Cost of Sustained and Burst Swimming to Juvenile Coho Salmon (*Oncorhynchus kisutch*)

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The relationship between oxygen consumption rate (milligrams per kilogram per hour) and sustained swimming speed (calculated from tailbeat frequency) was determined for 1.2-g juvenile coho salmon (*Oncorhynchus kisutch*) at 15°C. The data are best described by the following equation: log oxygen consumption rate = 2.2 + 0.13(body lengths·s^{-1}). This relationship is very similar to that extrapolated for sockeye salmon (*O. nerka*) of the same size, thus potentially enabling researchers to utilize the extensive sockeye data base to predict metabolic rates of coho. The oxygen consumption rate during burst swimming (9 body lengths·s^{-1}) was also determined. The burst swimming metabolic rate (38 000 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$) is nearly 40 times greater than the maximum sustained swimming metabolic rate.

On a déterminé la relation entre la consommation d'oxygène (milligrammes par kilogramme par heure) et la nage prolongée (évaluée d'après la fréquence des battements de la queue) chez les saumons coho (*Oncorhynchus kisutch*) juvéniles de 1,2 g à 15°C. La meilleure représentation des résultats de cette étude est l'équation log de la consommation d'oxygène = 2,2 + 0,13 (dimensions corporelles·s^{-1}). Comme cette relation se rapproche beaucoup de celle qu'on obtient par extrapolation pour le saumon nerka (*O. nerka*) de même taille, les chercheurs pourraient peut-être se servir de la banque de données très complète dont ils disposent sur ce poisson pour déterminer le métabolisme du saumon coho. On a également déterminé la consommation d'oxygène durant la nage d'accélération (9 fois les dimensions corporelles·s^{-1}). Le métabolisme durant ce type de nage (38 000 mg d'$O_2 \cdot kg^{-1} \cdot h^{-1}$) est presque 40 fois supérieur à la valeur maximum mesurée durant la nage prolongée.

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The standard and active metabolic rates of fishes have been studied extensively (reviewed by Brett and Groves 1979). This accumulated knowledge and refinement of technique has enabled researchers to determine the metabolic costs associated with such ecologically relevant activities as escape from predators, prey capture, migration, and territorial defense (Feldmeth and Jenkins 1973; Brett 1983; Feldmeth 1983).

We investigated the energetics of feeding territoriality in juvenile coho salmon, *Oncorhynchus kisutch*. Our ultimate goal was to relate field swimming speeds to laboratory-determined oxygen consumption data, thus enabling us to calculate activity energy budgets that would reflect natural stream conditions. In this paper we examine the relationship between swimming speed and oxygen consumption.

Fish use streambed heterogeneities, and possibly position in relation to other fish, to their hydrodynamic advantage (Feldmeth and Jenkins 1973; Weihs 1973). Thus, in the field, and in a simple respirometer, a water velocity measurement is insufficient as an indicator of swimming speed because the exact stream flow against which the fish is working is not known. Bainbridge (1958), working with trout (*Salmo gairdneri*), dace (*Leuciscus leuciscus*), and goldfish (*Carassius auratus*), determined the relationships between tailbeat frequency, tailbeat amplitude, total fish length, and swimming speed. Several other investigators repeated this work with various species and usually found a similar relationship (Hunter and Zweifel 1971; Smit et al. 1971; Webb 1975). Tailbeat frequency is a powerful tool for quantifying swimming speeds in unrestrained fish (Feldmeth and Jenkins 1973), and was used here.

We test whether the relationship between tailbeat frequency and swimming speed in juvenile coho is similar to that described by the general equation of Bainbridge (1958). We then examine the metabolic rates associated with sustained swimming (sensu Hoar and Randall 1978) at various speeds (calculated from measured tailbeat frequencies). Finally, we present data on the metabolic cost of burst swimming to underyearling coho salmon. The ability to accelerate quickly, and to maintain high speeds for a few seconds, is a critical part of fish locomotion. Juvenile coho salmon, for example, routinely "charge" at conspecifics during territorial defense. Despite its ecological importance, the metabolic cost of burst swimming has not been empirically investigated, although it has received extensive theoretical consideration (reviewed by Webb 1975; Hoar and Randall 1978).

