THE SWIMMING ENERGETICS OF TROUT

II. OXYGEN CONSUMPTION AND SWIMMING EFFICIENCY

By P. W. WEBB*

Department of Zoology, University of Bristol, Bristol

INTRODUCTION

In the preceding paper (Webb, 1971) the thrust and power output of rainbow trout swimming at subfatigue levels were calculated from the effects of extra drag loads on the frequency and amplitude of the tail beat. These data can be compared with the expected power made available to the propulsive system, calculated from the oxygen consumption of the fish, in order to calculate the aerobic efficiency of swimming. The calculation of aerobic efficiency, and the assumptions involved, have been discussed by Brett (1962, 1963) and Smit (1965). One of these assumptions is that no portion of the total energy expenditure is obtained from anaerobic respiration. This assumption does not apply where increasing velocity increments have been used, culminating in fatigue (Brett, 1964). No data are available on the anaerobic respiration of fish in an increasing-velocity test. However, since these tests lead to exhaustion of the fish, the total anaerobic fraction can be calculated from measurements of oxygen and/or lactate debt following exhaustion (see Black *et al.* 1962). An attempt is made in this paper to extend the efficiency calculations to include the anaerobic fraction of energy expenditure, on the basis of total debt measurements reported in the literature.

In studies of fish propulsive energetics the expected thrust power output has sometimes been calculated from oxygen-consumption data (Smit, 1965) or body-fuel depletion (Osborne, 1961) by assuming values for the efficiency of the muscles and caudal propeller. It is usually assumed that fish muscles have similar properties to other animal muscle systems, and that the caudal propeller will be as efficient as man-made propellers. The latter assumption is supported by mathematical models of swimming (see, for example, Taylor, 1952; Lighthill, 1960, 1970; Hertel, 1966); however, no experimental evidence is available. Therefore, the aerobic efficiency has been calculated for five groups of fish, four with extra drag loads attached. The loads caused changes in the parameters of the propulsive wave (Webb, 1971) and these can be related to expected changes in muscle efficiency in order to calculate the efficiency of the caudal propeller.

MATERIALS AND METHODS

The methods used were basically similar to those described by Webb (1971). A Brett respirometer with a circular chamber (Brett, 1964) was used in its original capacity as a water treadmill. The upstream half of the chamber was covered with

* Present Address: Fisheries Research Board of Canada, Biological Station, Nanaimo, B.C.

black Polythene sheeting, while the downstream half was strongly illuminated. This improved the station-holding ability of the fish.

Experiments were performed on five groups of fish: a control group, and groups 1–4 with extra drag loads. The values of these loads were calculated from the data in Webb (1971).

The water velocity in the fish chamber was increased in 0·2 ft/sec increments for the control group and groups 1–3, and in 0·1 ft/sec increments for group 4, until the fish was exhausted. The time to fatigue was recorded. The critical swimming speed was calculated by adjusting the last velocity increment in proportion to the time for which the fish swam after that increment (Brett, 1964; Webb, 1971). The experimental procedure differed from that described earlier in that the test period was increased to 60 min.

During the 45 min of the test period, water was recirculated through an aerating system to maintain the dissolved oxygen content of the water close to air-saturation. During the 30th–45th min of any test period the respirometer was isolated from the aerating circulation. The decrease in dissolved oxygen content of the water was measured from two sets of 150 ml water samples, taken at the beginning and the end of the 15 min period, using the Alstberg modification of the Winkler Method (Standard Methods, 1967). From the decrease in water oxygen content, the oxygen consumption of the fish was calculated in mg O_2/kg/h.

The dissolved oxygen content of the respirometer water never fell below 60 % air-saturation. At the highest swimming speeds, and oxygen consumption rates, the oxygen content did not usually fall below 75 % air saturation.

It was observed that each velocity increment was associated with a limited amount of unsteady swimming, lasting for a maximum of 5 min. The time period selected for the measurement of oxygen consumption gave sufficient time for the fish to settle down after this period. There was also sufficient time to replace the oxygen used during the 15 min period before the next velocity increment.

All experiments were performed at $15 \pm 0·2$ °C, which was the same as the acclimation temperature for the fish. The experiments were performed in spring and summer months.

The characteristics of the fish used are shown in Table 1.

Table 1. *Characteristics (mean and 2 standard errors) of the fish used to measure oxygen consumption*

Group	Length (L, cm)	Depth (d, cm)	Width (w, cm)	Wetted surface area (S, cm²)	Mass (M, g)	Muscle mass (M_m, g)	Speed correction
Control	29·2±0·7	5·7±0·3	2·9±0·2	— —	263·7±26·6 = 0·01L^3	128·9±17·9 = 0·49M	1·12
Group 1	29·4±0·4	5·8±0·2	3·0±0·1	348·4±14·1 = 0·40L^2	270·9±26·7 = 0·01L^3	138·2±4·3 = 0·50m	1·14
Group 2	30·1±0·5	6·1±0·2	3·1±0·1	354·9±27·8 = 0·39L^2	291·4±33·6 = 0·01L^3	145·4±19·4 = 0·50M	1·13
Group 3	29·7±0·3	5·9±0·2	3·0±0·1	357·9±28·0 = 0·41L^2	258·4±29·4 = 0·01L^3	137·0±18·9 = 0·53M	1·14
Group 4	30·0±0·3	5·9±0·2	3·1±0·1	359·9±13·1 = 0·40L^2	278·9±16·2 = 0·01L^3	145·5±10·3 = 0·52M	1·12

RESULTS

Oxygen consumption

Relationship between oxygen consumption and swimming speed

The results for the oxygen consumption of trout at various cruising speeds are given in Table 2. The relationship between the logarithm of oxygen consumption and swimming speed was found to be linear in all five groups of fish (Fig. 1) with the slope increasing with the size of the extra drag loads. The linear relationship supports Brett's (1964) hypothesis that this sort of relationship would be typical for fish. The regression equations relating logarithm oxygen consumption to swimming speed are given in Table 3.

