Energetic costs of migration through the Fraser River Canyon, British Columbia, in adult pink (*Oncorhynchus gorbuscha*) and sockeye (*Oncorhynchus nerka*) salmon as assessed by EMG telemetry

Emily M. Standen, Scott G. Hinch, Michael C. Healey, and Anthony P. Farrell

Abstract: Adult Pacific salmon (*Oncorhynchus* spp.) depend on energy reserves to complete their upriver spawning migration. Little is known about how flow patterns and bank characteristics affect energetics or how species differ in reach-specific energy use. In 1999, electromyogram (EMG) radiotelemetry was used to describe activity levels and estimate energy use of 12 adult pink salmon (*Oncorhynchus gorbuscha*) during their upstream migration in a 7-km section of the Fraser River Canyon. Data collected previously on sockeye salmon (*Oncorhynchus nerka*) in the same study area provided a species comparison. We could not identify any strong differences in energetics between species. Although sex had some influence, reach characteristics were the primary factors affecting migration activity and energetics. Fish increased their activity levels when they migrated through reaches constricted by islands or gravel bars compared with nonconstricted reaches. The former contained higher velocity currents and more complex hydraulic conditions than the latter. Two behavioural responses, with similar energetic consequences, occurred in constricted reaches. Either fish swam slowly and took more time, presumably searching for lower velocity areas for migration thus increasing passage time, or they swam quickly through higher velocity flow fields.

Résumé : Les saumons du Pacifique (*Oncorhynchus* spp.) adultes utilisent leurs réserves énergétiques lors de leurs migrations de frayé vers l’amont des rivières. On connaît encore mal les conséquences énergétiques des patterns de courant et des caractéristiques des berges, ainsi que l’utilisation de l’énergie chez les différentes espèces dans les sections particulières du cours d’eau. En 1999, l’électromyographie (EMG) par radio-télémétrie nous a permis de décrire les niveaux d’activité et d’estimer l’utilisation de l’énergie chez 12 saumons roses (*Oncorhynchus gorbuscha*) durant leurs migrations de frayé dans une section de 7 km du canyon Fraser. Des données récoltées antérieurement sur le saumon rouge (*Oncorhynchus nerka*) dans la même région d’étude ont servi de point de comparaison pour établir les différences inter-spécifiques. Aucune différence importante n’est apparue dans la dynamique énergétique entre les deux espèces. Bien que le sexe du poisson ait une influence, ce sont les caractéristiques de la section de la rivière qui affectent le plus la migration et l’utilisation de l’énergie. Les poissons augmentent leur niveau d’activité lorsqu’ils traversent des sections rétrécies par la présence d’îles ou de bancs de gravier, par comparaison aux sections non rétrécies. Les sections rétrécies contiennent des courants plus forts et des conditions hydrauliques plus complexes que les autres. Deux réactions comportementales, à incidences énergétiques semblables, se produisent dans les sections rétrécies. Les poissons nagent lentement et mettent plus de temps à leur migration, sans doute parce qu’ils recherchent des points de courant plus faible et ainsi ils augmentent la durée de leur passage, ou alors ils nagent rapidement à travers les champs de courant plus rapide.

[Traduit par la Rédaction]
**Introduction**

Upriver migration of anadromous fish can be energetically expensive, particularly when travel distances are long and river environmental conditions adverse (Bernatchez and Dodson 1987; Brett 1995; Leonard and McCormick 1999). Body constituent analyses on Pacific salmon (*Oncorhynchus* spp.) reveal that depending on migratory conditions, more than 50% of body energy may be used to complete migration (reviewed by Brett 1995). Such high levels of energy depletion are thought to cause en route or prespawning mortality (Rand and Hinch 1998; Hinch and Bratty 2000; Macdonald 2000). However, very little is known about the mechanisms responsible for high levels of energy use. Constituent analyses provide only a coarse-grained measure of how a stock uses its energy reserves and cannot be used to measure how specific habitat features influence energy use. Because fish must be killed to measure body energy, different individuals must be examined each time; therefore, the influence of behaviour or morphology cannot be evaluated by this method. By contrast, electromyogram (EMG) radiotelemetry enables one to quantify swimming speeds of individual migrating fish and thus provide fine-scale information on energy-use patterns (McKinley and Power 1992; Hinch et al. 1996).

EMG telemetry has been used for several years to investigate the factors responsible for variability in migratory energetics of sockeye salmon. Earlier research found that sex, size, and individual swimming speed patterns are important factors affecting energy use (Hinch et al. 1996; Hinch and Rand 1998; Hinch and Bratty 2000). Physical habitat features have also proven to significantly influence sockeye energy use. Specifically, river constrictions and their associated multidirectional currents appear to cause relatively high passage costs (Hinch et al. 1996; Hinch and Rand 1998). However, there has been little investigation into the behaviour and energetics of other salmon species during their upriver spawning migrations.