Materials and Methods

Speed and Tailbeat Frequency

Fish taken from the Salmon River, Langley, B.C., in May 1980 were transported to the Bamfield Marine Station. The fish

were held as a group in well water for 1 wk before experimentation. A Brett respirometer (Brett 1964, 1965) was used, since it had been specifically designed to reduce wall effects, turbulence, and eddy formations, making it possible to equate swimming speed with water velocity.

Three fish, 40-mm fork length, were tested simultaneously in the respirometer to determine the relationship between water velocity and tailbeat frequency. Water temperature in the respirometer was 13 ± 0.2°C. (Statistical limits are reported as ±1 SD unless otherwise stated.) The test was repeated using the same group of fish on five different days. Fish were placed in the respirometer and allowed to acclimate by swimming at less than 6 $cm \cdot s^{-1}$ for 12–14 h. The water velocity was then increased to 24 $cm \cdot s^{-1}$ and after 15 min the tailbeat frequency was recorded. Velocity was increased in increments of about 3 $cm \cdot s^{-1}$ every 0.5 h until the fish could no longer swim against the current.

Tailbeat frequency was recorded using an overhead video camera, and tapes were later viewed in slow or stop motion. Ten tailbeats were counted at one to six different tape locations (i.e. replicates) depending on clarity of the record. The time elapsed was noted (from a stopwatch) and tailbeat frequency was calculated from these measurements.

A few samples of tailbeat amplitude were measured from the most outside lateral position of the caudal fin on one side of the body axis to the most outside lateral position on the other side. There was no significant difference between the tailbeat amplitudes measured at the different speeds within the range we considered. The mean amplitude was 0.88 ± 0.04 cm, giving a ratio of mean amplitude to total length of 0.20. (Fork length was converted to total length using the equation of Dahlberg et al. 1968) for juvenile coho.) In all conversions of tailbeat frequency to swimming speed, amplitude was assumed to be constant.

Sustained Swimming

A different, small Brett-type respirometer was designed to measure the cost of swimming to 40- to 60-mm fish. The experimental chamber consisted of a 27-cm-long, 2.3-cm-I.D. cylindrical glass tube with wire mesh at either end. The downstream mesh was electrified and delivered a 1- to 2-V shock to the fish upon contact. A piece of black tape was wrapped around the outside of the experimental chamber to act as a visual reference for the fish.

Tygon tubing connected the experimental chamber to a 93-W centrifugal water pump and to an air-saturated water box. The pump was connected to a rheostat making it possible to alter water velocity. Temperature and oxygen probes were inserted into PVC ports in the tubing section which passed through the box. Snapping apart tubing connectors inside the box opened the system. The entire respirometer (total volume = 440 cm^3) and the water box were submerged in a large water bath for precise temperature control (15 ± 0.3°C).

Each fish was allowed to swim at a low speed overnight and then the velocity was increased to just less than 1 $L \cdot s^{-1}$ (body lengths per second, judged from tailbeat frequency) for 3 h before an experiment began. The respirometer was then closed for 30–45 min while the metabolic rate and tailbeat frequency at this speed were determined simultaneously. The respirometer was opened and flushed with air-saturated water for 15 min. Water velocity was then increased by increments of approximately 0.7 $L \cdot s^{-1}$ until no further pump output was possible, oxygen consumption being measured in 30- to 45-min periods separated by 15-min reoxygenation periods. All oxygen consumption rates represent total consumption minus a blank (oxygen depletion in the absence of a fish). Swimming activity was recorded on video tape, and the tapes were later reviewed to determine the tailbeat frequencies associated with each oxygen consumption datum. At the end of an experiment the fish was removed from the respirometer, anesthetized, weighed, and measured (fork length). Average fish size was 4.9 ± 0.18 cm (fork length) and 1.2 ± 0.14 g (wet weight). A total of 81 oxygen consumption measurements were made on 14 different fish collected in 1980 on the Salmon River.

Burst Swimming

During June and July 1981, coho fry were collected from the Salmon River and held separately in visually isolated aquaria for at least 1 wk before experimentation. The light regime was 16 h light : 8 h dark at 150 lx. The water temperature was kept at 15 ± 0.2°C. Fish ate brineshrimp three times per day (at irregular intervals) for a total ration of 3% body weight per day.