Table 2. *Oxygen consumption and swimming speeds for the five groups of trout*

| Swimming speed (cm/sec, mean)	2 S.E.S	Oxygen consumption (mg O_2/kg/h, mean)	2 S.E.S	No. fish
		Control group		
10·2	0·7	147·3	10·4	4
16·9	0·4	150·2	18·5	10
24·2	0·3	199·4	12·1	10
30·6	0·6	237·9	20·2	10
37·4	0·8	294·4	18·0	10
44·2	0·9	355·1	27·5	10
51·0	1·1	488·0	62·1	10
57·9	1·3	657·4	58·7	7
64·2	—	954·3	—	2
		Group 1		
10·3	0·3	112·4	16·7	8
17·3	0·6	150·7	15·6	12
24·7	0·62	206·1	21·9	11
31·1	0·8	268·7	22·8	9
38·0	1·0	365·2	30·2	9
44·7	1·4	486·2	40·9	7
52·0	—	614·4	—	1
		Group 2		
10·3	0·2	127·3	10·8	11
17·2	0·3	166·6	10·9	11
24·1	0·4	226·3	29·0	11
30·9	0·6	336·3	26·8	10
37·9	0·8	474·6	41·6	10
		Group 3		
10·4	0·5	142·7	24·5	10
17·3	0·8	211·5	27·5	10
24·7	0·7	354·5	61·3	10
31·2	1·7	496·6	53·8	7
		Group 4		
10·3	0·5	141·5	24·5	11
13·7	0·6	169·9	11·2	10
17·11	0·7	229·1	21·2	11
20·5	0·9	314·0	47·4	10
23·9	1·1	354·8	27·8	8
27·5	—	524·1	—	1
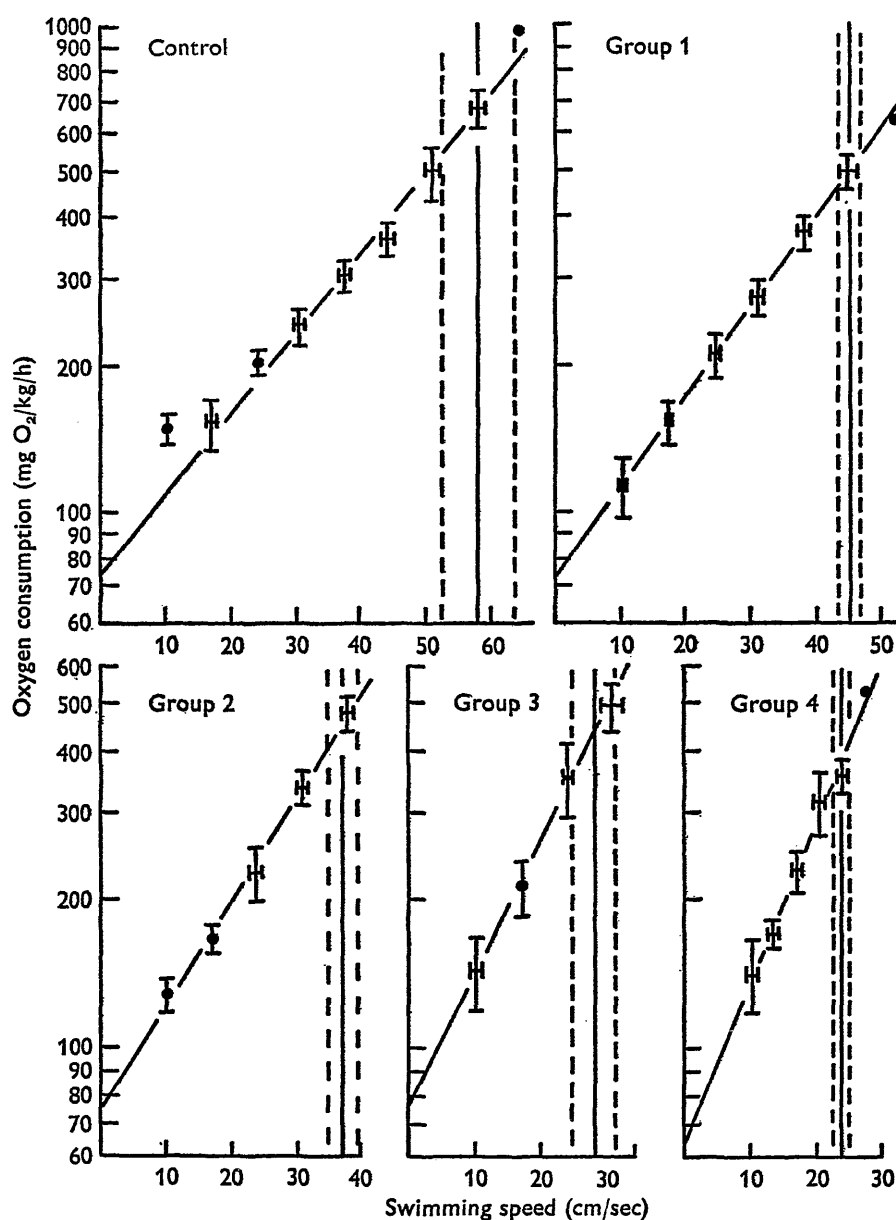
Fig. 1. Relationship between oxygen consumption and swimming speed in the five groups of trout. Vertical and horizontal bars represent two standard errors about the mean oxygen consumption and swimming speed. The vertical solid lines represent the critical swimming speed, the vertical dotted lines 2 standard errors about the mean.

Standard oxygen consumption

The standard rate of oxygen consumption was calculated by extrapolating the log oxygen consumption/speed relationship to zero swimming speed. The mean standard rate for all five groups of fish was 72·5 mg O_2/kg/h, with the control group and groups 1–3 falling between 74 and 76 mg O_2/kg/h. The value for group 4, with the steepest slope, was 63·4 mg O_2/kg/h. The values for standard oxygen consumption agree reasonably well with the standard rate of 95 mg O_2/kg/h measured by Skidmore (1970)

for fish of the same size and stock, confined in a small darkened chamber. Brett (1965) obtained a value of 73 mg O_2/kg/h for sockeye salmon of the same weight using the same method as used in the present paper.

Table 3. *Linear regression equations relating log oxygen consumption and swimming speed calculated for the data in Table 2*

(Critical swimming speeds and standard and active rates of oxygen consumption also shown.)

	Linear regression	Critical swimming speed (cm/sec)	Standard oxygen consumption (mg/kg/h)	Active oxygen consumption (mg/kg/h)
Control	$Log O_2 = 1.878 + 0.016V$	58.1 ± 5.5	75.5	658
Group 1	$Log O_2 = 1.870 + 0.018V$	45.1 ± 2.1	74.1	480
Group 2	$Log O_2 = 1.870 + 0.021V$	37.2 ± 2.3	74.1	447
Group 3	$Log O_2 = 1.878 + 0.027V$	28.6 ± 3.2	75.5	435
Group 4	$Log O_2 = 1.802 + 0.033V$	23.7 ± 1.3	63.4	378

Active oxygen consumption

The active rate of oxygen consumption was 658·5 mg O_2/kg/h in the control group, and fell in groups 1–4 as the size of the extra drag load increased. This is expected, as although all fish are assumed to make their maximum effort at the critical swimming speed, the rate at which they work is proportional to the critical swimming speed. This falls with increasing size of the load, and therefore so does the power output and hence oxygen consumption.

The critical swimming speed

The critical swimming speed for the control group was 58·1 cm/sec (2 body lengths/sec). Critical swimming speeds for all the groups of fish were about 10 % higher than those measured in the previous paper (Webb, 1971). Usually, a decrease in the test period is associated with an increase in the critical speed (Bainbridge, 1962; Brett, 1964, 1967; Dahlberg, Shumway & Doudoroff, 1968). Brett (1967) found that decreasing the test period from 60 to 45 min increased the critical swimming speed of sockeye salmon from 4·1 to 4·2 L/sec. However, Brett (1964) found that there was a greater difference in the critical swimming speed dependent on the time of year at which the measurements were made. Thus, winter sockeye salmon reached a critical speed of 3·2 L/sec. while summer fish swam at 4·0 L/sec. This is a decrease of 20 % in the winter fish. The same phenomenon is probably the source of the higher summer speeds obtained here.

DISCUSSION

Aerobic efficiency of cruising swimming

The cruising efficiency is defined as:

$$\eta_{aerob} = \frac{\text{energy required to develop thrust}}{\text{energy available from consumed oxygen}}.$$

$$= E_r/E_{aerob}. \tag{1}$$

This efficiency is identical to that considered by Brett (1963) and Smit (1965), who calculated E_r from the drag of a dead fish and of an equivalent rigid body, respectively.

The proportion of oxygen used in swimming

The oxygen consumed for locomotion is usually calculated as the difference between the oxygen consumption at any speed, and the standard rate (Brett, 1963, 1964, 1965; Smit, 1965). At the critical swimming speed this difference is

active − standard = metabolic scope   (Fry, 1957).

The validity of this method depends on the standard rate remaining constant during swimming activity, and on no oxygen being used elsewhere as a result of activity. Brett (1963) stresses that the standard rate is the *lowest* deductable value from the total oxygen consumption at any speed.

Two factors could give rise to error in the calculation of the oxygen used in swimming. These are increased activity of the ventilatory muscles and the heart. Webb (1971) has suggested that the extra ventilatory work would mainly be performed by the propulsive muscle, and therefore contribute to drag. Although fish like the trout ventilate during swimming (i.e. use opercular movements), the changes in rate and depth of ventilation with increasing speed and oxygen demand are not significant. Hence it is doubtful if increased ventilation during swimming is mediated by the ventilatory muscles.

Cameron & Cech (1970) have measured the weight of the ventilatory muscle in several species of mullet (*Mugil*). The mean ventilatory muscle weight was 1.5% of the body weight. If the trout had a similar amount of ventilatory muscle, and if it consumed oxygen at the same rate as the red muscle, representing 8.6% of the body weight (Webb, 1970), then a maximum error of 16% would be introduced in the calculation of the oxygen used in swimming at the critical swimming speed. The error will, in practice, be very much lower than this, as it is doubtful if the ventilatory muscle increases the amount of work done during swimming. In addition, some of the muscle is white muscle, which has a lower rate of oxygen consumption than red muscle (Wittenberger & Diatcuic, 1965).

