Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics

Scott G. Hinch and Peter S. Rand

Abstract: We used electromyogram (EMG) radiotelemetry to assess swimming activity (e.g., swim speeds), behaviour, and migration speeds (e.g., ground speeds) of individual adult sockeye salmon (*Oncorhynchus nerka*) migrating through several reaches of the Fraser and Nechako rivers in British Columbia. Using a laboratory swim flume and volitionally swimming adult fish carrying EMG transmitters, we developed relationships between EMG pulse intervals and swim speeds. A bioenergetics model was used to estimate reach-specific energy use per metre for each individual based on the average swim speed, migration time, body size, and river temperature. Migration was most energetically efficient (i.e., migration costs per unit distance traveled were relatively low) for females compared with males, large males compared with small males, and 1995 males compared with 1993 males. In all three cases, differences in swim speed patterns were primarily responsible for differences in energy use. For both sexes and in both years, migrations through reaches that contained a constriction (caused by an island, gravel bar, or large rock outcropping) were energetically inefficient compared with that through reaches with no constrictions. The high energetic costs at constrictions seem to result from long travel times probably caused by turbulent flow patterns that may generate confusing migrational cues.

Résumé : Nous avons utilisé la radiotélémétrie avec électromyogramme (EMG) pour évaluer l'activité natatoire (p. ex., vitesses de nage), le comportement et les vitesses de migration (p. ex., vitesses sol) de saumons rouges (*Oncorhynchus nerka*) adultes migrant dans plusieurs portions du Fraser et de la Nechako, en Colombie-Britannique. Nous avons fait nager librement des poissons adultes portant des émetteurs EMG dans un rapide de laboratoire pour établir une relation entre, d'une part, les intervalles entre impulsions et, d'autre part, les vitesses de nage. Nous avons utilisé un modèle bioénergétique pour estimer l'utilisation d'énergie par mètre dans les différents tronçons des cours d'eau pour chaque individu à partir de la vitesse de nage moyenne, du temps de migration, de la taille des individus et de la température de l'eau. L'efficacité énergétique de la migration était plus grande (c'est-à-dire que les coûts de la migration par unité de distance franchie était relativement faibles) chez les femelles que chez les mâles, chez les gros mâles que chez les petits mâles et chez les mâles de 1995 que chez les mâles de 1993. Dans les trois cas, les différences dans l'utilisation de l'énergie étaient principalement attribuables à des différences dans les profils des vitesses de nage. Chez les deux sexes et dans les deux années, l'efficacité énergétique dans les migrations qui se déroulaient dans les tronçons comportant un étranglement (du à la présence d'une île, d'un banc de gravier ou d'un gros affleurement rocheux) était inférieure à celle observée dans les migrations dans les tronçons dépourvus d'étranglement. Les coûts énergétiques élevés associés aux étranglements semblent être liés à un allongement du temps de passage, probablement causé par la turbulence des eaux qui peut rendre confus les signaux migratoires.

[Traduit par la Rédaction]

Introduction

The upriver spawning migration of adult Pacific salmon can be energetically expensive. Many stocks travel extremely long distances (i.e., over 1000 km) and, because feeding stops prior to migration, all must rely on stored energy. Based on analyses of body composition before and after spawning migrations, swimming activity by long-distance migrants usually depletes 75–95% of body fat (reviewed in Brett 1995). Despite a fairly good understanding of the total energetic costs of spawning migration for several stocks of Pacific salmon, we know relatively little about the swim speeds and behaviours that are responsible for the depletion of body energy associated with migration. Such studies are needed if we are to understand ecological and evolutionary aspects of the energetics of anadromous fish migrations.

From a fisheries management perspective, understanding habitat-specific swim speeds is critical for discerning river reaches that may prove difficult for fish migration. River reaches with high-velocity and turbulent flows may impose large energetic costs on upriver migrants (Hinch et al. 1996) and could substantially reduce the limited stores of energy

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available for successful migration and spawning. The placement of fish passage structures by management agencies could be aided by identifying sites where swim speeds and travel times are high.

There are several approaches that have been used to estimate in situ swim speeds of adult fish. Tail beat frequencies, recorded from visual observations, have been converted to swim speeds using laboratory swim tunnel relationships between tail beat frequency and swim speed (Feldmeth and Jenkins 1973). Upstream migration speeds, also measured by visual observation, have been converted to swim speeds by adding them to downstream flow speeds (Ellis 1966); proper use of this technique assumes that investigators can determine the exact flow speeds encountered by fish and the drag on the fish imposed by the currents, both of which are difficult tasks. More recently, underwater video systems that incorporate stereogrammetric imaging techniques have been used to directly measure swim speeds (Krohn and Boisclair 1994). However, all of the above approaches require that fish pass close to fixed observation sites and that water clarity is good, conditions that do not normally prevail for anadromous fish migrating up large river systems. Furthermore, these approaches are not practical for making continuous observations of fish, as they migrate long distances through diverse habitats.

An alternative approach to direct observations is physiological telemetry which has been used to examine activity levels and other correlates of oxygen consumption in adult fish (reviewed by Lucas et al. 1993). In particular, electromyogram (EMG) telemetry has proven to be effective for examining continuous swimming activity, over large spatial scales, of lake sturgeon (*Acipenser fulvescens*) (McKinley and Power 1992), sockeye salmon (*Oncorhynchus nerka*) (Hinch et al. 1996), and bass (*Micropterus* spp.) (Demers et al. 1996). However, EMG measures of swimming activity have not been used to describe patterns of swim speeds in the field or the energy use associated with these swim speeds.

The main objective of our study was to evaluate the role of local river features (e.g., bank morphology, current complexity) and fish characteristics (e.g., size, sex) as contributors to variability in swim speed, migration speed (i.e., travel rate), and energy use. We accomplished this in two steps. First, we developed a relationship in the laboratory whereby swim speeds of migrating salmon could be estimated from EMG radiotelemetry signals. Second, we carried out a multiyear field study in which sockeye from one Fraser River stock were radio tracked through sections of their 1200-km migration; for each fish, we determined swim and migration speeds with EMG telemetry and estimated energy expenditure using a bioenergetics model.

Methods

Laboratory study

A description of the EMG radio transmitters and specific details about their surgical implantation are outlined in Hinch et al. (1996). EMG electrode tips were positioned about 1.0 cm apart from each other, secured below the dorsal fin in the lateral red muscle which is used primarily in steady, nonbursting aerobic swimming (George 1962). These electrodes appear to also be sensitive to contractions of the relatively larger white muscle (McKinley and Power 1992; Hinch et al. 1996) which is recruited primarily during burst, anaerobic swimming. EMG signals should therefore be associated with tail beat frequency.

To quantify the relationship between swim speeds and EMG signals, we constructed a spontaneous swim chamber at the Canadian Department of Fisheries and Oceans' Cultus Lake Laboratory by modifying a fibreglass fish tank (300 cm length, 85 cm width, 45 cm depth). A plexiglass sheet (115 cm length, 85 cm width) was positioned at one end of the tank, sloping downward at a 20° angle from the top of the end wall to the centre of the tank bottom. Cultus Lake water (15°C) entered the chamber at the end with the plexiglass sheet via four 2.5-cm pipes passing through honeycomb-shaped flow straighteners before pouring onto the inclined plane and then flowing across the flat bottom and exiting through holes on the far wall.

