



## Swimming patterns and behaviour of upriver-migrating adult pink (*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon as assessed by EMG telemetry in the Fraser River, British Columbia, Canada

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### Abstract

Little is known about the behaviour patterns and swimming speed strategies of anadromous upriver migrating fish. We used electromyogram telemetry to estimate instantaneous swimming speeds for individual sockeye (*Oncorhynchus nerka*) and pink salmon (*O. gorbuscha*) during their spawning migrations through reaches which spanned a gradient in river hydraulic features in the Fraser River, British Columbia. Our main objectives were to describe patterns of individual-specific swim speeds and behaviours, identify swimming speed strategies and contrast these between sexes, species and reaches. Although mean swimming speeds did not differ between pink salmon (2.21 BL s<sup>-1</sup>) and sockeye salmon (1.60 BL s<sup>-1</sup>), sockeye salmon were over twice as variable (mean CV; 54.78) in swimming speeds as pink salmon (mean CV; 22.54). Using laboratory-derived criteria, we classified swimming speeds as sustained (<2.5 BL s<sup>-1</sup>), prolonged (2.5–3.2 BL s<sup>-1</sup>), or burst (>3.2 BL s<sup>-1</sup>). We found no differences between sexes or species in the proportion of total time swimming in these categories – sustained (0.76), prolonged (0.18), burst (0.06); numbers are based on species and sexes combined. Reaches with relatively complex hydraulics and fast surface currents had migrants with relatively high levels of swimming speed variation (e.g., high swimming speed CV, reduced proportions of sustained speeds, elevated proportions of burst speeds, and high rates of bursts) and high frequency of river crossings. We speculate that complex current patterns generated by river constrictions created confusing migration cues, which impeded a salmon's ability to locate appropriate pathways.

### Introduction

Adult Pacific salmon (*Oncorhynchus spp.*) do not feed during their upriver spawning migrations and must rely entirely on energy reserves to complete migration and spawn. Migrations can be energetically expensive, particularly when environmental conditions are adverse (e.g. caused by elevated discharge or temperature) or when travel distances are long (Gilhausen,

1980; Bernatchez & Dodson, 1987; Brett, 1995). Body constituent analyses on Pacific salmon reveal that more than 50% of total energy is often utilized to complete migrations (reviewed in Brett, 1995). Relatively high levels of energy use are thought to cause enroute or prespawning mortality (Rand & Hinch, 1998; Macdonald, 2000).

With the advent of electromyogram (EMG) radio telemetry, it has become possible to examine activity