Heart rate increases markedly during swimming (Smith, Brett & Davies, 1967; Stevens & Randall, 1967; Sutterlin, 1969). Jones (1971) has calculated that the heart could consume about 6% of the active rate of oxygen consumption, when working under optimum conditions.

The contributions of the heart and ventilatory muscle to the swimming oxygen consumption will result in the calculation of a value for η_{aerob} slightly lower than that expected for the mechanical system. However, the values calculated for η_{aerob} will include the costs of supply of metabolites and removal of waste from the skeletal tissues, and as such are more meaningful in terms of the overall locomotor activity.

A further factor affecting the validity of calculating the oxygen availability for swimming appears to apply here. Critical examination of the active rate of oxygen consumption for the control group suggests that the value is high. The active rate of 658 mg O_2/kg/h for the trout swimming at 58.1 cm/sec is higher than the value 532 mg O_2/kg/h recorded by Rao (1968) for fish of the same species swimming at speeds greater than 58 cm/sec. The value measured here is only a little lower than the value of 690 mg O_2/kg/h measured by Brett (1965) for sockeye salmon swimming at 96 cm/sec. Both these active rates were measured for fish of the same weight as

those used in the present paper. The fish used here have already been shown to have a poor swimming ability in comparison with other salmonids (Webb, 1971). It therefore appears unlikely that they should have such a relatively high active rate.

The active rate of oxygen consumption also appears high in comparison with the values for the other four groups with extra drag loads. This is readily seen when the results for the four groups are normalized with respect to mechanical parameters of the propulsive system, as is shown in Fig. 6. The control group can only be fitted on this figure after the active rate has been reduced to a more typical level.

It might be considered that the latter effect is a result of the extra drag loads interfering with the fish. However, fish were allowed to recover for about 30 h after the operation, which is longer than the time recommended for recovery from dorsal aortic cannulation (Houston, DeWilde & Madden, 1969). Furthermore, active rates of oxygen consumption for the loaded groups are more similar to the rates expected in comparison with other salmonids.

The active rate in the loaded groups is expected to be depressed to some extent, not only through a decrease in the maximum power output of the fish with increasing load, but also through a reduction in the efficiency of ventilation. This is basically ram-jet, and therefore as the critical swimming speed falls with increasing load, so will the pressure of the water at the mouth. However, it appears that this effect is small, as the active rates of oxygen consumption in groups 1–4 do not fall in the same way as the fall from the control group to group 1. Furthermore, normalization of the data with reference to the mechanical properties of the propulsive system (see Fig. 6) would be expected to show efficiency reductions from group 1 to group 4 which were not correlated with these mechanical properties. In practice this is not found.
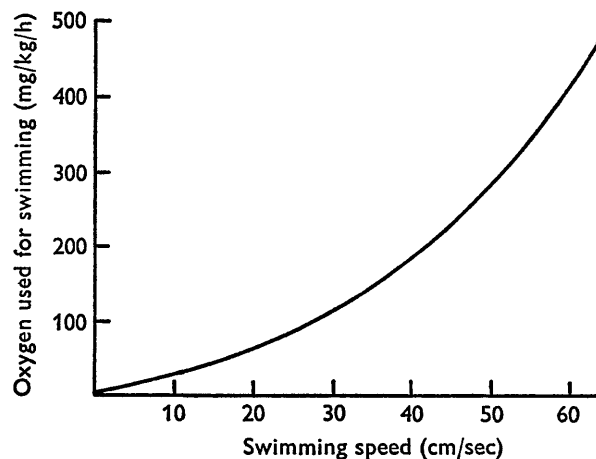

Fig. 2. The oxygen consumption used in swimming for the control group of fish.

A further factor that might be expected to result in high control values is excessive excitement in the control group. Brett (1964) found that excitement tended to affect the standard rates, rather than the active rates. Since the standard rates are comparable between the various groups, and it is the active rate that is apparently affected, it is doubtful if the high active rate of oxygen consumption in the control group is the result of excitement.

No explanation can be given for the high active rate in the control group, but it is apparently not typical of this stock. An active rate of 480 mg O_2/kg/h has therefore been taken in order to calculate the oxygen used by the fish for swimming. This is the mean value for all the active rates measured in the present paper, and is more consistent with values reported in the literature for salmonids swimming at the same speeds. The amount of oxygen used at the various swimming speeds is shown in Fig. 2.

Table 4. *Power available* (E_{areob} *and* E_{glyc}), *power required* (E_r) *and efficiency* (η_{aerob} *and* η_r) *during cruising-swimming of trout*

| Swimming speed (cm/sec)	Power available			Power Required (thrust power, (ergs/sec)	Efficiency	
	Aerobic E_{aerob} (ergs/sec)	Anaerobic E_{glyc} (ergs/sec)	Total $E_{aerob}+E_{glyc}$ (ergs/sec)		Aerobic η_{aerob} (%)	Overall η_{glyc} (%)
10·2	$3·2 \times 10^5$	$0·18 \times 10^3$	$3·2 \times 10^5$	$0·04 \times 10^5$	1·2	1·2
16·9	$5·9 \times 10^5$	$0·54 \times 10^3$	$5·9 \times 10^5$	$0·30 \times 10^5$	5·1	5·1
24·2	$9·4 \times 10^5$	$0·76 \times 10^3$	$9·4 \times 10^5$	$0·58 \times 10^5$	6·2	6·2
30·6	$13·2 \times 10^5$	$2·5 \times 10^3$	$13·2 \times 10^5$	$1·14 \times 10^5$	8·6	8·6
37·4	$18·4 \times 10^5$	$5·8 \times 10^3$	$18·4 \times 10^5$	$2·02 \times 10^5$	11·0	11·0
44·2	$23·8 \times 10^5$	$7·2 \times 10^3$	$23·8 \times 10^5$	$3·06 \times 10^5$	12·8	12·8
51·0	$32·6 \times 10^5$	$1·3 \times 10^5$	$33·9 \times 10^5$	$4·51 \times 10^5$	13·8	13·3
57·9	$42·6 \times 10^5$	$1·9 \times 10^5$	$44·8 \times 10^5$	$6·33 \times 10^5$	14·8	14·1
64·2	$53·1 \times 10^5$	$2·4 \times 10^5$	$55·5 \times 10^5$	$8·39 \times 10^5$	15·8	15·1
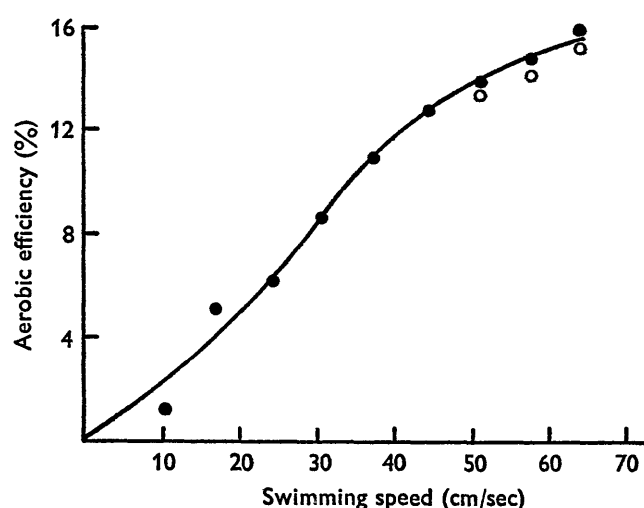
Fig. 3. Efficiency of swimming of trout at cruising swimming speeds. The line and solid circles represent the aerobic efficiency and the open circles represent the estimated overall efficiency.

The energy available for swimming

The energy released by aerobic metabolism depends on the fuel used by the tissues, whether fat, carbohydrate, or protein derivatives. Oxy-calorific equivalents for these fuels are 4·74, 5·05 and 4·46 Kcal/mole O_2 used, respectively (Brody, 1945). The normal fuel in cruising salmonids is apparently fat (Idler & Clemens, 1959). Kutty (1968) found that the respiratory quotient for swimming trout was 0·93, which implies that some carbohydrate could be used in addition. However, the oxy-calorific

equivalent for fat has been used here to calculate the energy available for swimming. This is close to the mean for all three fuels, and its use can only introduce a maximum error of $\pm 6\%$ (Brett, 1962).

