The Respiratory Metabolism and Swimming Performance of Young Sockeye Salmon[1,2]

By J. R. Brett

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

ABSTRACT

The rate of oxygen consumption in young sockeye salmon (*Oncorhynchus nerka*) was determined for various swimming speeds, including fatigue levels, at temperatures of 5, 10, 15, 20, and 24°C. A logarithmic increase in oxygen demand with increase in swimming speed characterized each acclimation temperature. Extrapolation to zero activity (standard metabolism) and maximum activity (active metabolism) provided differences of the order of 10 to 12 times the minimum rate.

The greatest scope for activity occurred at 15°C with an average active metabolic rate of 895 mg O_2/kg/hr for a swimming speed of 4.1 body lengths per second, just maintained for 1 hr. Above 15°C active metabolism was limited, apparently by oxygen availability.

Rate of replacement of oxygen debt following fatigue was determined by tracing the return to a resting state of metabolism, and confirmed by re-tests at fatigue velocities. In most instances the rate declined logarithmically with time; in some there was an initial or secondary slump. Times to recovery (return of spontaneous activity) averaged 3.2 hr, independent of acclimation temperature.

Swimming speed–fatigue tests indicated a sustained level of performance at about 200–300 min. Comparison with other fish suggests a marked change in slope of the fatigue curve at about 20 sec. The effect of temperature was greatest on sustained speeds and least on burst speeds.

CONTENTS

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INTRODUCTION

ALTHOUGH MANY STUDIES have been made on the respiratory metabolism of fish (Winberg, 1956; Fry, 1957) none has been concerned with the exact requirements for swimming at various levels of sustained capacity. The majority of studies have aimed at obtaining either the minimum resting rate (standard) or maximum sustained rate (active) while considering the consequences of altering one or more environmental variables such as temperature (Job, 1955), oxygen and carbon dioxide concentrations (Basu, 1959), salinity (Hickman, 1959), and photoperiod (Evans *et al.*, 1962).

Since fish are neither continuously resting nor persistently active there has been a need to determine the metabolic cost for intermediate levels of some well-defined activity (Brett, 1962). Because of this need and the particular concern over the energy requirements for migration in salmon (Idler and Clemens, 1959), a detailed study of the respiratory metabolism and swimming capacity of yearling sockeye was undertaken.

It was first necessary to develop a respirometer which would impose precise water velocities on the fish, minimizing any advantage from wall effect or irregular flow patterns. In addition ample space for free swimming was desirable without sacrificing sensitivity to oxygen change by involving too large a volume of circulating water. By determining the rate of oxygen consumption over a series of increasing velocity steps it was expected that the necessary parameters of metabolism in relation to swimming speed would be obtained.

Beyond meeting the hydrodynamic requirements, there were other essential problems to be solved. These included stimulating the fish to swim without inducing excessive excitement or unnecessary energy dissipation, accounting for the possible involvement of oxygen debt, and ensuring that the fish performed maximally without injury.

Various units of measurement, either in the foot-pound or metric system, occur throughout the text. In order to avoid re-expression of one in terms of the other in every instance, a conversion table appears as an Appendix. Where suitable, both systems have been included in the figures. Unless otherwise stated, statistical limits are given as ± one standard error.

MATERIALS AND METHODS

RESPIROMETER

The respirometer was designed as a recirculating water tunnel incorporating an acrylic plastic fish-chamber ($4\frac{1}{2}$-inch inside diameter × 12 inches long) connected to a pump through fibreglass contraction and expansion cones (Fig. 1 and 2; Mar, 1959). The drive unit (3 hp electric motor, top-mounted on a variable-speed hydraulic gear) and centrifugal pump were separately mounted from the tunnel section, and connected to it through rubber expansion joints to reduce vibration transfer. Maximum output was 235 gal/min against a developed head of 40 ft, providing a maximum velocity of 3.7 ft/sec through the chamber. Total volume of circulated water was 7.32 gal.

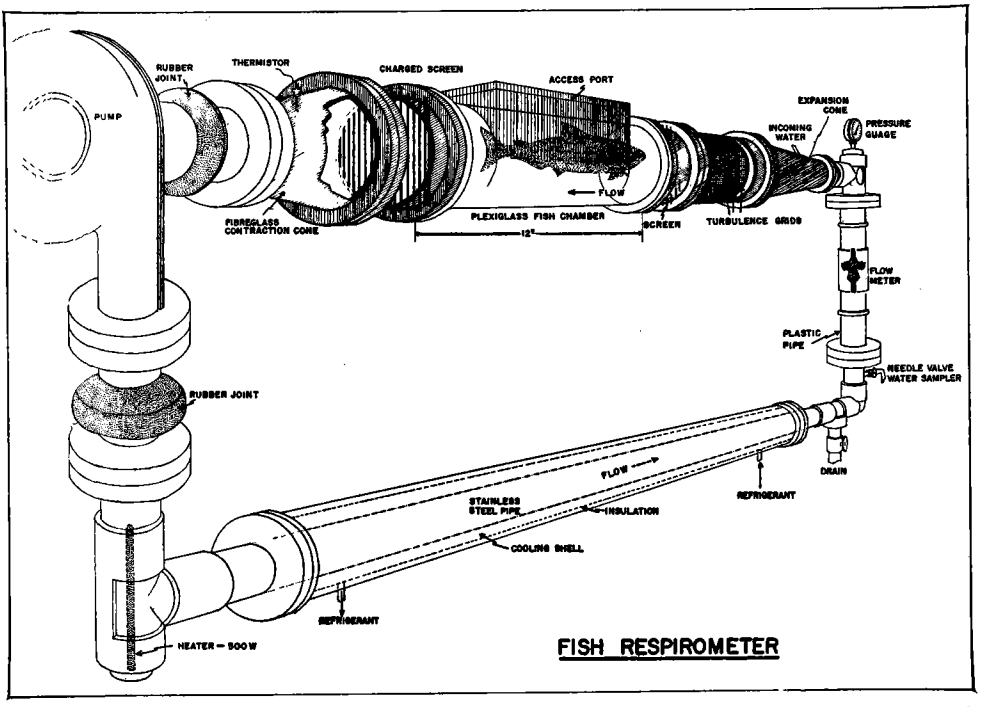

FIG. 1. Semidiagrammatic drawing of respirometer, expanded to show charged screen and turbulence grids.

A relatively consistent, flat velocity profile occurred over the range of velocities at which fish were forced to swim (0.3–3.3 ft/sec). This was achieved by the use of an appropriately designed diffuser section (expansion cone) followed by a series of three turbulence grids (mesh opening = .0755 inch, approximately 2 mm) leading to the fish chamber. These served to eliminate any massive turbulence or eddies by producing a streamlined flow of minutely turbulent water. The pattern was observed by the use of threads and dyes, and by introducing supersaturated water which resulted in a fine stream of bubbles evenly dispersed downstream from the grids.

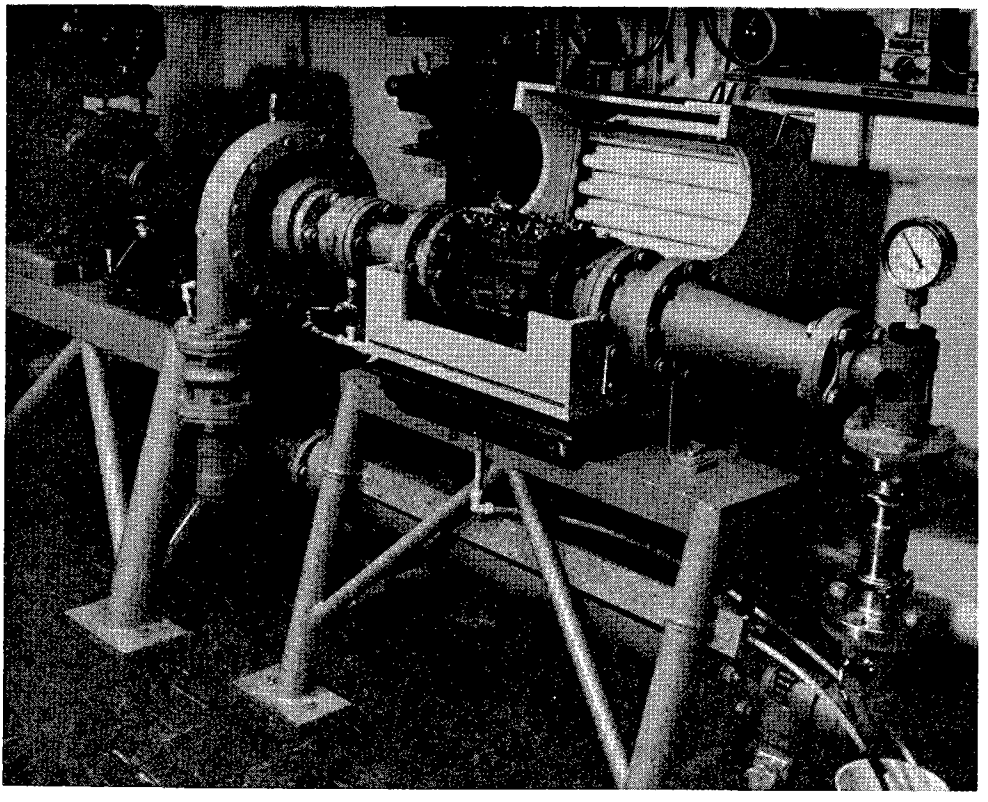

FIG. 2. Photograph of respirometer to show complete assembly.

The characteristics of the velocity profile in the chamber are important in the consideration of swimming speed. Laminar flow is not desirable since the velocity front is curved. Fine-meshed grids or honeycombs overcome this by producing a rectilinear front of statistically uniform turbulence. However, the turbulence has a characteristic rate of decay depending on the mesh size of the grids and water velocity. Eventually turbulent flow subsides to laminar flow. Calculations based on wind tunnel results (Goldstein, 1938) would indicate a probable decay from 2% to 0.7% turbulence over the length of the fish chamber. It would appear that sufficient turbulence persists to eliminate any advantageous wall effect developing at the downstream end of the chamber.

Temperature was controlled within ±0.1°C by continuous flow of a refrigerant through a chilling jacket, counterbalanced by a 500-watt heater and relay. A turbine-type flow meter provided direct read-out of chamber velocity. Since the maximum cross-section of an average fish did not exceed 7% of the cross-section of the chamber, no adjustment for swimming speed error from this source was applied.

New water could be introduced to the system at any time from a reservoir located above the respirometer. Water from the reservoir was adjusted to be slightly higher in temperature and oxygen content than the circulating water.

By increasing the oxygen percentage under normal atmospheric pressure and causing slight cooling on introduction to the respirometer, supersaturation was avoided. The average oxygen content during the closed-circuit period approximated 100% of atmospheric oxygen (started at about 105% and respired down to 95%).

Fish Chamber

Movement of the fish was confined to the chamber by an array of vertical piano wires ($\frac{3}{8}$-inch spacing) imbedded in moulded fibreglass sections at either end of the chamber (Fig. 3). The downstream screen was electrified (60 cycle A.C.) through an isolated, variable transformer with an applied charge of 3–5 v. This was sufficient to cause definite avoidance without strong reaction. Fish quickly learned to occupy positions at least one or more inches upstream from the screen.

Voltage-controlled incandescent lighting from the top of a light-box provided good visibility. A forward cover area, darkened by a wide ring of black plastic, was provided and was frequently used by the fish. In addition, on the under side of the clear plastic chamber a dark rubber mesh was slung as a bottom reference plane. A wide access port, machined to fit exactly to the inside curvature of the tunnel, permitted ready loading with fish. By such means as these,

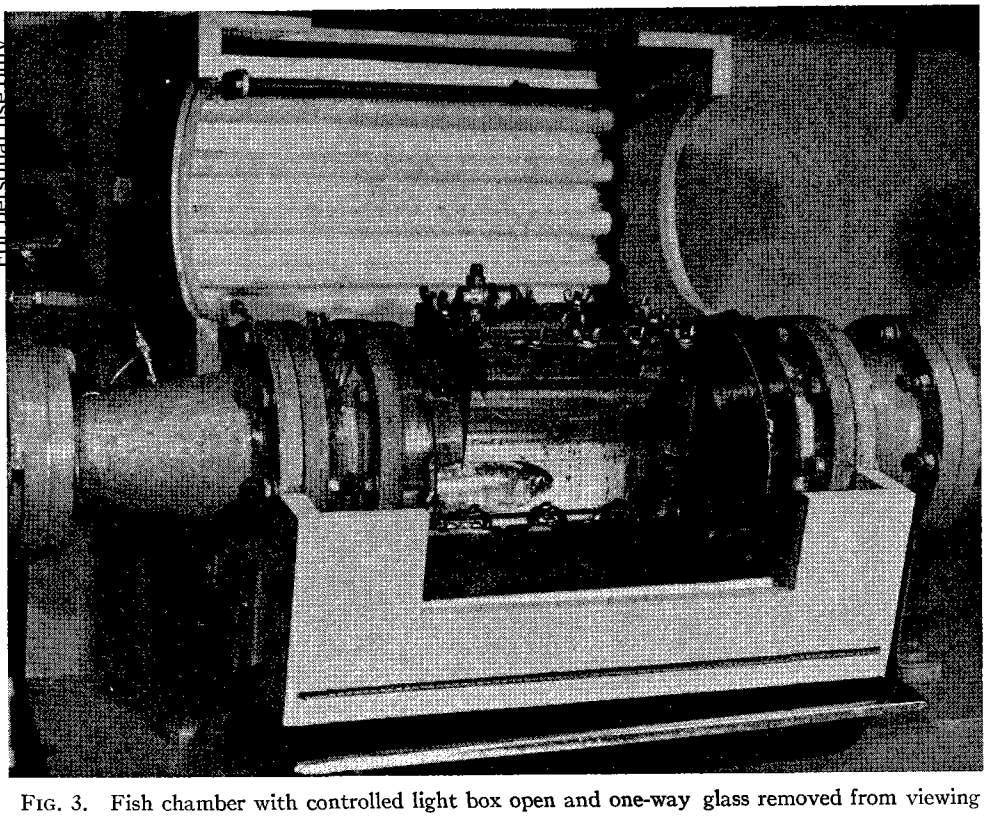

Fig. 3. Fish chamber with controlled light box open and one-way glass removed from viewing window.

an attempt was made to reduce excitement and promote good performance within the respirometer.

Fish Culturing and Preparation

Sockeye between 14 and 18 months of age were used (Table I). The fish were raised on a diet of Clark's pellet feed (J. R. Clark & Co., Salt Lake City, Utah) and a wet mix of canned salmon, pablum, cod liver oil, and yeast, bound with iodized salt. Pressure water-jets installed vertically in oval culture tanks produced an average velocity of about 0.7 ft/sec (range, 0.5–0.9) against which the fish swam constantly (Alderdice *et al.*, 1964).

Acclimation temperatures of 5, 10, 15, 20, and 24°C were maintained for at least 2 weeks within ±0.3°C of the desired final temperature. At temperatures above 10°C, intermediate steps of 5°C increments were maintained for 1 week. The 5°C fish were tested in April to coincide with the natural rise of environmental temperature above 4°C. All tanks were exposed to normal photo-period.

