

POWER OUTPUT OF TWO SIZES OF ATLANTIC SALMON (*SALMO SALAR*) AT THEIR MAXIMUM SUSTAINED SWIMMING SPEEDS

BY J. TANG AND C. S. WARDLE

SOAFD Marine Laboratory, Victoria Road, PO Box 101, Aberdeen, UK

Accepted 13 January 1992

Summary

The maximum sustained swimming speeds (U_{ms}) for large (0.45 m long) and small (0.15 m) Atlantic salmon were respectively 0.91 m s^{-1} and 0.54 m s^{-1} . Video and ciné films of fish swimming close to U_{ms} were analysed to obtain variables required for the application of two hydrodynamic models, those of Lighthill and Yates, to determine the mean thrust (\bar{T}) and mean power output (\bar{P}) at these swimming speeds (U) close to U_{ms} . A large fish ('Salmon') and a small fish ('Smolt') were selected for analysis. For salmon using Lighthill's model, $\bar{T}=0.30 \text{ N}$ and $\bar{P}=0.26 \text{ W}$, and using Yates' model, $\bar{T}=0.28 \text{ N}$ and $\bar{P}=0.25 \text{ W}$ ($U=0.87 \text{ m s}^{-1}=0.96U_{ms}$). For smolt using Lighthill's model, $\bar{T}=0.0052 \text{ N}$ and $\bar{P}=0.0019 \text{ W}$, and using Yates' model, $\bar{T}=0.0065 \text{ N}$ and $\bar{P}=0.0024 \text{ W}$ ($U=0.37 \text{ m s}^{-1}=0.69U_{ms}$). The power output for smolt swimming at $0.69U_{ms}$ was corrected to that required to swim at U_{ms} , giving $\bar{P}=0.0059 \text{ W}$ (Lighthill's model) and $\bar{P}=0.0074 \text{ W}$ (Yates' model).

At U_{ms} it was assumed that all the red muscle was used. Two fish were selected from each size group and cross-sectioned to estimate their red muscle masses. Using a maximum mass-specific power output of $5\text{--}8 \text{ W kg}^{-1}$ for slow red muscle fibres allowed us to calculate that the large and small fish have a power output capacity of $0.125\text{--}0.3 \text{ W}$ and $0.007\text{--}0.019 \text{ W}$, respectively.

The power output values at U_{ms} derived from the different approaches for the large ($0.25\text{--}0.26 \text{ W}$) and small ($0.0059\text{--}0.0074 \text{ W}$) salmon agree closely. Effects of scaling are discussed.

Introduction

He and Wardle (1988) studied the endurance at intermediate swimming speeds of Atlantic mackerel *Scomber scombrus* L., herring *Clupea harengus* L. and saithe *Pollachius virens* L. and determined the maximum sustained swimming speed [U_{ms} , the greatest swimming speed that can be maintained for 200 min, as defined by He and Wardle (1988) for these three marine fish]. Their technique involved training the fish to swim with a moving light pattern which allowed the authors to vary the swimming speed of these fish. The present study made use of this same technique with two sizes of Atlantic salmon to determine their maximum sustained

Key words: *Salmo salar*, fish, muscle, swimming, power output.

swimming speeds (U_{ms}) and endurance swimming characteristics. This procedure also allowed the swimming speed of the fish to be controlled during filming for the application of two hydrodynamic models.

Lighthill's (1971) large-amplitude elongated-body theory has been applied to cod (*Gadus morhua*) by Wardle and Reid (1977), Videler and Wardle (1978) and Videler (1981) to obtain the thrust and power required to swim at different speeds. This model requires overhead views of swimming fish to obtain the required parameters.

Yates (1983) developed an alternative model and applied it to data supplied by Webb (1975) on trout (*Salmo gairdneri*) to obtain estimates for mean thrust and power output. The parameters for this model are obtained from simultaneous overhead and side views of the swimming fish. The swimming movements of Atlantic salmon are similar to those of cod and trout, and it is considered that these two hydrodynamic models will provide independent assessments of its power output.

Several authors have discussed the view that red muscle alone is involved in swimming at speeds at or below U_{ms} (Bone *et al.* 1978; Kashin *et al.* 1979; Rome *et al.* 1984; Higgins and Thorpe, 1990). Such an assumption allows an assessment of the red muscle mass of a fish to be used to provide another independent approach for estimating the power output capacity of a fish.

Johnston and Salamonski (1984) determined mass-specific power output values for red and white muscle of Pacific blue marlin (*Makaira nigricans*). Langfeld *et al.* (1989) obtained values for fast-type muscle fibres, and Altringham and Johnston (1990) for fast- and slow-type muscle fibres of *Myoxocephalus scorpius*. The mass of red muscle present in individuals of 'large' and 'small' Atlantic salmon may thus give an indication of the power output capacity of these fish when related to mass-specific muscle power output figures in the literature.

In this study, the values suggested by Altringham and Johnston (1990) of $5\text{--}8\text{ W kg}^{-1}$ obtained for the slow muscle fibres of *Myoxocephalus scorpius* are used to obtain an estimate of the power output of salmon red muscle when the fish are swimming at their maximum sustained swimming speeds.

The endurance curves were first measured to determine the maximum sustained swimming speeds of two size groups (large salmon and small salmon). Filmed bouts were selected for steady swimming from each size group. Following this selection, detailed hydrodynamic analysis was carried out on two filmed individuals called 'Salmon' (length, $L=0.45\text{ m}$) from the group of large salmon and 'Smolt' ($L=0.15\text{ m}$) from the group of small salmon. Then a study of the distribution of the red and white muscle masses was carried out on two large salmon and two small salmon of similar size and shape to Salmon and Smolt.