The energy equivalent of the consumed oxygen is therefore taken as $1\cdot47 \times 10^8$ ergs/mg O_2. The amount of energy released by aerobic respiration, E_{aerob} is shown for the various swimming speeds of the control group in Table 4.

Aerobic efficiency

Values for the power output of the fish taken from Webb (1971) are included in Table 4. These are the values of E_r. The values for E_r were used to calculate η_{aerob} from equation (1), and are shown graphically in Fig. 3. The maximum η_{aerob} was about 15%. This is comparable with values reported for sustained activity in man, calculated by a similar method (Malomsoki & Nemessuri, 1967).

Overall efficiency

The fish were exhausted at the end of any experiment, and it is probable that some portion of their total energy expenditure was derived from anaerobic respiration. Therefore, an overall efficiency can be defined:

$$\eta_T = \frac{E_T}{\text{energy released by anaerobic respiration} + E_{aerob}} \qquad (2)$$

$$= \frac{E_T}{E_{glyc} + E_{aerob}}.$$

The amount of energy made available from anaerobic respiration is unknown. The total amount of E_{glyc} could, in principle, be calculated from measurements of the oxygen debt; alternatively, it could be calculated from the total fuel depletion on exhausting the fish. The fuel is probably carbohydrates (Black *et al.* 1962). The anaerobic energy fraction could therefore be measured in terms of lactate production or carbohydrate depletion.

Oxygen debt

Brett (1964) measured the oxygen debt in sockeye salmon following exercise. The debt was measured as the oxygen consumption in excess of the standard rate. It was not possible to measure the total debt directly since the fish began to move spontaneously after about 3–4 h, and before oxygen consumption levels had returned to normal levels. Black (1957*a, b, c*) has shown that a lactate debt persists in the blood for 8–12 h following exercise to exhaustion. It is also possible that the oxygen debt is not completely paid back. This would occur if some of the lactate produced during exercise were excreted (Black *et al.* 1962). Thus the oxygen debt is likely to be an unreliable method for measuring the total E_{glyc} used in swimming.

Lactate debt

The lactate debt is related to the amount of glycolytic metabolism, and could be related to E_{glyc}. Extensive studies on the relation between lactate debt and exercise have been made particularly by Black and his collaborators (1962). However, because of the extended periods for which the lactate is present in the blood and tissues, it

is difficult to calculate the total debt. Moreover, some lactate may be excreted, and it is possible that some could be produced during recovery, for example, from the ventilatory muscles.

Glycogen depletion

The most promising method of calculating the total anaerobic debt is from the amount of glycogen used up to exhaustion. The use of glycogen in the calculation assumes that no other source of energy is used. Black *et al.* (1960), Black, Robertson & Parker (1961) and Stevens & Black (1966) have shown that strenuous exercise does not result in the depletion of either muscle glucose or blood glucose or liver glycogen. Apparently, salmonids are unable to utilize glucose at a sufficiently high rate during locomotion for it to make a significant contribution to the total energy budget (Mac-Leod, Jonas & Roberts, 1963). Other carbohydrates are used in glycolytic metabolism – for example, inositol – but only in negligible quantities (Black *et al.* 1961).

Glycogen is the usual source of energy for the high levels of exercise which lead to exhaustion. In man, the amount of glycogen depleted is directly proportional to the intensity and duration of such exercise (Ahlborg *et al.* 1967). This is probably also true for the trout, as there is a direct correlation between the levels of lactate produced at different levels of activity and the amount of glycogen used (Black *et al.* 1960).

In salmonids, glycogen is apparently not used during cruising levels of activity. Moderate activity is associated with very small levels of lactate in the blood, and negligible decreases in glycogen (Miller, Sinclair & Hochachka, 1959; Black *et al.* 1960; Black *et al.* 1962; Connor *et al.* 1964).

The amount of glycogen used up to exhaustion should, therefore, be representative of the total amount of anaerobic respiration. The problem is further simplified because the rate of resynthesis of glycogen is low. As a result, the debt in terms of glycogen is accumulative in the time used in these experiments (Stevens & Black, 1966). Therefore, the total amount of glycogen up to exhaustion was calculated from data in Miller *et al.* (1959), Black *et al.* (1960), Black *et al.* (1962), Miller & Miller (1962) and Wendt (1965, 1967). The mean value from these sources was 0·19 g/100 g muscle wet weight. The mean weight of the fish used was 140 g. The muscle mass of the fish used here, comparable with that sampled by the above authors, was 130 g. Hence the total amount of glycogen used up to exhaustion is of the order of 0·247 g.

Anaerobic respiration of glycogen results in the production of two moles of lactate and three moles of ATP (see for example Prosser & Brown, 1961). The free energy change on hydrolysis of one mole of ATP is about 12 kcal. Thus 1 mole of glycogen could make about 36 kcal available to the fish. This represents about $8·36 \times 10^9$ ergs, so that the energy made available from anaerobic respiration for these trout is of the order of $2·06 \times 10^9$ ergs.

Anaerobic metabolism at cruising speeds

It has already been mentioned that moderate (cruising) activity is not associated with any significant levels of anaerobic respiration. However, in experiments of the sort where the swimming speed is increased by discrete increments, an oxygen debt of some sort is found at all levels of activity (Brett, 1964; Kutty, 1968). Furthermore

this debt is apparently accumulative (Brett, 1964) and has the effect of reducing the expected maximum swimming speed.

In man the commencement of any exercise period is associated with an increase in the blood lactate levels (Saiki, Margaria & Cuttica, 1967). This is apparently the result of anaerobic respiration by the active tissues until the cardiovascular system is able to adjust to the new demands (di Prampero, Cerretelli & Piiper, 1970). It was observed that the trout swam irregularly for a period of about 3–5 min after each velocity increment. This is of the same order of time required by the cardiovascular system to adjust to a step increase in swimming speed (Stevens & Randall, 1967). Furthermore, when salmonids are forced to swim at cruising speeds for long periods, the amount of lactate in the blood falls.

Therefore, it is suggested that there is an anaerobic energy fraction used in the first few minutes of each increase in exercise level. This will be the source of the observed oxygen debt, and lactate levels in the blood at low swimming speeds.

At higher cruising speeds greater than 80% of the critical speed, Webb (1970) observed that the white muscle system was used as well as the red muscle system. The white muscle probably operates anaerobically (see Bone, 1966; George, 1962) and hence these speeds are probably associated with a continual anaerobic energy fraction contributing to the total swimming budget.

The amount of anaerobic energy used in swimming

From the above discussion it is concluded that a small amount of anaerobic energy is used at the start of each swimming period. Otherwise, the total swimming energy requirements are supplied aerobically, except at speeds greater than 80% of the critical speed. Then, some proportion of the total energy expenditure is continuously derived anaerobically.

The total amount of anaerobic energy has been distributed in proportion to the time for which the system operates and the rate at which energy is dissipated. This is proportional to $V^{2 \cdot 8}$ (Webb, 1971), where V represents the swimming speed. Then, E_{glyc} at some swimming speed is proportional to $V^{2 \cdot 8}t$ (Fig. 4), where t is 5 min at speeds less than 80% of the critical swimming speed, and 60 min at speeds greater than this (Fig. 4). The total E_{glyc} is then

$$E_{\text{glyc}} = \Sigma(V^{2 \cdot 8}t)$$

for all values of V. Then, at some speed V_i, the anaerobic fraction $E_{i\,\text{glyc}}$ is given by

$$E_{i\,\text{glyc}} = \frac{2 \cdot 06 \times 10^9}{\Sigma(V^{2 \cdot 8}t)} V_i^{2 \cdot 8}t \text{ ergs.} \tag{3}$$

The anaerobic energy expenditure in ergs/sec is calculated by dividing $E_{i\,\text{glyc}}$ by 3600 sec (the test period). Values for E_{glyc} at each swimming speed have been calculated, and are shown in Table 4. These have been added to the aerobic energy fraction to calculate the overall efficiency from equation (2).

