. This value has sometimes been applied to fish (Bainbridge, 1961). k may take any value as appropriate to describe the drag on a swimming fish. According to Lighthill (1971) and Webb (1971*a*) k may be approximately four times greater than for a flat plate or an equivalent solid body.

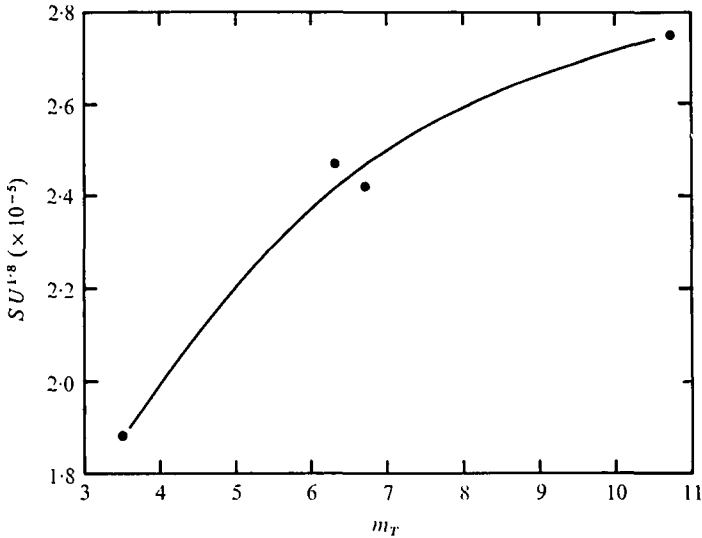


Fig. 3. The relationship between m_T and $SU^{1.8}$ at U_{crit} from equation 7.

will be small and may be neglected. For the conventional drag equation, k would be the same for all groups. Then, equation 6 can be rewritten

$$m_T Un = SU^{2.8} m. \quad (7)$$

For intact fish, S takes values of the order $0.4L^2$ (Bainbridge, 1961; Webb, 1971 *a, b*). Taking into account differences in area following amputation of parts of the caudal fin, then from equation 7, m_T should be linearly related to $SU^{1.8}$. This relationship is shown in Fig. 3, but is curved. A similar curve can be obtained by plotting E_T against $SU_{crit}^{2.8}$ from equation 6 (not shown).

Clearly, either the model giving E_T is in error, or the equation for E_D does not represent the drag-power for a swimming fish. The hydromechanical model takes into account fish-type movements, but the traditional form of the drag equation 4 does not do so. It neglects the effect of the additional drag that is likely to arise from higher resultant, W_R , of the caudal fin that is an inevitable consequence of that organ's lateral motion. The resultant velocity is given by:

$$W_R = \sqrt{(W^2 + U^2)} > U. \quad (8)$$

In addition, the oscillating nature of the caudal-fin lateral movements undoubtedly prevents the boundary-layer from growing to the thickness expected for steady-state motion of U or W_R . The consequence of such reduced boundary-layer thickness will be an increased drag on the caudal fin substantially augmenting the total drag of the fish. This phenomenon has been termed boundary-layer thinning (Bone, in Lighthill, 1971) and has been advanced by these authors to partially explain the relatively high drag values computed for swimming fish.

Taking into account boundary-layer thinning and increased W_R for the caudal fin implies a substantial drag cost associated with swimming movements. This drag would be reduced by removal of parts of the caudal fin. E_T will also be reduced