Materials and methods

Fish

The fish used in this study were two groups of Atlantic salmon. One group

consisted of 30 large fish which had been feeding in sea water for a year ($L=0.30-0.50$ m). The second group consisted of 21 small fish which had recently adapted to sea water ($L=0.10-0.20$ m). They were obtained from commercial fish farms in Scotland. The large and small fish were fed on food pellets (Mainstream Salmon Diets Grower 4 and Ewos Crumb Size 3, respectively).

Endurance swimming trials

Determination of the endurance swimming characteristics of the large and small salmon followed the procedures used by He and Wardle (1988) using a similar moving light pattern in a 10 m diameter gantry tank at the Marine Laboratory in Aberdeen (see He and Wardle, 1988, Fig. 1). Seawater temperatures were 11.2°C (s.d. 0.6°C) and 15.8°C (s.d. 0.9°C) during the endurance swimming trials and the filming of the groups of large and small fish, respectively.

Filming the fish and selection for hydrodynamic analysis

In obtaining film of the fish for analysis, four demanding criteria had to be satisfied: clear simultaneous overhead and sideview images of swimming fish, fish swimming at constant velocity, at the required speed (U_{ms} or as close as possible) and filmed with a minimum of 16 frames per tailbeat cycle.

For the large fish, two video cameras (Panasonic, CCTV) filming at 50 frames s^{-1} were used to obtain simultaneous overhead and sideview images as the fish swam at close to U_{ms} , following a moving light pattern (Fig. 1). From 60 min of video film (U-matic, JVC model CR-6600E), in which the group of large fish passed the camera approximately 100 times, the large fish that best satisfied the criteria ('Salmon', $L=0.45$ m, $U=0.867$ m s^{-1}) was selected for further analysis.

For the small fish, which had a higher tailbeat frequency whilst swimming at U_{ms} , a 16 mm ciné camera running at 100 frames s^{-1} (Photosonics IPL) was used. A video camera was used simultaneously to select successful ciné shots for processing. Both cameras were positioned overhead. Sideviews were provided by a 45° angled mirror placed in the swimming channel directly below the cameras such that simultaneous overhead and sideview images of the small fish were obtained on each camera image as they swam through the field of view. Water depth was reduced to 0.6 m to make the small fish swim alongside the angled mirror and so increase the successful yield of simultaneous overhead and sideview images. The set-up was similar to the arrangement shown in Fig. 1A in all other respects.

4200 feet of ciné film (Kodak Eastman Ektachrome, 7250 tungsten ISO400; KEE, 7251 daylight ISO400) was shot and, of this, 2200 feet was developed after identifying likely swimming bouts from the video tapes shot simultaneously. Despite many attempts to modify the set-up, the small fish that swam at U_{ms} in other parts of their 30 m swimming channel slowed as they approached the mirror. For this reason, we were forced to accept a reduced speed from the small fish. The small fish ('Smolt', $L=0.15$ m, $U=0.37$ m s^{-1}) that best satisfied all the other criteria had a swimming speed of $0.69U_{ms}$.

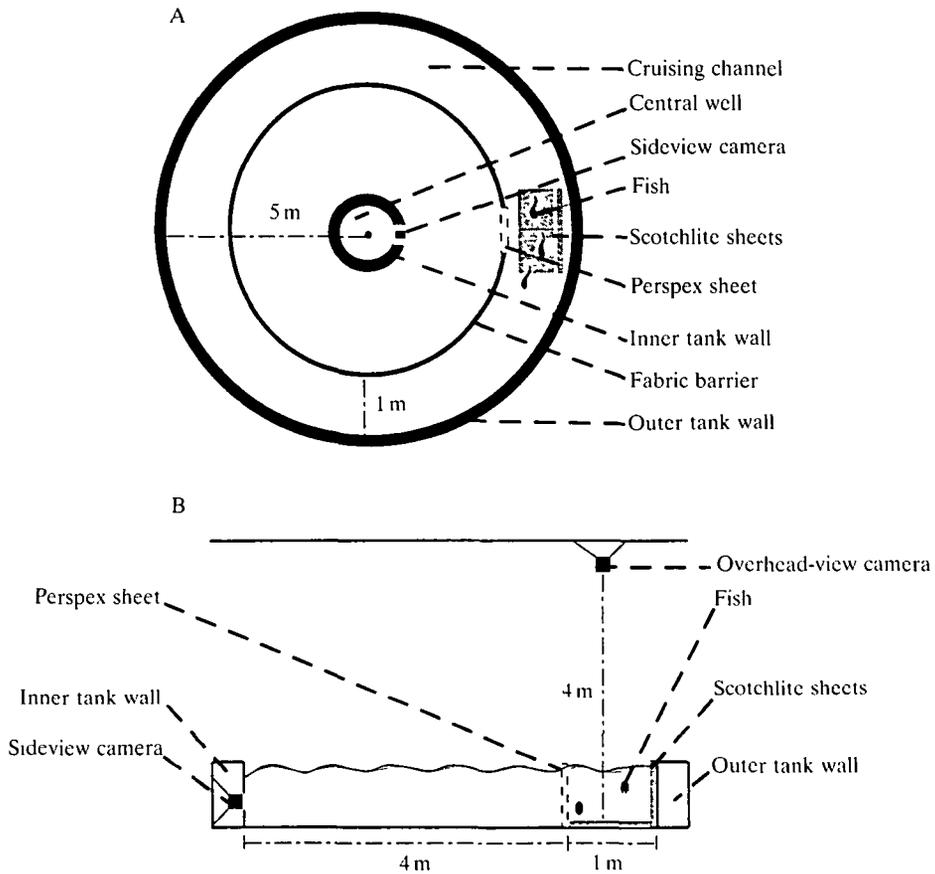


Fig. 1. Experimental design for filming the large fish. (A) Overhead view. (B) Side view.