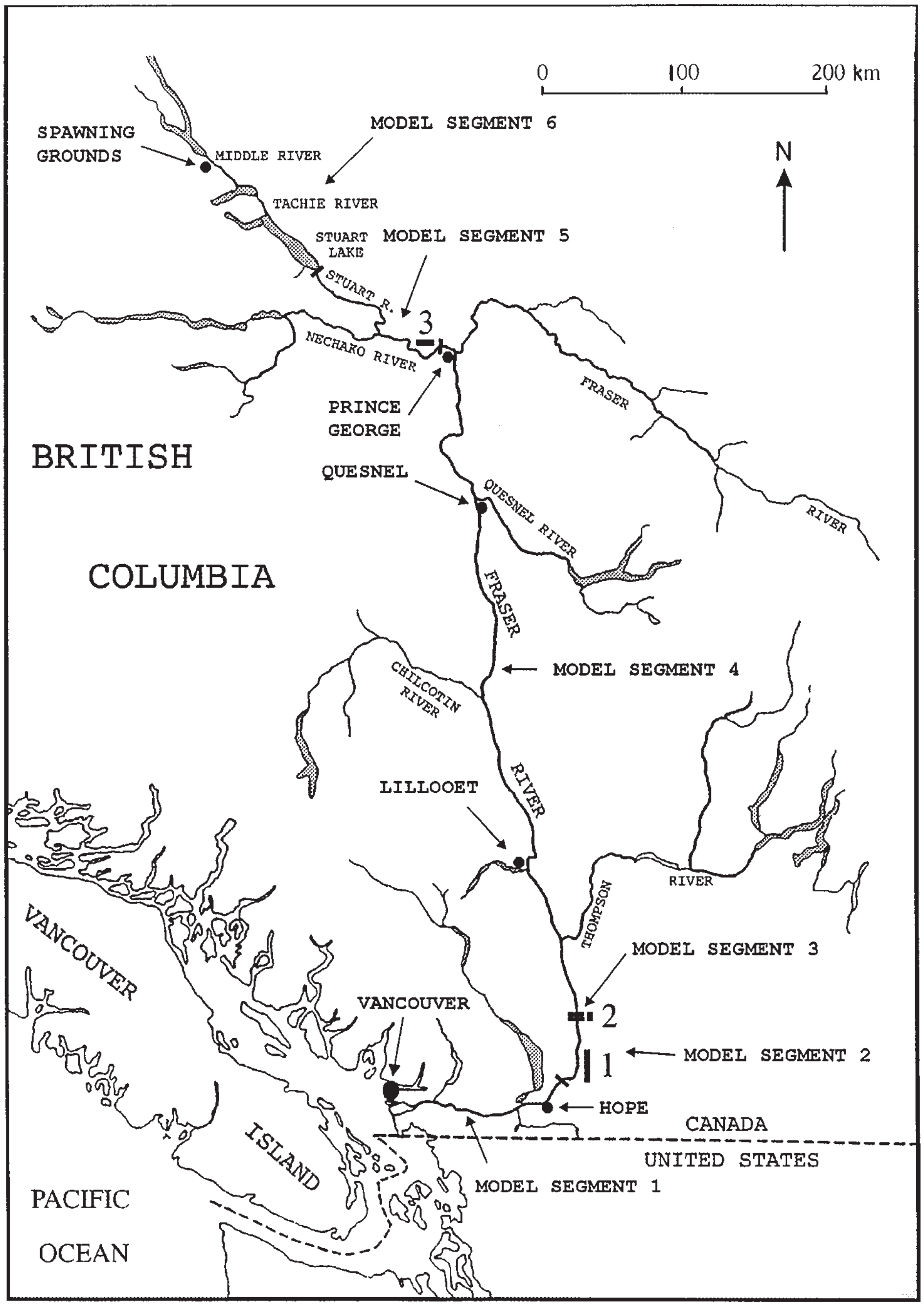
In August and September 1995, adult Fraser River sockeye were captured at two locations (Hell's Gate fishways and Sweltzer Creek, 180 and 100 km upriver from Vancouver, B.C., respectively) and transported to the laboratory where they were held at 15°C. Four males and four females (mass 1.4–3.9 kg, fork length 53.0–69.1 cm) were implanted with transmitters. Swim chamber trials were conducted after at least 1 day had past since surgery. A trial consisted of placing a fish in the chamber and allowing it to swim volitionally for 2 h. The chamber was large enough to permit unimpeded swimming, and preliminary trials showed that nearly all volitional swimming movements were towards or up the inclined plane. Further, preliminary trials demonstrated that sockeye would exhibit a complete range of swim speeds in this chamber. Typically, fish would swim rectilinearly up the incline and could attain swim speeds that were far greater than the flow speeds. The angle and smooth surface of the plane would result in fish swimming "in place" on the plane. Slow-swimming fish would remain in position at the bottom of the plane whereas fast-swimming fish may maintain, for a short period of time, a position near the top of the plane.

A video camera with a wide-angle lens was positioned 150 cm above the swim chamber. It was connected to a video image splitter and a time-lapse VCR. Another video camera, which was also connected to the image splitter, was positioned facing the LED screen on the front of the EMG signal data logger. The resultant video image recorded an EMG pulse interval (EMGPI) in one corner of the video image with the remaining area of the image occupied by the swim chamber (see Hinch et al. (1996) for a detailed description of EMGPI). We viewed the videotapes in slow motion and located all instances when fish were swimming straight into the flow and were being propelled by a complete tail beat (i.e., one complete oscillation of the caudal peduncle); observations were not considered if fish were near a wall or not swimming rectilinearly. We transcribed the EMGPI that accompanied the initiation of a tail beat, counted the number of video images to complete a tail beat, and were able to determine tail beat frequency (TBF) because 60 video images were recorded per second. Linear regression was used to describe associations between TBF and EMGPI.

Field study

Adult sockeye salmon from the early Stuart stock, enroute to spawning regions 1000 km upriver from the ocean, were radio tracked with EMG telemetry through three sections of their migration (Fig. 1). These sections were chosen to reflect the variability in river habitat encountered by early Stuart sockeye, the first sockeye stock to migrate up the Fraser each year. The start of the first section was situated at Yale, B.C., 150 km upriver from the Fraser River mouth. This section was 7.6 km in length and was divided into 10 contiguous reaches based on river bank features (e.g., the presence of constrictions, large bends, or straight parallel banks). Reach length, measured along the river centre from 1:4000 air photographs, ranged from 200 to 1100 m; maximum width within each reach ranged from 50 to 500 m (see Fig. 2). The first two reaches were situated immediately before the start of the Fraser River Canyon and had an average gradient of 75 cm·km^{-1}; the remaining reaches, with an average gradient of