Overall efficiency

The overall efficiency is shown in Fig. 3 and Table 4. At all speeds the anaerobic energy fraction is very small in comparison with the aerobic energy. The overall

efficiency is only smaller than the aerobic efficiency by detectable amounts at higher swimming speeds, greater than 80% of the critical speed.

It must be realized that the above calculations are only rough approximations of E_{glyc}. However, they do suggest that future studies on the sustained activity of fish may ignore this factor of anaerobic energy release, which is, in any case, an artifact of the experimental procedure.
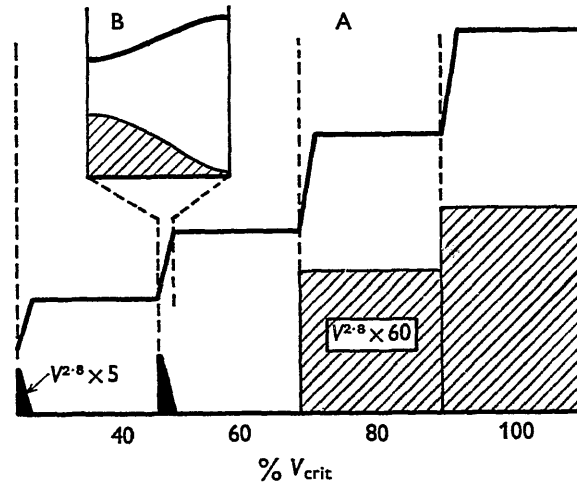

Fig. 4. (A) Diagram illustrating the proposed use of anaerobic energy sources in an increasing-velocity test. Four speeds are represented, corresponding to 40, 60, 80 and 100 % of the critical swimming speed. The solid line represents the energy made available from aerobic energy sources. The shaded areas represent the energy made available continuously from anaerobic energy sources, and the solid shading represents the anaerobic energy requirements at a velocity increment. At speeds greater than 80 % V_{crit}, the latter energy contribution is assumed negligible in comparison with the continual anaerobic energy contribution. (B) Proposed energy changes over a 5 min period after a velocity increment. Note: the scales are not the same for the aerobic and anaerobic contributions.

The efficiency of the muscles and caudal propeller

The efficiencies η_r and η_{aerob} are the products of the efficiencies of the muscles and caudal propeller. Thus

$$\eta_{aerob} = \eta_{m0} \times \eta_p, \tag{4}$$

where

η_{m0} = aerobic muscle efficiency

$$= \frac{\text{muscle mechanical power output}}{E_{aerob}} \tag{5}$$

and

η_p = caudal propeller mechanical efficiency

$$= \frac{\text{thrust power output } (E_r)}{\text{muscle mechanial power output}}. \tag{6}$$

Muscle efficiency

No data are available on the efficiency of fish muscle, so it must be assumed that changes in efficiency are related to some factor, like shortening speed during contraction as in the muscles of other groups of animals (see Hill, 1950). Thus when the shortening speed is constant, it may then be assumed that efficiency is constant when

the load is the same. It is assumed that the muscle mechanical efficiency is dependent on the shortening speed, and that the aerobic efficiency of the muscles in converting fuel to useful energy substrates (ATP) is constant. Then, the aerobic efficiency from equation (5) can also be considered to vary with shortening speed.

The propulsive muscles form an integral part of the propeller system. Therefore the characteristics, frequency and amplitude of the propeller system (Webb, 1971) will also represent the activity in terms of shortening speed of the muscles. In addition, the characteristics of the propeller system are linearly related to swimming speed (Bainbridge, 1958; Webb, 1971) and hence swimming speed will also be directly related to muscle-shortening speeds.

Webb (1971) has shown that different groups of fish with extra loads of different sizes can be compared with reference to their maximum levels of activity (the critical swimming speed). Five levels of activity, representing 20, 40, 60, 80 and 100% of the critical swimming speed (% V_{crit}) will therefore be considered. These levels of activity will represent muscle-shortening speeds which are the same in each group. It is assumed that the maximum red muscle power output will occur at V_{crit}. This implies that the maximum efficiency will occur at some lower level of activity, probably about 70% V_{crit} on the basis of Hill's (1950) observations. The swimming speed represented by this value of V_{crit} would be more similar to a speed maintained for about 200 min, which Brett (1967) has suggested would be more representative of true sustained activity. The implication is, then, that true sustained activity would be associated with maximum red muscle efficiency.

Assuming further that the maximum value of η_{m0} is 20%, then the diagram given by Hill (1950) can be used to construct a curve relating aerobic muscle efficiency to % V_{crit}. This is included in Fig. 7. The calculations suggest that there is a variation of only 3% in η_{m0} over the upper 80% of the cruising speed range. η_{m0} will be lower than shown in Fig. 7, above 80% V_{crit}, because of white muscle activity at these swimming speeds. These muscles may be assumed to be working at a low efficiency, as the white muscle would be contracting at low speeds under low loads. The usual optimum range of operation is probably at higher speeds and larger loads as found at sprint speeds.

Propeller efficiency

The ratio V/V_w has generally been assumed to be representative of η_p (Gadd, 1952; Taylor, 1952; Lighthill, 1960; Hertel, 1966), where

$$\frac{V}{V_w} = \frac{\text{forward swimming speed of fish}}{\text{backward speed of propulsive wave}}. \tag{7}$$

This follows because V/V_w represents the ratio between the increase in momentum given to the water by the propulsive wave, and the amount of kinetic energy required to accelerate that water. The ratio also reflects the pressure difference across the moving portions of the body, and hence the energy lost in cross flows.

The relationship between V/V_w and η_{aerob} can be tested by means of the results for groups 1–4, on the basis of the assumptions made above for the muscle system. Thus at any value of % V_{crit}, η_{aerob} should vary only with η_p or V/V_w.

η_{aerob} has been calculated for each level of % V_{crit}. The value of the thrust for each

fish was calculated from the data in Webb (1971) from the sum of the drag of the fish and the drag of the load at each swimming speed. The thrust power output was calculated from the product of thrust and swimming speed. The oxygen consumption and aerobic power output was similarly calculated from the data presented here, and the aerobic efficiency was calculated from equation (1). The results of these calculations are included in Table 5, together with values of V/V_w from Webb (1971).

Table 5. *Aerobic power available* (E_{aerob}), *power required* (E_r) *aerobic efficiency* (η_{aerob}) *and* V/V_w *for groups 1–4 for five levels of* % V_{crit}

V_{crit} (%)	Group 1	Group 2	Group 3	Group 4	
20	37	38	34	31	$E_{aerob} \times 10^{-4}$
	0·54	0·37	0·27	0·21	$E_r \times 10^{-4}$
	1·4	1·0	0·8	0·7	η_{aerob} (%)
	0·19	0·17	0·15	0·15	V/V_w
40	91	93	82	77	$E_{aerob} \times 10^{-4}$
	3·76	2·59	1·73	1·36	$E_r \times 10^{-4}$
	4·1	2·8	2·1	1·8	η_{aerob} (%)
	0·30	0·27	0·18	0·19	V/V_w
60	169	171	152	140	$E_{aerob} \times 10^{-4}$
	12·06	8·35	5·68	4·37	$E_r \times 10^{-4}$
	7·1	4·8	3·7	3·1	η_{aerob} (%)
	0·39	0·35	0·28	0·24	V/V_w
80	283	284	251	233	$E_{aerob} \times 10^{-4}$
	26·99	19·66	13·41	10·2	$E_r \times 10^{-4}$
	9·5	6·9	5·2	4·4	η_{aerob} (%)
	0·45	0·40	0·33	0·31	V/V_w
100	447	444	391	364	$E_{aerob} \times 10^{-4}$
	50·20	37·19	25·32	19·16	$E_r \times 10^{-4}$
	11·2	8·3	6·4	5·3	η_{aerob} (%)
	0·45	0·40	0·33	0·32	V/V_w

Four curves relating η_{aerob} and % V_{crit} have been drawn (Fig. 5A) in which the only variable at any value of % V_{crit} should be V/V_w. The values for the latter are plotted out in Fig. 5B.