For analysis, x, y -coordinates were recorded from the video tape using an image digitiser (Hampton Video Image VP112) and from the ciné film using a $0.57 \text{ m} \times 0.57 \text{ m}$ digitising pad (GTCO Corporation, Rockville MD, USA). The simultaneous overhead and side views of Salmon and Smolt ensured that the results from the two models of Lighthill (1971) and Yates (1983) were directly comparable.

Application of the models

Lighthill's (1971) large-amplitude elongated-body theory was applied to the digitised film images of Salmon and Smolt which satisfied his criterion of 16 frames per tailbeat cycle. A calculation was also carried out for the suggested approximation $[\frac{1}{2}mwz]_{a=0}$ of the integral term, where m is virtual mass, w is the velocity component perpendicular to the tangent on the fish spine at the tail-tip (i.e. position $a=0$) and z is the lateral velocity component of the tail-tip (Lighthill, 1971; Wardle and Reid, 1977; Videler, 1981).

Yates' (1983) hydromechanical model was applied to the swimming of Salmon and Smolt as shown in the example given by the author (Yates, 1983, Table 6-1, pp. 193–196).

Cross-sectional area and muscle mass

Two small and two large salmon, with dimensions closest to the filmed Salmon and Smolt, were killed at the end of the filming procedures, using MS 222 anaesthetic ($50\text{--}100\text{ mg l}^{-1}$), suspended by the mouth and frozen (-20°C) overnight to maintain an undistorted body shape. The frozen specimens were then cross-sectioned carefully at equal distances along the body of each fish. This started from the posterior edge of the opercula to the caudal peduncle, such that there were six sections of equal width. This was done with a sharp knife, immediately after each fish had been taken from the freezer (-20°C).

The rostral face of each section was then photographed and the areas of red and white muscle were identified and measured. Knowing the fish density and the thickness of each section, an estimate was made of the red and white muscle mass for each section and hence for the whole fish.

Results

Endurance curves and maximum sustained swimming speed

Fig. 2 shows the two endurance curves for the two size groups of fish. The curve for the large fish was determined using the two best swimmers. The curve for the small fish was determined using the complete school of 21 small fish. U_{ms} for the large fish is 0.91 m s^{-1} (2.03 L s^{-1} where $L=0.45\text{ m}$). U_{ms} for the small fish is 0.54 m s^{-1} ($5.4\text{--}3.6\text{ L s}^{-1}$ where $L=0.10\text{--}0.15\text{ m}$).

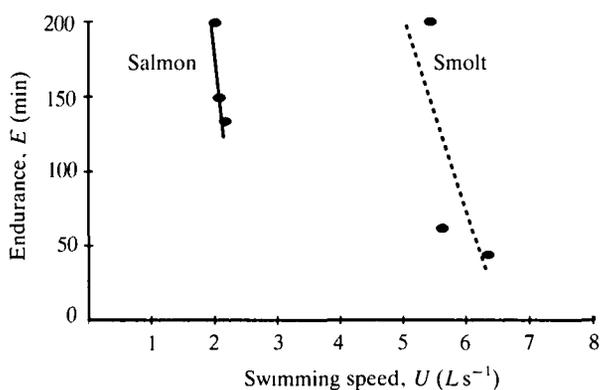


Fig. 2. Endurance curves of the large fish (solid line) and the small fish (dashed line). Linear regression equations are: large fish $E=1134-464U$ ($r=0.94$), small fish $E=864-141U$ ($r=0.75$), where E is the longest endurance at the test speed in minutes for four repeat trials and U is swimming speed in lengths per second ($L s^{-1}$).

Table 1. Mean thrust \bar{T} (N) and mean power \bar{P} (W) output values for Salmon ($L=0.45$ m, $U=0.87$ m s⁻¹, where $U_{ms}=0.91$ m s⁻¹) and Smolt ($L=0.15$ m, $U=0.37$ m s⁻¹, where $U_{ms}=0.54$ m s⁻¹)

	Salmon \bar{T} at U_{ms} (N)	Salmon \bar{P} at U_{ms} (W)	Smolt \bar{T} at $0.69U_{ms}$ (N)	Smolt \bar{P} at $0.69U_{ms}$ (W)	Smolt \bar{P} at U_{ms} (W)
Lighthill (1971)	0.30	0.26	0.0052	0.0019	0.0059
Yates (1983)	0.28	0.25	0.0065	0.0024	0.0074
Red muscle power	N/A	0.10–0.30	N/A	N/A	0.007–0.019

Note the discrepancy in the figures for Smolt between the red muscle power estimate (for swimming at U_{ms}) and the hydrodynamic models (for swimming at $0.69U_{ms}$).

The corrected hydrodynamic power figures ($\times 3.1$, see text) for Smolt swimming at U_{ms} are shown in the last column.

N/A, not applicable; L , fish length; U , swimming velocity; U_{ms} , maximum sustained swimming velocity.

Hydrodynamic models

The mean thrust (\bar{T}) and mean power output (\bar{P}) obtained from each model for Salmon and Smolt are shown in Table 1. The hydrodynamic parameters for Salmon and Smolt used in Yates' (1983) model are shown in Table 2. Examples of the parameters and instantaneous thrust values obtained for Salmon using Lighthill's model are shown in Table 3, for one swimming cycle.

Instantaneous thrust values from Lighthill's model are related to tail-tip position for Salmon and Smolt in Figs 3 and 4, respectively. Negative thrust values obtained from this model were found at the extremes of each tail-sweep cycle (Figs 3 and 4). These negative values were plotted as zero as it was considered a reasonable approximation that both the lateral velocity (dz/dt) and the angle of attack of the tail-blade (θ) are momentarily zero at these points (Table 3). This approximation was based on observations of the behaviour of the caudal fin trailing edge seen when filmed from behind during swimming motions (see also Fig. 1 in Bainbridge, 1963). It was noted that, at the extremes of each tail-sweep, the caudal fin slackened, losing its tension as the fin became momentarily stationary (similar to 'tacking' in the sport of sailing). These assumptions have the effect of removing the negative thrust values and augmenting the mean thrust and power obtained from Lighthill's model.