Test fish were not fed for a 24-hr period prior to being transferred in water to the respirometer. They were then set at a velocity of 0.3 ft/sec for an overnight conditioning period of 12–14 hr. Thus, a total of at least 36 hr fasting preceded any determinations of metabolic rate. An interval of this order has been shown by Beamish (1964a) to be necessary for determining the standard metabolism of brook trout. Where attempts were made to measure respiratory metabolism under resting conditions the water velocity was lowered to 0.1 ft/sec, which permitted the fish to rest on the bottom, and lighting reduced to 20 ft-c. In order to minimize vibration and sound transfer the usual drive unit was supplanted by a quiet $\frac{1}{3}$ hp Zero-Max torque converter, hooked up to the pump by a rubber V-belt. During the preliminary conditioning a continuous exchange of water was flushed through the respirometer.

Experimental Procedure

Following the introductory phase the fish were subjected to 75-min periods of swimming at fixed velocities. Commencing at 1.0 ft/sec the velocity was increased in steps of 0.3 ft/sec until the fish fatigued, usually after about 5–7 hr of performance, depending on size and condition. In each 75-min interval, exchange of water was cut off for the first 60 min; the last 15 min were used for flushing to re-establish the initial oxygen level. Three oxygen determinations were made at exactly 0, 30, and 60 min, each involving three samples. The first two were titrated, using the unmodified Winkler method. If the results differed by more than 0.02 ml sodium thiosulphate (0.1*N*), the third was titrated and the nearest two averaged. The repeatability was usually within ±0.01 ml thiosulphate (±0.016 ppm O_2).

Measurements of pH were taken before and after a test to obtain some indication of the effect of soluble excretory products. The initial readings averaged 6.8±.08 whereas those at fatigue time were 6.4±.11. The difference, most probably due to CO_2 and NH_3, was significant but not sufficient to cause

TABLE I. Metabolic rates and critical swimming speeds of yearling sockeye at five acclimation temperatures. The maximum and minimum observed oxygen consumptions are included together with the derived active and standard levels (by extrapolation).

Acclimation temperature	Total length	Wet weight	Condition factor	Maximum O_2-cons.	Minimum O_2-cons.	Active metabolism	Standard metabolism	Critical swimming speed	
	(*cm*)	(*g*)	(W/L^3)	(*mg/kg/hr*)	(*mg/kg/hr*)	(*mg/kg/hr*)	(*mg/kg/hr*)	(*ft/sec*)	(*L/sec*)
5°C									
Number	(9)	(9)	(9)	(9)	(9)	(9)	(9)	(9)	(9)
Mean	16.6	36.7	.769	537	66	514	41	1.76	3.26
S.D.	2.0	12.0	.076	...	...	94	9.7	...	.36
S.E.	0.7	4.0	.025	...	...	31	3.2	...	.12
10°C									
Number	(11)	(11)	(11)	(9)	(4)	(10)	(11)	(10)	(10)
Mean	16.2	32.9	.729	622	94	627	60	1.90	3.65
S.D.	2.3	13.1	.057	...	...	85	10.4	...	.30
S.E.	0.7	3.9	.017	...	...	27	3.2	...	.09
15°C									
Number	(10)	(10)	(10)	(8)	(7)	(8)	(10)	(8)	(8)
Mean	18.8	55.2	.786	988	121	895	71	2.52	4.12
S.D.	2.1	23.8	.098	...	...	123	11.4	...	.49
S.E.	0.8	9.5	.040	...	...	49	4.0	...	.19
20°C									
Number	(9)	(9)	(9)	(8)	(6)	(9)	(9)	(8)	(8)
Mean	19.5	62.6	.799	904	146	852	120	2.43	3.90
S.D.	3.0	24.6	.066	...	...	89	18.2	...	.40
S.E.	1.0	8.2	.022	...	...	30	6.1	...	.14
24°C									
Number	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)	(5)
Mean	18.5	52.2	.822	882	259	848	196	2.25	3.75
S.D.	2.0	20.2	.090	...	...	87	29	...	.75
S.E.	0.9	9.0	.040	...	...	39	13	...	.34

concern (Brett, 1962). The high levels of metabolism obtained lend confirmation to this assumption.

Fatigue was considered present when the fish, by repeated efforts, could no longer hold itself off the electric screen. At this stage of near collapse the velocity was immediately lowered to 0.1 ft/sec, the electric charge turned off, and oxygen readings taken every 30 min to determine the rate of replacement of oxygen debt. Flushing was conducted only if the oxygen level fell below 70% air-saturation, in order to minimize disturbance yet not limit oxygen supply. In some instances after the rate of oxygen consumption had reached a minimum plateau and spontaneous movements had resumed, the same velocity as the final fatigue rate was re-imposed to test the recovery state. In others the "recovered" fish was returned to a culture tank and checked for condition on the following day.

Swimming Speed

The system of applying successive 75-min increments of increasing velocity resulted in the determination of a final swimming speed, maintained for some fraction of that time. In most instances fatigue occurred within 15–20 min of the start of the last imposed velocity. To allow for comparison on a uniform time basis it was decided to use 60-min sustained speeds as a standard, comparable with the time of steady performance set forth by Brett *et al.* (1958). Speed corrections for times less than 60 min were made on a proportional basis. Thus, if a fish having swum at 2.0 ft/sec successfully was required to swim at 2.3 ft/sec and fatigued in 20 min, its *critical swimming speed* was calculated as: $2.0 + (20/60 \times 0.3)$ ft/sec $= 2.1$ ft/sec. This arbitrary system was at least consistent, permitting comparison, and turned out to be surprisingly representative of threshold levels (see Results).

To answer the question of how the 60-min period related to longer or shorter intervals, a *fatigue time* vs *velocity* curve was determined by applying preset, fixed velocities and maintaining these until exhaustion set in. Two difficulties immediately arose, viz. how to ensure "resting fish" at the start, and how to eliminate interference from excited, erratic behaviour during a test. The method adopted was to accustom the fish for a number of weeks to swimming fairly rapidly in a large oval tank at approximately 1.0–1.2 ft/sec. They were then quickly transferred in water to the respirometer at the accustomed speed of 1.0 ft/sec for $\frac{1}{2}$ hr. The velocity was next raised to 2.0 ft/sec for 5 min to overcome extreme excitement from more rapid velocity increase (yet still within their capacity), then raised to the prescribed level. A maximum performance time was arbitrarily set at 1000 min (approximately 17 hr) for the first series, and subsequently lowered to 600 min (10 hr) for the second. One 4-day test was conducted.

Fish Composition

Since the metabolic rate for any organism is dependent on the total demand of all the tissues, it is desirable to know the composition of those tissues. A preponderance of stored fat, excessive body fluids, or heavy skeletal structure would reduce the proportion of "active tissues" and hence decrease the overall

rate. Active metabolism might be expected to depend on the amount of protein, or more grossly the body nitrogen, provided the pool of non-protein nitrogen was not large. A 50-g sockeye is about 50% body musculature by weight.

Because of the relative ease of determinations, it was decided to compare the metabolic rate for wet weight, dry weight, and dry weight minus lipid, the latter being an approximation of the major protein fraction. Wet weight was determined immediately after an experiment by carefully removing external moisture with absorbent paper. The fish was then frozen at −10°C, and subsequently ground to a fine homogenate. A weighed fraction (approximately $\frac{1}{2}$) was oven-dried at 100°C for 18 hr. The balance was further ground with addition of distilled water to the original moisture level. Lipid determinations were then made in triplicate, following the method of Folch *et al.* (1957). No evaluation was made of the possible small lipid loss from different times of cold storage (up to 8 months).

RESULTS AND OBSERVATIONS

Preliminary Tests

In order to establish the nature of the relation between oxygen consumption and swimming speed, preliminary experiments with repeated measurements at the same velocity were conducted, including a prolonged series at 0.1 ft/sec.

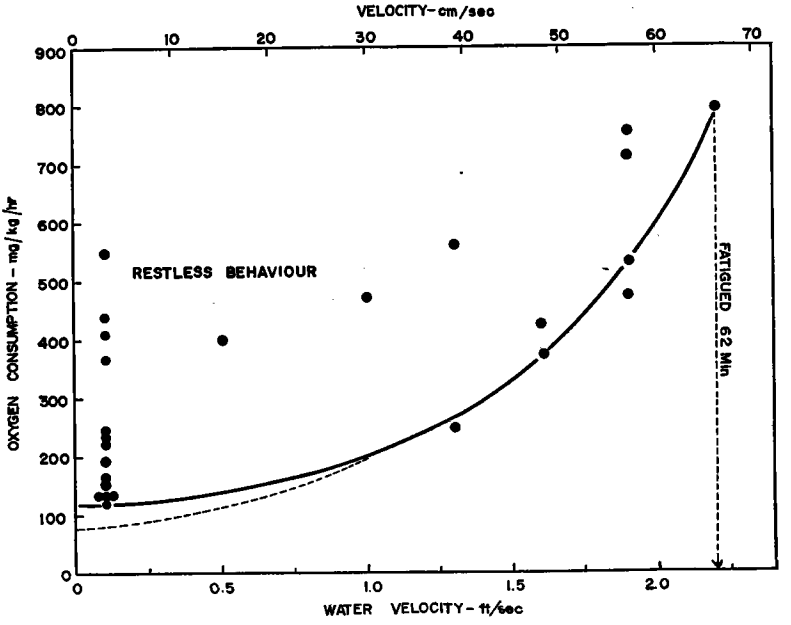

FIG. 4. Oxygen consumption and activity of a 16.5-cm, 30.3-g sockeye at 10°C. Repeated observations over 24 hr are shown at a near-resting velocity of 0.1 ft/sec. Other repeated measurements at higher velocities indicate the elevated rates which occur due to excitement, frequently accompanied by fluttering. The solid line represents the provisional relation; the broken line is the shape for a true exponential curve.

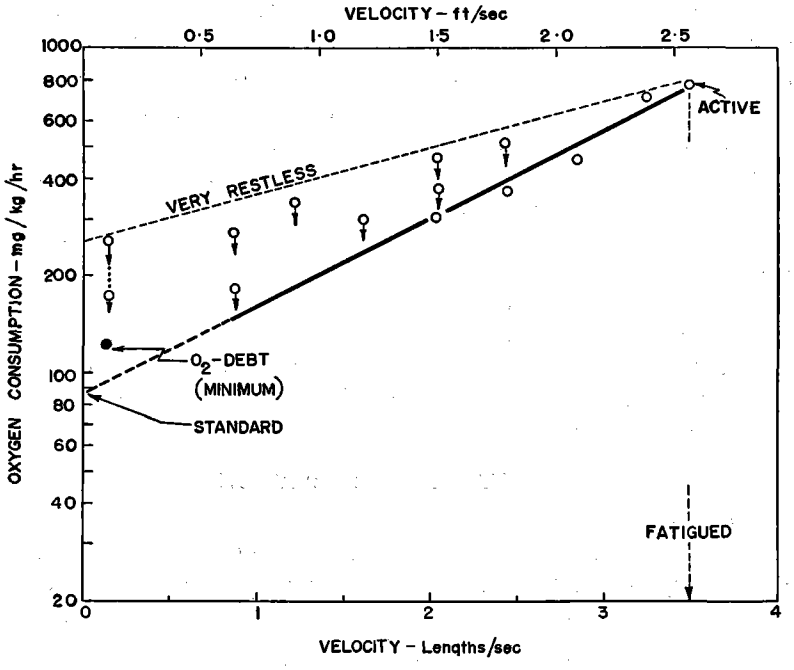

FIG. 5. Oxygen consumption and activity of a 22.4-cm, 83.8-g sockeye at 20°C. Arrow indicates that a lower value would be expected because of observed restless behaviour at the indicated velocity. Broken heavy line is extrapolated below minimum value obtained during recovery from oxygen debt.

The results of such an experiment are plotted in Fig. 4 and transformed in Fig. 5 to the logarithm of oxygen consumption in relation to velocity in terms of fish lengths per second (L/sec). The latter unit (ratio of speed to total lengths of fish) allows for comparison of fish of different lengths, and has been shown by Bainbridge (1958) to be a useful basis for more general comparisons. It was apparent that excitement or restlessness (spontaneous activity) could elevate the metabolism at low velocities to that accompanying much higher velocities. The reverse, in the form of lowered respiration at high velocities, was not observed although slight variations below a line drawn through the lowest points did occur. These were considered to be either experimental error or cases where partial oxygen debt had accumulated with the result that the measured rate of oxygen consumption was less than the actual energy required. There appeared to be a lower plateau of metabolism below which young sockeye would not readily reduce their level of excitement.

In a few cases the last metabolic rate preceding fatigue showed a slump below the previous reading obtained at a lower velocity. The reason is not known; it may relate to partial cardiac failure. In such cases the active metabolic rate was determined by extrapolation to the maximum 60-min sustained speed. Still others showed an increase above expected values, apparently related to bursts of swimming against the forward screen. This accounts for the difference

in Table I between the maximum observed oxygen consumption and the estimated active metabolism.

Metabolic Rates

The results for an average of ten sockeye at each of the various acclimations from 5°C to 20°C are presented in Table I. Difficulty in holding stocks at 24°C and in obtaining satisfactory behaviour in the respirometer at this near-lethal level reduced the number of completed runs to five.

For any one acclimation temperature fish can vary in the position, slope, and terminal point (fatigue level) of their metabolic rate in relation to swimming speed (Fig. 6). These differences may result from variation in composition, or in body form for the same weight or length (affecting drag and speed in terms of length/sec), or from differences in physical condition related to previous exercise (Brett *et al.*, 1958; Hochachka, 1961). If the mean is plotted for each acclimation, a series of lines in the form depicted in Fig. 7 is obtained showing the increase in metabolism with temperature in relation to swimming speed (Table II).