The relationship between η_{aerob} and V/V_w is shown in Fig. 6. The two parameters are related at each value of % V_{crit}. Furthermore, the relationship between them at neighbouring values of % V_{crit} tends to overlap, so that it could be expressed as a single line. This implies that there is very little change in muscle efficiency, and that the proposition made above on η_{m0} is more or less correct.

In Fig. 7 an attempt has been made to summarize this discussion on propulsive efficiency. Values for η_{aerob} are shown from Fig. 3. These have been used with the values for η_{m0} shown in Fig. 7A to calculate values for η_p in Fig. 7B. These are compared with values of η_p calculated from the model proposed by Lighthill (1969) as described by Webb (1971). The discrepancy between the two sets of values for η_p occurs because the fish do not realize the conditions of the model at low swimming speeds (Webb, 1971). It is expected that the fish would meet these conditions at higher swimming speeds.

Webb (1971) found that fish were reluctant to swim at low speeds. At such speeds, less than 10 % V_{crit}, the overall efficiency will be very low, and hence the costs of swimming disproportionally high. This may be an explanation for the observed behaviour of the fish.
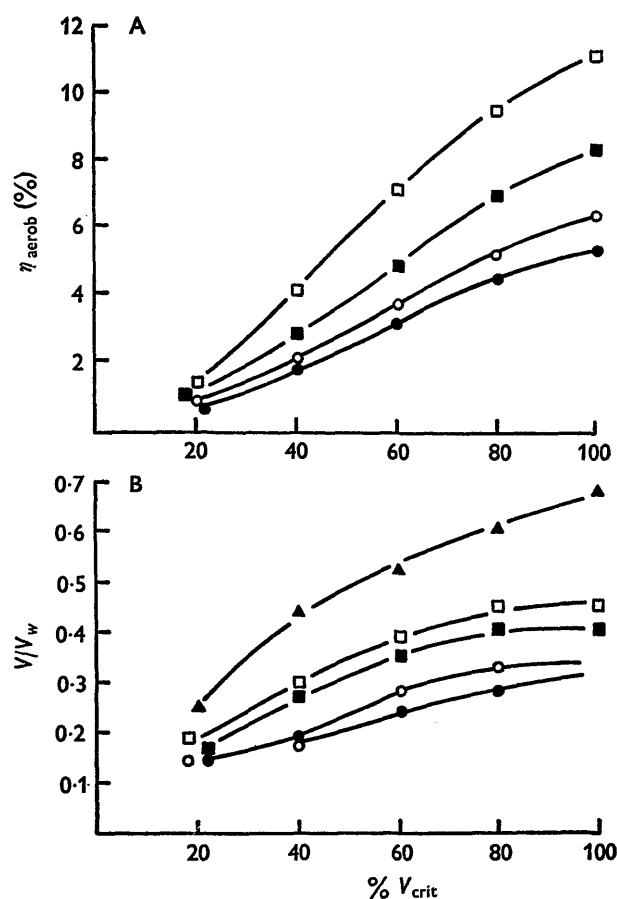
Fig. 5. (A) Relationship between the aerobic efficiency and swimming speed (expressed a percentage of V_{crit}) for groups 1–4. The points have been calculated for values of 20, 40, 60, 80 and 100 % V_{crit}. (B) Values for V/V_w as a function of % V_{crit} for all five groups of fish. ▲, Control group; □, group 1; ■, group 2; ○, group 3; ●, group 4.

Table 6. *Calculations of V/V_w at swimming speeds from 0 to 300 cm/sec (0–10 L/sec) for rainbow trout using Bainbridge's equation (1958)*

Swimming speed		Wave velocity	
V (cm/sec)	V/L	V_w (cm/sec)	V/V_w
5	0·17	31·7	0·16
10	0·33	36·3	0·27
15	0·50	40·8	0·37
20	0·67	45·3	0·44
30	1·00	54·5	0·55
40	1·33	63·4	0·63
50	1·67	72·5	0·69
60	2·00	81·6	0·73
70	2·33	99·8	0·80
90	3·0	108·7	0·82
100	3·33	117·9	0·85
150	5·0	163·2	0·92
200	6·67	208·5	0·96
250	8·33	253·8	c·08
300	10·00	299·3	1·00

Propeller efficiency at high swimming speeds

The difference between η_p calculated here and that predicted by Lighthill (1969) becomes smaller at higher cruising speeds. It is at these speeds that Lighthill's model becomes truly applicable to the swimming trout. Then the propeller efficiency is expected to reach values of about 90 % as V/V_w reaches about 0·8.

It has also been shown that η_p can be related to V/V_w. Values for V/V_w can be calculated by means of Bainbridge's equation (1958) as described by Webb (1971). This has been done for the fish used here up to a maximum sprint speed of 300 cm/sec
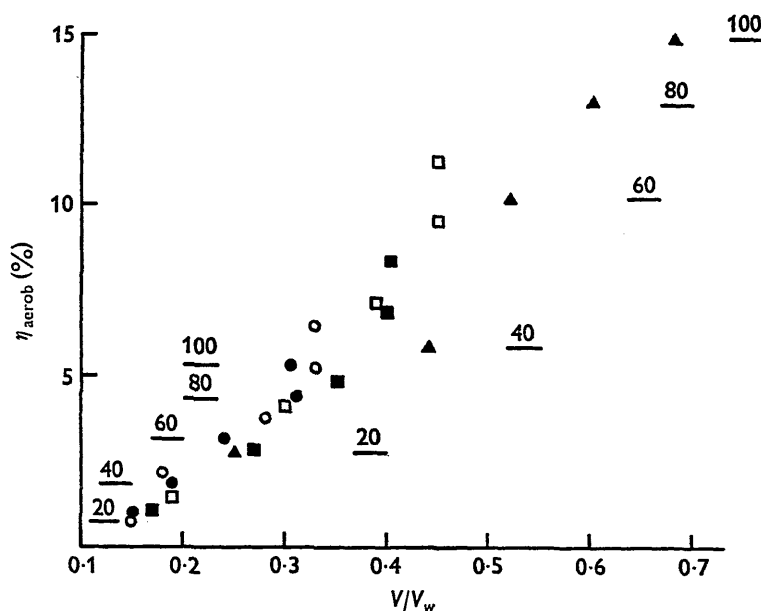

Fig. 6 .The relationship between η_{aerob} and V/V_w with % V_{crit} as parameter. Numbered lines on the left of the points represent the minimum values of η_{aerob} at each value of % V_{crit}, and the lines on the right represent the maxima. Key as for Fig. 5.

Table 7. *Values for V/V_w reported in the literature and values for*
the control group of fish from the present experiments

Fish	V/L	V (cm/sec)	V_w (cm/sec)	V/V_w	Reference
Whiting	0·91*	16·8	25·0	0·67 ⎫	Gray, 1933a
Mackerel	1·06*	42·5	77	0·55 ⎭	
Bream	2·37*	45	59	0·76 ⎫	
Goldfish	2·87*	46	65	0·71 ⎬	Bainbridge, 1963
Dace	1·68*	42	57	0·74 ⎭	
Rainbow trout	0·36	10·1	43·2	0·23 ⎫	
	0·61	16·9	49·5	0·34 ⎪	
	0·85	23·6	47·8	0·49 ⎪	
	1·09	30·4	59·4	0·51 ⎬	Webb, 1971
	1·33	37·2	68·0	0·55 ⎪	
	1·57	43·9	74·5	0·59 ⎪	
	1·83	50·7	75·3	0·67 ⎪	
	2·05	58·1	84·8	0·69 ⎭	

* From Webb (1970).

(10 L/sec) in Table 6. V/V_w is shown plotted against specific swimming speed (V/L) in Fig. 8. The figure shows that the propeller conditions for optimum efficiency occur at a swimming speed of about 4 L/sec. This is similar to the maximum cruising speeds observed in many fish (see tables in Webb, 1970, 1971).