The magnitude of the integral term approximation $[\frac{1}{2}mwz]_{a=0}$ for Salmon and Smolt proved to be negligible (see Table 3). The contribution of the term $[\frac{1}{2}mwz]_{a=0}$ to the mean power for Salmon was 0.0048 W, and it was less than 0.0001 W for Smolt.

Red and white muscle distribution

Fig. 5 shows the red and white cross-sectional areas of the two large and two

Table 2. *Yate's parameters measured from film images of Salmon and Smolt*

Parameters	Salmon	Smolt
U (m s^{-1})	0.867	0.3676
L (m)	0.45	0.1512
h_1 (m)	0.0345	0.0134
b_L (m)	0.0376	0.0105
f (Hz)	3.125	3.8
c (m s^{-1})	1.1613	0.5301
b_p/b_L	0.4706	0.3548
L^*/L	0.4984	0.5283
σ	10.1917	9.82
θ	1.2876	1.5903
A_L/L^2	0.0219	0.0151
C_T	0.0036	0.0041
C_{Ph}	0.0041	0.0046
η_h	0.8942	0.8843
\bar{T} (N)	0.2838	0.0065
\bar{P} (W)	0.2752	0.0027
$\bar{T}U$ (W)	0.2460	0.0024
$\bar{P} - \bar{T}U$ (W)	0.0292	0.0003

The symbols and units used are the same as those shown in Yates (1983) Table 6-1, p. 195, after applying his equations 31-40, pp. 193-195.

Note that the useful power $\bar{T}U$ is quoted in the comparisons of power output.

A_L , area of circle circumscribing the body cross section; b_L, b_p , dorso-ventral body height at tail tip (L) and tail peduncle (p); c , velocity of propulsive wave; C_T , mean thrust coefficient; C_{Ph} , mean power coefficient; f , frequency; h_1 , amplitude of lateral movements; L , fish length; L^* , dorsal fin to caudal fin separation; \bar{P} , mean power; \bar{T} , mean thrust force; U , swimming velocity; η_h , efficiency; θ , proportional feathering parameter; σ , reduced frequency.

small fish selected for their morphological similarity to Salmon and Smolt. Note that cross-sectional area is proportional to muscle mass per section.

Applying the figure of $5-8 \text{ W kg}^{-1}$ for the maximum red muscle power output capacity (Altringham and Johnston, 1990) to the mean masses of red muscle in the large and small fish indicates that the power output capacity is approximately $0.125-0.3 \text{ W}$ for Salmon and $0.007-0.019 \text{ W}$ for Smolt.

Discussion

Power output at maximum sustained swimming speed

Table 1 compares the results from the three approaches used to assess the power output of Salmon and Smolt swimming at or close to their maximum sustained swimming speeds (U_{ms}). The Salmon was filmed swimming at 0.87 m s^{-1} , close to its maximum sustained swimming speed of 0.91 m s^{-1} . The assumption is that all the red muscle is used when the fish swims at U_{ms} .

Several different approaches indicate that the whole length of the red muscle

Table 3. An example of the Lighthill parameters used in the analysis of Salmon for one tailbeat cycle (frame numbers every 0.02 s are listed in the first column)

Frame number	dx/dt ($m s^{-1}$)	dz/dt ($m s^{-1}$)	$\cos\theta$	$\sin\theta$	w ($m s^{-1}$)	Thrust (N)	$\frac{1}{2}mwz$ (N)	Power (W)
1	0.8710	0.0000	1.0000	0.0000	0.0000	0.0000	0.0000	0.000
2	0.7631	0.0000	1.0000	0.0000	0.0000	0.0000	0.0000	0.000
3	0.8526	0.0000	1.0000	0.0000	0.0000	0.0000	0.0000	0.000
4	0.8954	-0.8198	0.8549	-0.5188	-0.2363	0.7718	-0.0055	0.669
5	0.7671	-0.7819	0.8267	-0.5627	-0.2148	0.6765	-0.0015	0.587
6	0.8343	-0.6285	0.9997	-0.0263	-0.6063	0.8965	0.0491	0.777
7	0.9898	-0.5090	0.9997	-0.0263	-0.4828	0.5871	0.0395	0.509
8	0.9918	-0.1066	0.9997	-0.0263	-0.0805	0.0243	0.0073	0.021
9	0.9092	0.2492	0.9997	-0.0263	0.2730	0.1398	-0.0272	0.121
10	0.9609	0.5784	0.9947	-0.1029	0.6742	0.7446	-0.0267	0.646
11	0.8807	0.6984	0.8707	0.4918	0.1749	0.4946	-0.0043	0.429
12	0.7916	0.5886	0.9567	0.2912	0.3326	0.6491	0.0046	0.563
13	0.8284	0.4583	0.9920	0.1260	0.3502	0.4528	0.0180	0.393
14	0.9585	0.3772	0.9997	-0.0263	0.4023	0.3220	0.0268	0.279
15	0.9459	0.1160	0.9940	-0.1092	0.2186	0.0073	0.0160	0.006
16	0.8383	-0.1485	0.9997	-0.0263	-0.1264	0.0490	-0.0091	0.043
17	0.9042	0.0000	1.0000	0.0000	0.0000	0.0000	0.0000	0.000
18	0.9687	0.0000	1.0000	0.0000	0.0000	0.0000	0.0000	0.000

Similar sets of parameters were obtained for Smolt.