The respirometer used in the sustained swimming experiments was also used for these burst swimming experiments, but with the following alterations: (1) a peristaltic pump reduced the total respirometer volume to 240 cm^3 (exps. 1–8) or 294 cm^3 (exps. 9–19), (2) a feeding port was added to facilitate stimulus introduction, and (3) the experimental chamber was increased in length to 39 cm (exps. 1–8 (27 cm)). The potential charge distance (black tape to front of chamber: 22 cm) was the same in all experiments.

An experiment refers to a full day of measurements. The first experiments consisted of a test sequence: subsequent experiments consisted of both a test and a control sequence. Each sequence consisted of five trials. During each trial, which lasted about 0.5 h, the decreasing oxygen concentration was measured by the in-line oxygen probe whose output was recorded graphically. At the end of a trial, oxygen-saturated water was circulated through the system until saturation values were reestablished (about 15 min). In experiments 9–12, the control sequence preceded the test sequence; the sequences were later reversed when a bias was suspected.

An idealized experiment is diagrammed with hypothetical results shown on two different scales (Fig. 1). The top scale depicts the oxygen concentration measurements as recorded over time by the chart recorder. The lower scale depicts the oxygen consumption rates (minus a blank) derived from the upper scale oxygen concentration measurements. Preliminary studies indicated that blanks remained constant throughout experiments and therefore these were measured only at the end of each experiment.

The experiment began when a coho fry was anesthetized lightly with MS-222 and placed into the respirometer the night before the measurements. Once the fish appeared calm, it was fed brineshrimp and trained to avoid the electrified grid. The fish in these experiments were never starved but kept on a 3% body weight ration, even in the respirometer. The daily ration was divided into three equal portions. The first portion was given just after the lights were turned on in the morning. A second portion was delivered to the fish during the first trial of the test sequence (T1) and a third portion delivered during the first trial of the control sequence (C1). To increase the number of charges possible from one portion, small brineshrimp were used; on average, about 15 brineshrimp made up one portion.

After the fish had learned to avoid the shocking grid it was left

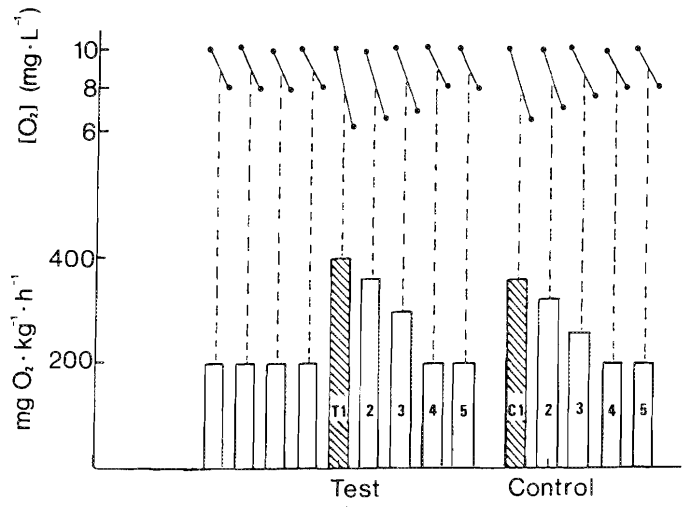

FIG. 1. Sequence of events in a hypothetical burst swimming experiment diagrammed with idealized results. Oxygen consumption rates (lower scale) were calculated from oxygen concentration data (upper scale). Test and control sequences (each consisting of five trials) are also shown, and hatched trials indicate that brineshrimp were delivered to the fish causing either burst swimming (T1) or nonburst swimming (C1).