The validity of the theoretical line in Fig. 8 can be indicated by putting in some values reported in the literature. Values for V/V_w have been given by Gray (1933 a),
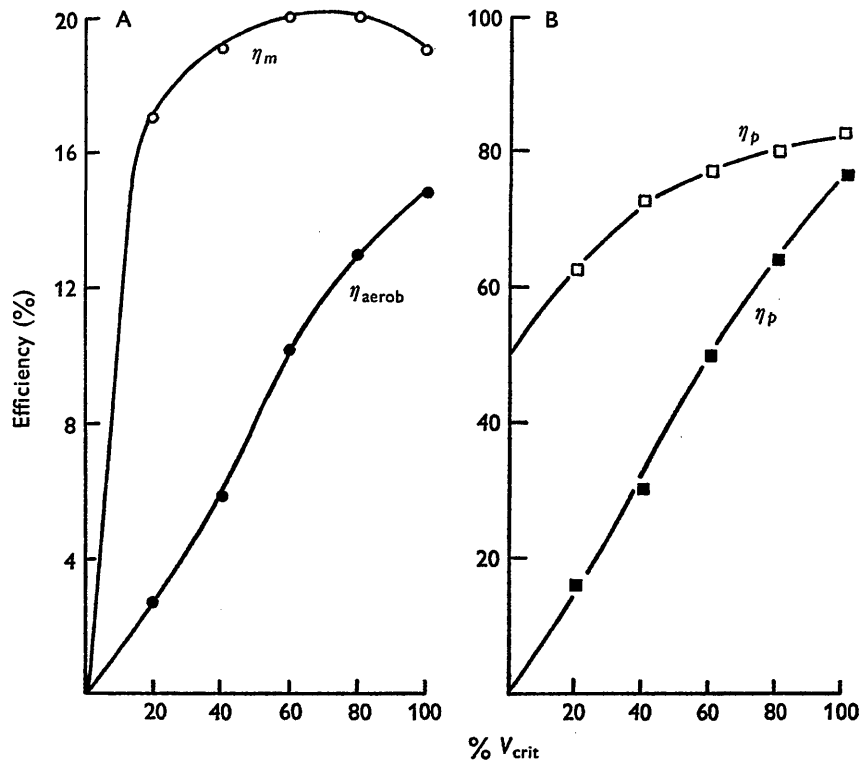

Fig. 7. Summary of the efficiency relationships for aerobic efficiency, muscle efficiency and propeller efficiency described in the text, at cruising speeds expressed as % V_{crit}. (A) Open circles represent red muscle efficiency, assuming that the muscles behave in the same way as other vertebrate muscle systems, with the maximum power output occurring at V_{crit}. Aerobic efficiency values (solid circles) are taken from the results in Fig. 3. (B) Propeller efficiency. The solid squares have been calculated from the values shown in (A). Open squares have been calculated from the model proposed by Lighthill (1969) from the values calculated from Webb (1971).

Bainbridge (1963) and Webb (1971). These are shown in Table 7. The agreement between these values and the theoretical line is good. Most values have been determined close to the optimum value predicted by Lighthill (1960).

The calculations of V/V_w imply that the propeller efficiency will be high over most of the cruising-speed range of fishes, and over the whole of the sprint-speed range.

SUMMARY

1. The oxygen consumption of rainbow trout was measured at a variety of sub-fatigue swimming speeds, at a temperature of 15 °C. Five groups of fish were used, a control group and four groups with extra drag loads attached to the body.

2. The logarithm of oxygen consumption was linearly related to swimming speed in all five groups, the slope of the relationship increasing with the size of the extra drag load. The mean *standard rate* of oxygen consumption was 72·5 mg O_2/kg wet weight/h. The *active rate* of oxygen consumption was highest for the control group (628 mg O_2/kg/h) and fell with increasing size of the attached drag load. The active rate for the control group was high in comparison with other salmonid fish, and in comparison with the value expected for the fish. This was not a result of the extra drag loads in the other groups. No explanation for this high value can be found.
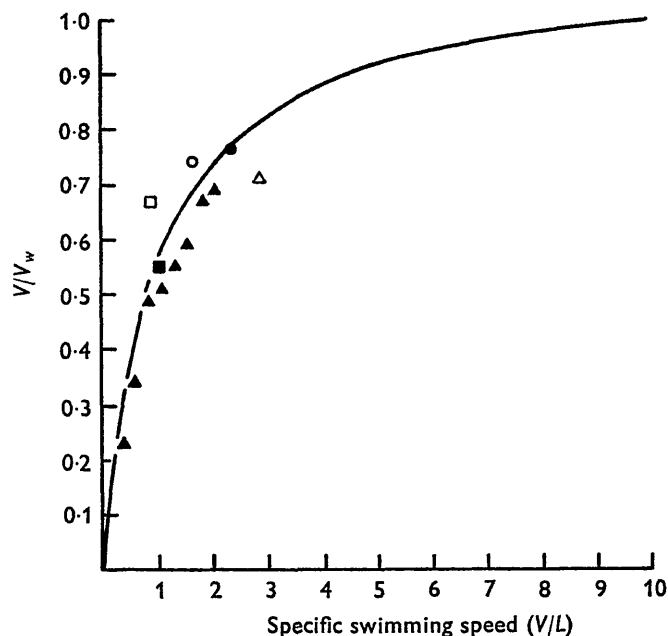

Fig. 8. The relationship between V/V_w and specific swimming speed (L/sec) for fish similar to the trout. The solid line was calculated from Bainbridge's equation (Bainbridge, 1958). Other points: ■, mackerel; □, whiting (Gray, 1933a); ●, bream, ○, dace, △, goldfish (Bainbridge, 1963); ▲, trout (Webb, 1971).

3. The *critical swimming speed* for a 60 min test period was 58·1 cm/sec (2·0 body lengths/sec) for the control group. The values for the critical swimming speeds were slightly higher than those measured for the same species in a previous paper (Webb, 1971). The difference between the two sets of critical swimming speeds is attributed to seasonal changes in swimming performance.

4. The *aerobic efficiency* was found to reach values of 14·5–15·5 % based on the energy released by aerobic metabolism in comparison with the calculated required thrust.

5. The anaerobic contribution to the total energy budget in increasing-velocity tests is considered to be small, and can be neglected.

6. It is concluded that the efficiency of the muscle system in cruising will be approximately 17–20 % over the upper 80 % of the cruising-speed range, while the caudal propeller efficiency will increase from about 15–75 % over the same range.

7. Consideration of the efficiency values for the caudal propeller calculated here, and those predicted by Lighthill's (1969) model of fish propulsion, suggest that the

efficiency of the propeller system will reach an optimum value at the maximum cruising speeds of most fish, and will remain close to this value at spring speeds.

REFERENCES

AHLBORG, B., BERGSTROM, J., EKELUND, L. & HULTMAN, E. (1967). Muscle glycogen and muscle electrolytes during prolonged physical exercise. *Acta physiol. scand.* **70**, 129–42.

BAINBRIDGE, R. (1958). The speed of swimming of fish as related to size and to the frequency and the amplitude of the tail beat. *J. exp. Biol.* **35**, 109–33.

BAINBRIDGE, R. (1962). Training, speed and stamina in trout. *J. exp. Biol.* **39**, 537–55.

BAINBRIDGE, R. (1963). Caudal fin and body movements in the propulsion of some fish. *J. exp. Biol.* **40**, 23–56.

BLACK, E. C. (1957a). Alterations in the blood level of lactic acid in certain salmonid fishes following muscular activity. I. Kamloops trout, *Salmo gairdneri*. *J. Fish. Res. Bd Can.* **14**, 117–34.

BLACK, E. C. (1957b). Alterations in the blood level of lactic acid in certain salmonid fishes following muscular activity. II. Lake Trout, *Salvelinus namaychus*. *J. Fish. Res. Bd Can.* **14**, 645–9.

BLACK, E. C. (1957c). Alterations in the blood level of lactic acid in certain salmonid fishes following muscular activity. III. Sockeye salmon, *Oncorhynchus nerka*. *J. Fish. Res. Bd Can.* **14**, 807–14.

BLACK, E. C., CONNOR, A. R., LAM, K. & CHIU, W. (1962). Changes in glycogen pyruvate and lactate in rainbow trout (*Salmo gairdneri*) during and following muscular activity. *J. Fish. Res. Bd Can.* **19**, 409–36.