Our first objective was to use EMG telemetry to estimate swimming speeds, ground speeds, and energy use of adult pink salmon (*Oncorhynchus gorbuscha*) during their migration through the Fraser River Canyon. We predict that as previously found with sockeye, female pink salmon will be more energetically efficient than males and that river constrictions will increase energy expenditures. The second objective was to compare pink salmon swimming energetics with those of sockeye salmon (*Oncorhynchus nerka*), previously described by Hinch and Rand (1998). To effectively make this comparison, a reanalysis of those data was required. Pink salmon are believed to be weaker swimmers than sockeye (Brett 1982) and, in particular, are thought not to be adept at negotiating high velocity barriers because of their relatively small body size (Heard 1991). We therefore predict that pink salmon will be less efficient in their use of energy for swimming during migration compared with sockeye salmon.

**Materials and methods**

**Calibrating EMG signals to swimming speeds**

A description of the EMG radio transmitters (Lotek Engineering, Newmarket, Ont.) and specific details about their surgical implantation are outlined in Hinch et al. (1996). EMG transmitters are surgically implanted into a fish’s abdomen. Sensing electrode tips are positioned approximately 1.0 cm apart, secured below the dorsal fin in the lateral red muscle. Although this muscle type is used primarily in steady, nonbursting aerobic swimming, the electrodes are also sensitive to contractions of the relatively larger white muscle (Hinch et al. 1996; Hinch and Rand 1998), which is recruited primarily during burst, anaerobic swimming. Intervals between EMG signals (termed EMG pulse intervals or EMGPI, measured in milliseconds, ms) are thus associated with tail beat frequency (TBF) and hence with swimming speed across the full range of aerobic and anaerobic speeds (Hinch and Rand 1998; Hinch and Bratty 2000).

We followed a two-step process to convert EMGPI values from pink salmon into estimates of swimming speed; a similar approach was used on sockeye salmon by Hinch and Rand (1998). The first step was to generate mathematical relationships for both sexes between EMGPI and TBF. To accomplish this, in October 1999, eight adult pink salmon, four males (fork length, 47.2–55.2 cm; mass, 1.25–2.00 kg) and four females (fork length, 49.6–55.0 cm; mass, 1.00–1.75 kg), were collected using dip nets from the fish ladder at the Seton Lake dam near Lillooet, British Columbia (B.C.; Fig. 1), and were implanted with EMG transmitters. These fish then swam in a large swimming tunnel following the methodology described in Jain et al. (1997). A detailed description and photographs of the tunnel and its components are provided at http://www.sfu.ca/biology/faculty/farrell/swimtunnel/swimtunnel.html. The tunnel has a volume of 471.2 L and was capable of creating water velocities up to 150 cm·s–1. However, we were able to record swimming speeds in the tunnel that were much greater than this because salmon often do not swim at a constant pace in swimming tunnels (e.g., they accelerate and decelerate), particularly at the higher water velocities and as they get more fatigued. We were able to generate EMGPI values in the tunnel that spanned the complete range of EMGPI values observed in the field. This is elaborated on in the results.

We recorded EMGPI and TBF data in the following manner. Individual fish were placed in the swimming tunnel and exposed, at sequential intervals, to water velocities that increased incrementally at 0.15 body lengths per second (BL·s–1). The intervals were 5–20 min in length and a trial lasted until the fish was exhausted and could not get off the rear grid. We were not interested in measuring oxygen consumption or relating water speed to EMGPI, so interval length did not matter. Our goal was simply to observe a range of EMGPI values that would be similar to that exhibited by migrating fish carrying transmitters. A stereo video camera system synchronously recorded onto a single video image the swimming fish and the digital face of the EMG radio receiver (model SRX 400; Lotek Engineering). The radio receiver displayed every EMGPI transmitted from the fish, usually 1–2·s–1. In the laboratory, after the field telemetry study was completed, we viewed the videotapes in slow motion and located instances when fish were swimming in the centre of the tunnel 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 the tunnel wall or back grid. EMGPI values clearly associated with the initiation of a tail beat were transcribed. Because the cam-
eras record 60 images·s\(^{-1}\), we could calculate TBF associated with the EMGPI value by counting the number of video frames required to complete the tail beat. For each fish, we developed a relationship between EMGPI values and TBF by transcribing approximately 100 EMGPI values from the videotapes. We ensured that the range of transcribed EMGPI values for each fish was at least as great as that observed from the field telemetry EMGPI values (ranges provided in Results).

The second step in estimating swimming speeds from EMGPI values was to use an equation from Brett (1995). He had adult pink salmon swim in a 184 cm wide, open flume and used movie cameras to record TBF and demonstrated a linear relationship between swimming speeds and TBF. His relationship would much better reflect reality than anything we could generate in our swimming tunnel, despite its relatively large size, because of the phenomenon of solid blocking and wall effects within a tunnel. We used his equation (swimming speed (cm·s\(^{-1}\)) = 0.739TBF (beats·min\(^{-1}\)) + 14.904; \(P < 0.0001; r^2 = 0.64\); standard error (SE) intercept = 22.513; SE slope = 0.121) to predict instantaneous swimming speeds from individual TBF values.