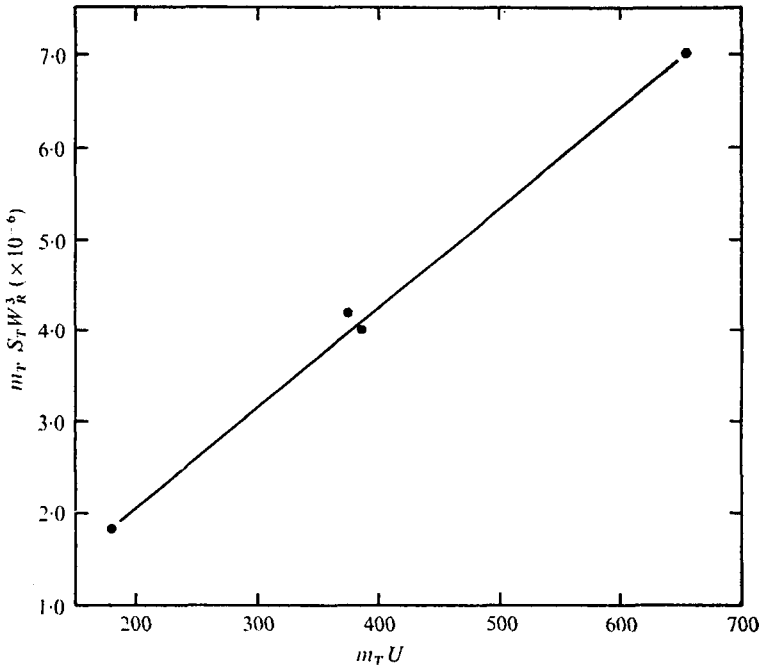


Fig. 4. The relationship between $m_T U$ and $S_T W_R^3$ at U_{crit} from equation 11.

because of the reduction in d_T following amputation. If the reduction in E_T through reduced d_T were of the same order as the reduction E_D , through reduced S_T then the situation can easily be visualized where caudal-fin-lobe amputation results in small changes in U_{crit} .

In order to test the hypothesis that the reduction in drag power required is of the same order as the decrease in thrust predicted by the model, equation 4 must be rewritten to include the special case of drag arising on the caudal fin.

Thus
$$E_D = E_{DB} + E_{DT}, \quad (9)$$

$$E_D = \frac{1}{2} \rho S_B U^3 C_B + \frac{1}{2} \rho S_T W_R^3 C_T.$$

Equating 3 and 9

$$m_T U (wW - \frac{1}{2} w^2 / \cos \theta) = \frac{1}{2} \rho S_B U^3 C_B + \frac{1}{2} \rho S_T W_R^3 C_T. \quad (10)$$

The assumptions concerning $(wW - \frac{1}{2} w^2 / \cos \theta)$ in equation 6 still apply. In addition, variations in E_{DB} are small enough to neglect since S_B will be the same in all groups; C_B is expected to be small (Schlichting, 1968) and variations in U_{crit} are relatively small. The magnitude of C_T is not known. However, the caudal fin, or any other part of the body of a swimming fish, can be compared with a hydrofoil (Taylor, 1952). Although this analogy is largely of heuristic value, it nevertheless suggests that changes in C_T with the various kinematic parameters will be small at given levels of mechanical scope. Thus at U_{crit} variations in C_T may be neglected.

Equation 10 can then be simplified in the same way as equation 6, so that

$$m_T U n = p + S_T W_R^3 q. \quad (11)$$

For the prediction of E_T to be valid, at U_{crit} , $m_T U$ should be linearly related to $S_T W_R^3$. Relevant data for equation 11 are included in Tables 1 and 4. The relation suggested by equation 11 is plotted in Fig. 4, and is linear. A similar relationship between E_T and $(E_{DB} + S_T W_R^3)$ can also be shown to be linear.

The more appropriate form of the drag equation thus validates the form of Lighthill's simplified bulk-momentum model in predicting E_T , and also supports the hypothesis that the laterally moving portions of the body experience an augmented drag (Bone, in Lighthill, 1971).

Breder (1926) and Gray (1933c) have suggested an alternative explanation for the small reductions in steady or sustained swimming performance following caudal-fin surgery. This considers that thrust generation is transferred from the caudal fin to the body. This explanation would require compensatory changes in the kinematics, and this is not supported by the present data. Even the differences observed in group 4, where most of both caudal-fin lobes were amputated, are small compared with other groups.