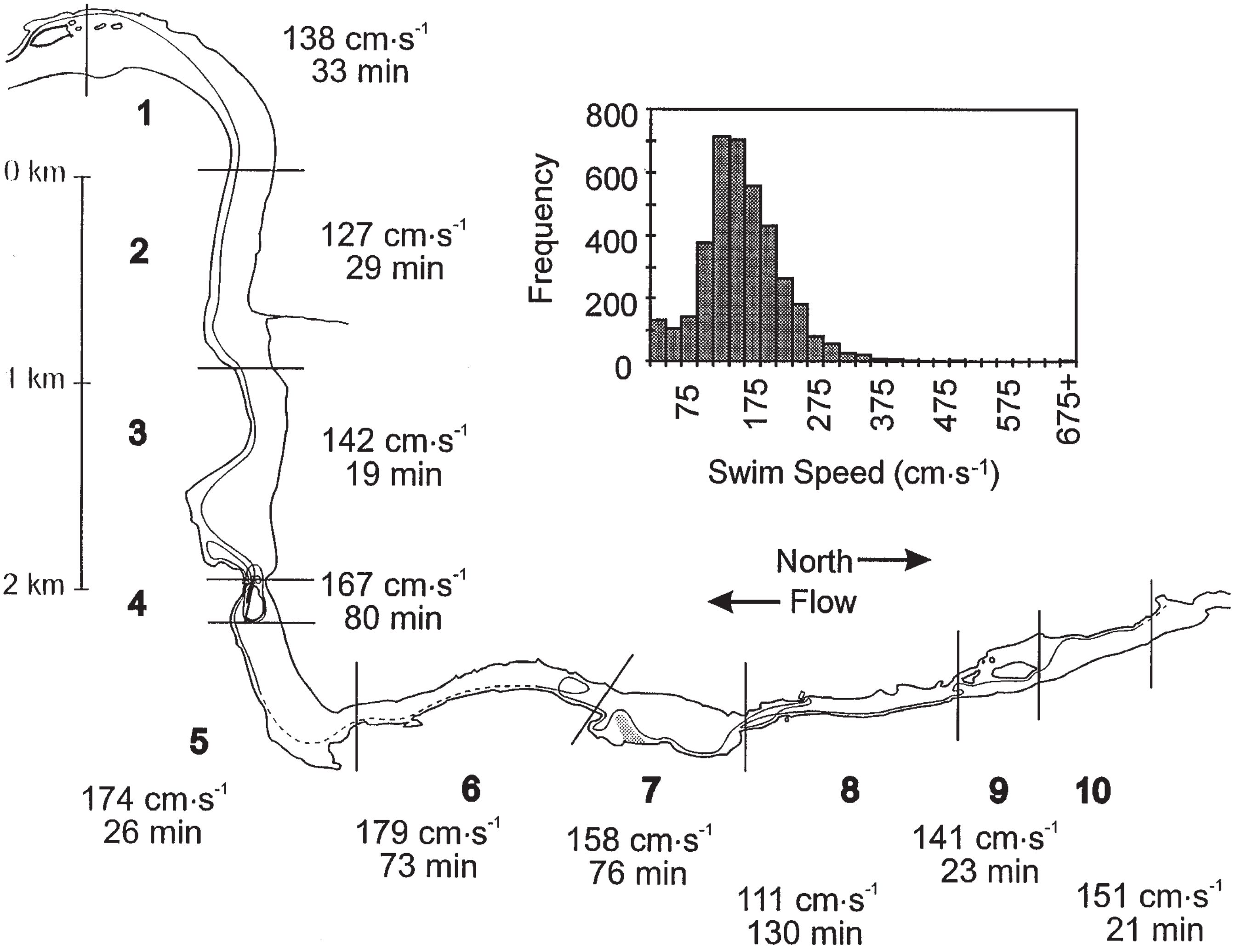
Fig. 1. Map of the Fraser River, its main tributaries, and the main juvenile sockeye salmon rearing lakes in the Fraser watershed. Our study population migrates north in the Fraser River and then west in the Nechako and Stuart rivers. They spawn throughout the region north of Stuart Lake but primarily in tributaries of the Middle River. The three river sections through which fish were radio tracked are indicated with numbers and solid bars next to the rivers. The Hell's Gate fishways are located in section 2. Model segments are delineated by bars that bisect the migration route; these segments apply to the bioenergetics model constructed in Rand and Hinch (1998).



120 cm·km^{-1}, were in the Fraser River Canyon and were more variable in their river bank morphology than reaches 1 and 2. Section 2 was situated at the Hell's Gate fishways, 180 km upriver from the Fraser River mouth near the end of the Fraser River Canyon (Fig. 1). We focused sampling on a 100-m reach located immediately downriver of the fishway entrances. It comprised steep canyon walls that were 120 m apart at the start of the reach which tapered to 30 m at a peninsular rock outcropping located a few metres before the main-level fishway entrance. A physical description and diagram of the Hell's Gate fishways are provided in IPSFC (1950). Section 3 comprised two noncontiguous reaches, both with straight and parallel banks, situated 17 and 21 km west of Prince George, B.C., respectively (Fig. 1). Their gradient was 120 cm·km^{-1}. The first was 500 m long with banks 50 m apart and the second was 100 m long with banks 100 m apart.

In all sections, water temperatures were recorded from the transmitters and river centre flow speeds were assessed using wooden surface floats (20 × 20 × 5 cm). Flow speeds were not assessed in 1993. We subjectively classified reach morphologically by the presence of parallel banks, the presence of large bends, or the presence of

Fig. 2. Map of river section 1 illustrating the position of the 10 reaches. The migration path of fish was east through reaches 1–5 and then north through reaches 6–10. The migration path for an individual male (fork length = 57.9 cm) tracked in 1993 is indicated by the thin solid line drawn between the river banks, and the broken line indicates the presumed path. The reach-specific average swim speed and migration time for this fish are indicated beside each reach. The histogram in the upper right corner demonstrates the swim speed frequencies for the migration of this fish through the entire river section. The most frequently exhibited speed was 125–175 cm·s^{-1} (about 2–3 BL·s^{-1}).



constrictions (e.g., large islands, gravel bars, large rock outcroppings) and hydrodynamically by the direction of the major surface flow patterns along their centreline (e.g., flows were primarily downstream, or flows were split and heading in multiple directions).

We tracked sockeye salmon through sections 1 and 2 during July 1993 and 1995. Fish were captured, implanted with transmitters, and tracked following Hinch et al. (1996). In 1993, five females (fork length 50.7–57.2 cm, mass 1.4–2.0 kg) and five males (fork length 55.2–61.7, mass 1.9–2.8 kg) were tracked, and in 1995, five males (fork length 56.2–63.4, mass 2.1–3.2 kg) were tracked. Individuals were tracked continuously through section 1 and their horizontal positions recorded on maps (see example of a migration path in Fig. 2). Based on preliminary tests, fish horizontal position could be ascertained to within ±5 m. Sex- and year-specific differences in fish size (e.g., length) and shape (e.g., length to mass ratio) were explored using ANOVA for the former and ANCOVA (comparing ln length versus weight regressions) for the latter. A subset of the individuals tracked through section 1, two males and one female in 1993 and three males in 1995, were tracked through Hell's Gate (section 2) by an automated receiver system. Three antennae, one situated each at the start, middle, and end of the reach, were linked to receivers and enabled us to monitor EMG activity and determine the time of entry and exit. We tracked fish through section 3 during August 1994 and 1995. Fish were captured by tangle net and implanted with transmitters at section 3. In 1994, two females (fork length 55.5–62.3 cm, mass 1.9–2.8 kg) and two males (fork length 57.3–57.8, mass 2.0–2.4 kg) were tracked through both reaches. In 1995, four females (fork length 55.4–60.9, mass 1.9–2.3 kg) and four males (fork length 60.2–61.7, mass 2.6–2.7 kg) were tracked only through the first reach.