Telemetry study
The Fraser River Canyon, situated in the southwest corner of British Columbia (Fig. 1), exhibits a diversity of flow...
conditions and habitat features that create challenges for upriver passage of salmon (Hinch and Rand 1998; Hinch and Bratty 2000). The study area in the Fraser River Canyon was from kilometre 150 to 157, the same as that used by Hinch and Rand (1998). Reach length, width, and gradient were determined using 1:4000 air photos. Reaches 1 and 2, located immediately downstream of the canyon, had an average gradient of 75 cm·km⁻¹. All other reaches were in the canyon and had an average gradient of 120 cm·km⁻¹. Reaches ranged in length from 200 to 1100 m and in width from 50 to 500 m. Surface water speeds along the centre line of each reach were estimated by timing the passage of wooden blocks (20 cm × 20 cm × 5 cm) over a known distance in the main current of the river. Blocks were floated during the middle of our study when discharge was about the same for both years. These values are intended to provide one, albeit coarse, measure of the broad differences in flow features that exist among reaches and are not intended to reflect the specific current speeds that salmon encounter while migrating. We subjectively classified reach bank morphology by the presence of parallel banks (termed “straight”), large bends (termed “bend”), or features (e.g., large islands, gravel bars) that cause flow constrictions (termed “constriction”).

During September and October 1999, six male pink salmon (fork length, 47.5–56.6 cm; mass, 1.50–2.25 kg) and six female pink salmon (fork length, 47.5–50.6 cm; mass, 1.00–1.35 kg) were collected from a fish wheel situated 200 m downstream of the study area, and transmitters were implanted at that site. The wheel was operated by the Yale First Nations Band (Yale, B.C.). Fish were held in a pen near the wheel for at least 1 h to recover from the surgery. Fish were released into a large slow water eddy at the edge of the river mainstem near the holding pen and individually tracked upstream using a hand-held directional three element Yagi antenna and EMG receiver. Only one fish was released per day and we tried to alternate sexes from one day to next. Fish were tracked by following them on foot along the river banks, and their positions could be ascertained to within 5 m (determined previously at our study sites using transmitters suspended on submerged lines at known depths (Hinch et al. 1996)). Migration time was measured as the amount of time it took a fish to swim through a reach from first entry to first exit. We found that pink salmon stopped their forward migration at dusk and did not migrate at night, so times from dusk to dawn were not included in the migration time. Ground speed was calculated by dividing the migration time by the reach length.

EMGPI values were recorded by the receivers at an interval of every 3–5 s. Each EMGPI value was converted to TBF in beats per second using the linear regression equations developed from the swimming tunnel trials (equations given in Results). Each TBF value was converted to an estimate of instantaneous swimming speed using the relationship developed by Brett (1982) and described above. Assuming receivers recorded an EMGPI value every 4 s and a reach takes 60 min to traverse, we would accumulate 900 EMGPI values and hence have 900 estimates of swimming speeds. These estimates of swimming speeds were averaged for each fish within reach. Individual specific energy use was estimated using a salmon bioenergetics model with variables average swimming speed through the reach, average river temperature, fish mass, and migration time through the reach (Hinch and Rand 1998). This model was originally developed by Beauchamp et al. (1989) and parameterized using adult sockeye salmon. A comparable model for adult pink salmon has not been developed.

Hinch and Rand (1998) used EMG transmitters to track five male and five female early Stuart sockeye salmon in 1993 through the same reaches described above. Using results from laboratory swimming experiments and the other approaches described above, they collected ground and swimming speeds and estimated reach specific energy expenditures. It is these data that are used for making comparisons with pink salmon. Preliminary analysis of the pink salmon data suggested that individual fish might be an important factor explaining variation in swimming and ground speeds as well as energy use. A reanalysis was conducted of Hinch and Rand’s (1998) data because they did not consider “individual fish” as a factor responsible for variation.

Daily average water temperatures (measured by Fisheries and Oceans Canada at Hell’s Gate, situated approximately 10 km upstream of the study area) were 13.9–15.4 and 14.0–17.0°C during the field seasons in 1999 and 1993, respectively. Daily average discharge (measured by Water Survey of Canada at Hope, B.C., approximately 20 km downstream of the study area) ranged from 1900 to 4030 (mean 2758) and 3170 to 3770 (mean 3295) m³·s⁻¹ for 1999 and 1993, respectively.