Although the data support the predictions of E_T for the simplified form of Lighthill's model, they do not support the predictions of E . The power input to the caudal propeller is the same at equivalent levels of activity, and therefore so should the total mechanical power output of the mechanical system. However, it can be seen from equation 1, that E as well as E_T will vary mainly with m_T , and consequently be reduced with d_T following caudal-fin surgery.

The explanation for this discrepancy follows mainly from the form of the model discussed here, that is, the model of greatest predictive potential to biologists studying *intact* fish. In treating mean bulk-momentum changes in the trailing-edge region, it neglects the distribution of momentum changes along the length of the body which are discussed by Lighthill's (1970, 1971) detailed treatment of locomotion and also by Wu (1971c).

One of the factors discussed in detail was the interaction of different parts of the body having different sectional designs as in the sockeye salmon. Such interactions occur between the leading edge of the caudal fin and trailing edges of the anal fin, and probably the posteriorly-thinning dorsal aspect of the body. Interactions result in energy economies without detriment to thrust. Clearly these advantages are lost by caudal-fin surgery of the form used here, and are not taken into account by the bulk-momentum form of the model. Lighthill (1970) also showed that tapering body sections tended to waste more energy than sections of deep caudal-fin type. Amputation tends to result in tapering body shapes, and energy lost because of this has not been accounted for.

In addition, the relations that apply to thrust and propeller-disc area (von Mises, 1945) will apply equally to the caudal fin. A large propeller generates thrust over a relatively large area, while the circumference available for energy loss through cross-flows is relatively small. Generation of an equivalent thrust/unit propeller-disc area for a smaller propeller would require a greater energy input, because proportionally more energy is lost in cross-flows around the relatively larger circumference. These losses are also neglected by the model.

In summary, kinematic data suggests that E_T is well predicted by the simpler model, but that E is not. The physiological data suggests that E will be the same for

Table 4. Derived values for U , W_R and E_T at various % U_{crit} used in the estimation of C_T

% U_{crit}	U	W_R	E_T	U	W_R	E_T
Group 1			Group 2			
10	6.2	10.5	2.01×10^3	6.0	10.4	1.14×10^3
20	12.3	17.1	7.72×10^3	11.9	16.8	4.40×10^3
30	18.5	24.0	1.84×10^4	17.9	23.5	1.06×10^4
40	24.6	30.8	3.50×10^4	23.8	30.3	2.02×10^4
50	30.8	38.0	5.84×10^4	29.8	37.1	3.37×10^4
60	37.0	45.0	8.89×10^4	35.7	43.9	5.17×10^4
70	43.1	52.0	1.28×10^5	41.7	50.8	0.75×10^5
80	49.3	59.0	1.75×10^5	47.6	57.6	1.03×10^5
90	55.4	66.0	2.31×10^5	53.6	64.4	1.36×10^5
100	61.6	73.1	2.97×10^5	59.5	71.3	1.76×10^5
110	67.8	80.1	3.73×10^5	65.5	78.2	2.22×10^5
Group 3			Group 4			
10	5.7	10.2	1.15×10^3	5.2	9.9	0.55×10^3
20	11.5	16.5	4.59×10^3	10.4	15.8	2.15×10^3
30	17.2	23.1	1.13×10^4	15.5	21.8	0.52×10^4
40	23.0	29.6	2.12×10^4	20.7	27.9	1.01×10^4
50	28.7	36.3	3.57×10^4	25.9	34.1	1.72×10^4
60	34.4	42.9	5.49×10^4	31.1	40.3	2.68×10^4
70	40.2	49.6	0.80×10^5	36.3	46.4	0.39×10^5
80	45.9	56.2	1.10×10^5	41.4	52.6	0.55×10^5
90	51.7	62.9	1.46×10^5	46.4	58.8	0.73×10^5
100	57.4	69.6	1.90×10^5	51.8	65.0	0.96×10^5
110	63.1	76.2	2.40×10^5	57.0	71.2	1.22×10^5

groups at similar activity levels, but is not well predicted by the model in the form considered most applicable in practical situations. Reasons are advanced suggesting that this is because energy losses exceed those predicted.