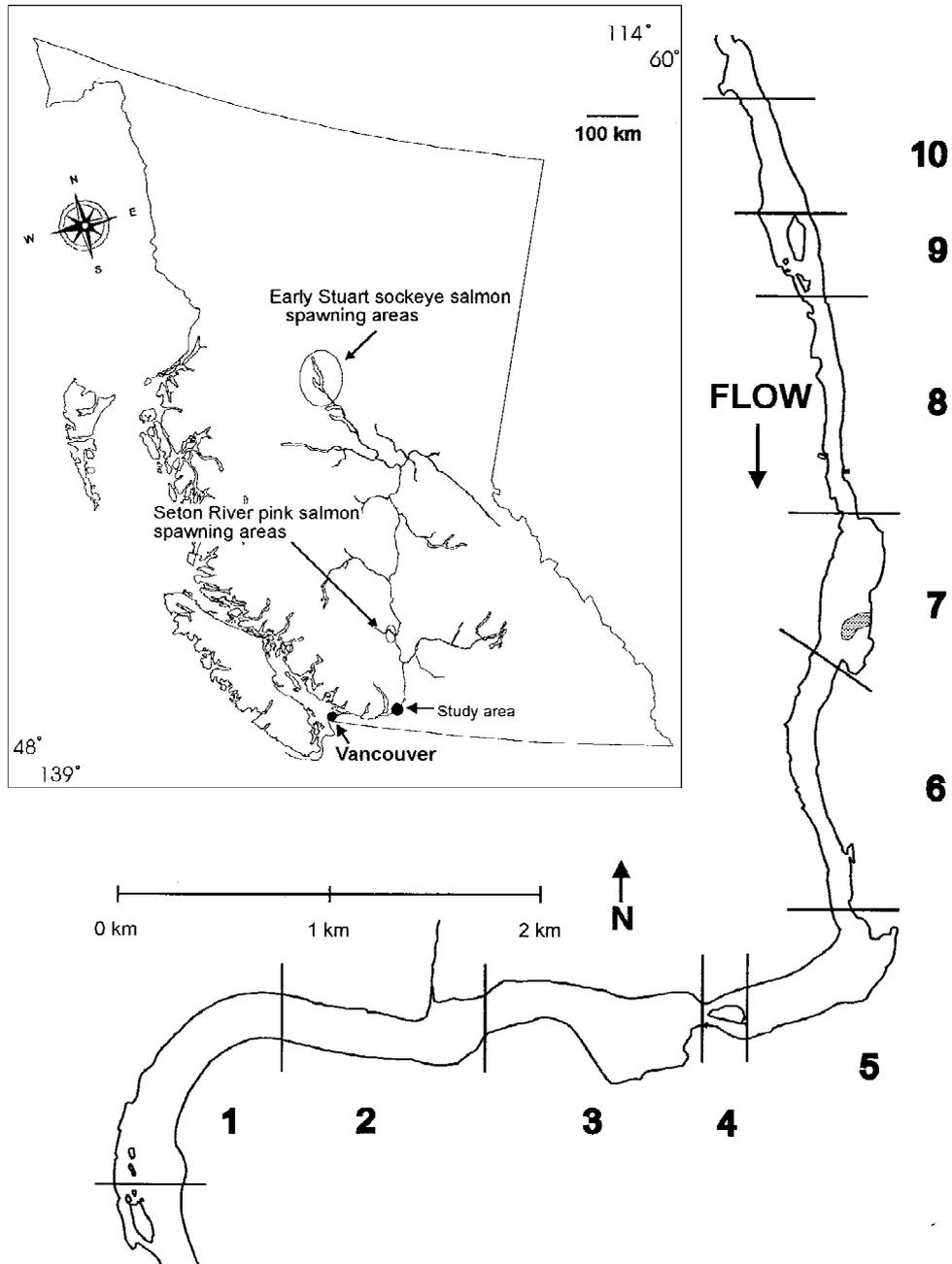


Figure 1. Map of Fraser River canyon indicating 10 reaches (numbered) that were studied by Hinch & Rand (1998). We used their reaches 2, 4, 7 and 9 in this study. Inset is a map of British Columbia, Canada showing the Fraser River and its main tributaries, the locations of spawning destinations for the two stocks of salmon in this study, and the location of our study area.

and behaviour in migrating fish (McKinley & Powers, 1992; Hinch et al., 1996; Økland et al., 1997; Hinch & Rand, 1998; Hinch & Bratty, 2000). Although still poorly understood, it is becoming apparent that behaviour is an extremely important factor affecting energy use and migration success in Pacific salmon (Rand & Hinch, 1998). The importance of behaviour was recently demonstrated by Hinch & Bratty (2000) who observed with EMG telemetry that hyperactive swimming patterns in sockeye salmon (*Oncorhynchus nerka* Walbaum) were associated with passage failure and mortality at Hell's Gate, a notoriously difficult site for passage in the Fraser River, British Columbia. With the exception of Hinch & Bratty, there has been little description or quantification of individual-specific variation in swimming speeds of upriver migrating anadromous fish, nor any examination of swimming speed patterns that are attributable to specific sexes, species, or habitat features.

In this study, we used EMG telemetry to estimate instantaneous swimming speeds for individual sockeye and pink salmon (*O. gorbuscha* Walbaum) during their upriver migration through the Fraser River, British Columbia. Our main objectives were to describe patterns of individual-specific swim speeds and behaviours, and contrast reach-specific swimming patterns between sexes and species. To address these issues, we utilized telemetry information that was previously collected as part of other studies (Hinch & Rand, 1998; Standen, et al., in press). However, these studies focussed on average energy use and only provided a brief summary description of average swim speeds. They did not report on swimming speed patterns, migration routes, or present any results or interpretation of species-, sex- or individual-specific activity levels.