These parameters were used in the equations of Wardle and Reid (1977, equations 1–7), which are based on the derivation of Lighthill (1971).

The approximation of the dz/dt values to zero occurs at the points where the resulting thrust was found to be negative. This occurred at the extreme points of the tail-sweep.

Note the low value of the integral term $[\frac{1}{2}mwz]_{a=0}$.

The swimming speed used in the calculations is $U=0.8670 m s^{-1}$ and the virtual mass $m=4.5438 kg m^{-1}$.

dx/dt , forward tail-tip velocity; dz/dt lateral tail-tip velocity; w , tail-tip velocity; x, z ; forward and lateral coordinates; θ , angle of attack of tail-blade.

cross section is involved in producing power for the sustained swimming cycle. Hess and Videler (1984) showed in saithe, *Pollachius virens*, that during steady swimming there is one instant of maximum bending moment all along the body as the tail-tip crosses the track of the fish (coincident with the peaks of instantaneous force shown in Figs 3 and 4 here). Studies of how muscle is used during swimming in carp *Cyprinus carpio* (Van Leeuwen *et al.* 1990) and saithe (J. D. Altringham, C. S. Wardle and C. Smith, in preparation) have suggested that, despite delays in onset of myotomal activity along the body, there is positive work in the anterior sections accompanied by negative work in the posterior sections. It seems possible that all sections can reach peak force at about the same time as the maximum bending moment (J. D. Altringham, C. S. Wardle and C. Smith, in preparation).

Bearing this in mind and using the maximum value of $5-8 W kg^{-1}$ suggested by Altringham and Johnston (1990) for sculpin red muscle, the range of power output

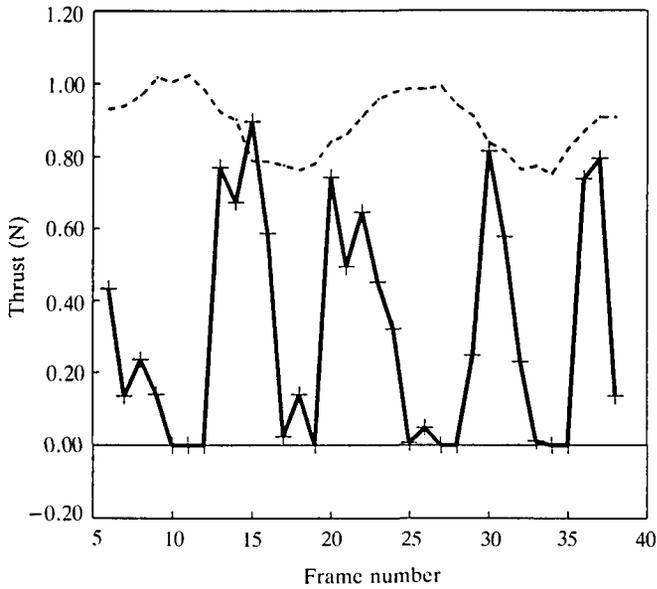


Fig. 3. Instantaneous thrust values for Salmon (solid line). Tail-tip position (dashed line, no scale) is shown only for phase comparison with the instantaneous power peaks. The amplitude (midpoint to extreme of tail-sweep) is 0.035 m. Each frame lasts 0.02 s.

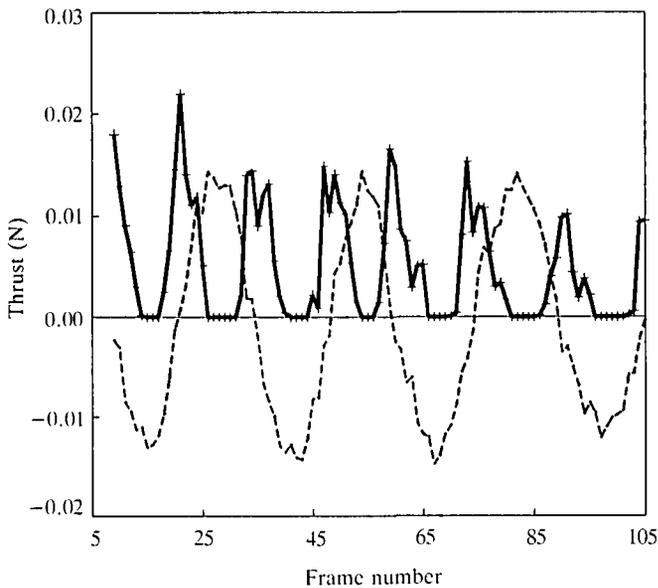


Fig. 4. Instantaneous thrust values for Smolt (solid line). Tail-tip position (dashed line, no scale) is shown only for phase comparison with the instantaneous power peaks. The amplitude (midpoint to extreme of tail-sweep) is 0.013 m. Each frame lasts 0.01 s.