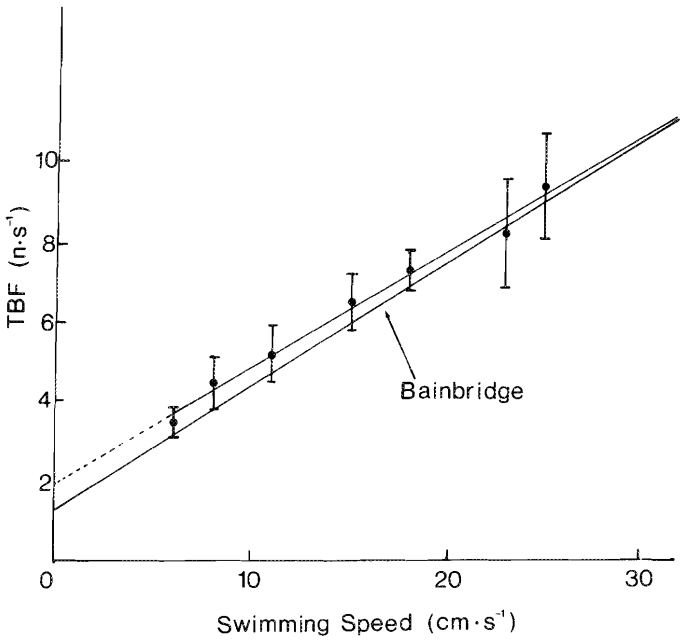

FIG. 2. Mean (±2 SD) tailbeat frequency (TBF) and swimming speed (water velocity) for three 40-mm coho. The upper line is the least squares regression ($r = 0.99$, $P < 0.01$). The lower line was calculated from Bainbridge's (1958) equation. One body length per second is approximately equal to 4.5 cm·s^{-1}.

undisturbed for 6–8 h. In the morning, the lights went on and the fish was fed. Two to four trials were then conducted to establish the baseline metabolic rate (BR) of the fish while it swam slowly behind the black tape. During T1, a single brineshrimp was forced through a syringe needle into the submerged, stoppered feeding port. The shrimp was moved by the water current into the upstream end of the experimental chamber. As the brineshrimp entered the chamber, the fish immediately became aware of its presence, charged at it, consumed it, and then returned (usually by gliding) to its former holding position behind the black tape. Once it had regained this position, other brineshrimp were introduced to the fish sequentially until all 15 shrimp had been eaten. The next four trials (2–5) reflect the oxygen consumption of the fish as it swam slowly behind the black tape (no brineshrimp offered) and were meant to measure oxygen debt caused from the burst swimming activity in T1. (All calculations of charge cost include the time between trials (used to reestablish oxygen saturation) by extending the mean oxygen consumption rate through the subsequent 15-m period.)

During C1, the fish was cued to a forthcoming feeding: 0.1 cm of freshwater, in which many brineshrimp had recently lived, was forced through a syringe needle into the feeding port. This stimulus caused the fish to move slowly to the upstream end of the experimental chamber. Immediately following the stimulus, 15 small brineshrimp were forced through the syringe needle into the feeding port of the respirometer. These tended to form a loosely defined clump and were eaten individually, or in clumps, immediately as they entered the experimental chamber. During the rest of the control sequence, the fish swam routinely behind the black tape. Thus, the behavior of the fish during the control sequence was similar in all respects, except charging, to their behavior during the test sequence. (A few charges sometimes occurred during C1 if the fish missed one of the shrimp the first time around and then charged at it as it entered the experimental chamber for the second time.) Any difference in oxygen consumption between control and test sequences can thus be attributed to the larger number of charges during T1.

At the end of the day, the fish was removed from the respirometer. After a 24-h starvation period, it was anesthetized, weighed, and measured (fork length). We completed 19 experiments using 14 different fish.

We used an overhead video camera to film fish activity and later viewed the tapes in slow motion to determine charge speed (average distance travelled over time during T1 from two experiments, $n = 25$).

Results

Speed, Tailbeat Frequency, and Sustained Swimming

We found no significant difference between the regression line fitted to our data relating swimming speed and tailbeat frequency and the curve for the same size fish derived from Bainbridge's (1958) equation (Fig. 2), supporting the application of this equation to convert tailbeat frequency to sustained swimming speed in juvenile coho salmon. The curve in Fig. 2 is only useful above 3 beats·s^{-1}. Caudal propeller efficiency apparently drops quickly at low speeds and fish switch to using their pectoral fins for locomotion (Hunter and Zweifel 1971).