### Description of study sites

The Fraser River drains approximately one third of British Columbia and is one of the largest producers of wild Pacific salmon in the world (Northcote & Burwash, 1991). Flows through the mainstem of the Fraser River are not regulated by humans. Our research was carried out in the lower section of the Fraser River mainstem (Fig. 1). This area exhibits a wide range of flow conditions and habitat features. All five species of Pacific salmon migrate through here (Groot & Margolis, 1991) making it an ideal location for interspecific comparisons of salmon migration behaviour.

Our study area was the same as that used by Hinch & Rand (1998). The area is bounded between river kilometre 150 and 157 (Fig. 1). Hinch & Rand divided their study area into 10 contiguous reaches and classified each based on bank morphology (e.g., constrictions, bends, or straight banks), 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), and centreline velocities. We chose four of their reaches (reaches 2, 4, 7, and 9) to focus attention on because they reflect the range in natural variability in river habitat encountered in the Fraser River (see Fig. 1) and because they had the most complete telemetry coverage out of all the reaches. Reach length, width and gradient were determined using 1:4000 aerial photographs; distances were measured from the center of the river. Reach 2, located immediately downstream of the Fraser River canyon, had an average gradient of  $75 \text{ cm km}^{-1}$ , all other reaches were in the canyon and had an average gradient of  $120 \text{ cm km}^{-1}$ . Reaches ranged in length from 200 to 973 m and in width from 117.5 to 192.5 m. Surface water speeds were estimated by timing the passage of floating wooden blocks ( $20 \times 20 \times 5 \text{ cm}$ ) downriver, over a known distance, above the main thalweg of the river. Reach 2 has parallel banks, no constrictions, unidirectional centreline flows, and centreline surface water speeds of  $147 \text{ cm s}^{-1}$ . Reach 4 is constricted by an island, has two channels, multidirectional centreline flows, and centreline surface water speeds of  $385 \text{ cm s}^{-1}$ . Reach 7 has parallel banks with a large gravel bar creating a constriction, multidirectional centreline flows, and centreline surface water speeds of  $246 \text{ cm s}^{-1}$ . Reach 9 is constricted by two large islands and three small ones, has several channels, multidirectional centreline flows, and centreline surface water speeds of  $292 \text{ cm s}^{-1}$ .

Water temperatures were measured hourly by Fisheries and Oceans Canada at Hell's Gate, situated approximately 10 km upstream of our study area. Daily mean water temperatures were  $13.9\text{--}15.4 \text{ }^\circ\text{C}$  during the 1999 field season and  $14.0\text{--}17.0 \text{ }^\circ\text{C}$  during the 1993 field season with mean temperatures of  $15.7$  and  $14.9 \text{ }^\circ\text{C}$ , respectively. Discharge measurements were made daily by the Water Survey of Canada at Hope BC, situated approximately 20 km downstream of our study area. During the 1999 field season, the mean daily discharge was  $2758 \text{ m}^3\text{s}^{-1}$  (range,  $1900\text{--}4030 \text{ m}^3\text{s}^{-1}$ ). During the 1993 field season, the mean

daily discharge was  $3295 \text{ m}^3\text{s}^{-1}$  (range, 3170–3770  $\text{m}^3\text{s}^{-1}$ ).

## Materials and methods

### *Study animals and telemetry approaches*

The sockeye salmon are from the early Stuart stock, which spawn in the Stuart Lake system (Fig. 1) and migrate through our study area in July. This is the longest distance migrating sockeye stock in the Fraser River system, traveling approximately 1200 km upriver. In 1993, we studied nine sockeye salmon (four males, mass 2.0–2.8 kg, fork length 57.9–61.7 cm; five females, mass 1.4–2.0 kg, fork length 50.7–57.2 cm). The pink salmon are from the Seton River stock, which spawn in the Seton River system (Fig. 1) and migrate through our study area in September and October. This is the longest distance migrating pink stock in the Fraser system, travelling approximately 400 km upriver. In 1999, we studied 12 pink salmon (six males, mass 1.50–2.25 kg, fork length 47.5–56.6 cm; six females, mass 1.00–1.35 kg, fork length 47.5–50.6 cm).