Using equations established from the laboratory relationships between EMGPI and swim speeds (see Results: Laboratory study), we converted all field EMGPI into instantaneous swim speeds for each fish. EMPGPI were recorded by the data logger about every 5 s. An individual's migration time through a given reach was determined as the time from first entry to first departure. Average swim speed was calculated for each individual at each reach based on swim speed values collected during the corresponding migration period. Migration speed, the speed at which fish traveled through a reach, was calculated by dividing reach length, determined by the straight-line distance up the centre of the reach, by migration time. Energy use was estimated for individuals migrating through each reach by inputting average swim speed, river temperature, fish weight, and migration time into a sockeye salmon bioenergetics model (Beauchamp et al. 1989). Parameters for dependence of weight, temperature, and swim speed on metabolism were taken from Beauchamp et al. (1989, their table 1). In our calculations of energy use, river temperatures for fish in sections 1 and 2 were set to 18°C and in section 3 to 21°C, which were average temperatures that we recorded in those sections during our study. We adjusted the intercept value for standard metabolism using estimates of whole-body energy density (Stewart et al. 1983). The energy density of early Stuart sockeye has been determined at set locations along the migration route (IPSFC 1980). We used these energy density values in our energetics model: 8368 $J \cdot g^{-1}$ for fish migrating through sections 1 and 2 and 5167 $J \cdot g^{-1}$ for fish migrating through section 3. Energy expenditure was expressed in joules per fish. Energy expended per unit distance traveled (i.e., per metre of forward progress) was determined for each individual by dividing energy use by reach length, and it was this estimate of energy use, ln transformed, that was used in statistical analyses. If we could not ascertain an entry and exit time, or EMG data were not collected over the majority of the reach, then average swim speed, migration speed, and energy use were not calculated.

To examine the relative influence of river reach, year, sex, and fish individual on swim speed, migration speed, and energy use, two-way and repeated-measures ANOVAs were carried out. Spearman correlations between fish length and swim speeds, migration speeds, and energy use were calculated, by sex, for each of the 10 reaches in section 1 in 1993 to assess possible relationships between body size and swimming activity.

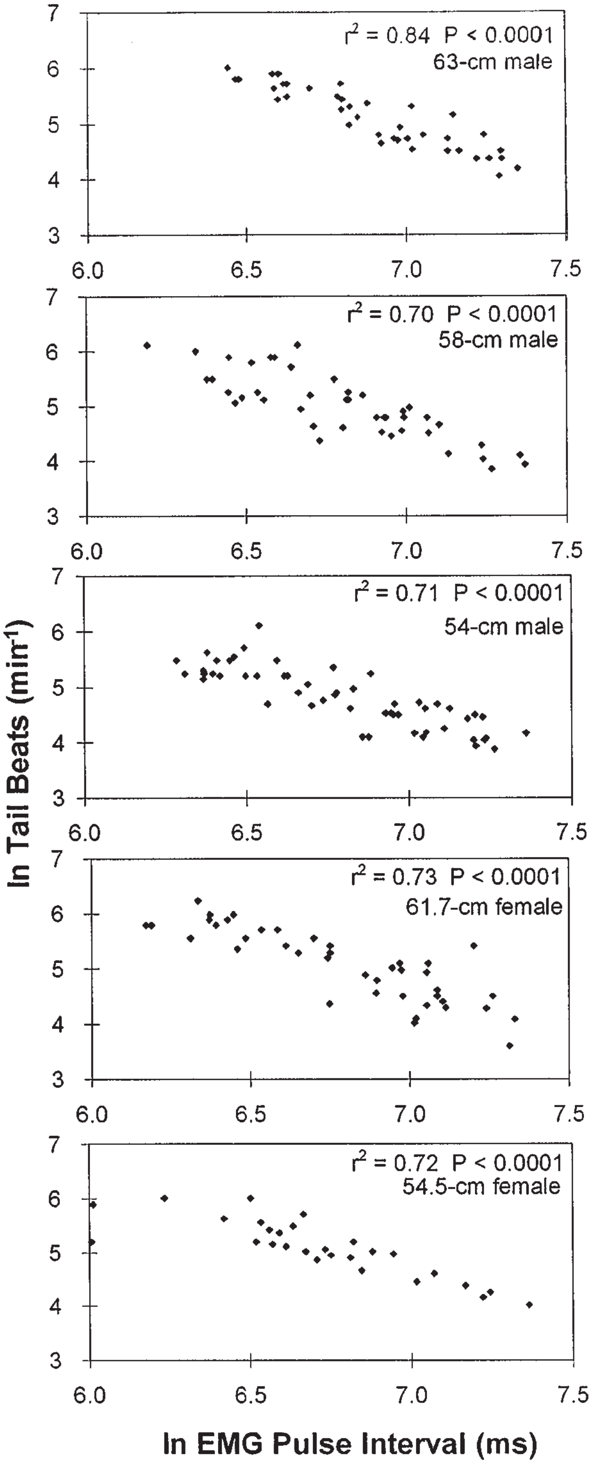
Results

Laboratory study

For each of the eight spontaneously swimming fish, low EMGPI values were associated with a high TBF ($P < 0.001$ for each regression relationship on ln-transformed data). However, the spontaneous swimming data were incomplete for three fish because TBFs and EMGPIs did not span the entire range that has been observed in field situations. For the remaining five fish, the regression relationships of ln TBF versus ln EMGPI (Fig. 3) differed in their slopes and intercepts (ANCOVA; $P < 0.001$ for both). These differences appeared to be related to fish size. We found a linear relationship between the intercept values and fish length ($P = 0.023$; Fig. 4) and a linear relationship between the slope values and fish length ($P = 0.031$; Fig. 4). Using the relationships in Fig. 4, we created a general equation that allowed the prediction of TBF (beats per minute) from EMGPI (milliseconds) for fish of particular lengths (L, centimetres): $\ln \text{TBF} = \ln \text{EMGPI}(1.2484 - 0.0498(L)) + (0.3767(L) - 5.7794)$.

Brett (1995) swam adult sockeye salmon in a 184-cm-wide open flume and demonstrated a strong linear relationship between swim speeds in body lengths per second (BL) and TBF: $\text{BL} = 0.023(\text{TBF}) - 1.286$ ($P < 0.001$, $r^2 = 0.97$). We used this equation to convert TBF to swim speeds for a given fish by multiplying predictions of BL by fork length. For TBF that were less than 58 $\text{beats} \cdot \text{min}^{-1}$, a value that corresponded to our laboratory observations of cessation of forward body motion in still water, we set BL equal to 0.00083(TBF), which represented a straight-line decline from 58 to the origin of the above regression. Thus, using the above equations, we were able to convert EMGPI values obtained in the field to estimates of instantaneous swim speeds.

Fig. 3. Relationships between ln tail beat frequency and ln EMGPI for five individual sockeye salmon. The coefficient of determination and probability of significance from regression analyses are indicated.



Physical habitat in the field

Of the 13 reaches within the three river sections through which we tracked fish, we characterized five reaches as having parallel banks; these same five had unidirectional surface flow patterns along their centrelines. The remaining eight reaches

Fig. 4. Regression relationships of slopes and intercepts on fork length. Slope and intercept data were obtained from the five regression relationships presented in Fig. 3. The coefficient of determination, probability of significance, and regression equation are indicated.