Standard metabolism rose from 41±3.2 mg O_2/kg/hr at 5°C to 196±13 mg O_2/kg/hr at 24°C. The active metabolic rates for the corresponding temperatures

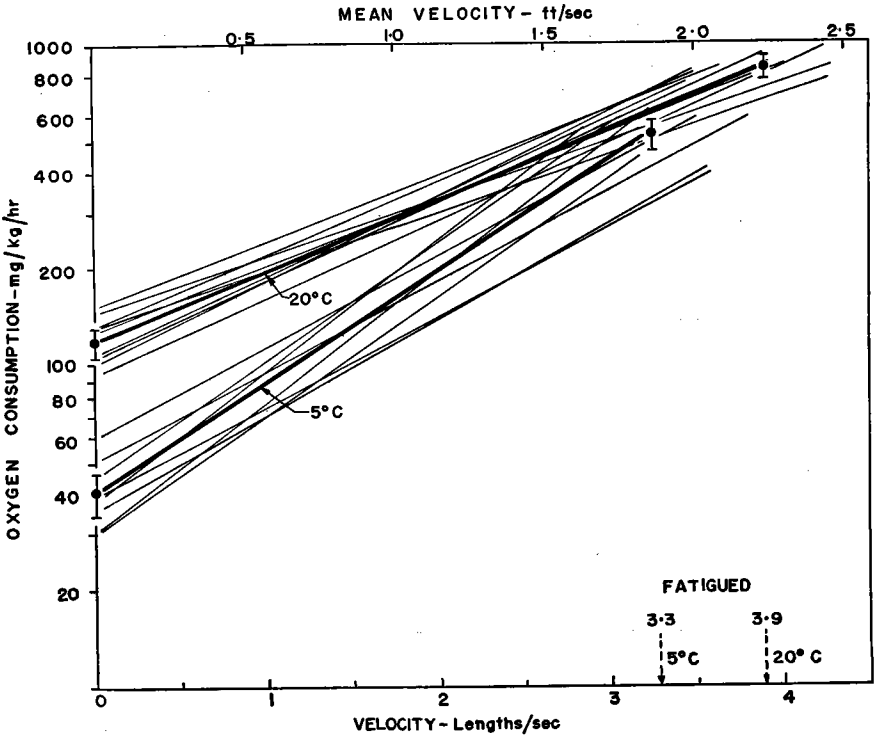

FIG. 6. Individual oxygen consumption rates in relation to swimming speed for yearling sockeye (average 18 cm, 50 g) at two acclimation temperatures (light lines). Mean lines of best fit are shown joining the mean ±2 S.E. of the standard and active metabolic rates (heavy lines).

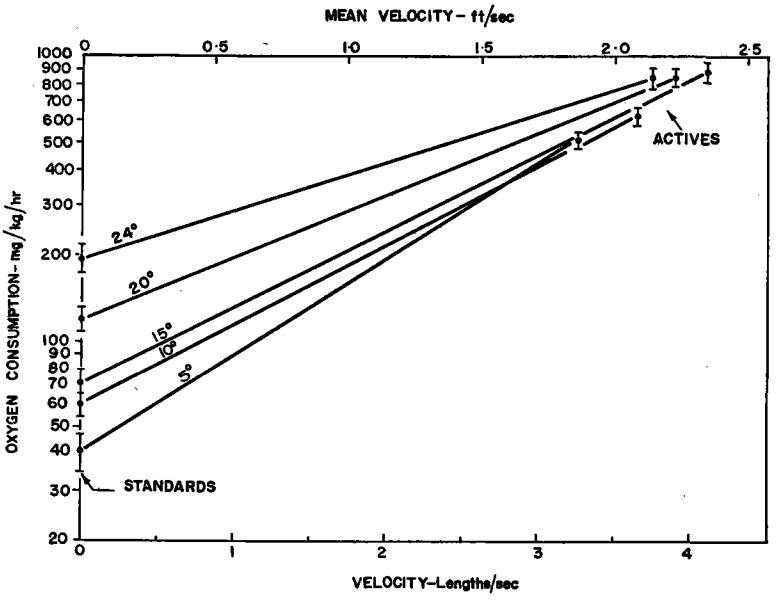

FIG. 7. Mean ±2 S.E. oxygen consumption rates in relation to swimming speed of young sockeye (18 cm, 50 g) for five acclimation temperatures. The crossing over the 5 and 10°C lines is within the expected limits of variability.

TABLE II. Equations for: A. relation of rate of oxygen consumption (Y in mg O_2/kg/hr) to swimming speed (X in Length/sec) at different acclimation temperatures, and B. relation for rate of oxygen replacement (Y in mg O_2/kg/hr) following fatigue (X in hours) (see Fig. 7 and 10).

Acclimation temperature		Equation
	°C	
A.	5	$\text{Log } Y = 1.61 + 0.34\,X$
	10	$\text{Log } Y = 1.78 + 0.28\,X$
	15	$\text{Log } Y = 1.85 + 0.27\,X$
	20	$\text{Log } Y = 2.08 + 0.22\,X$
	24	$\text{Log } Y = 2.29 + 0.17\,X$
B.	5	$\text{Log } Y = 2.40 - 0.16\,X$
	10	$\text{Log } Y = 2.55 - 0.18\,X$
	15	$\text{Log } Y = 2.64 - 0.15\,X$
	20	$\text{Log } Y = 2.65 - 0.12\,X$
	24	$\text{Log } Y = 2.66 - 0.06\,X$

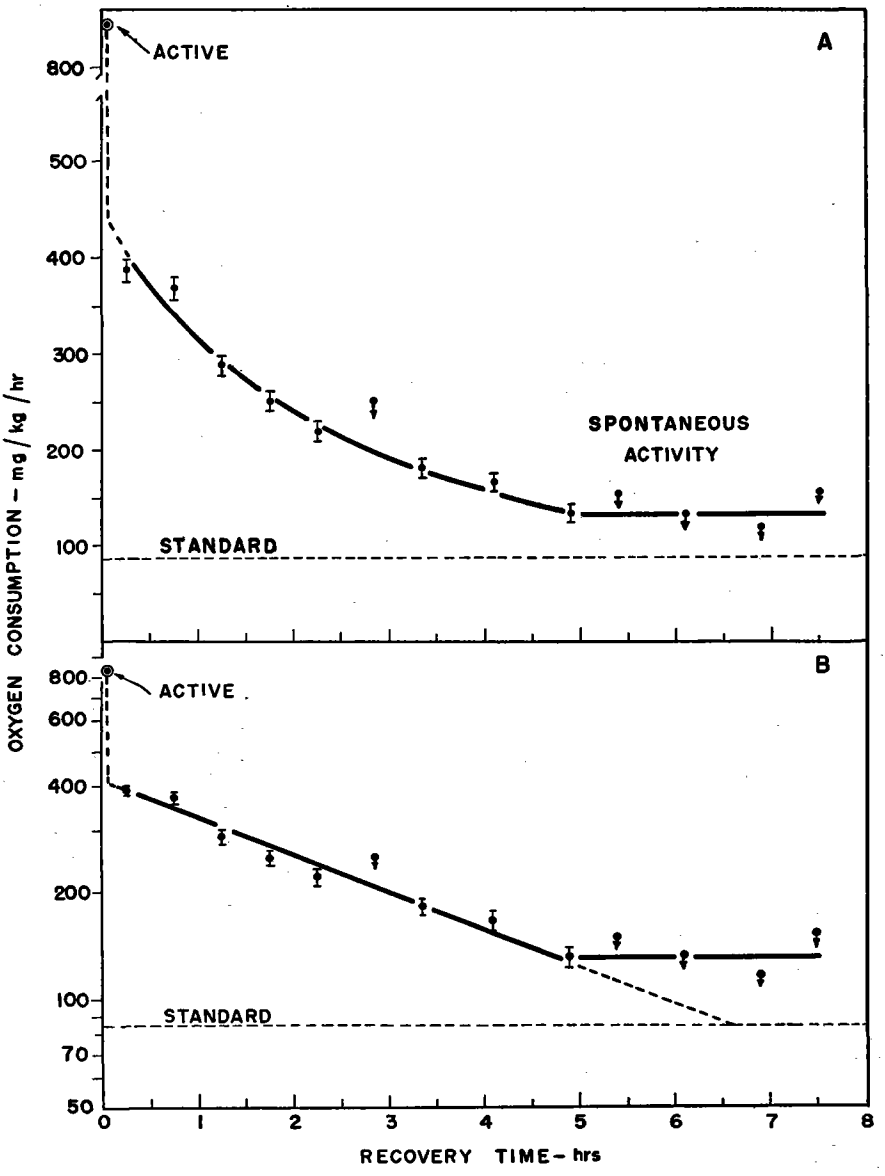

FIG. 8. Oxygen debt replacement in a yearling sockeye (21.5 cm, 87.9 g, 15°C) at rest following fatigue. Last recorded metabolic rate when swimming indicated by Active rate. Arithmetic plot in A transformed to semi-log relation in B. Extrapolation to zero time gives maximum non-swimming rate of oxygen consumption; extrapolation to standard rate gives expected time to complete recovery. Limits are shown equivalent to ±.04 ppm, involving two values (subtracted). Arrows as in Fig. 5.

were 514±31 and 848±39 mg O_2/kg/hr. Maximum active metabolism occurred at 15°C with a rate of 895±49 mg O_2/kg/hr. Although the latter is not significantly different from either the 20°C or the 24°C rate ($P \approx 0.5$ in both cases, by "*t*" test) the decreasing trend at higher temperatures suggests that oxygen availability was limiting, and that the differences were real (see Discussion).

Oxygen Debt

Following fatigue (with water velocity reduced) the exhausted fish would lie quietly in the forward part of the chamber, respiring deeply. Not infrequently the caudal fin would arch upwards almost in reflex reaction to more extreme ventilation gasps. In many instances this behaviour would persist for 2–4 hr, interspersed with an odd restless movement or exploratory turn. Spontaneous activity of a more continuous nature followed, elevating or affecting metabolism in such a way that the further replacement of oxygen debt could not be distinguished. The rate of decrease in oxygen consumption during the recovery period was discovered to be exponential (Fig. 8 and 18). Exceptions occurred in 29% of cases (n = 38) in which either a primary or secondary slump in metabolic rate occurred, followed by a return to a normal pattern of decrease. Frequently the lowest oxygen consumption recorded during recovery was lower than any obtained while trying to determine standard metabolism directly, yet not quite as low as the extrapolated estimate (see Fig. 5).

Having obtained a suitable linear transformation it was possible to treat the data on recovery rate much as those for swimming requirements. An eyed line-of-best-fit was drawn for each applicable case, and the mean value determined

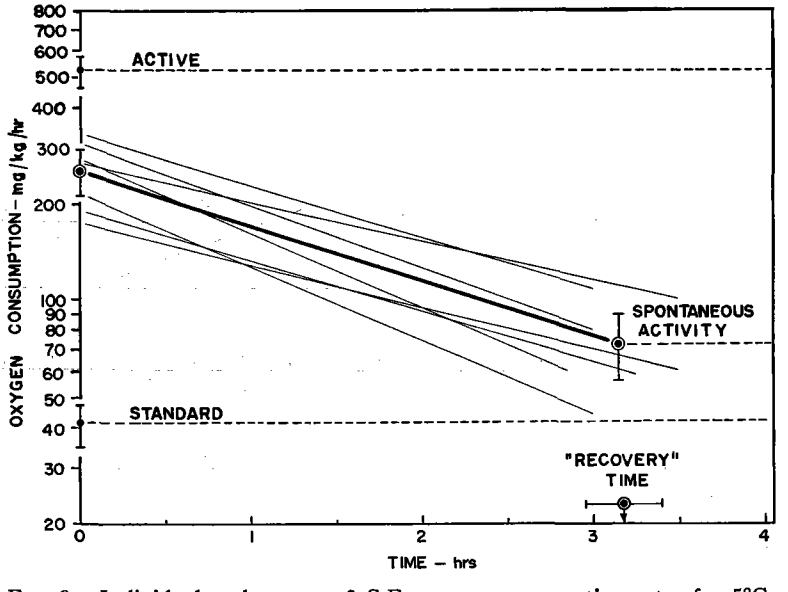

FIG. 9. Individual and mean ±2 S.E. oxygen consumption rates for 5°C-acclimated yearling sockeye during replacement of oxygen debt. Mean time ±2 S.E. to start of spontaneous activity shown.

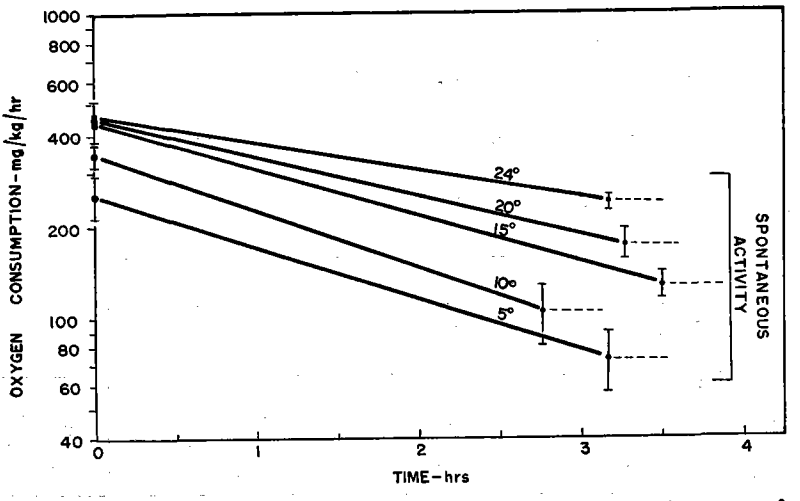

FIG. 10. Mean ±2 S.E. oxygen consumption rates during replacement of oxygen debt in yearling sockeye at five acclimation temperatures.

for initial metabolic rate, final rate (before start of spontaneous activity), and the time to this stage of recovery (Fig. 9 and 10). The areas under each curve for each acclimation were then computed to provide a measure of the total sustained debt as mg O_2/kg (Table III).

No deaths occurred in the recovery phase for acclimations up to 15°C. In the cases examined for a number of days after fatigue, normal feeding had commenced on the following morning (about 18 hr later).

At 20°C, greater irregularity in recovery rate occurred with some loss of equilibrium; one out of nine fish died. Increased problems of recovery were apparent in the 24°C group where, as stated, only five fish out of an original ten could be tested successfully. Of these five, two were highly irregular in metabolic rate but recovered, and two died (see Fig. 19).

SWIMMING SPEED AND FATIGUE TIME

The first series of tests to determine a velocity–fatigue curve were performed from June 11 to 15, 1962, on 17 yearling sockeye (Table IV). Difficulty in obtaining a mean fatigue time for a given velocity resulted from the great range of fatigue times at intermediate velocities, which suggested poor response in some fish. In addition, assigning a fatigue time for those fish still swimming at the end of the test period posed a problem.

A second series was conducted from February 11 to 14, 1963, using 35 fish to supplement the data for the first group (Table V). Although at the same acclimation temperature and approximately the same size, these fish had a reduced capacity to perform.

Similar experiments, conducted with larger numbers of adult salmon during the following spring showed normal distribution of fatigue times when the proportion of a sample showing fatigue was plotted as probits against the logarithm of time-to-fatigue. This system of plotting is essentially the approach of

TABLE III. Metabolic rate, recovery time and magnitude of oxygen debt following fatigue of yearling sockeye at five acclimation temperatures. The maximum rates were obtained by extrapolation (see Fig. 8) For comparison the observed rates in the first ½-hr are shown. Column 5 shows the ratio of maximum recovery rate (non-swimming) to the active metabolic rate. Two recovery times are given, one as the time observed to the start of spontaneous activity and the other as the time determined by extrapolation to reach standard metabolism (Fig. 8). The former provides an "overload" oxygen debt and the latter a calculated total debt.