Fish were collected in the Fraser River canyon and EMG radio transmitters (Lotek Engineering Inc., Newmarket, Ontario) were implanted on site. One fish was released per day downstream of reach 2 and tracked upstream on foot using a hand-held directional three-element Yagi antenna. EMG pulse interval data were recorded on a 3–5 s interval by hand-held radio receivers (Model SRX 400; Lotek Engineering). Fish positions could be ascertained to within 5 m. Details on fish collection, release and position-finding methodologies are given in Hinch & Rand (1998) and Standen et al. (in press). A description of the EMG radio transmitters and details about their surgical implantation are outlined in Hinch et al. (1996). Fish were normally released in the morning and tracked continuously during daylight hours, typically completing migration through our study area during that day. Early Stuart sockeye salmon will migrate up-river during night times (Hinch & Rand, 1998) but Seton pink salmon appeared to migrate only during daylight.

Hinch & Rand (1998) studied volitionally swimming adult sockeye containing EMG transmitters in the laboratory and showed that EMG pulse interval signals were strongly correlated to tail beat frequency. They developed predictive relationships for sockeye salmon between EMG pulse intervals and instantan-

eous swim speeds (in body lengths per second,  $\text{BL s}^{-1}$ ). Standen et al. (in press), conducted similar trials on adult pink salmon and developed relationships for the prediction of instantaneous swim speeds from EMG data. We used these two sets of predictive relationships to estimate swimming speeds that were associated with EMG pulse intervals recorded in the field from sockeye and pink salmon. Others studies on salmonids have demonstrated that EMG pulse intervals are strongly correlated with swimming speeds (Thorstad et al., 2000, and references within).

### *Behavioural observations*

Travel time through a reach was determined for each fish by subtracting time of reach first exit from time of reach first entry. We calculated travel rate (also termed ground speed) by dividing reach length by travel time. To explore swimming patterns, we calculated the mean and coefficient of variation (CV) for swimming speeds for each individual at each reach. We also calculated the proportion of total within-reach time that each individual spent swimming under sustained speeds, prolonged speeds, and burst speeds. The three swimming speed categories are defined from laboratory results of swimming performance and fatigue trials and are described below. Although each category encompasses a broad range of swimming speeds, they provide a convenient and well-understood convention for describing swimming patterns. We also calculated the number of bursts per second (i.e., rate of burst swimming) that were elicited by each individual at each reach because burst swimming could be a very important behaviour enabling migrating salmon to pass through relatively fast currents.

Defined as speeds which can be maintained without fatigue for 200 min or more (Beamish, 1978), sustained swimming is the slowest class of speeds but may be the most common ones elicited by fish during non-migratory phases of life (Beamish, 1978). Prolonged swimming reflects the fastest class of speeds that can be elicited while still performing predominantly under aerobic metabolism, although high prolonged speeds are not usually attained without some component of anaerobic metabolism (Burgetz et al., 1998). Prolonged speeds may be the ones most commonly elicited during migration (Beamish, 1978). Burst swimming is the fastest class representing speeds generated by swimming entirely under anaerobic metabolism. These speeds are often defined as those that cannot be continuously maintained for

more than 20–60 s (Beamish, 1978). Based on swimming performance and fatigue information provided in Brett (1967), Brett & Glass (1973), and Beamish (1978) for adult sockeye, we classified sustained speeds as those under  $2.5 \text{ BL s}^{-1}$ , prolonged speeds as  $2.5\text{--}3.2 \text{ BL s}^{-1}$ , and burst speeds as greater than  $3.2 \text{ BL s}^{-1}$ . Detailed swimming performance experiments have not been performed on adult pink salmon. Williams & Brett (1987) determined that the critical swimming speed (the  $U_{\text{crit}}$ ) for adult pink salmon was very similar to that for adult sockeye salmon so we will assume the same swimming performance criteria for both species.

We quantified three characteristics of the pathways used by individual fish as they migrated through each reach and examined these values for strong and consistent trends, between species and sexes. First, because fish tended to migrate near riverbanks, we determined the percentage of fish exiting a reach along a different bank than was entered (termed ‘bank infidelity’). Banks associated with islands (e.g., in reaches 4 and 9), were also considered. Second, we counted the number of times within a reach that individuals crossed from one bank to another (termed ‘crossings’). Third, we counted the number of times individuals backtracked to a previous downstream position (termed ‘backtracking’). Backtracking involved relocation downstream directly in a straight-line path, or indirectly in a circular path which may have resulted from a failed crossing.