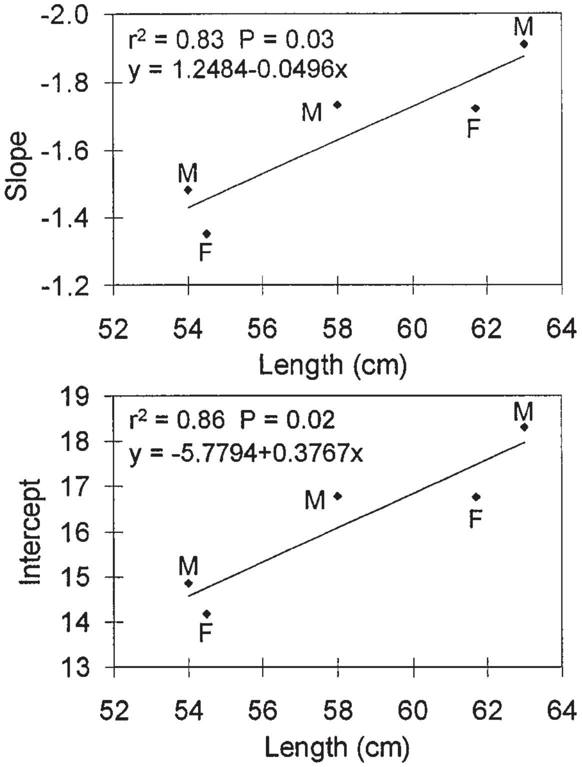
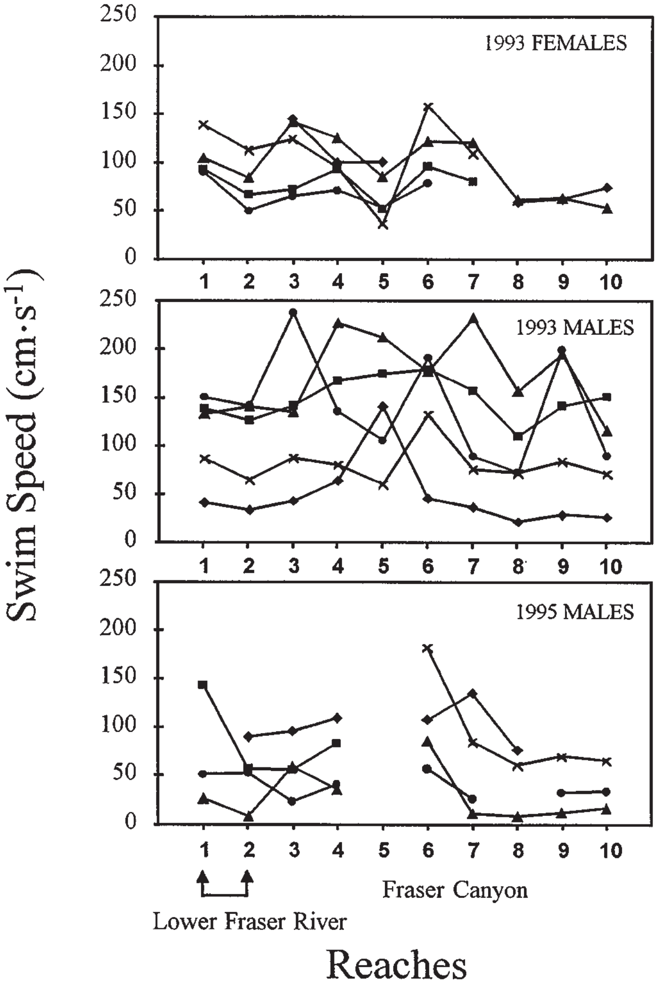


Fig. 5. Average reach-specific swim speeds through the 10 reaches in river section 1 for individual males in 1995 and 1993 and females in 1993. Within each sex- and year-class, individual fish are denoted by the same symbol.



exhibited multidirectional surface flow patterns; four were characterized as containing large river bends and the other four contained prominent constrictions. Surface velocity ranged from 2.3 to 6.0 $\mathrm{m \cdot s^{-1}}$ through constricted reaches, from 2.2 to 2.5 $\mathrm{m \cdot s^{-1}}$ through reaches with large bends, and from 0.9 to 3.4 $\mathrm{m \cdot s^{-1}}$ through reaches with straight parallel banks. During tracking, across all years, water temperatures ranged from 16 to 19°C in sections 1 and 2 (reaches 1–11) and from 20 to 22°C in section 3 (reaches 12 and 13). Average daily river discharge (data collected at Hope, B.C., and provided by the Water Survey of Canada) near river sections 1 and 2, corresponding to the days that fish were tracked, was 4236 $\mathrm{m^3 \cdot s^{-1}}$ in 1995 and 3260 $\mathrm{m^3 \cdot s^{-1}}$ in 1993. Average daily river discharge (data collected at Isle Pierre, B.C., and provided by the Water Survey of Canada) near river section 3, corresponding to the days that fish were tracked, was 516 $\mathrm{m^3 \cdot s^{-1}}$ in 1994 and 486 $\mathrm{m^3 \cdot s^{-1}}$ in 1995.

Fish description in river section 1

In 1993, average male fork length (59.14 cm) and mass (2.22 kg) were greater than the female average fork length (54.42 cm) and mass (1.68 kg) ($P = 0.026$, $P = 0.021$, respectively). There were no differences, between 1993 and 1995, in average male length or mass ($P = 0.854$, $P = 0.117$, respectively). The general shape (ln length versus mass) of males and females in 1993 was similar ($P = 0.475$ for slopes, $P = 0.633$ for intercepts). The general shape of males in 1993 and 1995 was also similar ($P = 0.919$ for slopes, $P = 0.067$ for intercepts).

Swim speeds in river section 1

Swim speeds of 1993 males were associated with variation among fish individuals but not among reaches (repeated-measures ANOVA; $P < 0.001$, $P = 0.109$, respectively). Two individuals swam at relatively slow speeds through each reach compared with the other three individuals (Tukey's test; $P < 0.05$; Fig. 5). Although we were unable to statistically analyse the 1993 female and 1995 male data sets in the same manner, it is evident from Fig. 5 that some individuals consistently swam at slow speeds whereas others consistently swam at fast speeds, a similar result to the 1993 males. There were no obvious differences among reaches in swim speeds in the 1993 female and 1995 male data sets. In 1993, small males generally swam at faster speeds than large males through all reaches; five out of 10 correlations were negative in sign and significant (Spearman $r \geq -0.90$, $P < 0.05$), and the remaining five were also negative in sign, although not significant (Spearman $r = -0.70$, $r = -0.60$, $r = -0.60$, $r = -0.60$, $r = -0.10$, $P > 0.05$ for all). We were only able to evaluate females at three reaches due to low sample sizes. Females exhibited positive correlations between length and swim speeds; however, only one of the three was significant ($P < 0.05$).

Swim speeds of males were 1.3 times faster than those of females (two-way ANOVA; $P = 0.008$; male mean = 118.28 cm·s^{-1}, SE = 8.32, $n = 50$ observations pooled among reaches; female mean = 89.85 cm·s^{-1}, SE = 5.06, $n = 36$ observations pooled among reaches). There were no significant differences among reaches (two-way ANOVA; $P = 0.510$), nor was there any interaction between reach and sex (two-way ANOVA; $P = 0.934$).

Male swim speeds in 1993 were almost two times faster than 1995 male swim speeds (two-way ANOVA; $P < 0.001$; 1993 mean = 118.28 cm·s^{-1}, SE = 8.32, $n = 50$ observations pooled among reaches; 1995 mean = 62.23 cm·s^{-1}, SE = 7.37, $n = 32$ observations pooled among reaches). There were no significant differences among reaches (two-way ANOVA; $P = 0.467$), nor was there any interaction between reach and year (two-way ANOVA; $P = 0.986$).