Acclimation temperature	Maximum rate	Rate in 1st ½-hr	Recovered rate	Max. rate of activity	Recovery time	Average test time	Deaths	Oxygen-debt		Time to "full recovery"	Successful retests
								Overload	Total		
	(*mg/kg/hr*)	(*mg/kg/hr*)	(*mg/kg/hr*)	(%)	(*min*)	(*min*)	(%)	(*mg/kg*)	(*mg/kg*)	(*min*)	(*no*)
5°C											
Number	(7)	(6)	(7)		(7)	(7)	(7)	(7)	(7)	(7)	(2)
Mean	253	212	73	49	190	244	0	252	350	278	2
S.D.	56	...	22		19			51.4			
S.E.	21	...	8.3		7.2			19.5			
10°C											
Number	(7)	(7)	(7)		(6)	(7)	(7)	(6)	(6)	(6)	(1)
Mean	343	308	105	55	167	243	0	292	457	245	0
S.D.	41	...	32		39			18.7			
S.E.	15	...	12		16			7.1			
15°C											
Number	(8)	(8)	(8)		(8)	(8)	(8)	(8)	(8)	(8)	(2)
Mean	439	384	128	49	211	297	0	504	680	315	2
S.D.	68	...	18		79			18.2			
S.E.	24	...	6.7		28			6.4			
20°C											
Number	(6)	(6)	(6)		(7)	(7)	(9)	(6)	(6)	(6)	(3)
Mean	448	392	175	50	196	288	11	450	585	274	3
S.D.	72	...	28		69			21.2			
S.E.	29	...	11		26			8.6			
24°C											
Number	(4)	(4)	(4)		(2)	(4)	(5)	(3)			
Mean	461	421	243	54	190[a]	300	40	287	...[a]	...[a]	
S.D.	33	...	7		...			13.5			
S.E.	16	...	4		...			7.8			

[a]Since death occurred in 40% of this sample, no entry has been made.

TABLE IV. Fatigue times for 17 yearling sockeye (17.57±0.29 cm, 42.08±2.37 g) tested in June, acclimated to 10°C. Geometric mean times for grouped velocity intervals of ±0.2 L/sec are given. Limit of test time = 1000 min (17 hr); this has been the assigned "fatigue time" for fish still swimming at the end of a test.

	Velocity — (*L/sec*)						
	3.7	3.9	4.1	4.3	4.5	4.7	4.9
Fatigue time (*min*)	1000 1000	1000	1000 5.8 11.6 1000	2.7 4.9 20.3 93.0	5.0	2.3 3.3 5.3	2.7 6.8
G.M. ±S. E.	1000	50.7 (174 / 15)		10.5 (20 / 5.5)		3.7 (6.5 / 2.1)	
Grouped velocity range	3.7±.1	4.0±.2		4.4±.2		4.8±.2	

TABLE V. Fatigue times for 35 yearling sockeye (18.61±.14 cm, 52.82±3.76 g) tested in February, acclimated to 10°C. Geometric mean times and time-to-50%-fatigue from Fig. 11 are given. Limit of test time = 600 min (10 hr).

	Velocity — (*L/sec*)								
	2.6	2.8	3.0	3.2	3.4	3.6	3.8	4.0	4.4
Fatigue time (*min*)	600 600 600	600	55 600 600	9.3 15 75 335	3.7 315 600	1.5 2.2 5.7 9.5 31 40 100	1.0 1.5 2.0 26.3 35 600[a]	2.0 3.3 5.3 6.1 9.0 20.0	0.1 0.6
G.M. ±S. E.	600+		94.9 (182 / 50.1)		20.8 (39.8 / 11.0)		5.3 (7.8 / 3.7)		0.25
FT_{50}	600+		112		13.2		4.7		....
Grouped velocity range	2.7±.2		3.1±.2		3.5±.2		3.9±.2		4.4

[a]Not included in G.M. Considered exceptional from probit plot, Fig. 12.

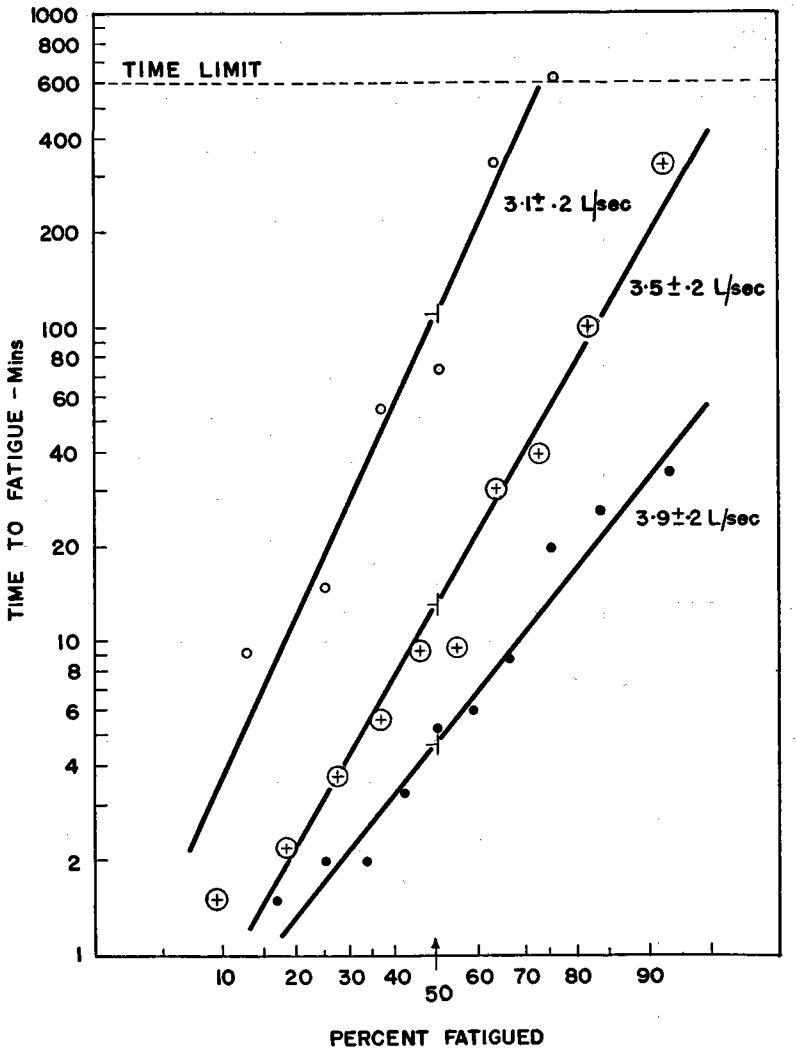

FIG. 11. Relation of fatigue time (log) to order of fatigue (probit) for sockeye yearlings (18.6±0.14 cm, 52.8±3.8 g, 10°C) at three velocities (L/sec).

bio-assay analysis using fatigue time as the response and velocity as the dose. The method made it possible to obtain a *time-to-50%-fatigue* (FT_{50}), providing determinable, representative values where up to half the fish were still swimming at the end of the test period.

Although undesirably low in numbers of fish, the yearling sockeye data were treated in the above manner for the February series (Fig. 11), and both groups were analysed for geometric mean fatigue time to permit comparison (Fig. 12; Tables IV and V).

For the standard test time of 60 min used in the metabolism experiments the June sockeye had a maximum swimming speed of 4.0 L/sec whereas the

February rate was 3.2 L/sec. The geometric mean time-to-fatigue and the interpolated time-to-50%-fatigue approximated closely, substantiating the use of the latter for comparison where not all the fish fatigue in the allotted time. There is some suggestion in the data that the capacity to continue performing, once 200–300 min have elapsed, is greater than that expected by extrapolation. Of the four smaller fish subjected to long-term swimming, two fatigued within 180 min, whereas one continued for 5520 min (3.8 days at 4.8 L/sec, 15°C) and

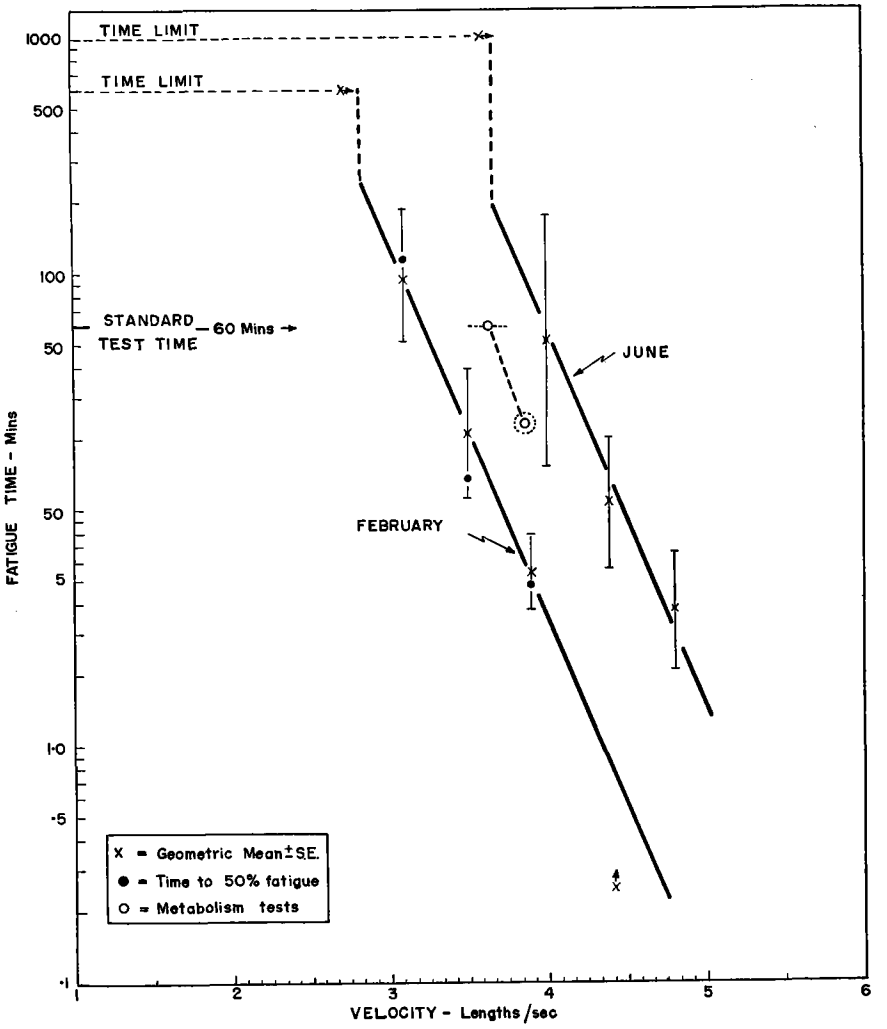

FIG. 12. Relation between geometric mean fatigue time and swimming speed for yearling sockeye at 10°C. June fish averaged 17.6 cm, 42 g, and February fish were 18.6 cm, 52.8 g. Time to 50% fatigue from probit plot (Fig. 11) falls within G.M. ±1 S.E. Mean fatigue time determined from metabolism tests is shown (circled) including 60-min calculated maximum speed. Point with arrow at bottom of graph involved only two excited fish. Points with arrows at top of graph indicate fish were still swimming at end of test time.

the fourth was still swimming at 5800 min (4+ days at 3.7 L/sec, equivalent to 92.3 miles). These latter performances demonstrate a remarkable sustained capacity beyond an apparent 200–300-min threshold level. For this reason dotted lines have been used in Fig. 12 suggesting a "break" in the fatigue curve.

The mean swimming speed and fatigue time in the metabolism studies using the step-type increase in velocity was 3.84 L/sec maintained for 23 min. Using the method described to determine a 60-min fatigue velocity, the result was 3.65 L/sec. These two values plotted in Fig. 12 are seen to parallel the fatigue curves, and by coincidence the value of 3.6 L/sec approximates the June threshold speed maintained for at least 1000 min. Hence it is quite likely that the values for "critical swimming speed" recorded in Table I approximate the threshold levels which would be obtained from fatigue curves.

DISCUSSION

Validity of Metabolic Rate–Swimming Speed Relation

Much of the essence of this study depends on the validity of the linearized relation between logarithm of oxygen consumption and swimming speed. The technique employed was expected to provide in a single test on individual fish both active and standard rates of metabolism, as well as maximum sustained swimming speeds. Since minimum and maximum activity levels would be obtained in a systematic way, it was further expected that the ultimate values for these extremes could be obtained within the limits of season and condition of the stocks tested.

The use of sensitive activity meters has served to show a direct (arithmetic) relation between the frequency of undefined, random movements and oxygen consumption (Spoor, 1946; Beamish and Mookherjii, 1964). This method has been employed mostly for determining standard metabolism by extrapolation to zero activity. Since the maximum observed metabolic rates are limited to those for spontaneous activity, estimates of active metabolism cannot be obtained. Fry and associates (Fry, 1957; Basu, 1959) used a rotating annular chamber, later modified into the form of a "doughnut", and induced fish to swim strongly by applying a localized electric field. Maximum rates of oxygen consumption were taken to be a good measure of active metabolism; however, no significant relation between speed of rotation and oxygen consumption was apparent (Basu, 1959). Saunders (1962) subsequently obtained considerably higher rates for two species at approximately the same calculated swimming speeds. The apparent lack of relationship between imposed velocity and metabolic rate in these cases was undoubtedly involved with excitement. Nevertheless, Fry (1957) was able to transform earlier data on a variety of species including four salmonids into an approximate linear relation between cruising speed and oxygen consumption, expressed as the square root of the difference between active and standard metabolism ($\sqrt{\text{"scope"}}$). Although the assumption that a full measure of active metabolism was obtained may not prove to be substantiated in every case, the derivation showed the possibility of an exponential relation between metabolism and swimming speed.

Wohlschlag (1957) and Wohlschlag and Juliano (1959) also used a rotating annular chamber, allowing the fish to swim "naturally" without particular persuasion from an applied stimulus. When corrected for weight and temperature, the logarithm of oxygen consumption was found to be directly related to velocity, although a fairly large standard error was involved. Hatanaka (personal communication) has approached the problem by studying the decrease in body weight in relation to swimming speed in a propeller-induced stream and found a linear relation between the logarithm of per cent decrease in body weight and velocity.

These related studies, conducted with somewhat less precision than that made possible in the present experiments, lend confirmation to the relation derived for the sockeye data[3]. It seems likely that the exponential transformation is one that applies to fish metabolism in general. However, the increase in drag on a non-flexing dead fish follows more standard hydrodynamic laws, where the log of "power to overcome drag" is directly related to the log of velocity, with appropriate constants (Brett, 1964). Blazka (1960) and Blazka *et al.* (1960) used a neatly devised respirometer with a small ratio of fish volume to water mass in which the fish almost brushed the walls of the respirometer chamber. They obtained a relation showing greater curvilinearity than that represented in Fig. 4. This may have arisen from proportionately increased drag due to acceleration of water past the body of the fish under the confined circumstances. The weight of evidence, however, supports the contention that the metabolic relation is best expressed in the form $Y = ae^{bX}$, where Y = oxygen consumption, X = swimming speed.

Metabolic Rates, Temperature, and Activity Relations

Accepting the validity of the relation plotted for the five acclimation temperatures in Fig. 7, it is possible to read off the metabolic rates accompanying intermediate velocities by interpolation and to construct the graph of Fig. 13. This shows the relation between given levels of activity and corresponding rates of oxygen consumption over the biokinetic range of the species.