### Statistical analyses

Split-plot repeated-measures ANOVAs (SAS Institute, 1988) were used to assess how variability in each salmon swimming behaviour was accounted for by sex, species, and reach type. Seven separate repeated-measures ANOVAs were conducted, one for each of the following behaviours (response variables): ground speed, mean swimming speed, CV of swimming speed, proportion of time in sustained swimming, proportion of time in prolonged swimming, proportion of time in burst swimming, and, number of burst swimming speeds. As type III sums of squares were used for calculating  $F$ -statistics, and individuals were nested both within a sex and a species, there was inadequate degrees of freedom to consider sex and species as separate main effects. Therefore it was necessary to consider sex and species as one variable, but with four separate classes (male pink, female pink, male sockeye, and female sockeye); henceforth called sex-

species class. Each analysis had sex-species class as a treatment (four classes = 3 df). River reach (four reaches = 3 df), a repeated measure with individual fish as replicates, was another treatment. This ANOVA design enabled us to test for interactions between reach and sex-species class (four reaches, four classes = 9 df). For each ANOVA, the treatment effect of sex-species class was tested for significance using fish individual as the error term. Fish individual (six fish in each class, four classes, three missing values = 17 df) was nested within sex-species class. We also used fish individual as a treatment. All tests of significance, other than that for sex-species class, used the general model error term (four reaches, six individuals in each class, four sex-species classes, 24 missing values = 36 df). See Kuchl (1994) for further details on split-plot repeated-measures designs. Statistical significance was assessed at the 0.05 level. Least square means (LSMs; SAS Institute, 1988) were used to assess, *a posteriori*, differences among the levels within the class variables. We used Bonferroni’s method to adjust the *a posteriori* significance levels when making multiple simultaneous contrasts of the LSMs. To minimize error variance heteroscedasticity variables were  $\log(x+1)$  transformed (or arcsine square root in the case of variables that were proportions) prior to conducting the ANOVAs. For sake of visual clarity and to prevent making *a posteriori* backtransformations, all LSM values presented in the text will be based on non-transformed variables.

We generated Pearson correlation’s between fish mass and each swimming behaviour, within-species and -reach, to assess the role that fish size may have in contributing to observed swimming patterns. We were unable to incorporate fish mass as an additional variable into the split-plot ANOVAs because of inadequate degrees of freedom. Statistical significance was assessed at the 0.05 level.

## Results

### Statistical analyses

The split-plot repeated-measures ANOVA accounted for 64% ( $P = 0.026$ ) of the variation in ground speed. Neither individual fish, sex-species class nor the interaction of reach and sex-species accounted for variation ( $P > 0.26$  for each). Only reach significantly explained variation in ground speed ( $P = 0.0004$ ). Specifically, ground speed through reach 2

(LSM 44.64 cm s<sup>-1</sup>) was nearly three times faster ( $P < 0.003$  for all contrasts) than through the other reaches. The other reaches did not differ in ground speed (for each  $P > 0.63$ ; LSMs: reach 4 17.83 cm s<sup>-1</sup>, reach 7 17.43 cm s<sup>-1</sup>, reach 9 15.55 cm s<sup>-1</sup>).

The split-plot repeated-measures ANOVA accounted for 97% ( $P < 0.0001$ ) of the variation in mean swimming speed. Individual fish and reach both accounted for significant variation in mean swim speed ( $P < 0.0001$  for each). Speeds through reach 9 were slower than through the other reaches ( $P < 0.002$  for each contrast), and speeds through reach 4 were faster than through the other reaches ( $P < 0.006$ ; Fig. 2). Speeds through reaches 2 and 7 did not differ ( $P = 0.20$ ). Sex-species class was not significant ( $P = 0.19$ ). The interaction between reach and sex-species class was significant ( $P = 0.036$ ) and was caused by a relatively low average swim speed by female sockeye at reach 9 (see Fig. 2).