Statistical analyses

Analysis of covariance (ANCOVA) was used to compare the slopes and intercepts of the linear relationships between TBF and EMGPI from the swimming tunnel trials to determine if separate predictive relationships were required for fish of specific sizes or sex. If error variance heteroscedasticity existed, TBF was log transformed prior to analysis. Differences in mass and length between the sexes of fish used in the swimming tunnel were determined by analysis of variance (ANOVA). To assess differences in condition between the sexes, sex-specific log mass versus length regression relationships were compared with ANCOVA.

To examine the speeds and energy use of upriver migrating pink salmon, three separate split-plot repeated-measures ANOVAs were used and then type III sums of squares were interpreted (SAS 1988). Separate analyses were performed using ground speed (cm·s⁻¹), swimming speed (cm·s⁻¹), and energy use (J·m⁻³) as dependent variables. In each analysis, sex was the treatment (two sexes = 1 degree of freedom (df)), river reach (nine reaches = 8 df) was the repeated measure with individual fish as replicates (six fish, two sexes = 10 df). Within this model, sex was tested using the fish nested in sex error term (10 df), and all other dependent variables were tested using the full model error. All models were described for interaction between sex and reach. If an interaction was detected, further two-way ANOVAs with sex and reach as main effects were conducted to isolate the interactive terms. Differences among individuals, sexes, and reaches were determined a posteriori using least square
means (LSM). Pearson’s correlation between weight and swimming speed, ground speed, and energy use were also examined to speculate on the role that fish size might have on the response variables. Differences in weight between fish were determined using two-way ANOVA and a least significant difference t test.

We combined our data with that used by Hinch and Rand (1998) to compare energy use of sockeye and pink salmon. Species and sex classes were combined into one main effect variable that was termed species–sex class that had four levels (sockeye females, sockeye males, pink females, and pink males, four classes = 3 df). Because a sex by species interaction could not be tested for in these analyses, two additional split-plot repeated-measures ANOVAs were conducted with sex and then species replacing sex–year class as main effects. One-way ANOVAs were used to compare fish body mass among the sex and species groups. LSM were used as effects. One-way ANOVAs were used to compare fish body mass among the sex and species groups. LSM were used as the a posteriori approach for assessing differences among levels within the class variables. Following each ANOVA, plots of residual versus predicted values were examined to look for error variance heteroscedasticity. If present, log transformations were applied and the ANOVAs redone. The coefficient of variation (CV) of energy use was calculated for each species–sex class. Two-way ANOVAs were then used to compare CV values among sex–species and reach. Statistical significance was assessed at the 0.05 level. Significance levels for all a posteriori contrasts were adjusted using Bonferroni’s method. All analyses were conducted using SAS (1988).

**Results**

**Swimming tunnel study**

There were no differences in mean length or mean mass between sexes for the pink salmon (P = 0.9642 and 0.4583, respectively; overall mean length 52.0 cm, overall mean mass 1.6 kg). Furthermore, neither the slopes nor intercepts of the log mass versus length regression relationships differed between sexes (P = 0.4991 and 0.5690, respectively). The TBF versus EMGPI regression slopes differed among individuals (P = 0.0001). These differences were primarily due to sex. When separate ANCOVAs for males and females were conducted, the slopes of the male fish did not differ (P = 0.3147), nor did those of the female fish (P = 0.2081). Therefore, common regression relationships were developed for males and females by pooling data within sexes (Fig. 2). Hinch and Rand (1998) found that fish size was also an important independent variable helping to predict TBF in sockeye salmon. We found with multiple regression that mass significantly contributed to explaining variation in TBF (for both sexes, P < 0.0001). Thus, the regression models used for predicting TBF from EMGPI are

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\text{log TBF} = -0.0004186\text{EMGPI} + 0.1731621\text{mass} + 0.5796416\text{for males (Fig. 2a, P < 0.0001, r^2 = 0.84, SE intercept = 0.036, SE mass = 0.016, SE EMGPI = 0.000022 and log TBF} = -0.0003026\text{EMGPI} - 0.1646564\text{mass} + 0.9171931\text{for females (Fig. 2b, P < 0.0001, r^2 = 0.53, SE intercept = 0.022, SE mass = 0.012, SE EMGPI = 0.000009). EMGPI values ranged from 1950 to 500 ms, which corresponded to predicted TBF values of 1.10 to 4.44 beats s\(^{-1}\) for an average-sized fish (1.6 kg).}

Estimated instantaneous swimming speeds associated with those TBF values ranged from 63.03 to 209.62 cm s\(^{-1}\). For females, the EMGPI values ranged from 1800 to 550 ms, which corresponded to predicted TBF values of 1.29 to 3.07 beats s\(^{-1}\) for an average-sized fish. Estimates of instantaneous swimming speeds associated with those TBF values ranged from 71.28 to 149.59 cm s\(^{-1}\).

**Telemetry study**

**Pink salmon**

Male pink salmon (mean mass 1.79 kg) used in the telemetry study were larger than the female pink salmon (mean mass 1.18 kg, P = 0.0090). However, there were no differences between mass of males used in calibration study and those used in telemetry study, nor between mass of females used in calibration study and those used in telemetry study (P > 0.05 for both).