Standard metabolism. The points for zero velocity, representing standard metabolism, are not significantly different between 10°C and 15°C ($P \approx .07$) although the means differ by 11 mg O_2/kg/hr. By graphic approximation (Fig. 14) it was determined that a line could be drawn to pass through the limits set by the mean ± 2 S.E. of each oxygen consumption rate with the equation:

$$\log (Y - 36) = 0.48 + 0.071\,X$$

where Y = oxygen consumption in mg O_2/kg/hr, and X = temperature in centigrade degrees.

This provided the most likely standard metabolic rate at each temperature and permitted extrapolation of the rates to the upper and lower lethal

[3]Observations on pumpkinseed (*Lepomis gibbosus*) also support the validity of this approach (Brett and Sutherland, MS, 1964).

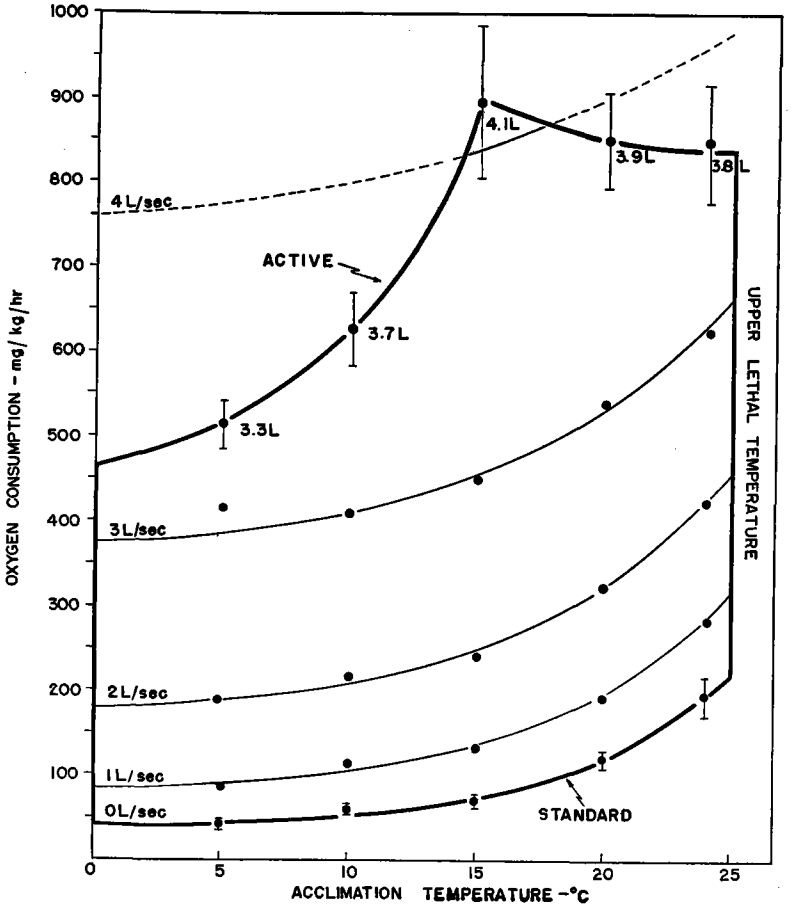

FIG. 13. Relation between oxygen consumption and temperature at various swimming speeds for yearling sockeye salmon (18 cm, 50 g). Standard and active rates are indicated as mean ±2 S.E. The 60-min "critical speed" accompanying each active rate is shown. Swimming speeds of 1–3 L/sec obtained by interpolation; those at 0 and 4 L/sec by extrapolation, except at 15°C. The broken line for 4 L/sec is drawn in an area where rapid fatigue would occur since the speed at these temperatures demands a metabolic rate in excess of the active rate.

temperatures of approximately 25°C and 0°C. The value of 36 mg O_2/kg/hr is considered to be the minimum threshold metabolism capable of supporting life of yearling sockeye at a low temperature. It is known that young sockeye can just survive freezing temperatures when acclimated to 5°C (Brett, 1952) and that young sockeye and chum salmon (*O. keta*) have an ultimate lower lethal of −0.1°C in 28‰ salt water (Brett and Alderdice, 1958). The extrapolated estimate for standard metabolism at 0°C was 39 mg O_2/kg/hr. Standard rates increased fairly rapidly above 15°C, with a calculated maximum of 220 mg O_2/kg/hr at 25°C.

These minimum and maximum levels of standard metabolism agree closely with what might be expected for brook trout (Beamish, 1964b). However, the concave relation of the sockeye data shows a somewhat lower rate at intermediate temperatures (Fig. 14).

ACTIVE METABOLISM. The sharp cut-off in active metabolic rate at 15°C (Fig. 13) suggested the presence of a limiting factor, suspected as being oxygen concentration. Although no significant difference was found between the maximum rates for 15, 20, and 24°C (page 1193) it is to be noted that the means do decrease. This circumstance was considered likely since the amount of oxygen per unit volume decreases with temperature (Fig. 15). To test this possibility, an experiment to determine the effect of relatively high levels of oxygen concentration (approximately 150% air-saturated) on active metabolism was performed at 20°C (Table VI). The initial results showed a highly signif-

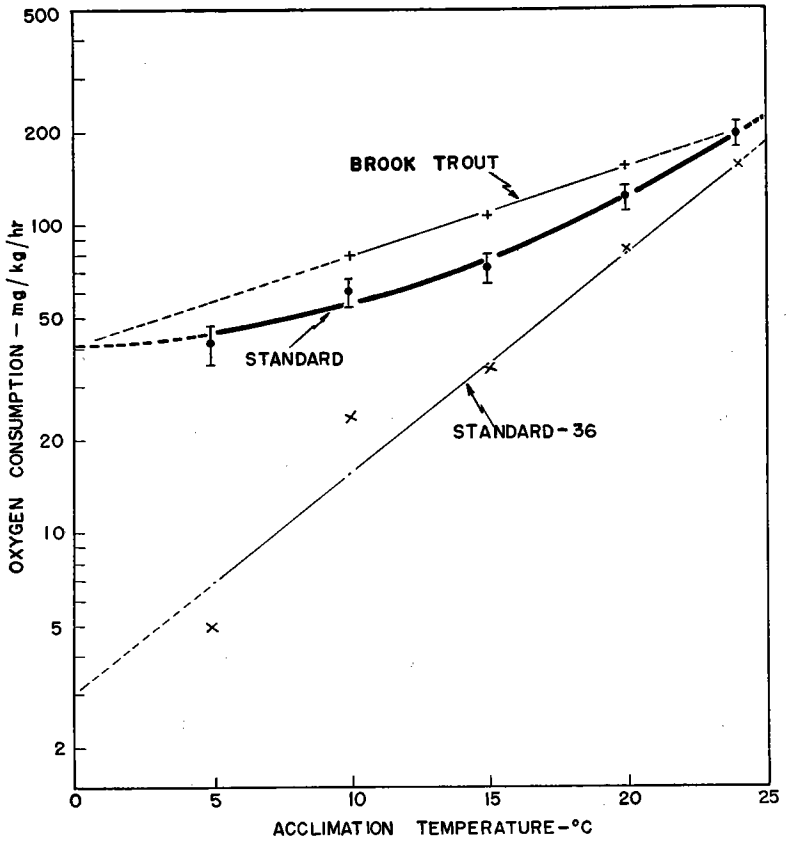

FIG. 14. Relation of standard metabolism to acclimation temperature for yearling sockeye (18 cm, 50 g). The line passing through the mean or within ±2 S.E. was obtained from the best straight line drawn through values of the *standard* –36. Standard rates for 100-g brook trout (Beamish, 1964b) are presented for comparison.

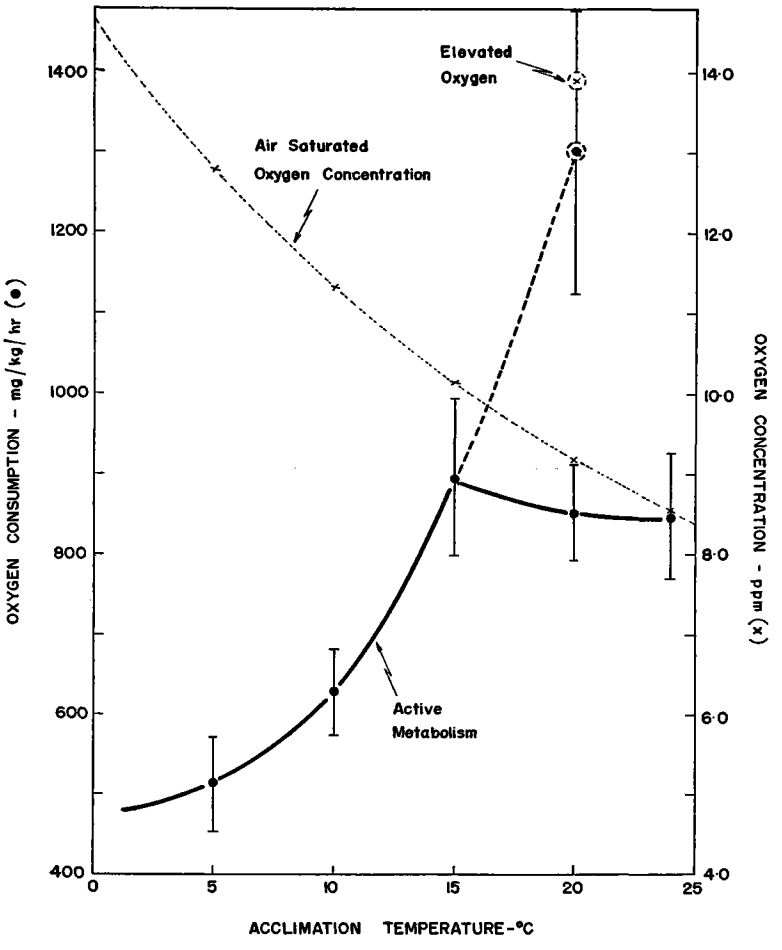

FIG. 15. Active metabolism of yearling sockeye (heavy line) tested at air-saturated oxygen levels (dotted line). Mean ±2 S.E. metabolic rate for elevated oxygen (13.9 ppm) determined at 20°C (circled points).

icant proportional increase in active metabolism which was elevated by an average of 50%. However, wide variation in the imposed oxygen levels occurred. A temporary halt was called in the tests in order to improve the controls. During this period the complete stock of yearling sockeye was accidentally lost. A new stock was obtained from a different source and found to be infected with a gill parasite (*Salmincola* sp.). The parasite was removed by cutting the hold-fast under anaesthetic.

A comparison of the new stock with the original stock revealed a lower active metabolic rate at 20°C, which was not quite significant ($P \approx .08$). In addition, elevated oxygen concentrations failed to bring about any significant increase in active metabolism (Table VI). Some slight "erosion" of gill lamellae had taken place as a result of the infection, but this did not appear to be sufficient

to produce such a marked difference in response between the two stocks. It was apparent that a thorough examination of the problem would be required before any satisfactory answer could be obtained.

The conclusion was that environmental oxygen concentration could be a limiting factor above 15°C, but that other factors of a physiological nature may occur to alter this relation.

The reason for fatigue at temperatures lower than 15°C must be sought beyond the respiratory circumstance in some incapacity to deliver available oxygen or maintain an adequate supply of metabolites. The maximum rate at 15°C of 895±45 mg O_2/kg/hr (Table I) is considerably higher than other maxima obtained for salmonids of about the same weight, e.g. 450 mg O_2/kg/hr for *Salvelinus fontinalis* (Job, 1955), and 460 mg O_2/kg/hr for *Salvelinus namaycush* (Gibson and Fry, 1954).

TABLE VI. Comparative rates of active metabolism for 20°C-acclimated yearling sockeye at various levels of oxygen concentration. Stock "A" is original stock from Great Central Lake; stock "B" is from Cultus Lake. See Table I for records on stock "A" at air-saturated levels of oxygen.

Stock	Active metabolism	Oxygen concentration		Critical speed	
	(*mg/kg/hr*)	(*ppm*)	(%)	(*ft/sec*)	(*L/sec*)
A					
Number	(6)	(6)	(6)	(5)	(5)
Mean	1302	13.9	152	2.39	4.27
S.D.	267	3.3	...	...	0.94
S.E.	89	1.3	...	...	0.43
B					
Number	(5)	(5)	(5)	(5)	(5)
Mean	740	8.71	95	1.94	2.98
S.D.	176	0.24	...	...	0.58
S.E.	80	0.11	...	...	0.26
B					
Number	(4)	(4)	(4)	(4)	(4)
Mean	755	13.02	142	1.98	2.84
S.D.	121	.50	...	...	0.28
S.E.	60	.25	...	...	0.14

METABOLIC SCOPE

One of the aims of this study was to determine the energy required solely for locomotion, at various levels of performance. By deducting the amount directed into maintenance (standard) the balance of oxygen consumption when swimming can be ascribed mostly to the mechanics of propulsion. This balance of "available energy" was termed the *scope for activity* by Fry (1957) when applied to the maximum metabolic difference at any one acclimation temperature (active minus standard). Beamish (1964b) has further introduced the term *routine scope* as the amount of metabolism devoted to spontaneous activity

(routine minus standard). A comparison of the power to overcome the drag on an average 50-g dead sockeye (freshly killed) and that expended by a 50-g living fish was made by Brett (1963) using metabolic scope determinations. The optimum relation in favour of the swimming fish occurred at about 4 L/sec. The metabolic scope for swimming at speeds of 1, 2, and 3 L/sec is depicted in Fig. 16. It is apparent that the respective requirements for standard metabolism and for swimming at 1 L/sec are approximately equal up to 12°C. A continuing rise in the maintenance fraction elevates the standard rate to almost that for 2 L/sec at 25°C. These relations serve to emphasize the dual increased costs imposed by temperature on metabolism. Not only does it cost more to swim at 1 L/sec with increasing temperature, but above about 12°C the maintenance fraction increases considerably.

Although slight but definite curvilinearity characterizes the distribution of points at low swimming speeds, a straight line has been used as a near approximation of the relation (maximum error = 6%). Using the general exponential equation (page 1203), the slopes for the speeds of 1, 2, and 3 L/sec are, respectively, .019, .013, and .007. The rate of decrease in slope is such that at 4.2

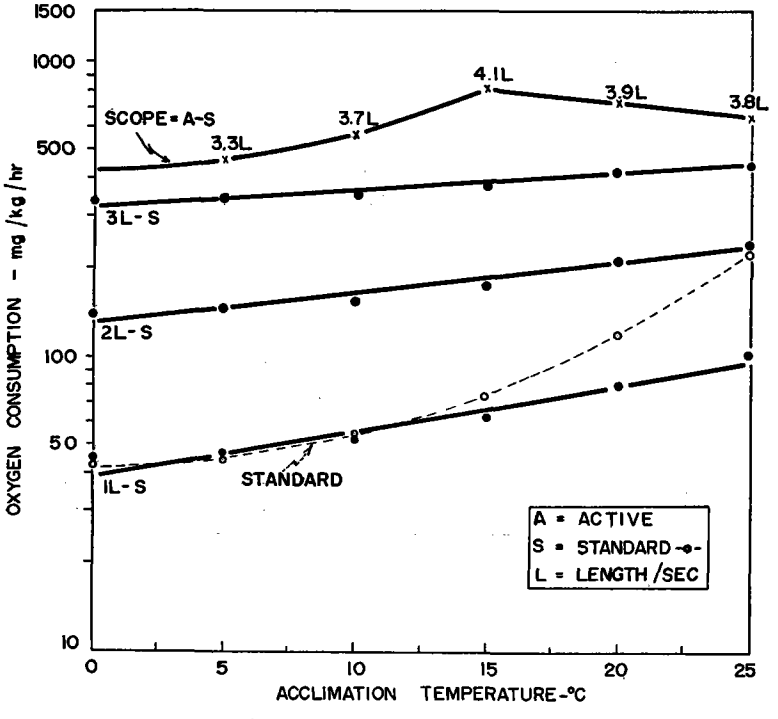

FIG. 16. Relation between metabolic scope (locomotor requirement) and acclimation temperature for various swimming speeds. The maximum scope with accompanying critical swimming speed is shown in the top line. The standard metabolic rate (*S*), the value subtracted in each case above, is included for comparison to show the "maintenance cost" at each temperature.