BLACK, E. C., ROBERTSON, A. C., HANSLIP, A. R. & CHIU, W. (1960). Alterations in glycogen, glucose and lactate in Rainbow and Kamloops trout (*Salmo gairdneri*) following muscular activity. *J. Fish. Res. Bd Can.* **17**, 487–500.

BLACK, E. C., ROBERTSON, A. C. & PARKER, R. R. (1961). *Comparative Physiology of Carbohydrate Metabolism in Heterothermic Animals* (ed. A. W. Martins), pp. 89–124. University of Washington Press.

BONE, Q. (1966). On the function of the two types of myotomal muscle fibre in elasmobranch fish. *J. mar. biol. Ass. U.K.* **46**, 321–49.

BRETT, J. R. (1962). Some considerations in the study of respiratory metabolism in fish, particularly salmon. *J. Fish. Res. Bd Can.* **19**, 1025–38.

BRETT, J. R. (1963). The energy required for swimming of young sockeye salmon with a comparison of the dead drag force. *Trans. R. Soc. Can.* **1** (ser. IV), 441–57.

BRETT, J. R. (1964). The respiratory metabolism and swimming performance of young sockeye salmon. *J. Fish. Res. Bd Can.* **21**, 1183–226.

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**, 1491–501.

BRETT, J. R. (1967). Swimming performance of sockeye salmon in relation to fatigue time and temperature. *J. Fish. Res. Bd Can.* **24**, 1731–41.

BRODY, S. (1945). *Bioenergetics and Growth.* New York: Reinhold.

CAMERON, J. N. & CECH, J. J. (1970). Notes on the energy cost of gill ventilation. *Comp. Biochem. Physiol.* **34**, 447–55.

CONNOR, A. R., ELLING, C. H., BLACK, E. C., COLLINS, G. B., GAULEY, J. R. & TREVOR-SMITH, E. (1964). Changes in glycogen and lactate levels in migrating salmonid fish ascending experimental 'endless' fishways. *J. Fish. Res. Bd Can.* **21**, 255–90.

DAHLBERG, M. L., SHUMWAY, D. L. & DOUDOROFF, P. (1968). Influence of dissolved oxygen and carbon dioxide on the swimming performance of the large-mouthed bass and coho salmon. *J. Fish. Res. Bd Can.* **25**, 49–70.

FRY, F. E. J. (1957). The aquatic respiration of fish. In *Physiology of Fishes*, vol. 1 (ed. M. E. Brown). Academic Press.

GADD, G. E. (1952). Some hydrodynamic aspects of swimming in snakes and eels. *Phil. Mag.* **48** (7th. ser.), 663–70.

George, J. C. (1962). A histophysiological study of the red and white muscles of the mackerel. *Am. Midl. Nat.* **68**, 487–94.

Gray, J. (1933). Studies in animal locomotion. I. The movement of fish with special reference to the eel. *J. exp. Biol.* **10**, 88–104.

Hertel, H. (1966). *Structure, Form and Movement*, English ed. New York: Reinhold.

Hill, A. V. (1950). The dimensions of animals and their muscular dynamics. *Sci. Prog.* **38**, 209–30.

Houston, A. H., DeWilde, M. A. & Madden, J. A. (1969). Some physiological consequences of aortic cannulation in the Brook Trout (*Salvelinus fontinalis*). *J. Fish. Res. Bd Can.* **26**, 1847–56.

Idler, D. R. & Clemens, W. A. (1959). Energy expenditure of the Fraser River sockeye salmon during migration, spawning and death *Int. Pacific Salmon Fish. Prog. Rep.* pp. 1–80.

Jones, D. R. (1971). A theoretical analysis of factors which may limit the maximum oxygen uptake of fish: The oxygen cost of the cardiac and branchial pumps. *J. theor. Biol.* (in the Press).

Kutty, M. N. (1968). Respiratory quotients in goldfish and rainbow trout. *J. Fish. Res. Bd Can.* **25**, 1689–728.

Lighthill, M. J. (1960). Note on the swimming of slender fish. *J. Fluid Mech.* **9**, 305–17.

Lighthill, M. J. (1969). Hydromechanics of aquatic animal propulsion. *A. Rev. Fluid Mech.* **1**, 413–46.

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

MacLeod, R. A., Jonas, R. E. E. & Roberts, E. (1963). Glycolytic enzymes in the tissues of a salmonid fish (*Salmo gairdnerii gairdnerii*). *Can. J. Biochem. Physiol.* **41**, 1971–81.

Malomsoki, J. & Nemessuri, M. (1967). Determination of the economic efficiency of muscular work by gas exchange measurements. *Acta Physiol. hung.* **31**, 57–72.

Miller, R. B. & Miller, F. (1962). Diet, glycogen reserves and resistance to fatigue in hatchery reared rainbow trout. Part II. *J. Fish. Res. Bd Can.* **19**, 365–75.

Miller, R. B., Sinclair, A. C. & Hochachka, P. W. (1959). Diet, glycogen reserves and resistance to fatigue in hatchery reared trout. *J. Fish. Res. Bd Can.* **16**, 321–8.

Osborne, M. F. M. (1961). Hydrodynamic performance of migratory salmon. *J. exp. Biol.* **38**, 365–90.

di Prampero, P. E., Cerretelli, P. & Piiper, J. (1970). Lactic acid formation on gastrocnemius muscle of the dog and its relation to O_2 debt contraction. *Resp. Physiol.* **8**, 347–53.

Prosser, C. L. & Brown, F. A. (1961). *Comparative Animal Physiology*. London: W. B. Saunders.

Rao, R. M. M. (1968). Oxygen consumption of rainbow trout (*Salmo gairdneri*) in relation to activity and salinity. *Can. J. Zool.* **46**, 781–6.

Saiki, H., Margaria, R. & Cuttica, F. (1967). Lactic acid production in sub-maximal work. *Int. Z. angew. Physiol.* **24**, 57–61.

Skidmore, J. F. (1970). Respiration and osmoregulation in rainbow trout with gill damaged by zinc sulphate. *J. exp. Biol.* **50**, 481–94.

Smit, H. (1965). Some experiments on the oxygen consumption of goldfish (*Carasius auratus* L) in relation to swimming speeds. *Can. J. Zool.* **43**, 623–33.

Smith, L. S., Brett, J. R. & Davies, J. C. (1967). Cardiovascular dynamics in swimming adult salmon. *J. Fish. Res. Bd Can.* **24**, 1775–90.

Standard Methods for the Examination of Water and Wastewater (1967). New York: American Public Health Ass.

Stevens, E. D. & Black, E. C. (1966). The effect of intermittent exercise on carbohydrate metabolism in rainbow trout (*Salmo gairdneri*). *J. Fish. Res. Bd Can.* **23**, 471–85.

Stevens, E. D. & Randall, D. J. (1967). Changes in blood pressure, heart rate, and breathing rate during moderate swimming activity in rainbow trout. *J. exp. Biol.* **46**, 307–15.

Sutterlin, A. M. (1969). Effects of exercise on cardiac and ventilatory frequency in three species of freshwater teleosts. *Physiol. Zool.* **42**, 36–52.

Taylor, G. (1952). Analysis of the swimming of long narrow animals. *Proc. R. Soc. Lond.* A **214**, 158–83.

Webb, P. W. (1970). Some aspects of the energetics of swimming of fish with special reference to the cruising performance of rainbow trout. Ph.D. thesis, University of Bristol.

Webb, P. W. (1971). The swimming energetics of trout. I. Thrust and power output at cruising speeds. *J. exp. Biol.* **55**, 489–520.

Webb, P. W. & Brett, J. R. (in preparation). The hydrodynamics of swimming of fishes.

Wendt, C. (1965). Liver and muscle glycogen and blood lactate in hatchery reared *Salmo salar* following exercise in winter and summer. *Rep. Inst. Freshwater Res. Drottningholm* **46**, 148–67.

Wendt, C. (1967). Mortality in hatchery reared *Salmo salar* after exercise. *Rep. Inst. Freshwater Res. Drottningholm* **46** 98–112.

Wittenberger, C. & Diatcuic, I. V. (1965). Effort metabolism in lateral muscles in carp. *J. Fish. Res. Bd Can.* **22**, 1397–406.