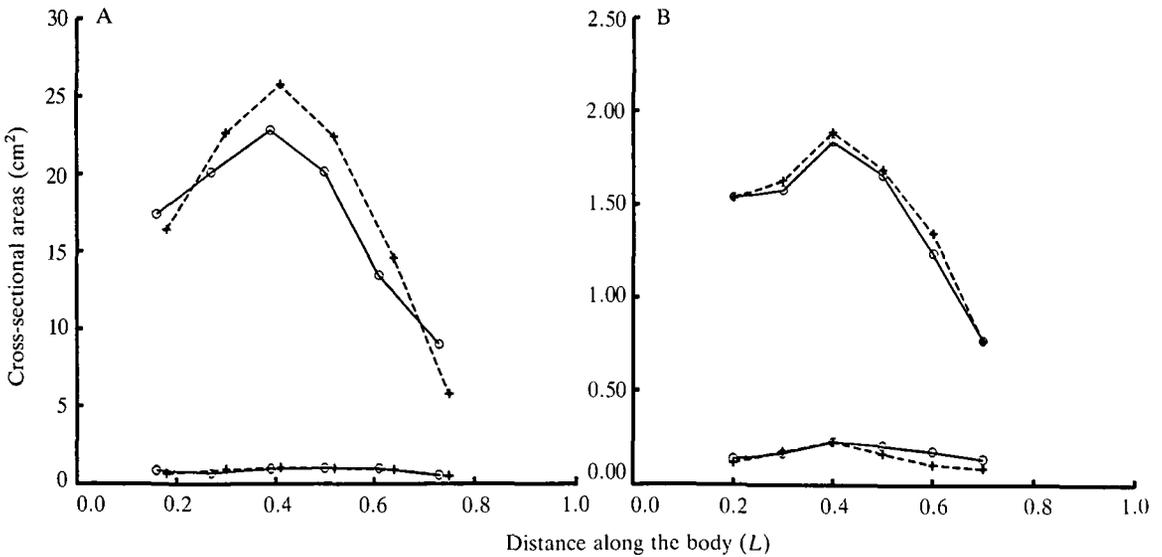


Fig. 5. (A) Distribution of red (lower lines) and white (upper lines) muscle cross-sectional areas for the two selected large fish (740 g, solid line, $L=0.44$ m; 770 g, dashed line, $L=0.44$ m) of similar morphology to Salmon (see text). Mean fish density was 1.0676 g cm^{-3} . Thickness of each cross section was 5 cm. (B) Distribution of red (lower lines) and white (upper lines) muscle cross-sectional areas for the two selected small fish (22.9 g, solid line, $L=0.148$ m; 26.0 g, dashed line, $L=0.155$ m) of similar morphology to Smolt (see text). Mean fish density was 1.0551 g cm^{-3} . Thickness of each cross section was 1.5 cm. L is fish length.

values estimated by measuring the whole salmon red muscle volume agrees closely with that obtained from the hydrodynamic models (see Table 1).

The Smolt was filmed at $U=0.37 \text{ ms}^{-1}$, which is $0.69U_{\text{ms}}$ (where $U_{\text{ms}}=0.54 \text{ ms}^{-1}$). The red muscle power output estimate (for swimming at U_{ms}) exceeds that obtained from the hydrodynamic models at $0.69U_{\text{ms}}$. Assuming that power required for swimming increases as the cube of the speed, at U_{ms} the power required would be increased by a factor of about 3.1. This factor increases the power values obtained from the models to the range suggested by the red muscle power output figures (see last column in Table 1). Hence, the agreement between these three approaches appears to be good.

A fourth independent approach to assessing power output at U_{ms} is by measuring oxygen consumption. Data from Brett and Glass (1973) indicate that a 700–800 g sockeye salmon *Oncorhynchus nerka* has an active metabolic rate of 700–800 $\text{mg O}_2 \text{ kg}^{-1} \text{ h}^{-1}$, equivalent to 2.65–3.03 W kg^{-1} using oxycaloric conversion values for fat from Elliot and Davidson (1975). The various metabolic processes, starting with the uptake of oxygen and ending with the swimming movements of the fish muscles, are subject to various efficiency factors. Webb (1975, Fig. 63) suggests an overall aerobic efficiency of 15.8% at U_{ms} for rainbow trout *Salmo gairdneri*. Applying Webb's efficiency correction to the range of values for

Oncorhynchus nerka adjusts it to 0.42–0.48 W kg⁻¹. The approximate mass-specific power output figure found here for Salmon (750 g) is 0.33 W kg⁻¹, assuming a mean power output of 0.25 W from Table 1.

Large- and small-amplitude models of fish swimming

Lighthill (1975, chapter 6) points out that his earlier note on the swimming of slender fish (Lighthill, 1960) regarded swimming motions as ‘a small perturbation of the stationary stretched-straight state’ only valid for small displacements about this central line. Thus, this and related models (such as Yates’ 1983 model applied here) assume that the amplitude of body movements is small, relative to body length.

Lighthill’s (1971) large-amplitude model differs by considering the ‘actual disturbed position of the animal’s centreline’ as the starting point, which may more realistically represent the swimming of fish at prolonged and sustained swimming speeds. Applying Lighthill’s (1971) and Yates’ (1983) models to Salmon and Smolt shows that the results obtained are similar (see Table 1). The difference between the mean power output values obtained from the two models for Salmon and Smolt lies within a factor of 2.

The ratio of amplitude, mid-point to extreme of tail-sweep (h_1), to body length (L) for Salmon at $U=0.867\text{ m s}^{-1}$ was 0.08 and that for Smolt at $U=0.37\text{ m s}^{-1}$ was 0.09. The slenderness ratio, maximum transverse dimension (d) to L , is 0.16 for Salmon and 0.17 for Smolt. The difference between the two models applied to fish swimming in similar modes to Atlantic salmon near or at U_{ms} is slight and it is suggested that, as long as the ratios h_1/L and d/L are within the limits noted above, either type of model will give a similar answer.

Red and white muscle distribution

Fig. 5 shows that the maximum cross-sectional area (and hence muscle mass) of white muscle occurs at about 0.4–0.45 L for the large and small salmon. The red muscle cross-sectional area and mass vary considerably less, remaining fairly constant along the body in fish from both size groups. The red muscle forms 3–4 % of the body mass of the two selected large fish and 5–7 % of the body mass of the two selected small fish.

Goolish (1989) found that for a rainbow trout *Salmo gairdneri* of similar length to Salmon ($L=0.45\text{ m}$), 3–4 % of the body mass is red muscle, which agrees well with the findings for Salmon. For rainbow trout of similar length to Smolt ($L=0.15\text{ m}$), Goolish (1989) found that only 1.25 % of the body mass was red muscle.