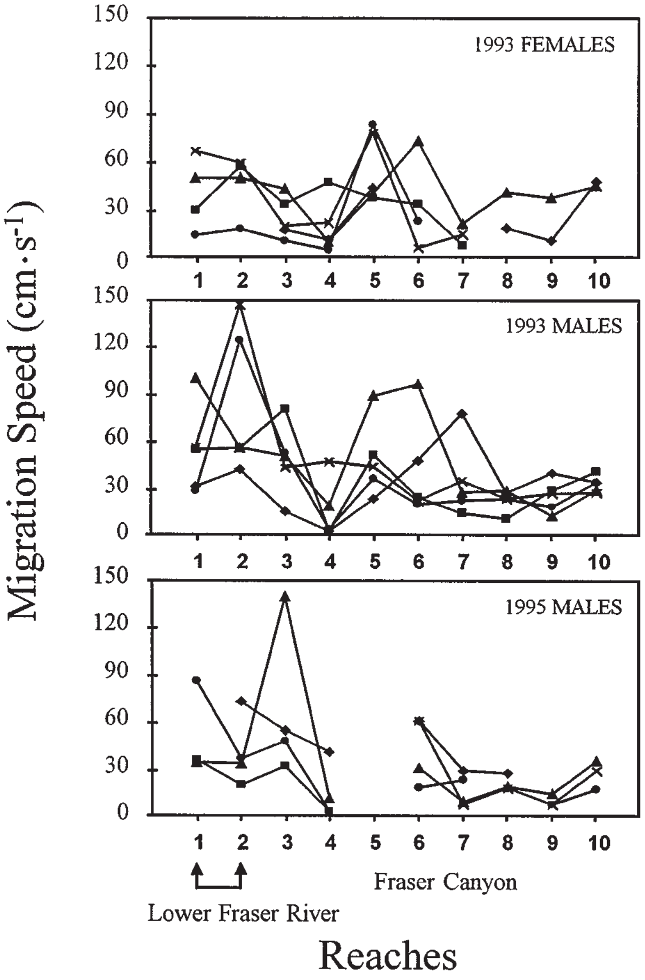
Migration speeds in river section 1

Migration speeds of 1993 males were associated with variation among river reaches but not among individuals (repeated-measures ANOVA; $P = 0.009$, $P = 0.498$, respectively). Migration speeds through reach 2 were significantly faster than speeds through reaches 4, 8, and 9 (Tukey's test; $P < 0.05$; Fig. 6). Although we were unable to statistically analyse the 1993 female and 1995 male data sets in the same manner, it is evident from Fig. 6 that individual fish did not consistently migrate at the same speeds through all reaches. In other words, some individuals that were relatively fast migrants through some reaches were relatively slow migrants through other reaches. Migration speeds of 1995 males seemed to demonstrate a similar pattern to those of 1993 males in that speeds through reaches 4, 8, and 9 were relatively slow. Unlike with the 1993 males, it was less clear that migration speeds of 1993 females were relatively fast through reach 2 and relatively slow through reaches 4, 8, and 9. There was no obvious association between fish length and migration speed. Five Spearman correlations were positive, with only one significant ($P < 0.05$), and five were negative, with only one significant ($P < 0.05$). None of the three Spearman correlation values for females was significant ($P > 0.10$).

Migration speeds in 1993 varied among reaches (two-way ANOVA; $P < 0.001$). They were faster (Tukey's test; $P < 0.05$) through reach 2 (mean = 68.20 cm·s^{-1}, SE = 13.60, $n = 9$) relative to reach 4 (mean = 17.77 cm·s^{-1}, SE = 5.37, $n = 10$), reach 7 (mean = 28.19 cm·s^{-1}, SE = 7.70, $n = 8$), reach 8 (mean = 25.49 cm·s^{-1}, SE = 3.47, $n = 7$), and reach 9 (mean = 25.67 cm·s^{-1}, SE = 4.30, $n = 7$). In addition, migration speeds were faster through reach 5 (mean = 53.19 cm·s^{-1}, SE = 7.06, $n = 10$) relative to reach 4 (Tukey's test; $P < 0.05$). There were no differences in migration speeds between sexes (two-way ANOVA; $P = 0.156$), nor was there any interaction between reach and sex (two-way ANOVA; $P = 0.411$).

Migration speeds of males varied among reaches (two-way ANOVA; $P < 0.001$). They were faster (Tukey's test; $P < 0.05$) through reach 2 (mean = 65.91 cm·s^{-1}, SE = 14.28, $n = 9$) relative to reach 4 (mean = 15.76 cm·s^{-1}, SE = 5.76, $n = 9$), reach 7 (mean = 28.05 cm·s^{-1}, SE = 6.94, $n = 9$), reach 8 (mean = 28.05 cm·s^{-1}, SE = 6.94, $n = 9$), and reach 9 (mean = 20.24 cm·s^{-1}, SE = 4.01, $n = 8$). In addition, migration speeds were faster through reach 3 (mean = 57.93 cm·s^{-1}, SE = 11.78, $n = 9$) relative to reach 4 (Tukey's test; $P < 0.05$). There were no differences between years in migration speeds (two-way ANOVA; $P = 0.205$), nor was there any interaction between reach and year (two-way ANOVA; $P = 0.393$).

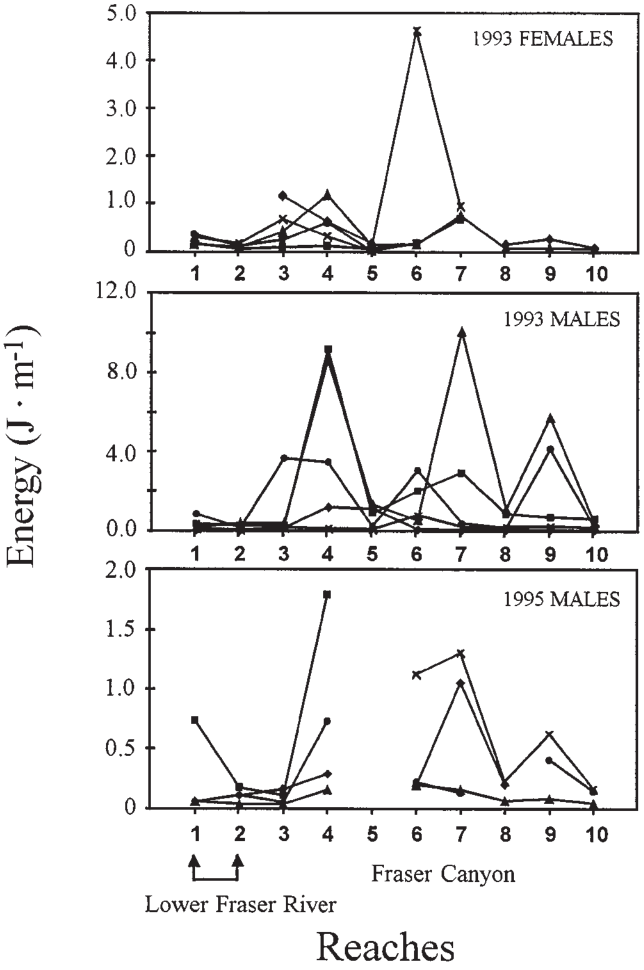
Fig. 6. Reach-specific migration speeds through the 10 reaches in river section 1 for individual males in 1995 and 1993 and females in 1993. Within each sex- and year-class, individual fish are denoted by the same symbol.