L/sec the slope would approximate zero. In other words, the temperature influence on locomotor metabolism is negligible at burst speeds (approximately 4–10 L/sec). As pointed out in a previous paper (Brett, 1964), it makes the thermal relations of metabolism for burst speeds comparable to those of a homeotherm. This important phenomenon was noted in a general way by Blaxter and Dickson (1959) while studying the burst speeds of a variety of marine species. The authors reported that "There was no consistent effect of temperature on the [burst][4] swimming speed over the range of temperature used", e.g. 5–18°C for herring.

Having established the relation for given swimming speeds, the further relation for the total scope (top line Fig. 16) can be seen to depend on the fact that increasing temperature permits a higher level of metabolic rate accompanied by a higher level of sustained performance. This increase is curtailed by available oxygen supply above 15°C, and performance and oxygen uptake both decline thereafter.

Weight Relations

A comparison of the weights between the sets of five acclimations showed that there were highly significant differences between the first group (5 and 10°C) and the second group (15 and 20°C), but not within these groups (Table VII). The 24°C-acclimated fish, with an intermediate mean weight, did not differ significantly from either of the other acclimation groups. The maximum difference in mean weight was that between 20°C and 10°C (62.6 g and 32.9 g, respectively).

As a result of this difference, a correction for weight would be necessary at each acclimation if there were a significant difference in rate of oxygen consumption with size (within the range considered), applied to standard and active rates.

Although there is abundant evidence for such corrections for standard metabolism, particularly the extensive series collected by Winberg (1956) at 20°C, nevertheless there are cases where the rates were almost directly proportional to weight (Wohlschlag and Juliano, 1959, July–Aug. equation; Hickman, 1959, winter starry flounder over 40 g; Beamish, 1964b, speckled trout, 10, 15, and 20°C). Comparable studies on active metabolism are scarce. Job (1955), investigating the active metabolism of speckled trout from 5 to 1000 g, demonstrated that at 5°C the exponent b equalled 0.94 indicating near proportionality, whereas at 20°C it was 0.75. Basu (1959) applied Job's b values to enable comparisons of active metabolism corrected for weight in speckled trout, and provided evidence for a value of 0.8 in carp at 30°C.

For the yearling sockeye data, over the range of weights studied, there was no significant correlation between weight and metabolic rate (mg O_2/kg/hr), either standard or active, for any of the acclimation temperatures. One series at 15°C acclimation did include a small group of underyearlings, introduced for weight comparison (Fig. 17). There was a correlation of −.45 for standard

[4]Durations of ½–1 min involved.

TABLE VII. Mean weight ±2 S.E. of yearling sockeye from each acclimation temperature. Significant difference between groups determined by "*t*" test (Goulden, 1952).

Mean weight (*g*)	±2 S.E.		Table of comparison between acclimation temperatures				
			5°C	10°C	15°C	20°C	24°C
36.70	± 8.0	5°C		N[a]	.10	.01[c]	N
32.85	± 7.8	10°C			.02[b]	.01[c]	.10
55.18	±19.0	15°C				N	N
62.58	±16.4	20°C					N
52.24	±18.0	24°C					

[a]N = not significant, by inspection.
[b]Significant.
[c]Highly significant.

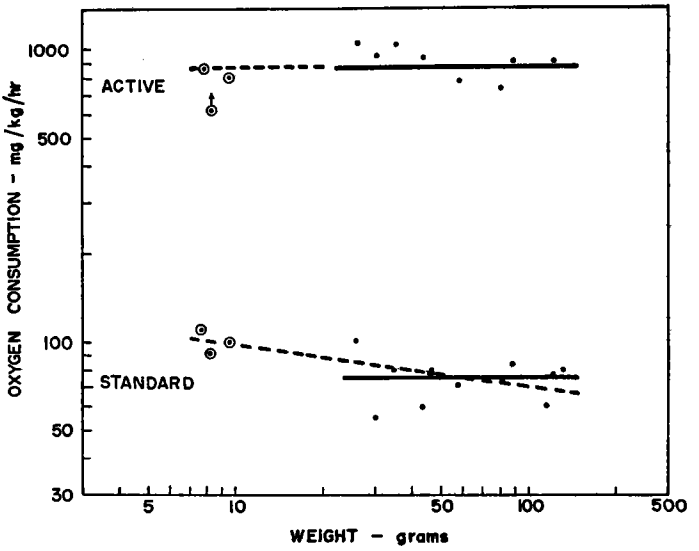

FIG. 17. Relation between weight and metabolic rate at 15°C for yearling sockeye (solid line) and that for a greater weight range including underyearlings (circled points). The latter were tested in groups of five fish; one series (with arrow) was not carried to maximum swimming speed.

rate and weight which was not quite significant ($P_{.05}$ = .53)[5]. If a line of best fit is employed, however, the difference in standard metabolism at 32 g and 62 g is 7%. Since no such difference exists for active metabolism, this possible small error at the resting level was not sufficient to warrant further consideration.

[5]Alternatively it can be shown that the slope of the line relating log weight to log mg O_2/hr does not differ significantly from 1.0 (Table VIII).

The metabolism data can therefore be considered to apply to an overall mean weight of 47.9±2.3 g and length of 17.8±1.6 cm (n = 44), i.e. approximately 50 g and 18 cm.

Condition Factor

A condition factor or index relating weight to length (W/L^3) has frequently been used to provide a relative measure of well-being of fish (Carlander, 1950). This is a different concept from condition in terms of physical fitness, but nevertheless the implication exists. Some support for this assumption is presented by Reimers (1963), when considering the survival of liberated hatchery-reared rainbow trout. He reports that those "in the range 0.60–0.70 may be considered marginal in vitality, tiring quickly in stamina tests". The basis of the tests is not clearly indicated, but appears to stem from field observations in an experimental stream (Nielson *et al.*, 1957).

The relation between the condition of the yearling sockeye and their ability to metabolize, and hence perform, was considered by correlation tests relating condition, active metabolism, critical swimming speed, weight, and length (Table VIII). The condition factor ranged from 0.64 to 1.04. The 10°C group had the lowest mean value (0.73±.02) while the 24°C fish had the highest (0.82

Table VIII. Correlation coefficients relating condition factor (W/L^3) to various parameters of yearling sockeye salmon (temperature = 15°C). W = wet weight in grams, L = total length in centimetres.

Variates	Correlation coefficients		Significance level		Significant
			P .05	P .01	
Condition × active metabolism	r_{12}	−.78	.71	.83	< .05
Condition × critical speed	r_{13}	−.27	.71	.83	Not
Condition × length	r_{14}	+.36	.71	.83	Not
Condition × weight	r_{15}	+.45	.71	.83	Not
Active metabolism × speed	r_{23}	+.38	.71	.83	Not
Active metabolism × length	r_{24}	−.16	.71	.83	Not
Active metabolism × weight	r_{25}	−.24	.71	.83	Not
Speed × length	r_{34}	−.56	.71	.83	Not
Speed × weight	r_{35}	−.57	.71	.83	Not
Condition × active metabolism (speed constant)	$r_{12\cdot3}$	−.75	.75	.87	.05
Condition × active metabolism (length constant)	$r_{12\cdot4}$	−.77	.75	.87	< .05
Condition × active metabolism (weight constant)	$r_{12\cdot5}$	−.78	.75	.87	< .05

±.04; Table I). There was a significant difference at a $P_{.05}$ level between the extremes but not between the balance.

Condition factor and weight were not significantly related. This point is worth noting since the power *3* for length (L) is arbitrarily used as a generally suitable exponent. If it were unsuitable in the present case a significant difference with weight would have been expected.

The only significant correlation was a negative relation between condition and active metabolism at 15°C ($r = -.78$; $P = .02$). The coefficients for the other four acclimations were all negative but none exceeded −.57 ($P_{.05} = .63$). Given that the fish were equally healthy, the negative correlation would be expected on the basis that the heavier fish contained more stored reserves not involved in active metabolism. Critical speed and condition were not related, nor were active metabolism and speed, which speaks highly of the physical fitness of all the fish independent of plumpness. Partial correlation coefficients were also determined. These did not alter the significance of any relation (Table VIII).

It can be concluded that the stock was indeed a healthy one and that the metabolic rate for unit weight is inevitably lowered for fish with a high condition factor, provided of course they are in good physical condition.

The lack of any significant relation above 15°C is explicable on the basis of oxygen as a limiting factor, masking the relation by restricting the full capacity to metabolize. Fish which had a still lower value than 0.64 for condition factor might well be inferior fish. This points up the need to consider the meaning of "condition factor", which would be particularly valuable if it reflected capacity to survive in nature. Size alone may have some advantage, but if it relates to poor performance it may at times be a greater handicap than advantage.

Fish Composition

Examination of the moisture and lipid fractions of the fish should be revealing in regard to the weight influence on metabolic rate and the condition factor–metabolism relation. The supposition is that variation in active metabolic rate for immature fish of the same weight and age is due to a difference in the proportion of moisture, lipid, and protein[6], and that if the moisture and lipid are subtracted then the variability in metabolic rate per unit weight of the "residue" would be significantly reduced. In addition the respiratory coefficient *b* would approach 1.0, i.e. directly proportional to the mass of residue rather than the 0.8 value of Winberg (1956).

To test this the results for 15°C yearling sockeye have been analysed (Table IX). From the regression equations it is apparent that the slope for wet weight is not significantly different from 1.0 (as might be expected from the lack of a significant correlation between standard metabolic rate and weight — page 1209) nor are those for dry weight and dry weight-less-lipid. The surprising point is that the variability is not reduced since it was thought likely that a major cause of difference would be removed.

[6]Carbohydrate makes up less than 2% (Love, 1957; Fontaine and Hatey, 1953).

TABLE IX. Values for exponent "b" for the equation: $\log Y = a + bX$, where Y = mg O_2 consumed/hr and X = weight (grams), as indicated below. Fiducial limits determined for P = .05 (Goulden, 1952).

X-factor	b-value	Fiducial limits
Wet weight	0.88±.26	0.62–1.14
Dry weight	0.83±.26	0.57–1.09
Dry weight — lipid	0.85±.27	0.58–1.12

In the face of a significant negative correlation between condition and active metabolism the conundrum remains, except to conclude that the moisture and lipid fractions reflect the capacity to metabolize, or are involved in the process in some indirect fashion. The consequence is that the wet weight is as suitable to use as the other weight measures, a point which Zeuthen (1953) was forced to conclude following a study of metabolism and weight in a wide variety of organisms.

One relation of interest that emerged was a highly significant negative correlation between the proportion of lipid and water ($r = -.84$, $P_{.01} = .37$, $n = 44$). Where there was proportionately a lot of fat there was little moisture and vice versa. Thus, although considerable differences in fat and moisture content occurred, they tended to balance out with the result that the dry weight minus lipid paralleled the wet weight.

OXYGEN DEBT

The fact that sockeye were exercised to the exhaustion point presented an opportunity to examine not only the extent of sustained debt, but also the effect of acclimation temperature on this load, the rate of recovery, and the *state* of recovery in terms of capacity to re-perform (Table III).

RECOVERY TIME. The primary phase of recovery in sockeye was rarely characterized by restless movements except at temperatures of 20 and 24°C. The start of spontaneous activity was accompanied by a levelling-off in the decline of metabolic rate, with some increase in metabolism when the movements included turns and roaming. An example of an 11-hr record is given in Fig. 18 in which only the last rate was within 12% of the standard metabolic rate. To assess the significance of return of spontaneous activity, the system of re-imposing the last fatigue-producing velocity was adopted. Most cases were curtailed when the fish demonstrated an ability to perform for as long as the previous fatigue time (Table III). Out of eight cases, only one was unsuccessful; by comparison, the time to fatigue in one successful case was over twice as long as the original time. It is perhaps unsound to make such a comparison as this, since the original test was a prolonged step-type one. It is appropriate, however, to conclude that recovery was sufficient to permit a high level of performance.

A comparison of the times to recovery for each acclimation showed no significant difference between the means. The overall mean, not including the

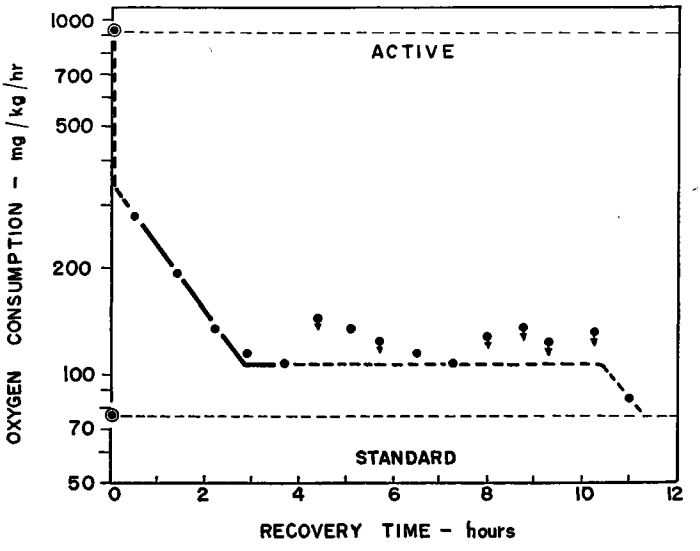

FIG. 18. Eleven-hour record of respiratory metabolism following fatigue in a yearling sockeye (25 cm, 121 g, 15°C). Active and standard rates previously determined from performance studies. The fish was not observed frequently after 5 hr so subsequent elevated points without an arrow may have been accompanied by unnoted spontaneous activity.

uncertain 24°C group, was 191±3.8 min (3.2 hr). This is somewhat faster than the recovery rate for adult coho salmon (*O. kisutch*) following fatigue in an annular chamber (Paulik *et al.*, 1957). Using the method of testing capacity to re-perform, recovery of the coho was approximately 67% complete after 180 min of rest. The rate of recovery was such that completion would be predicted within 5 hr at most; however, only tests at 18–24 hr were conducted beyond the 3-hr recovery stage. These showed complete recovery.