With this discrepancy in mind, two specimens of small trout ($L=0.15\text{--}0.20\text{ m}$) were examined. They were not the same shape as Smolt but had a much deeper body and hence a greater body mass than Smolt of a similar length. Cross-sectioning also revealed visibly less red muscle compared to cross sections of Smolt at corresponding positions along the body. These differences account for the factor of about 4 between the findings of Goolish (1989) for rainbow trout and

those for Smolt. It appears that the greater proportion of red muscle found in Smolt is real and supports the sustained aerobic swimming required for the migratory phase of its life as it leaves the river and enters the sea.

Effects of scale

The lengths of Salmon ($L=0.45$ m) and Smolt ($L=0.15$ m) differ by a factor of 3. Measurements of the wetted surface areas (S) using a gravimetric method by wrapping graph paper around similar-sized specimens of each size group supported the general rule that surface area scales as the square of the length (Salmon, $S=0.064$ m²; Smolt, $S=0.00675$ m², where the scaling factor is about 9.5, close to 3²).

The masses of Salmon (750 g) and Smolt (25 g) differ by a factor of 30 (densities of fish from each group were similar) and follow approximately the rule that mass scales as the cube of the length (3³), as fish densities for the large and small salmon were similar.

The U_{ms} values for Salmon ($U_{ms}=2.03$ L s⁻¹=0.91 m s⁻¹) and Smolt ($U_{ms}=3.62$ L s⁻¹=0.54 m s⁻¹) lie on the slope compiled by McMahon and Bonner (1983), and the endurance curves also fit into the series of curves (where swimming speed is in m s⁻¹) compiled by Wardle (1988).

The mean power outputs of Salmon and Smolt swimming at U_{ms} differ by a factor of 10–15. Assuming that the swimming speed of U_{ms} is a valid speed for comparison of these two sizes, from the standard power (\bar{P}) formula $\bar{P}=1/2\rho U^3 S C_D$ (where ρ is water density, U is swimming speed, S is wetted surface area and C_D is drag coefficient) the wetted surface area may account for this difference, assuming that the friction drag component predominates over energy losses due to anterior recoil, as the salmon has a relatively shallow body depth anteriorly (see Lighthill 1960, 1969, 1970, 1971, 1975, 1977*a,b*; Hess and Videler, 1984; Webb, 1992).

Using the values given above for the ratios h_1/L and d/L for Salmon and Smolt, the Reynolds numbers ($Re=UL/\nu$, where ν is the kinematic viscosity of sea water) for Salmon and Smolt at the swimming speed U at which they were filmed are about 4.0×10^5 ($U=0.87$ m s⁻¹, $L=0.45$ m) and 5.6×10^4 ($U=0.37$ m s⁻¹, $L=0.15$ m), respectively. At these Reynolds numbers with these fineness ratios, the corresponding C_D values of Salmon and Smolt from Hoerner (1965, chapter 6, Fig. 22) are 0.0035 and 0.01 for Salmon and Smolt, respectively.

Lighthill (1971) notes a discrepancy ('Lighthill's paradox', see Ferrari, 1975) between the C_D values obtained from rigid bodies (the values from Hoerner, 1965, for example) and those obtained from undulatory swimmers such as the salmon in this study. If his example is followed with the mean thrust (\bar{T}) values obtained from his model for Salmon ($\bar{T}=0.30$ N) and Smolt ($\bar{T}=0.0052$ N), the calculated C_D values come to 0.012 and 0.011, respectively. Hence Lighthill's paradox appears to hold for Salmon (0.012/0.0035=3.4) but not for Smolt (0.011/0.01=1.0).

Lighthill's (1971) example of a 0.30 m long dace *Leuciscus leuciscus* swimming at

0.48 m s⁻¹ with a Reynolds number of 1.4×10^5 showed a calculated discrepancy (a 'paradox factor') of about 4. Lighthill's paradox here appears to be size-dependent: the discrepancy between rigid and undulatory swimming bodies scales very approximately inversely with Reynolds number.

The metabolic power coefficients C_{ph} shown in Table 2 for Salmon and Smolt are lower than those obtained by Yates (1983, Figs 6–8) using Brett's (1965) data. The lower values obtained here may be because the fish swam through still water rather than in flume-type respirometers (Gehrke *et al.* 1990).

Measurement of power used by a swimming fish is not yet a routine process. Comparisons of different methods, as made here, can only be carried out in closely controlled situations. The current trends towards more appropriate measurements of muscle power output, and knowledge of how this muscle is coordinated to produce swimming motions at different speeds, may lead to more accurate values for the power used by swimming fish. The hydrodynamic models are only suitable for swimming at constant velocity. Fish rarely swim steadily and future models, if they are to be more practical, should take this into account and deal with those fluctuations of power consumption that are found in real situations.