The split-plot repeated-measures ANOVA revealed that swimming speeds varied among individual fish (F\(_{10,66}\) = 77.48, P = 0.0001) and among reaches (F\(_{8,66}\) = 10.38, P = 0.0001) but did not vary between sexes (F\(_{1,10}\) = 0.00, P = 0.9625). Swimming speeds of pink salmon ranged from 51 to 183 cm s\(^{-1}\) (mean 114 cm s\(^{-1}\), n = 93, SE = 2.9) among fish and reaches. Swimming speeds were fastest through reaches 4 and 6 and slowest through reach 8 (Table 1). Pink salmon ground speed data required log transformation. The split-plot repeated-measures ANOVA revealed no differences among individual fish (F\(_{10,64}\) = 1.27, P = 0.2643) or between sexes (F\(_{1,10}\) = 0.09, P = 0.7758) in pink salmon ground speeds; however, differences were evident among reaches (F\(_{8,64}\) = 6.80, P = 0.0001). Average ground speeds varied from 21.2 to 114.3 cm s\(^{-1}\) (mean = 57.1, n = 9, SE = 11.13) among reaches. Among reaches, ground speeds fell into two general groups: fast (reaches 1 and 5) and slow (reaches 3, 4, 7, 8, and 9) (Table 1).
Means and standard errors (SE) of swimming speeds, ground speeds and energy use of pink salmon migrating through the nine reaches.

Table 1.

<table>
<thead>
<tr>
<th>Reach</th>
<th>Bank morphology class</th>
<th>Bend</th>
<th>Constricted</th>
<th>Straight</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
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Note: Data were pooled for these calculations. Means and SE are based on raw nontransformed data. Fish sample sizes are presented on Fig. 3. Bonferroni contrasts are based on analysis of variance (ANOVA) results, which examined log-transformed ground speeds and energy use. Reaches with similar letters are not different. Bank classes and mean centre-line current speeds are given for each reach. Current speeds could not be obtained at reach 7 because of dangerous access and flow conditions. 

Means, standard errors (SE) of swimming speeds, ground speeds and energy use of pink salmon migrating through the nine reaches.

<table>
<thead>
<tr>
<th>Bank morphology class</th>
<th>Mean centre-line current speed (cm·s–1)</th>
<th>Mean swimming speed (cm·s–1)</th>
<th>Bonferroni contrasts of swimming speed</th>
<th>Mean ground speed (cm·s–1)</th>
<th>SE ground speed (cm·s–1)</th>
<th>Bonferroni contrasts of ground speed</th>
<th>SE energy use (J·m–1)</th>
<th>Bonferroni contrasts of energy use</th>
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<tr>
<td>Constricted</td>
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<td>147</td>
<td>B</td>
<td>88.52</td>
<td>0.29</td>
<td>B</td>
<td>0.12</td>
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<tr>
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<td>116.93</td>
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<td>12.9</td>
<td>A</td>
<td>12.9</td>
<td>0.17</td>
<td>A</td>
<td>0.06</td>
<td>A</td>
</tr>
<tr>
<td>Reach 5</td>
<td>6</td>
<td>12.9</td>
<td>B</td>
<td>12.9</td>
<td>0.17</td>
<td>B</td>
<td>0.06</td>
<td>B</td>
</tr>
<tr>
<td>Reach 6</td>
<td>7</td>
<td>12.9</td>
<td>C</td>
<td>12.9</td>
<td>0.17</td>
<td>C</td>
<td>0.06</td>
<td>C</td>
</tr>
<tr>
<td>Reach 7</td>
<td>8</td>
<td>12.9</td>
<td>A</td>
<td>12.9</td>
<td>0.17</td>
<td>A</td>
<td>0.06</td>
<td>A</td>
</tr>
<tr>
<td>Reach 8</td>
<td>9</td>
<td>12.9</td>
<td>B</td>
<td>12.9</td>
<td>0.17</td>
<td>B</td>
<td>0.06</td>
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Contrasting pink and sockeye salmon