The sustained swimming metabolic rate data set is described by an exponential model ($\log O_2$ consumption rate = $\log a + b$(speed)). The mean regression coefficients describing the 14 individual experiments are 2.2 ± 0.18 ($\log a$) and 0.14 ± 0.03 (b). We pooled these data (Tytler 1969; Smit et al. 1971) and calculated a mean line of best fit: $Y = 2.2 + 0.13X$ (Fig. 3).

Burst Swimming

The burst swimming (test) sequence is more costly than the control sequence (Table 1), as easily seen when these data are plotted (Fig. 4). The cost per charge was calculated as the difference between the areas under these two curves (80 mg O_2·kg^{-1}) divided by the mean net number of charges (the number of charges during T1 minus the number of charges

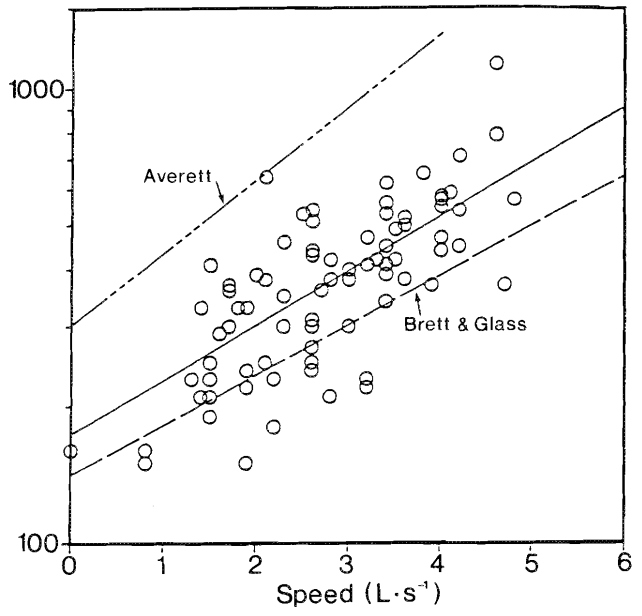

FIG. 3. Sustained swimming metabolic rates for juvenile coho from our data (circles and solid line) and those of Averett (1969) (upper broken line). Each datum represents one oxygen consumption rate determination at a given speed (calculated from tailbeat frequency). The lower broken line is an extrapolation of Brett and Glass' (1973) equation for sockeye. All regression lines are for 1.2-g fish at 14–15°C.

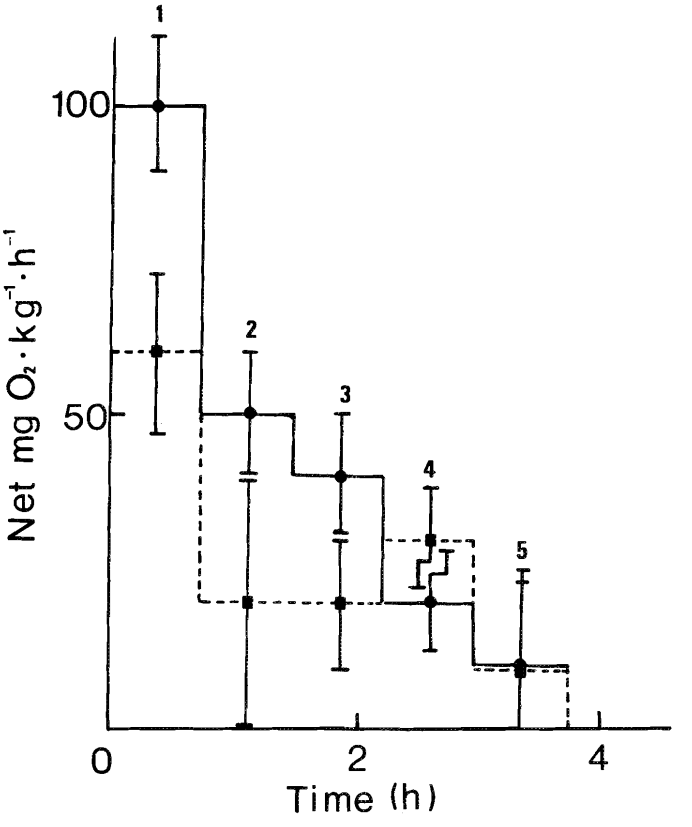

FIG. 4. Net burst oxygen consumption rates ($\bar{x} \pm 1$ SE) as a function of time from the start of the test (solid line and circles) or control (broken line and squares) sequence. Trial number is indicated above each pair of means.

using C1 (usually 1 or 2)). The average net number of charges was 14. Thus, the estimated cost per charge is 80/14 = 5.7 mg $O_2 \cdot kg^{-1}$.