Much of this wasted energy is associated with forces of viscous origin, which are not included in the model. However, for normal fish swimming at typically high R_L , Lighthill (1960, 1970) has indicated that such forces will be negligible compared with inertial forces. Lighthill (1969, 1970) and originators of other models (see Webb, 1971 *a* for references) have repeatedly indicated the desirability of a composite model treating inertial and viscous forces, but as they have observed, the current problems in formulating such a model are immense.

On the basis of the foregoing discussion, it might be thought that the simpler form of Lighthill's model is not appropriate for applied use with fish. Certainly the detailed form is more desirable. However, it requires an arduous analysis of the type that Taylor (1952) does not recommend, high-quality film records, and is virtually confined to the laboratory.

In contrast, it must be noted that the discussion of fish propulsion mechanics given here is for a highly abnormal situation, specifically designed to obtain insight into both practical models and drag mechanisms. Such extreme caudal-fin modification is not usually found in normal fish populations where observed caudal-fin damage does not usually destroy its composite functional integrity. Thus, normal populations of fish would not require the detailed model. In fact, it has been shown that Lighthill's simpler model gives a good description of propulsive energetics for trout, especially in its prediction of E_T (Webb, 1971 *a, b*). Thus, it is considered that

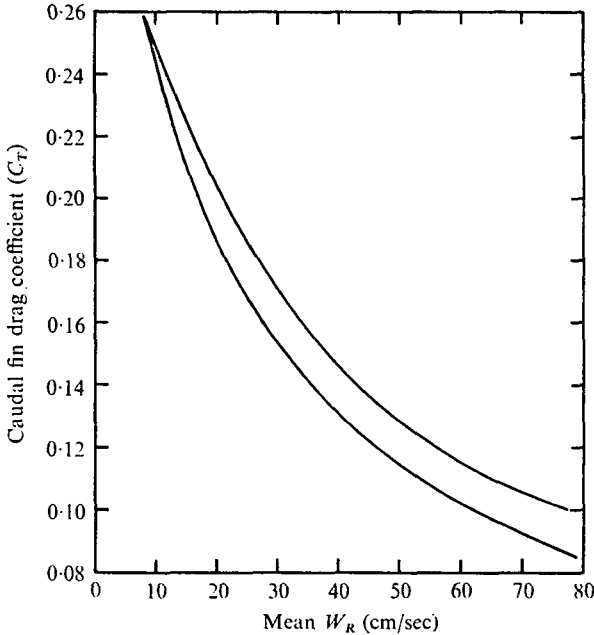


Fig. 5. Estimations of the caudal-fin drag-coefficient (C_T) shown as a function of mean trailing-edge resultant velocity (W_R) calculated from equation 12. The lower curve is based on data for group 1 compared with that for groups 2 and 3, and the upper curve for group 1 compared with group 4.

this model is applicable to normal fish, and as such its potential for the evaluation of locomotory activities in both laboratory and wild fish populations cannot be underestimated.

So far, the various equations describing thrust and drag have been treated generally, with no attempt at their numerical solution. Using control group 1 data, a value for E_T of 2.97×10^5 ergs/sec is obtained at U_{crit} . Brett (1963) and Webb (1971*b*) have shown that overall efficiency of conversion of metabolic power to mechanical thrust is greatest at this level of activity. The mean metabolic scope for activity (the oxygen available for locomotion at U_{crit}) has a mean value $514 \text{ mg O}_2/\text{kg h}$ for the four groups. The c.g.s. energy equivalent for oxygen can be taken as 1.47×10^8 ergs/mg O_2/sec (Alexander, 1967; Webb, 1971*b*). Then, at U_{crit} , the overall efficiency as described by Webb (1971*a*) is 22%. This value is of the same order commonly found for other vertebrates working at similar levels of activity (see Webb, 1971*b*).