Male sockeye salmon (mean mass 2.64 kg) were larger than female sockeye salmon (mean mass 1.75 kg, P < 0.0001). In contrasting sex–species classes, only pink males and sockeye females were not different in mass (P > 0.05). The repeated-measures ANOVA examining the combined data sets for pink and sockeye salmon swimming speeds revealed significant differences between individual fish (F[17,111] = 6.53, P = 0.0001), reach (F[9,111] = 6.53, P = 0.0001), and an interaction between reach and species–sex class (F[24,111] = 2.18, P = 0.0035). The main effect of species–sex class was not significant (F[3,17] = 0.57, P = 0.6392). We reduced the number of reaches in our a posteriori contrasts to more easily interpret the interaction term. We took this approach because the Bonferroni adjustment of α = 0.05/16 is a highly conservative interpretive tool and resulted in no significant differences being detected in any comparisons, despite the ANOVA revealing a significant interaction term. Reaches 2, 4, 7, and 9 were scrutinized because they represented the full, among-reach range of hydraulic conditions in this study (Table 1). Pink females (PF) swam faster than sockeye females (SF) in reaches 4 (PF mean = 121 cm·s–1, SF mean = 97 cm·s–1, P = 0.0613), 2 (PF mean = 117 cm·s–1, SF mean = 78 cm·s–1, P = 0.0181), and 9 (PF mean = 95 cm·s–1, SF mean = 63 cm·s–1, P = 0.0060) but not in reach 7 (P = 0.5211). Pink females swim faster than sockeye males (SM) in reach 2 (PF mean = 117 cm·s–1, SM mean = 91 cm·s–1, P = 0.0608) but not in the other reaches (all P ≥ 0.26). Pink males (PM) swim faster than sockeye males in reach 2 (PM mean = 117 cm·s–1, SM mean = 91 cm·s–1, P = 0.0576) but not in reaches 4, 7, and 9 (P ≥ 0.2885). Pink males also used less energy than sockeye females in reach 2 (PM mean = 117 cm·s–1, SM mean = 91 cm·s–1, P = 0.0576) but not in reach 7 (P = 0.5040).

Ground speed data for all species–sex classes required log transformation. For ground speed, species–sex class (F[17,111] = 3.45, P = 0.0402) and reach (F[8,109] = 9.67, P ≤ 0.0001) were significant. Individual fish was not a significant variable (F[17,111] = 0.82, P = 0.6642) and there was no interaction between species–sex class and reach (F[24,109] = 0.85, P = 0.6702). Both pink females (mean = 54.2 cm·s–1, n = 46, SE = 6.3, P = 0.0003) and pink males (mean = 63.4 cm·s–1, n = 46, SE = 10.1, P = 0.0017) migrated faster than sockeye females (mean = 33.9 cm·s–1, n = 34, SE = 3.8). All sex–species classes had slower ground speeds through reaches 4 (mean = 31.6 cm·s–1, n = 20, SE = 4.9), 7 (mean = 28.5 cm·s–1, n = 18, SE = 4.3), and 9 (mean = 24.0 cm·s–1, n = 12, SE = 3.6) than through reach 2 (mean = 77.6 cm·s–1, n = 20, SE = 19.1).

Pink salmon energy-use data required log transformation. The split-plot repeated-measures ANOVA revealed that variation in energy use was attributed to differences among individual fish (F[9,64] = 11.29, P = 0.0001) and among reaches (F[8,64] = 8.36, P = 0.0001) but not between sexes (F[1,10] = 0.75, P = 0.4058). Average energy use varied from 0.002 to 1.73 J·m–1 (mean = 0.26, n = 92, SE = 0.032) among reaches and individuals. Energy use fell into two general reach groupings: low (reaches 1 and 5) and high (reaches 3, 4, 6, 7, and 9) (Table 1).
Energy-use data for all species–sex classes required log transformation. Energy use varied among individuals ($F_{17,109} = 9.44, P \leq 0.0001$) and there was interaction between species–sex class and reach ($F_{24,109} = 2.01, P = 0.0082; \text{Fig. 3}$). Again we used the reduced data set to interpret the interaction as outlined above for the swimming speed data. In reach 4, pink females and pink males used less energy than sockeye males ($P < 0.001$ for both; Fig. 3). Averaging among sex–species classes, reaches 4 and 7 had higher energy use than reach 2 ($P \leq 0.0001$ for both contrasts; Fig. 3). When sex–species class was replaced with sex as a main effect in the same ANOVA, energy use varied among reaches ($P \leq 0.0001$) but not between sexes ($P = 0.3294$). Likewise when species was used as the main effect, energy use varied strongly among reaches ($P \leq 0.0001$) but not between species ($P = 0.0986$).

Within-group variation in swimming speed differed among sex–species classes ($F_{8,23} = 22.26, P = 0.0001; \text{Fig. 3}$). Swimming speeds for pink salmon females (mean CV = 13.2) were less variable than those for pink salmon males (mean CV = 36.6; LSM, $P = 0.0005$). Sockeye salmon females (mean CV = 22.6) did not differ in swimming speed variation from pink salmon females (LSM, $P = 0.0972$) or pink salmon males (LSM, $P = 0.0275$). Swimming speeds for sockeye salmon males (mean CV = 55.0) were more variable than those for female pink salmon ($P = 0.0001$), male pink salmon ($P = 0.0001$), and female sockeye salmon (LSM, $P \leq 0.0001$). Within-group variation in log ground speed ($F_{8,23} = 0.75, P = 0.5361$) or log energy use ($F_{8,23} = 0.99, P = 0.4168$) did not differ among sex–species classes. Within species–sex group variation in swimming speed ($F_{8,23} = 0.42, P = 0.8987$), log energy use ($F_{8,23} = 0.99, P = 0.4666$), and log ground speed ($F_{8,23} = 1.54, P = 0.1964$) did not differ between reaches (Fig. 3). As a summary of energy-use variability among reaches, CV was calculated based on the four species–sex mean energy-use values at each reach (presented in Fig. 3).