The values for T1 were higher when the control sequence was run first ("C" under Exp. No., Table 1) than when it was not. This difference is significant ($t = 2.95$, $P < 0.01$). A second estimate of cost per charge of 5.0 mg $O_2 \cdot kg^{-1}$ is obtained if this "C" first group is excluded from the T1 column mean. The values for the "C" groups listed under other columns (test or control sequences) are not significantly different from the rest of the values.

The second estimate is probably the most accurate, since higher estimates may include excitement. For example, the control-first oxygen consumption rates were thought to be high even during the experiments, and this was part of the motivation for changing to the test sequence first. In general, the fish displayed considerably more excitement if they were fed many brineshrimp at once (as in C1) followed by brineshrimp fed singly (as in T1). Control-first fish tended to take longer before returning to the black tape holding position between individual shrimp feedings and to make more irregular movements. It appears that two regular 4-h feedings were sufficient to cue the fish to expect another clumped feeding in 4 h. Having the test sequence first tended to prevent any such cueing. Brett (1976) showed that fish can readily be trained to expect food and that they show an immediate metabolic rate increase under such circumstances. Before we used a fish in an experiment, it was fed three times daily but not at regular times, to avoid such problems.

Metabolic rate during a charge can be calculated from the cost per charge and the average charge duration of 0.48 ± 0.15 s as 43 000 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ (estimate No. 1) or 38 000 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ (estimate No. 2). The average distance travelled per charge was 18.8 ± 3.08 cm. The average speed was therefore 39 cm·s^{-1} + 4.5 cm·s^{-1} (water velocity) = 43.5 cm·s^{-1} (9 L·s^{-1}).

Discussion

Juvenile coho salmon defend feeding territories soon after emerging from the gravel streambed. The fish search from stationary swimming positions, facing upstream. Prey items from the drift float past the salmon and they dart out to pursue these prey or to fend off intruders. The metabolic cost of this activity likely influences the overall growth and fitness of salmon.

In this portion of our study on the energetics of feeding territoriality we have reported burst swimming metabolic costs and sustained swimming metabolic costs as a function of swimming speed (calculated from tailbeat frequency). The data relating swimming speed and tailbeat frequency are in good agreement with the general equation derived by Bainbridge (1958). We have used this relationship to convert both laboratory (this study) and field (Puckett and Dill 1985) measurements of tailbeat frequency to swimming speed.

The plot of oxygen consumption rate as a function of swimming speed (Fig. 3) demonstrates that there is considerable scatter in the data. Excitement (this need not be observable) could lead to an overestimate of low velocity values whereas anaerobic metabolism at medium and high velocities would underestimate these values. Juvenile coho are easily excited (Brett et al. 1958; Averett 1969) and anaerobic metabolism contributes to the energy utilized at intermediate and prolonged speeds (Beamish 1978; Wokoma and Johnston 1981; Duthie

TABLE 1. Oxygen consumption rates during and after burst swimming. The "C" under "Exp. No." indicates that the control sequence was run first; control sequences were not run until experiment 9. Experiments 1 and 2, 5 and 6, and 7 and 8 are duplicate pairs, run on the same day. "Charges" listed are those counted during the first trial of test sequence (T1) minus those counted during the first trial of the control sequence (C1). Baseline metabolic rates (BR) represent total oxygen consumption ($mg \cdot kg^{-1} \cdot h^{-1}$) before T1 or C1. All other metabolic rates represent net consumption (total metabolic rate minus BR).