Energy use in river section 1

Energy use of 1993 males was associated with variation among fish individuals (repeated-measures ANOVA; $P < 0.002$); two of the five fish used relatively small amounts of energy in each reach (Tukey's test; $P < 0.05$; Fig. 7). Energy use was also associated with variation among reaches (repeated-measures ANOVA; $P = 0.011$); energy use through reach 4 was greater than that through reaches 2 and 10 (Tukey's test; $P < 0.05$; Fig. 7). Although we were unable to statistically analyse the 1993 female and 1995 male data sets in the same manner, it is evident from Fig. 7 that some 1995 males consistently used small amounts of energy through each reach whereas others consistently used relatively large amounts, a similar result to the 1993 males. However, this phenomenon was less obvious for 1993 females. Also similar

Fig. 7. Estimates of reach-specific energy use for migrating through the 10 reaches in river section 1 for individual males in 1995 and 1993 and females in 1993. Within each sex- and year-class, individual fish are denoted by the same symbol. Note that the scales on the energy use axis are different for each figure.



to the 1993 males, both the 1993 females and 1995 males used relatively more energy at reach 4 compared with that at reaches 2 and 10 (Fig. 7). In 1993, small males generally used more energy per metre than large males through all 10 reaches. Two correlations were significant (Spearman $r \geq -0.90$, $P < 0.04$), another was close to significant (Spearman $r = -0.80$, $P = 0.10$), and the remaining seven were all negative in sign, although not significant (Spearman $r = -0.70$, $r = -0.70$, $r = -0.60$, $r = -0.60$, $r = -0.50$, $r = -0.30$, $r = -0.20$, $P > 0.05$ for all). In contrast with males, the three reaches where data were sufficient to examine females revealed positive and weak correlations between length and energy use (Spearman $r = 0.50$, $r = 0.50$, $r = 0.20$, $P > 0.30$ for all).

Male energy use was over three times greater than female energy use (two-way ANOVA; $P = 0.008$; male mean = 1.36 J·m^{-1}, SE = 2.37, $n = 50$ observations pooled among reaches; female mean = 0.43 J·m^{-1}, SE = 0.79, $n = 36$ observations pooled among reaches). Male energy use also varied among reaches (two-way ANOVA; $P = 0.025$); energy use through reach 4 (mean = 2.54 J·m^{-1}, SE = 1.10, $n = 10$ observations pooled between sexes) was 17 times greater than that through reach 2 (mean = 0.15 J·m^{-1}, SE = 0.04, $n = 9$ observations pooled between sexes). There was no interaction between reach and sex (two-way ANOVA; $P = 0.609$).

Energy use by males in 1993 was four times greater than in 1995 (two-way ANOVA; $P < 0.005$; 1993 mean = 1.36 J·m^{-1}, SE = 2.37, $n = 50$ observations pooled among reaches; 1995 mean = 0.33 J·m^{-1}, SE = 0.08, $n = 32$ observations pooled among reaches). There were also significant differences among reaches (two-way ANOVA; $P = 0.023$). Energy use through reach 4 (mean = 2.84 J·m^{-1}, SE = 1.20, $n = 9$ observations pooled between years) was 20 times greater than energy use through reach 2 (mean = 0.14 J·m^{-1}, SE = 0.04, $n = 9$ observations pooled between years) and 13 times greater than energy use through reach 10 (mean = 0.22 J·m^{-1}, SE = 0.07, $n = 8$ observations pooled between years) (Tukey's test; $P < 0.05$). There was no interaction between reach and year (two-way ANOVA; $P = 0.769$).

Speed and energy use through all river sections

Because interactions were not evident among year, sex, and river reach in section 1, we pooled data among years and sexes and contrasted the 13 reaches with ANOVA. We found that swim speeds differed only between reach 6 and reach 12 ($P = 0.032$), being twice as fast in the former (Tukey's test; $P < 0.05$; Fig. 8). On the other hand, several differences existed among reaches in migration speeds ($P < 0.001$), with those in reach 2 being greater than those in reaches 4, 7, 8, 9, and 11 (Tukey's test; $P < 0.05$; Fig. 8) and those in reaches 4 and 11 being greater than those in reaches 1, 3, and 5 (Tukey's test; $P < 0.05$; Fig. 8). Energy use also varied among reaches ($P < 0.001$), being over six times greater in reach 11 than in reaches 1, 2, 3, 5, 8, 10, 12, and 13 (Tukey's test; $P < 0.05$; Fig. 9) and over 10 times greater in reach 4 than in reaches 2 and 12 (Tukey's test; $P < 0.05$; Fig. 9).

Discussion

Fish individual, fish sex and year were all relatively strong contributors to variation in swim speeds. In contrast, only reach accounted for significant amounts of variation in migration speeds. Because energy use was calculated using both swim and migration speed data, it was not surprising to find that the environmental and fish characteristics that were significantly associated with either swim or migration speed variability also explained significant amounts of variation in energy use. We did not consider the anaerobic component of swimming metabolism in our estimates of reach-specific energy use; thus, our estimates are low. However, the relative importance of anaerobic processes to the overall migration energy budget of sockeye salmon is examined in Rand and Hinch (1998) and further elaborated in Burgetz (1996).

Potential role of fish characteristics and year

Fish swam at individual-specific speeds that were fairly consistent among reaches; this consistency may be a phenomenon related to an individual's size. In males, where our data were most complete, small fish swam faster than large fish. However, there was little evidence that small males were migrating any faster than large males, implying that small fish were less energetically efficient at migrating. Why small males seem to adopt this behaviour of higher TBF is not entirely

Fig. 8. Average swim speed (top line) and migration speed (bottom line) for each of the 13 reaches contained within the three river sections. Averages (and 1 SE) are based on all fish that migrated through each reach (left axis). For illustrative purposes, we divided average speeds by average fork length to display speeds in BL·s^{-1} (right axis). The broken lines indicate that adjacent reaches were not contiguous. The geographic location of the reaches is indicated at the bottom and bank classification (B, bend; S, straight; C, constriction) is indicated at the top.