In the extensive experiments of Black *et al.* (1962) on recovery from fatigue in hatchery-reared rainbow trout at 11.5°C, muscle pyruvate was mostly dissipated after 4 hr of recovery, but blood and liver levels of pyruvate and lactate remained elevated for nearly 12 hr. Muscle lactate was less than $\frac{1}{2}$ reduced by 4 hr, continuing to decrease for 8 hr before reaching normal concentrations. Heath and Pritchard (1962) obtained similar times for return of normal levels of blood lactic acid, but report that respiratory metabolism remained elevated beyond 10 hr.

For "trained" rainbow trout Hochachka (1961) did not observe a return of muscle glycogen in less than 18 hr. However, pre-exercise respiration rates were re-established in 4–6 hr after fatigue, a situation not unlike the sockeye recovery. Since the sockeye could re-perform successfully, Hochachka's deduction is pertinent, namely that "all the accumulated lactate need not be oxidized when the oxygen debt has disappeared, but only that it bear a certain relationship to pyruvate, so that metabolic oxidations can return to normal".

SUSTAINED DEBT. The debt replaced up to the start of spontaneous activity was plotted against acclimation temperature (Fig. 19, "overload debt"). For comparison the mean rates of replacement (Fig. 8 and 10) were extrapolated to the respective levels of standard metabolism, thereby making it possible to compute a total sustained debt. The difference between these two levels of debt probably represents the sort of tolerable load readily sustained by the fish. Temperature effect was pronounced. At an optimum of 15°C the total debt (680 mg O_2/kg) exceeded the 5°C level (350 mg O_2/kg) by almost two times. The decline appears to relate to an inability to extract oxygen at an increased rate at higher temperatures, coupled with an elevated standard metabolism. This is revealed by the decreasing slope in the recovery rate above 15°C (Fig. 10).

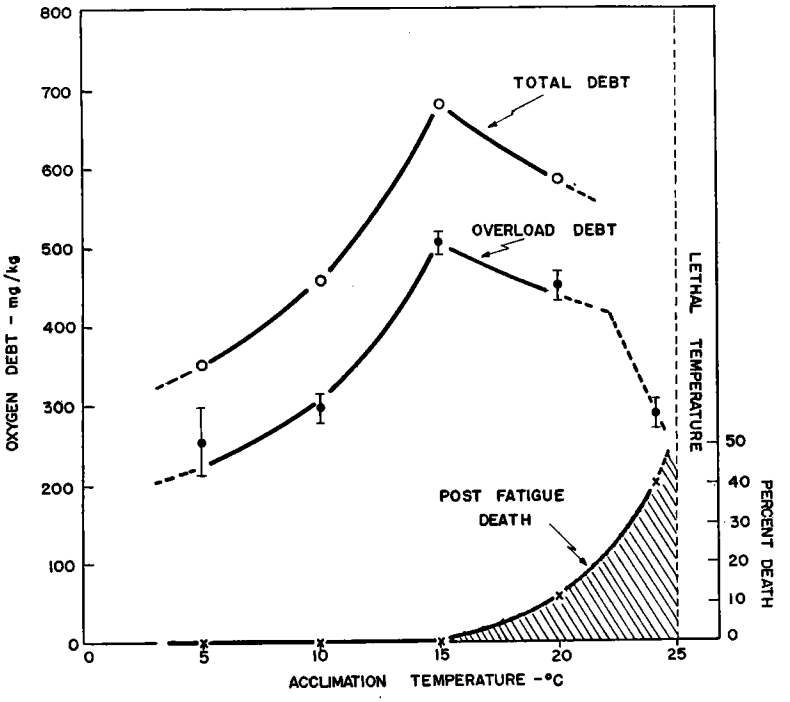

FIG. 19. Magnitude of oxygen debt replaced following fatigue in yearling sockeye at different acclimation temperatures. Amount replaced (mean ±2 S.E.) to start of spontaneous activity labelled "overload debt", and amount calculated to the level of standard metabolism labelled "total debt". Incidence of death during recovery is shown.

Having determined the amount of oxygen debt which young sockeye could sustain at each acclimation temperature, and also the relation between rate of oxygen consumption and swimming speed, it was possible to predict the time-to-fatigue for burst performances. For example, at 10°C the active metabolic rate was 627 mg O_2/kg/hr at a critical speed of 3.65 L/sec (Table I). The calculated demand for swimming at 4.5 L/sec is approximately 1080 mg O_2/kg/hr; a

differential of 453 mg O_2/kg/hr exists. Since a debt of at least 328 mg O_2/kg can be accumulated at this acclimation temperature, the time-to-fatigue would be expected to be about 43 min. At best the observed performance was not more than 8 min (Fig. 12).

The differential can be accounted for by assuming that considerable debt is carried from one sustained swimming stage to another, and that in the speed tests there is already an accumulated debt from excitement and preliminary performance before the final burst. This is a recognized phenomenon in muscular activity of man in which long-distance runners may build up a sizeable debt although not be exhausted at the end of the race (Karpovich, 1959).

To check the possibility of oxygen debt under "normal load" a few experiments were conducted, switching to resting conditions during a sub-fatigue swimming performance. These confirmed the presence of a definite debt, replaced within an hour of recovery. It is apparent that the greatest precautions to avoid complications from oxygen debt have to be used in exploring respiratory metabolism in relation to prescribed activities.

MAXIMUM OXYGEN CONSUMPTION. One comparison of interest turned up from the linearized relation on rate of replacing oxygen debt which permitted extrapolation to the instantaneous metabolic rate immediately following fatigue (Fig. 8 and 18; Table III). This represents the maximum uptake of oxygen during deep opercular ventilation when lying almost motionless in water of 0.1 ft/sec velocity. When swimming, flushing of the gills is achieved usually by holding the mouth and opercula slightly open. Maximum velocities ranged from 1.8 ft/sec (5°C) to 2.5 ft/sec (15°C). One of the signs of approaching fatigue was the onset of irregular gasps. The comparative rates of respiratory metabolism under the two circumstances showed that the maximum achieved while swimming was *twice* that for resting with deep respiration.

These findings are in contrast to those reported by Saunders (1962) for gill irrigation in swimming and resting white suckers, brown bullheads, and carp, when stimulated by low levels of oxygen or high levels of carbon dioxide. In the presence of these stimulating agents the non-swimming fish had the larger respiratory volume. Since oxygen debt probably stimulates respiration in the manner of decreased oxygen, the difference could be one of species characteristics. Alternatively fatigue may be accompanied by cardiac depression or loss of blood volume resulting in circulatory insufficiency. Black *et al.* (1962) have suspected this. In the present experiments, as stated previously, 29% showed a primary or secondary slump in respiration during recovery. However, in the cases not involved with such respiratory irregularities, an inability to increase the rate significantly at temperatures above 15°C has been attributed to limiting oxygen. Furthermore, ability to re-perform within 3 hr is an indication of the integrity of the metabolic and supporting circulatory and excretory systems.

SWIMMING SPEED

PERFORMANCE TIME. To establish a complete fatigue curve, experiments must be continued until a definite "break" in the relation of fatigue time and

velocity is obtained indicating a true sustained capacity. From burst speed studies on trout, dace, and goldfish, Bainbridge (1960) thought that "by 20 seconds the low steady cruising speed seems generally to have been reached", whereas steady performance appeared to require up to 40 min for young sockeye (Brett *et al.*, 1958). Subsequently, Bainbridge (1962) extended the test period to 5 min and still obtained a levelling off in less than 60 sec; data for six trout which fatigued from 32 to 104 min are given but cannot be directly related to the shorter experiments. Swimming performance of immature Atlantic herring has been presented by Boyar (1961) and re-drawn as endurance curves by Blaxter and Holliday (1963). None of these reaches a terminal plateau.

A comparison of the results obtained by Bainbridge (1962) and those for sockeye are presented in Fig. 20. It is apparent that a change in the relation occurs between 0.2–0.4 min (12–24 sec) with a distinct alteration in slope, but not terminating the fatigue curve. Since the mean speeds are plotted in the upper curve involving different species, temperatures, and apparatus the individual records on rainbow trout are included in the lower curve (Bainbridge, 1962). These support the general relation showing the same inflection at about 0.3 min. To complete the fatigue curve the transition to a true sustained speed at about 300 min is included in the figure.

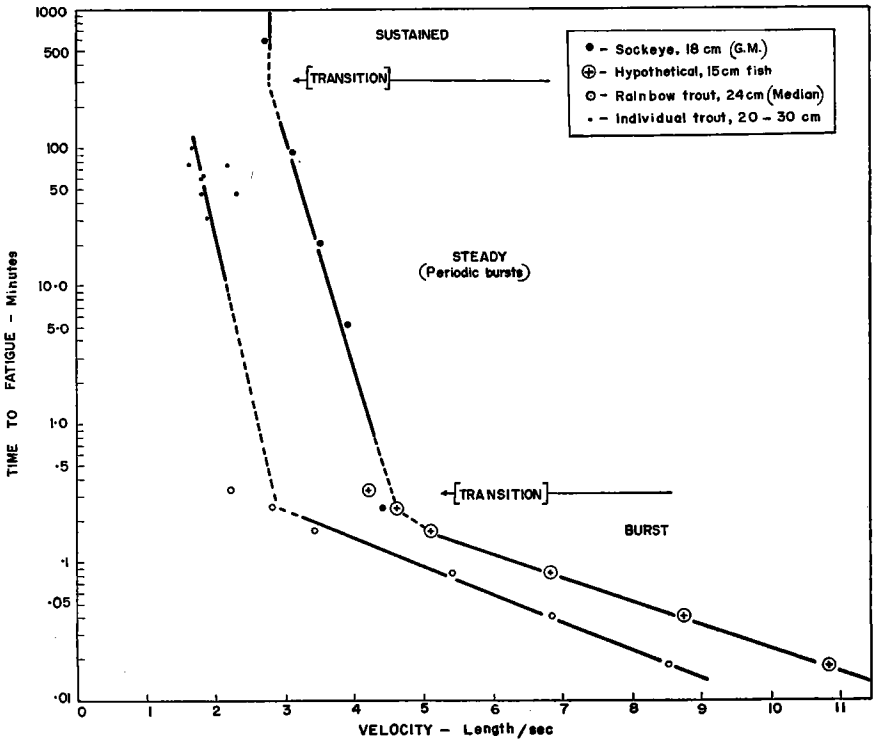

FIG. 20. Fatigue curve for yearling sockeye compared with results obtained by Bainbridge (1960, 1962). Two transition zones (broken lines) appear to exist where variability might be expected to be greatest.

It is very likely that these data represent three stages of availability of fuels for muscular contraction, interrelated with the limiting circumstances of accumulated by-products of anaerobic metabolism and the problem of oxygen supply to the tissues. The rapid fatigue phase (burst) would represent an exhaustion of the available cellular source of energy. The observation by Black *et al.* (1962) that muscle glycogen is reduced to less than one-half the resting level within 2 min with rapid elevation of pyruvate and lactate supports the basis for early collapse when maximum muscular effort is involved. Performance which can be steadily maintained for from 2 to 200 min is more likely to relate to the supply of metabolites delivered by the blood to the muscles and the capacity of the liver to maintain adequate levels from its reserves of glycogen. Hochachka (1961) has shown in a comparison of hatchery and wild trout that liver glycogen levels are dependent on recent feeding and "were reduced to very low levels during transportation" for planting. Finally, beyond 200 min a state of balance must exist between supply and demand, involving a continuous conversion of fat and protein to provide utilizable carbohydrate. This implies that circulation and respiration are not limiting. Indeed this is an obvious conclusion for sustained performance. The middle "link" would appear to be the critical phase where such systemic mechanisms could act as limiting factors.

It is apparent that for sockeye a reliable estimate of sustained speed could not be obtained under a test period of about 5 hr. This may not apply more generally but until explored in other species it remains as one of the reasons why such differences in reported "sustained" speeds occur. The values given for sockeye by Brett *et al.* (1958) were recorded for fork length. If these are converted to total length (by adding 6.4%) and expressed as speed in L/sec the relation for underyearlings (7.4 cm) and yearlings (15.4 cm) is seen in Fig. 21.

SIZE EFFECT. Since form changes with size, the combined effect can be tested by correlating speed with length (Table X). A significant negative correlation was obtained for three of the four acclimations; apparently as the fish grows its *relative* capacity to perform decreases. This was recognized by Bainbridge (1958) for burst speeds. The relation was more pronounced in goldfish than trout. Blaxter and Dickson's (1959) treatment of burst speeds in herring showed the relation between body length (L) and swimming speed (V) to be in the form $V = 7.6\ L^{0.94}$, indicating an almost direct dependence of speed on length. Using the same log–log relation Bainbridge (1960) obtained a variety of slopes for different sustained times (.5–20 sec) with a mean slope of 0.58 for trout. Similar determinations for sockeye using the 1-hr sustained speeds at 15°C resulted in a value of 0.49. There is a suggestion in the goldfish values (Bainbridge, 1960) that low values are associated with longer test times.

The conclusion is that large fish swimming for a long time would have a relatively low ratio of sustained speed to length (L/sec).

TEMPERATURE EFFECT. The effect of temperature on swimming speed, as indicated previously, has been subject to some conflicting reports. These have been resolved by the evidence for the relative temperature-independence of

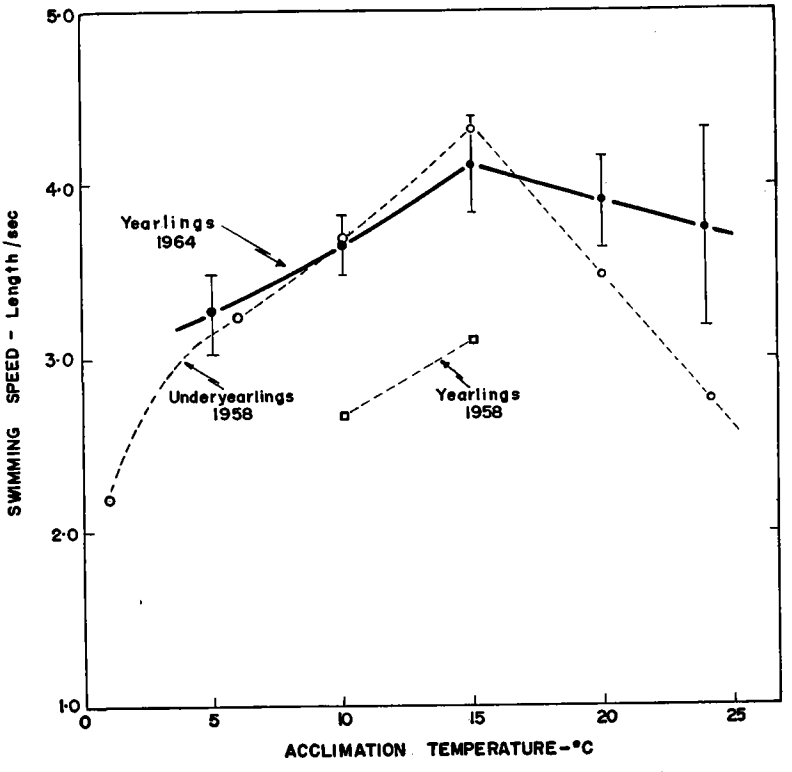

FIG. 21. Relation between swimming speed and acclimation temperature for sockeye tested in a rotating circular trough without an electric screen (1958), and in the respirometer (1964).

burst speeds. The temperature-dependent cruising speeds determined by Brett *et al.* (1958) at various acclimation temperatures have been plotted for comparison with the critical speeds obtained in the respirometer (Fig. 21). A Q_{10} of 1.4 applies to the effect between 5 and 15°C. Some differences exist but the general pattern of temperature effect is comparable. The differences pertain to lower performance (about 25%) among the yearlings tested in the circular trough.