**Discussion**

As we found in our reanalyses of their data, Hinch and Rand (1998) found that reaches with constrictions were the most energetically costly for migration of sockeye salmon. We also found this for pink salmon, although it is somewhat more complicated. Certainly constricted reaches (e.g., 4, 7, and 9) caused high energy use for pink salmon, but so did reaches 3 and 6. The latter had large bends and relatively fast surface currents (unlike the other reaches with bends that had relatively slow currents). The common feature among these five reaches is that the combination of their bank morphologies and current speeds would result in extremely complex surface and subsurface flow patterns. Energy use is accelerated by increased swimming speeds or increased ground speeds, and our results indicate that depending on the reach, either one or both are responsible for high energy-use values. Flow complexity can cause an increase to both swimming speeds and ground speeds. Hinch and Rand (2000) used underwater video to examine swimming speed, encountered water velocities, and ground speeds of upriver-migrating sockeye salmon and found that at non-turbulent and slow water sites, fish adjusted their swimming speeds to achieve ground speeds that resulted in energetically minimal costs. However, when encountered currents were relatively fast and turbulent, fish chose to swim relatively fast and not elicit this energy-saving behaviour. They speculated that at fast, turbulent sites, salmon might be attempting to minimize their travel times because they only have a short while to live and significant migration impediments could seriously affect arrival times on spawning grounds and hence negatively affect spawning success.
It is equally likely that complex, turbulent, and fast currents prevent fish from readily locating migration cues thus taking longer to find a desired path and therefore having decreased ground speeds. The diminished ability to locate cues and paths is supported by the among-reach variability (as measured by the CV) in energy use that we found. Reaches with complex flow patterns probably have the greatest diversity of hydraulic conditions, allowing for a greater number of possible migratory routes, which could explain the relatively higher among-individual variation in energy use that we found at these complex flow reaches. A closer examination of migration path choice suggests that migrating fish cross the river and backtrack more often at reaches with constrictions (Standen 2001; Hinch et al. 2002). This may be evidence that the fish are being diverted by strong, turbulent flows or that they are attempting to locate small-scale low velocity fields for upriver migration. Whenever the reason, small-scale hydraulic conditions appear to be of great importance in determining behaviour and resultant energy use in migrating salmon. In sum, whether caused by a desire to reduce travel time thereby elevating swimming speed or by an inability to locate appropriate paths thereby decreasing ground speed, river reaches with constrictions and those where currents are fast and deflected by river bends cause pink and sockeye salmon to use relatively high levels of energy during migration.

Hinch and Rand (1998) found that during migration, male sockeye used more energy than female sockeye. The present reanalysis of their data suggests that this depends upon reach. Male sockeye exhibited the most costly migrations at constricted reaches (e.g., reaches 4, 7, and 9). Our present results differ from those of Hinch and Rand (1998) for two reasons. First, to analyze their data, they chose to use a two-way ANOVA that did not take individual variation into consideration, unlike the repeated-measures split plot used in this analysis. Large individual variation may be masking stronger differences between sexes. Of equal importance, this analysis used only a subsample of their sites. They included three very low velocity sites on the Nechako River as well as the much more constricted Hell's Gate site on the Fraser River. Hinch and Rand found strong differences between sexes at Hell's Gate, which supports the findings of this study that differences between the sexes become more apparent in areas of difficult passage.

In pink salmon, we found no statistically significant differences in energy use between males and females. Although not statistically different, male energy use at each reach was always higher than that of females, and as with sockeye, differences were most evident at our constricted, fast-flowing reaches (reaches 4 and 9) where males used over 4 times the energy of females. Based on swimming tunnel experiments, Williams and Brett (1987) estimated that male pink salmon use 15% more energy than females to swim the same distance. Thus it is likely that sex differences exist but our sample size may have been too low for adequate detection.

Several factors can explain why adult male salmon seem to use more energy than adult females during migration through reaches with fast and complex flows. Increased selective pressure for migration efficiency likely exists for females because they must allocate relatively more energy to egg production than males do for milt production (Gilhousen 1980; Jonsson et al. 1991; Brett 1995). Also males undergo a much more distinct morphological change. Males develop a large dorsal hump and extended kype (Brett 1995). This change in shape may increase their hydrodynamic drag (Weihs and Webb 1983; Videler 1993) and potentially force them to increase their swimming speed and energy expenditure to reach the spawning grounds at the same time as females. A difference between sexes in hydrodynamic drag may be most evident at reaches with fast and complex flows. There may also be increased physiological differences in the cardiac and metabolic processes between males and females as they near reproductive maturity. During respirometer trials with sockeye salmon, males swam at consistently higher $V_{O_{2}}$max (the maximum volume of oxygen consumed by a swimming fish) than females of the same size, indicating that females are more efficient swimmers (Christopher G. Lee, Biology Department, Simon Fraser University, Burnaby, B.C., unpublished data). Webb's (1995) theory that fish can minimize energy use by swimming at metabolic and hydrodynamic optimal speeds suggests that differences in physical shape and metabolism between the sexes could cause them to have different energy-use minima.