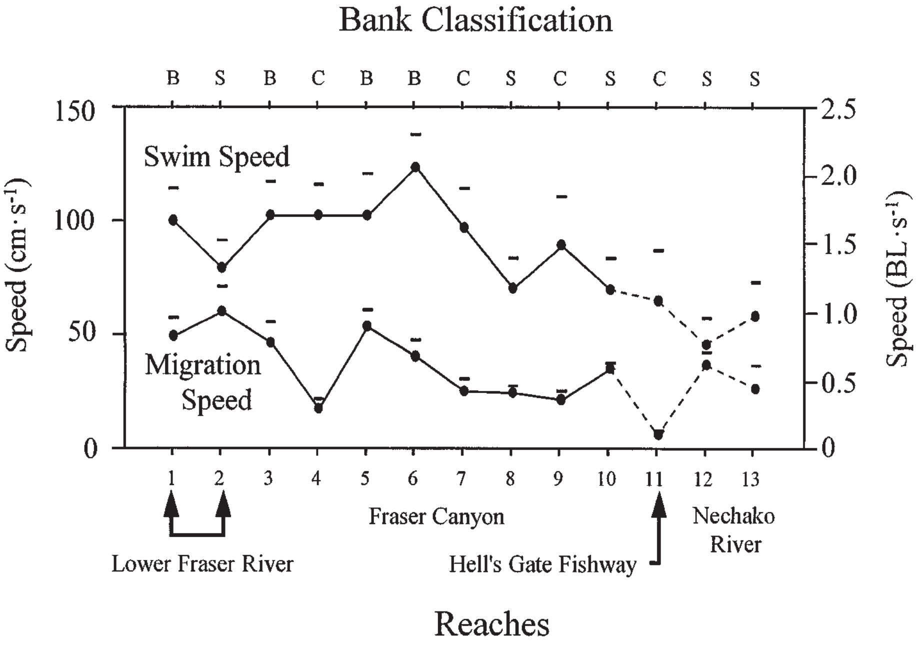
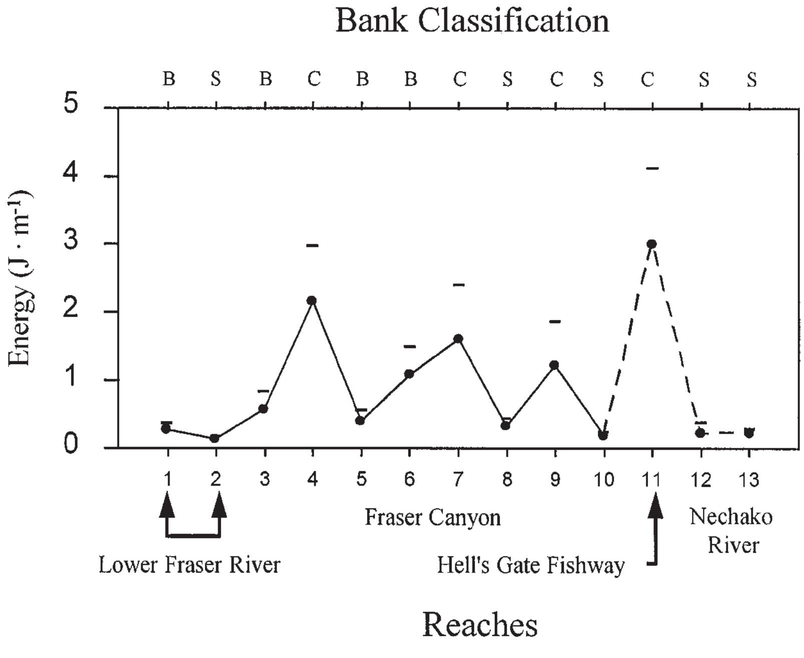


Fig. 9. Average energy use (and 1 SE) for passage through each of the 13 reaches contained within the three river sections. See Fig. 8 for additional details.



clear. Small males may have less thrust-generating abilities than large males, or there may be subtle differences in shape between large and small males that make small males more readily influenced by drag imposed by downstream currents. Regardless, if small males are to arrive on the spawning grounds at the same time as large males and thus not lose breeding opportunities to larger males, they would probably need to swim at relatively faster speeds to maintain migration rates similar to those of large males.

Fish sex contributed to variation in swim speeds and energy use per metre. Generally, males swam faster and used more energy per metre than females; however, males did not achieve a faster migration rate than females. These facts suggest that relative to males, females were more energetically efficient at migrating. Males and females had identical length–mass relationships indicating a general similarity in their shapes; however, subtle shape differences could exist that we did not measure and that could account for sex-specific differences in migration energetics. For instance, the emergence of secondary sexual characteristics (e.g., the development of the humped back and kype) during the migration would make males less streamlined and increase their drag. It is probably advantageous for males to arrive on the spawning grounds simultaneously with females to maximize mating opportunities. Thus, males may need to swim faster than females to overcome drag and maintain similar migration rates to females. It is also possible that agonistic interactions among migrating males, which are prominent and relatively energetically expensive for males on spawning grounds (R. Lake, Institute for Resources and Environment, University of British Columbia, unpublished data), could contribute to additional energy expenditures. Selection for energy efficiency during the migration should be greater for females because they utilize a much higher percentage of their total body energy reserves during the migration (at the completion of their migration, early Stuart sockeye females have used 20–30% more energy than males (IPSFC 1959, 1980)) and are thus probably at greater risk of prespawning energy exhaustion.

Energy use was greater in 1993 males compared with 1995 males, and this difference was primarily due to differences in swim speeds which were typically twice as fast in 1993 compared with 1995. Fish length and weight were similar between 1993 and 1995; thus, it is unlikely that general differences in fish size or shape were responsible for differences in energy use. Of the environmental features that we examined, the major difference between years was in river discharge which was 30% greater in July 1995 compared with July 1993; the latter was the lowest July discharge ever recorded in the Fraser Canyon (based on daily observations from 1912 to the present, Water Survey of Canada). Webb (1995) suggested that upriver-migrating salmon could minimize energy use by swimming at metabolic and hydrodynamic optimal speeds, and Brett (1995) suggested that optimal swim speeds of river-migrating adult sockeye should be relatively lower for individuals that encounter relatively high river velocities. Thus, it is plausible that sockeye salmon may have exhibited relatively slow swim speeds in 1995 (a year of moderately high discharge and presumably moderately high velocities) as a tactic to optimize energy use.

Potential role of river bank morphology and flow patterns

River flow velocities are moderated by the presence of river banks with relatively slow, unidirectional flows near the banks of straight reaches and complex, multidirectional flows near the banks of reaches that contain constrictions. Because adult sockeye migrate nearshore and use downstream flow as a migrational cue during migration, any bank feature that alters the downstream direction of flow could lengthen migration paths and accelerate energy use. Furthermore, any bank feature that increases the downstream speed of river flow could cause sockeye to swim at greater speeds to make forward progress, which also would increase energy use.

Migration speeds were generally slowest through the Hell's Gate fishways reach and several of the reaches in the Fraser River Canyon (Fig. 8). Of the five reaches with the slowest migration speeds, four contained a constriction (Fig. 2) whereas the fastest migration speeds occurred through reaches with no constrictions. Unlike migration speeds, swim speeds did not vary much among reaches, implying that sockeye may have a preferred or optimal speed at which to swim through most reaches in any particular year. However, two reaches did differ from each other; slowest swim speeds were exhibited in the Nechako River (reach 12, average = $50\ \mathrm{cm\cdot s^{-1}}$; Fig. 8) and fastest swim speeds in the Fraser River Canyon (reach 6, average = $120\ \mathrm{cm\cdot s^{-1}}$; Fig. 8). Neither reach contained a constriction. To prevent erosion, this Nechako River reach has had its banks armoured with riprap material. We have observed that these artificially created banks generate small reverse flow fields (e.g., eddie vortices) along the shore, and migrating sockeye appear to be exploiting these to facilitate their forward progress. At this reach, migration speed of some individuals exceeded their swim speed, suggesting that these individuals were receiving some form of upriver assist. In contrast, swim speeds were relatively fast at that Fraser Canyon reach, and although we are uncertain of the reasons for this occurrence, this reach had very turbulent surface flow patterns throughout its entirety; thus, it is possible that sockeye were forced to swim at an elevated speed to successfully pass.

The relationship between energy use and bank characteristics was clear. Migration through reaches with constrictions was more costly and less efficient energetically than migration through reaches with parallel, straight banks (Fig. 9). Migration through reaches with nonparallel, curving banks seemed to be intermediate in energetic costs. The high costs of migration through constricted sites seem to be caused by a combination of long passage times (i.e., slow migration speeds) *and* a relatively large difference between migration and swim speeds. This combination probably occurred because flows at these reaches were usually multidirectional, turbulent, and often fast. In addition, this type of environment would be difficult for sockeye to locate appropriate migrational cues in, hence contributing to delays in upriver passage.

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