Numerical solutions can also be used to obtain estimates of C_T . Amputation of portions of the caudal fin result in a decrease in E_T , ΔE_T , that can be related to a reduction in caudal-fin area, ΔS_T . Rearrangement of equation 10 and taking a mean value for W_R^3 gives

$$C_T = \frac{\Delta E_T}{\frac{1}{2}\rho\Delta S_T[W_{iR}^3 + W_{iiR}^3]}, \quad (12)$$

where the subscripts i and ii designate the values of W_R^3 for any two groups. Measured and derived values for equation 12 are included in Tables 1 and 4 computed for various % U_{crit} .

Estimates for C_T are shown in Fig. 5 as a function of the mean W_R . The lower line was computed for data from group 1 and groups 2 and 3, and the upper line for data from groups 1 and 4. Fig. 5 indicates that the caudal-fin drag coefficient will be highest at low W_R , and hence usually at low U . At such swimming speeds V is relatively greater than U , in comparison with higher swimming speeds (Webb, 1971 *a, b*). Therefore, the angles subtended by the body to the flow will tend to be high, and drag will, tend to be elevated in a similar fashion to that on a hydrofoil (von Mises, 1945). However, C_T decreases as W_R (and usually U) increase, so that at higher speeds it approaches minimal values. This would make for good energetic economy as energy available for locomotion becomes limiting at higher speeds. At U_{crit} , C_T is approximately one order of magnitude higher than expected in the absence of lateral movements of the caudal fin.

It should be noted that values for C_T given are approximations and will err on the high side. This is because W_R is calculated for trailing-edge motions, and consequently does not apply to the whole caudal fin. The mean value for W_R over the whole fin would be lower, and hence C_T higher. Consequently the form of Fig. 5 is more important than the absolute values estimated.

The general observation of the small effect of caudal-fin amputation on steady and sustained swimming performance of fish swimming in the sub-carangiform mode raises the question of the utility of that structure. The ability of the caudal fin to suffer extensive damage without reducing sustained performance is of obvious selective value. But this does not explain the evolutionary pressures that would give rise to a large, not particularly strong structure of no selective value for sustained activity.

Recent studies by Weihs (1972) on turning manoeuvres in *Carassius auratus* and *Cyprinus erythrophthalmus*, and on acceleration in *Salmo trutta* and *Esox esox* (Weihs, 1973) indicates that a well developed caudal-fin of large depth is necessary for these activities. It is therefore suggested that the deep caudal fin shapes characteristic of a majority of fish have evolved in response to requirements of high acceleration, fast turning and high speed manoeuvrability.

SUMMARY

1. Propulsive wavelength, tail-beat frequency, trailing-edge amplitude, critical swimming speed and oxygen consumption rates have been measured for sockeye salmon in which the trailing edge depth and caudal-fin area were variously reduced by partial caudal-fin amputation. The swimming mode was sub-carangiform.

2. The 45 min critical swimming speed for intact fish was 61.6 cm/sec (3.0 l/sec). The critical speed was not significantly reduced by removal of either the epaxial or hypaxial caudal-fin lobes, but was reduced significantly ($P < 0.05$) to 51.8 cm/sec (2.5 l/sec) when both lobes were removed.

3. The mean length of the propulsive wave was 1.00 body length, and was not affected by the caudal-fin surgery.

4. Both tail-beat frequency and amplitude increased with speed, their product linearly so. Normalization of data in relation to the physiological maximum at the critical swimming speed showed no relative changes in frequency and amplitude.

5. No significant differences were observed in standard or active metabolic rates.
6. General equations describing thrust (Lighthill, 1969) and drag were compared. It was shown that the drag on the caudal fin was markedly increased by lateral propulsive movements as suggested by Bone's boundary-layer thinning hypothesis (Lighthill, 1971). Drag coefficients for the caudal fin were one to two orders of magnitude higher than would be expected in the absence of lateral movements.
7. It is considered that the principal function of the caudal fin is in manoeuvre and acceleration.

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