References

- ALTRINGHAM, J. D. AND JOHNSTON, I. A. (1990). Modelling muscle power output in a swimming fish. *J. exp. Biol.* **148**, 395–402.
- BAINBRIDGE, R. (1963). Caudal fin and body movement in the propulsion of some fish. *J. exp. Biol.* **40**, 23–56.
- BONE, Q., KICENIUK, J. AND JONES, D. (1978). On the role of the different fibre types in fish myotomes at intermediate swimming speeds. *Fishery Bull. Fish Wildl. Serv. U.S.* **76**, 691–699.
- BRETT, J. R. (1965). The relation of size to the rate of oxygen consumption and sustained swimming speeds of sockeye salmon *Oncorhynchus nerka*. *J. Fish Res. Bd Can.* **22**, 1491–1501.
- BRETT, J. R. AND GLASS, N. R. (1973). Metabolic rates and critical swimming speeds of Sockeye salmon *Oncorhynchus nerka* in relation to size and temperature. *J. Fish. Res. Bd Can.* **30**, 379–387.
- ELLIOT, J. M. AND DAVIDSON, W. (1975). Energy equivalents of oxygen consumption in animal energetics. *Oceologia* **19**, 195–201.
- FERRARI, C. (1975). Considerations on fish locomotion. *Meccanica* Dec. 1975 (2nd National Congress of Amieta, Naples, October 1974), pp. 300–311.
- GEHRKE, P. C., FIDLER, L. E., MENSE, D. C. AND RANDALL, D. J. (1990). A respirometer with controlled water quality and computerized data acquisition for experiments with swimming fish. *Fish Physiol. Biochem.* **8**, 61–67.
- GOOLISH, E. M. (1989). The scaling of aerobic and anaerobic muscle power in rainbow trout *Salmo gairdneri*. *J. exp. Biol.* **147**, 493–505.
- HE, P. AND WARDLE, C. S. (1988). Endurance at intermediate swimming speeds of Atlantic mackerel *Scomber scombrus* L., herring *Clupea harengus* L. and saithe *Pollachius virens* L. *J. Fish Biol.* **33**, 255–266.
- HESS, F. AND VIDELER, J. J. (1984). Fast continuous swimming of saithe *Pollachius virens*: a dynamic analysis of bending moments and muscle power. *J. exp. Biol.* **109**, 229–251.
- HIGGINS, P. J. AND THORPE, J. E. (1990). Hyperplasia and hypertrophy in the growth of skeletal muscle in juvenile Atlantic salmon *Salmo salar* L. *J. Fish Biol.* **37**, 505–519.
- HOERNER, S. F. (1965). *Fluid-Dynamic Drag*. Brickton, New Jersey: S.F. Hoerner.
- JOHNSTON, I. A. AND SALAMONSKI, J. (1984). Power output and force-velocity relationship of red and white fibres from the Pacific blue marlin *Makaira nigricans*. *J. exp. Biol.* **111**, 171–177.

- KASHIN, S. M., FELDMAN, A. G. AND ORLOVSKY, G. N. (1979). Different modes of swimming of the carp *Cyprinus carpio* L. *J. Fish Biol.* **14**, 403–405.
- LANGFELD, K. S., ALTRINGHAM, J. D. AND JOHNSTON, I. A. (1989). Temperature and the force-velocity relationship of live muscle fibres from the teleost *Myoxocephalus scorpius*. *J. exp. Biol.* **144**, 437–448.
- LIGHTHILL, M. J. (1960). Note on the swimming of slender fish. *J. Fluid Mech.* **9**, 305–317.
- LIGHTHILL, M. J. (1969). Hydromechanics of aquatic animal propulsion. *A. Rev. Fluid. Mech.* **1**, 413–446.
- LIGHTHILL, M. J. (1970). Aquatic animal propulsion of high efficiency. *J. Fluid Mech.* **44**, 265–301.
- LIGHTHILL, M. J. (1971). Large-amplitude elongated-body theory of fish locomotion. *Proc. R. Soc. Lond. B* **179**, 125–138.
- LIGHTHILL, M. J. (1975). *Mathematical Biofluidynamics*. Res. Conf. Nat. Sci. Found., 1973, New York Soc. Ind. Appl. Math. SIAM, 281pp.
- LIGHTHILL, M. J. (1977a). Aquatic animal locomotion. *Trans. N.E. Coast Inst. Eng. Shipbuild.*, 11th Blackadder Lecture, 21st Feb., pp. 121–135.
- LIGHTHILL, M. J. (1977b). Mathematical theories of fish swimming. In *Fisheries Mathematics* (ed. J. H. Steele), pp. 131–144. London, New York, San Francisco: Academic Press.
- MCMAHON, T. A. AND BONNER, J. T. (1983). *On Size and Life*. New York: Scientific American Books Inc. pp. 255.
- ROME, L. C., LOUGHNA, P. T. AND GOLDSPIK, G. (1984). Muscle fibre activity in carp as a function of swimming speed and muscle temperature. *Am. J. Physiol.* **247**, R272–R279.
- VAN LEEUWEN, J. L., LANKHEET, M. J. M., AKSTER, H. A. AND OSSE, J. W. M. (1990). Function of red axial muscles of carp *Cyprinus carpio*: recruitment and normalised power output during swimming in different modes. *J. Zool. (Lond.)* **220**, 123–145.
- VIDELER, J. J. (1981). Swimming movements, body structure and propulsion in cod *Gadus morhua*. *Symp. zool. Soc., Lond.* **48**, 1–27.
- VIDELER, J. J. AND WARDLE, C. S. (1978). New kinematic data from high-speed ciné film recordings of swimming cod *Gadus morhua*. *Neth. J. Zool.* **28**, 465–484.
- WARDLE, C. S. (1988). Understanding fish behaviour can lead to more selective gears. *Proceedings of the World Symposium on Fishing Gear and Fishing Vessel Design*. Marine Institute, St John's, Newfoundland, Canada. pp. 12–19.
- WARDLE, C. S. AND REID, A. (1977). The application of large-amplitude elongated-body theory to measure swimming power in fish. In *Fisheries Mathematics* (ed. J. H. Steele), pp. 171–191. New York, San Francisco, London: Academic Press.
- WEBB, P. W. (1975). Hydrodynamics and energetics of fish propulsion. *Bull. Fish. Res. Bd Can.* **190**, 158pp.
- WEBB, P. W. (1992). Is the high cost of body/caudal fin undulatory swimming due to increased friction drag or inertial recoil? *J. exp. Biol.* **162**, 157–166.
- YATES, G. T. (1983). Hydromechanics of body and caudal fin propulsion. In *Fish Biomechanics* (ed. P. W. Webb and D. Weihs), pp. 177–213. New York: Praeger.