TABLE X. Correlation coefficients between critical swimming speed (sustained for 60 min) and length, for various acclimation temperatures.

Acclimation temperature	Correlation coefficient	Significance
(°C)	(r_{xy})	(*P value*)
5	−.71	$P < .05$
10	−.51	$P \approx .1$
15	−.88	$P < .01$
20	−.86	$P < .01$

Underyearlings, however, achieved the same relative performance (L/sec) in the circular trough as the yearlings did in the respirometer for 5, 10, and 15°C. At lower and higher temperatures there was a significant reduction in the cruising speed, probably due to a behavioural difference requiring a stronger stimulus than was applied in the circular trough to achieve the performance induced in the respirometer.

GENERALIZED RELATIONS

Some of the factors which govern the rate of metabolism and set limits to its magnitude are apparent in the foregoing presentation. Earlier work on yearling sockeye set forth the limits which temperature sets for survival. Within these boundaries the metabolic rates for various levels of activity have been illustrated (Fig. 13). With the emphasis of the effect of activity on metabolism, the relation has been drafted on arithmetic axes in the form of Fig. 22. Upper and lower lethal temperatures provide the boundaries at the top and bottom of the figure. Limits of activity, from resting states to temperature-dependent critical speeds, provide the remaining boundaries, except for the apex which

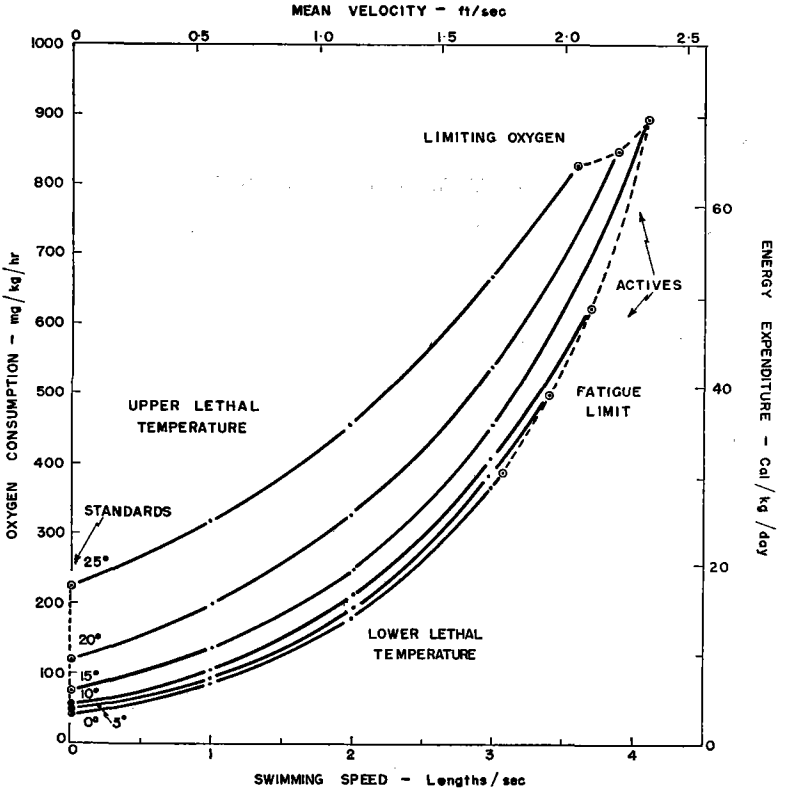

FIG. 22. General relation between oxygen consumption and swimming speed for yearling sockeye salmon in air-saturated fresh water, showing the factors governing the limits of performance.

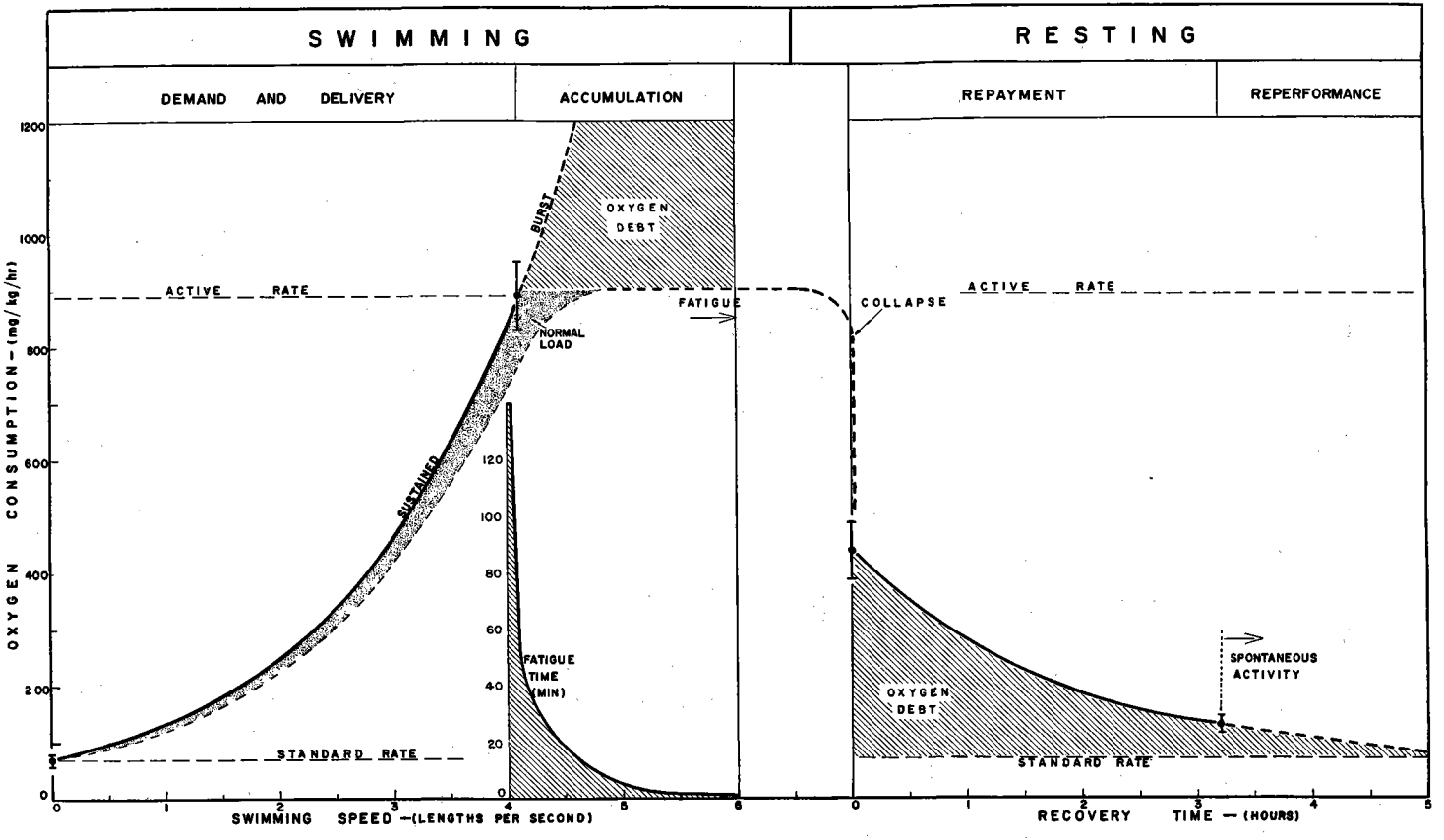

FIG. 23. General relation of oxygen consumption, swimming speed, fatigue time, oxygen debt, and recovery time for an 18-cm, 50-g yearling sockeye performing in air-saturated fresh water at 15°C.

appears to be limited by environmental oxygen. It is seen that *external* factors provide the limits on all sides except the fatigue boundary. It would appear that some temperature-dependent factor of *internal* origin is setting this limit. As has been suggested, in all likelihood this is the supply of metabolic fuels together with the influence of anaerobic products.

The interrelations of oxygen uptake, performance, fatigue times, and oxygen debt repayment are depicted in Fig. 23. Although derived from the total data and distilled into one figure, the relation is within the confidence limits obtained for 15°C-acclimated 50-g sockeye. Broken lines indicate the extrapolated path of increasing oxygen requirement above the active metabolic rate which forces the fish into a cumulative oxygen debt, inducing collapse. The length of time which the excessive rate can be maintained is defined by the fatigue curve. Following exhaustion, deep ventilation in the non-swimming fish for about 3 hr pays off the immediate oxygen debt leaving the fish free to commence spontaneous activity and to re-perform at a successful burst level again. It must be concluded that although the fish is unlikely to be back to resting levels of blood constituents, the capacity to re-perform certain swimming feats ensures a reinstatement of survival capacity.

SUMMARY AND CONCLUSIONS

1. The relation between respiratory metabolism and swimming speed in young sockeye salmon was found to be exponential, described by the general equation $Y = ae^{bX}$, where Y = rate of oxygen consumption (mg O_2/kg/hr) and X = speed (L/sec). The relation applied to all acclimation temperatures from 5°C to 24°C. Values for a ranged from 1.61 to 2.29, and those for b from 0.34 to 0.17.

2. At 5°C the standard metabolic rate was 41 ± 3.2 mg O_2/kg/hr which rose to 196 ± 13 at 24°C. From the basic equation ultimate minimum and maximum levels of 36 mg (0°C) and 200 mg (25°C) were derived, a maximum difference of approximately $5\frac{1}{2}$ times.

3. Active metabolism rose from 514 ± 31 mg O_2/kg/hr at 5°C to a maximum of 895 ± 49 mg O_2/kg/hr at 15°C, with some decrease at higher temperatures.

At temperatures up to 15°C active rates were about 10–12 times the standard level. Above 15°C the ratio fell to about 4 times the standard rate for an acclimation temperature of 24°C. The combined action of temperature and activity elevated respiratory metabolism by a factor of 22 times, equal to the influence of activity on metabolic rate in many mammals.

4. The general level of standard metabolism, supported by evidence from recent literature, is sufficiently below that reported in earlier literature to suggest that excitability has not been accounted for sufficiently to provide an accurate measure of the standard rate. In addition, the high active levels indicate that this parameter has possibly not been determined in its maximum expression. In consequence, calculations based on these indices could be in considerable error.

5. A near linear transformation for the effect of temperature on locomotor metabolism was obtained by relating the logarithm of the swimming requirement *less* the standard rate (locomotor scope) to acclimation temperature. The slopes of the lines decreased with increasing speed, approaching 0 at 4.2 L/sec.

It can be concluded that burst speeds of this level and above are virtually independent of temperature, placing the poikilotherm on a common basis with the homeotherm in this regard.

6. In air-saturated fresh water, oxygen became a limiting factor for active metabolism above 15°C in one group of yearling sockeye. In consequence any reduction in saturation could be expected to further reduce maximum activity above this temperature.

7. Within the range of weight studied (25–130 g) there was no significant correlation between weight and standard or active metabolism at any acclimation temperature, except at 15°C where, by including some underyearlings, a range of 8–130 g was provided. The slope of this line for standard metabolism was 0.88±.26. The error is such that a slope of 1 could apply throughout.

8. Despite a range in condition factor of 0.64–1.04, only the 15°C group showed a significant correlation between plumpness and active metabolic rate ($r = -.78$; $P = .02$).

Studies on the composition of the fish did not support an expected improved relation between weight and active metabolism by using dry weight minus lipid. A high negative correlation between the relative proportion of lipid and water ($r = -.84$; $P < .01$) provided a partial explanation for the results.

It can be concluded that wet weight was as useful a basis for expressing metabolic rate as either dry weight or dry weight minus lipid.

9. The rate of replacement of oxygen debt following fatigue was found to be exponential with time in the majority of cases. Irregularities occurred in the form of primary or secondary slumps. These were more frequent at temperatures of 20 and 24°C, where post-fatigue death occurred in from 10% to 40% of cases.

Time to return of spontaneous activity was 191±3.8 min, independent of acclimation temperature. At this stage of recovery successful re-performance of the fatigue velocity was possible.

10. The *extent* of debt sustained at the time of fatigue, however, was influenced by acclimation temperature, rising from 252±20 mg O_2/kg at 5°C to a maximum of 504±6 mg O_2/kg at 15°C.

This represents the "overload" debt replaced by the time of the start of spontaneous activity. Total debt, determined by extrapolation to standard metabolism, was about 30% greater. The difference was considered to represent the normal load, demonstrated by a determinable debt present at sub-fatigue velocities.

11. Fatigue curves determined at 10°C were linearized by relating the logarithm of the geometric mean time-to-fatigue to the swimming speed. Two breaks in the relation appear to exist, one between 200 and 300 min defining the

sustained speed and the other at about 20 sec (from data of Bainbridge) where only burst speeds occur.

The geometric mean fatigue time and time-to-50%-fatigue (FT_{50}) determined by plotting log time-to-fatigue against per cent fatigued (probits) were comparable. The latter approach provides a useful basis for comparative studies of performance under different environmental conditions and allows the use of data where not all the fish fatigue by the end of the test time.

ACKNOWLEDGMENTS

The extent to which it has been possible to make relatively rapid progress in these studies stems from the stimulation and consultation which Drs F. E. J. Fry and E. C. Black have continued to provide in the field of respiratory metabolism. The metabolic problems for Pacific salmon with their extensive migrations and consequent large energy demands have received increased attention as a result of Dr W. A. Clemens' efforts to provide for biochemical studies on energy expenditure. It is a pleasure to acknowledge these sources of inspiration.

The diligence and hydrodynamic insight of Mr John Mar of the Pacific Naval Laboratories brought the biological requirements for a tunnel respirometer into an effective, precision instrument. The excellence of the design continues to provide an unusual opportunity for research.

Throughout the many tedious hours of preparation, operation and recording required to obtain the data, Mr D. B. Sutherland has faithfully persevered in all technical matters. His ability and patience have meant much to the successful completion of the project.

The determinations of dry weights and lipid fractions were made by Mr C. T. Shoop, who also assisted in many of the statistical calculations. This help is gratefully acknowledged.

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APPENDIX

1 ft/sec = 0.305 m/sec = 0.682 mile/hr

1 cfs = 28.3 l/sec = 449 gal/hr

1 L/sec = 1 total fish-length/sec

1 mg O_2/l = 0.70 cc O_2/l = 1 ppm

1 Cal/kg/day = 12.9 mg O_2/kg/hr (assuming an average oxycalorific equivalent of 4.75 Cal/l O_2)

5°C = 41°F; 10°C = 50°F; 15°C = 59°F; 20°C = 68°F; 24°C = 75°F