Contrary to our original prediction, pink salmon were not less efficient (used less energy per metre) than sockeye salmon. There were no statistical differences between the species, and there was a trend towards pink salmon actually being more efficient. This was most noticeable at the reaches with fast water speeds (e.g., reaches 4 and 6). Interspecific differences in migration paths probably exist and these may be responsible for any differences in energy use between species. Using a split-beam echosounder, Xie et al. (1997) found that pink salmon migrated in tight groups close to shore near the bottom of the river, whereas sockeye migrated in less dense aggregates further from shore and throughout the water column. River velocities generally increase with distance away from the bank and bed of the river (Henderson 1966), which would suggest that sockeye are encountering faster currents that could be more costly to migrate. As well, Seton River pink salmon migrate only one-third the distance of the Early Stuart sockeye salmon. Because of the longer migration distance they travel to reach their spawning grounds and the small temporal window they have in which to do it, Early Stuart sockeye salmon may be swimming at faster, more energy-demanding speeds.

Two assumptions were made to compare the migration energetics of pink and sockeye salmon. First, although pink and sockeye salmon were studied through the same reaches in the Fraser River, they were studied in different years. However, temperature and river discharge were very similar during the periods of study of the two species, particularly when one considers how variable these features can be inter-annually (Macdonald 2000). Second, a sockeye salmon bioenergetics model (Hinch and Rand 1998) was used to predict energy use for pink salmon. Currently a sockeye salmon bioenergetics model for pink salmon does not exist. Williams and Brett (1987) determined that the $U_{crit}$ (the swimming velocity at which a fish can sustain itself for 60 min before reaching exhaustion and failing to swim) for pink salmon was similar to that for sockeye, suggesting that bioenergetics parameters may be similar between species, yet Brett (1982) found that pink salmon required higher amounts of energy to maintain $U_{crit}$.
swimming. These types of conflicting results may reflect the fact that different stocks of pink salmon were used in those two studies. Studies of swimming metabolism on Seton pink salmon and Early Stuart sockeye salmon are needed to better understand their endogenous swimming abilities. Lastly, although not an assumption, sample size was a general limitation to this study. The lack of strong differences between sexes and species may be due to small sample size and resulting large individual variation within each species-sex group.

Our interpretations of EMG data from migrating fish are determined by our laboratory EMG – swimming speed relationships. Other laboratory swimming tunnel studies in which EMG technology has been used to assess swimming speeds of salmonids have found that individual fish can vary in their EMG – swimming speed relationships, resulting from size, sex, and transmitter-specific factors (reviewed in Thorstad et al. 2000). Within this study we have minimized these potential differences by including size and sex as covariates in the models. In terms of transmitter-specific factors, EMG information can vary with the muscle insertion position of the sensing electrodes and with subtle technical differences among transmitter electronics. We implanted electrodes using methods and insertion positions that were identical for each fish, although there may have been minor differences among fish. We have no control over factory-generated differences in transmitter electronics. However, there is no reason to suspect that these transmitter factors have caused a bias in our interpretations. In other words, they should not affect one sex, species, or reach more than another. Transmitter factors should contribute to the levels of unexplained variation that we report in individual-specific EMG data. The fact that we can detect consistent and strong differences among reaches in EMG patterns indicates just how influential this variable is in the face of these other potential sources of variation. Ideally, one should develop EMG – swimming speed calibration relationships for each individual fish (and transmitter) that is being tracked in the wild (e.g., first swim the fish in vivo before studying it in situ) (e.g., Geist et al. 2002).

We have found that this is not possible with mature Pacific salmon, and Early Stuart sockeye salmon are needed to better understand their endogenous swimming abilities. Lastly, all other laboratory swimming tunnel studies in which EMG technology has been used to assess swimming speeds of salmonids have found that individual fish can vary in their EMG – swimming speed relationships (e.g., Hinch et al. 2002). Using the same EMG data summarized in the present study, Hinch et al. (2002) calculated that 5–10% of the time, burst speeds (which are fueled by anaerobic metabolism) were being elicited by both species in our reaches. The higher percentage values were at the reaches with constrictions, indicating that these reaches are more energetically costly than our present results suggest. Furthermore, if figured into total energetic costs, these additional anaerobic costs could thus make the migrations of pink salmon males more expensive than those of pink salmon females, thereby strengthening our original prediction that male salmon are less energetically efficient at migration than females.

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