Exp. No.	WT (g)	Length (mm)	No. of charges	Test sequence BR	T1	2	3	4	5	Control sequence BR	C1	2	3	4	5
1	1.1	48	14	190	90	80	40								
2	1.1	48	14	230	140	40	0								
3	1.2	49	12	220	60	90	100		−80						
4	1.2	49	10	210	140	20									
5	1.2	48	16	180	80	50	50	40	0						
6	1.2	48	17	180	80	70	40	0							
7	1.2	49	14	180	100	120	50	30	70						
8	1.2	49	14	230	80	−30									
9 C	1.1	48	15	170	90	30	20	20		120	130	60	70	40	
10 C	1.1	47	20	200	160	80	50	10		250	20	−70	−30		
11 C	1.1	47	21	120	130	100	60	50		150	70	70	0		−20
12 C	1.1	48	17	200	200	20	30	50	10	200	60	−10	50	0	
13 E	1.3	50	14	140	30	20	−40	−20	−20	120	20	20			
14 C	1.0	48	11	290	160	−10	30	−20	20	260	80	70		50	30
15 E	1.2	50	14	150	70	50	−20	0	0	150					
16 E	1.2	50	13	130	50			0	40	130	50		−10	50	
17 E	1.6	53	13	160	70	30		−20	20	170	30	50	20	30	
18 E	1.3	51	8	110	100		80	50		160	50		30	30	30
19 E	1.2	50	15	110	160		50	70		200	100	−60		10	
Mean	1.2	49	14	180	100	50	40	20	10	170	60	20	20	30	10
SD	0.12	1.47	3	50	50	40	40	30	40	50	40	60	30	20	30

1982; Jones 1982). The combined effect of these two factors would be to underestimate the slope and overestimate the intercept.

Figure 3 also compares our data with extrapolated relationships from the work of Brett and Glass (1973) on sockeye (*Oncorhynchus nerka*) and Averett (1969) on juvenile coho. Because there is no significant difference in the slope, or the *y*-intercept, between Brett's relationship and ours, we suggest that there is little difference between juvenile coho and juvenile sockeye metabolism, at least at this one fish size and water temperature. We cannot explain the discrepancy between our data and those reported by Averett (1969).

Several factors in the burst swimming experiments reduce the precision of the cost estimate, including the use of food as the charge stimulus and the aerobic measurement technique. For example, although burst swimming is anaerobic (Jones 1982), oxygen consumption was measured as the indicator of cost (see Brett 1964). Measurements of oxygen debt assumes that all lactate produced during the anaerobically powered activity is subsequently oxidized to carbon dioxide and water or converted to glucose in the presence of oxygen, but not excreted (Beamish 1978). Unfortunately, the exact fate of lactate in fishes is not known. Nevertheless, oxygen debt should be a reasonable indicator of the minimal cost of burst swimming in our experiments, since (1) salmon are not hypoxia adapted, (2) the ambient oxygen concentration was near saturation at all times, and (3) the activity was of short duration (less than 15 s total) and the oxygen measurement period was long (4 h).

The metabolic cost of burst swimming has not been determined empirically until now, but estimates based on power–performance data sets do exist (Brett 1970, 1983). These estimates are calculated by extrapolating experimentally determined relationships between swimming speed and oxygen consumption to burst swimming speeds. The estimates vary greatly and the value presented in this paper (38 000 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$) is about 5–20 times greater than extrapolated values (including our own) for small coho. Fast start acceleration is thought to be very inefficient (Webb 1982) and our data support this argument.

Our estimate of the metabolic cost of burst swimming seems surprisingly high until one considers the number of charges at this rate that would be necessary to double the routine metabolic rate of a fish in the field. Suppose that a juvenile coho has an average routine activity cost of 350 mg $O_2 \cdot kg^{-1} \cdot h^{-1}$ (Puckett and Dill 1985). In a 16-h day the fish would consume 5600 mg $O_2 \cdot kg^{-1}$. The cost per charge is 5 mg $O_2 \cdot kg^{-1}$. To double the daily activity cost the fish would need to charge 1120 times (every 51 s). Even including feeding motions this is unlikely. In fact, territorial fish charge only about 12 times per hour (9 foraging plus 3 aggressive), resulting in only 192 charges in 16 h (Puckett 1983).

Furthermore, 14 consecutive bursts increased the routine metabolic rate by only about 30% for the 1st h. The scope for activity is far larger than this so that the fish can be repaying the glycogen debt and still remain very active aerobically. In addition, young coho have a greater aerobic capacity than adult fish (Giles and Randall 1980) and this may help them cope with the large cost of territorial activity.

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