The split-plot repeated-measures ANOVA accounted for 94% ( $P < 0.0001$ ) of the variation in swimming speed CV. Individual fish, reach, and sex-species class accounted for significant amounts of variation ( $P < 0.0001$  for each). Fish passing through reach 9 had a larger CV than when they passed through the other three reaches ( $P < 0.008$  for each of the three contrasts; Fig. 3). Fish passing through reach 2 had a smaller CV than when they passed through the other reaches ( $P < 0.01$  for each of the three contrasts). CV did not differ for passage through reaches 4 and 7. There is a species effect on CV; pink salmon males and females had lower values than sockeye salmon males and females ( $P < 0.0001$  for each contrast; Fig. 3). Female pink salmon had lower CV values than male pink salmon at each reach ( $P < 0.0001$ ) and a similar among-reach trend was noted for female and male sockeye salmon (Fig. 3) but this was not statistically significant ( $P = 0.20$ ). There was no interaction between reach and sex-species class ( $P = 0.48$ ).

The split-plot analysis explained 91% ( $P < 0.0001$ ) of the variation in the proportion of time spent swimming at sustained speeds. Individual fish ( $P < 0.0001$ ) and reach ( $P = 0.0004$ ) accounted for significant amounts of variation. There was no significant effect of sex-species class ( $P = 0.66$ ). Sustained speeds were elicited for higher proportions of time at reach 9 relative to reaches 4 and 7 ( $P < 0.0035$  for both; Fig. 4), and higher proportions of time at reach 2 relative to reach 4 ( $P = 0.002$ ; Fig. 4). Reaches 2 and 9 did not differ ( $P = 0.064$ ) nor did reaches 4 and 7 ( $P = 0.11$ ). We detected a weak interaction between

reach and sex-species class ( $P = 0.066$ ) which arose because female sockeye salmon at reach 9 had a disproportionately elevated duration of sustained speeds (LSM 98% of total time).

The split-plot analysis explained 86% ( $P < 0.0001$ ) of the variation in the proportion of time spent swimming at prolonged speeds. As with sustained speeds, individual fish ( $P < 0.0001$ ) and reach ( $P = 0.016$ ) explained significant amounts of variation, and there was no effect of sex-species class ( $P = 0.40$ ). Prolonged speeds were elicited for lower proportions of time at reach 9 relative to reaches 4 and 7 ( $P < 0.0027$  for both; Fig. 4). There were no differences among reaches 2, 4 and 7 ( $P > 0.065$ ). We detected a weak interaction between reach and sex-species class ( $P = 0.056$ ) which arose because female pink salmon at reach 4 had a disproportionately elevated duration of prolonged speeds (LSM 45% of total time).

The split-plot analysis explained 83% ( $P < 0.0001$ ) of the variation in the proportion of time spent swimming at burst speeds. As with sustained and prolonged speeds, individual fish ( $P < 0.0001$ ) and reach ( $P = 0.041$ ) explained significant amounts of variation, and there was no effect of sex-species class ( $P = 0.24$ ). Burst speeds were elicited for higher proportions of time at reach 4 relative to reach 2. There were no differences among any other combinations of reaches ( $P > 0.058$  for each contrast). There was no interaction between sex-species class and reach ( $P = 0.28$ ).

The split-plot analysis explained 85% ( $P < 0.0001$ ) of the variation in number of bursts elicited per second. Individual fish ( $P < 0.0001$ ) and reach ( $P = 0.011$ ) explained significant amounts of variation. There was no effect of sex-species class ( $P = 0.15$ ). Burst rates were twice as high at reaches 4 and 7 (both LSMs 0.011 bursts s<sup>-1</sup>) relative to that at reach 2 (LSM 0.005 bursts s<sup>-1</sup>;  $P < 0.0054$  for both contrasts). Burst rates at reach 9 (LSM 0.008 bursts s<sup>-1</sup>) did not differ from that at the other reaches ( $P < 0.23$  for all contrasts). A significant interaction between sex-species class and reach ( $P = 0.022$ ) was caused primarily by male sockeye salmon having relatively high burst rates at reaches 4, 7 and 9 (LSMs 0.020, 0.027 and 0.021 bursts s<sup>-1</sup>, respectively) compared to all other sex-species and reach combinations (LSMs range from 0.001 to 0.010 bursts s<sup>-1</sup>).

Within-species, we pooled data from both sexes and calculated Pearson correlations for each reach, between fish mass and each of the seven transformed swimming behaviour variables. We found positive cor-

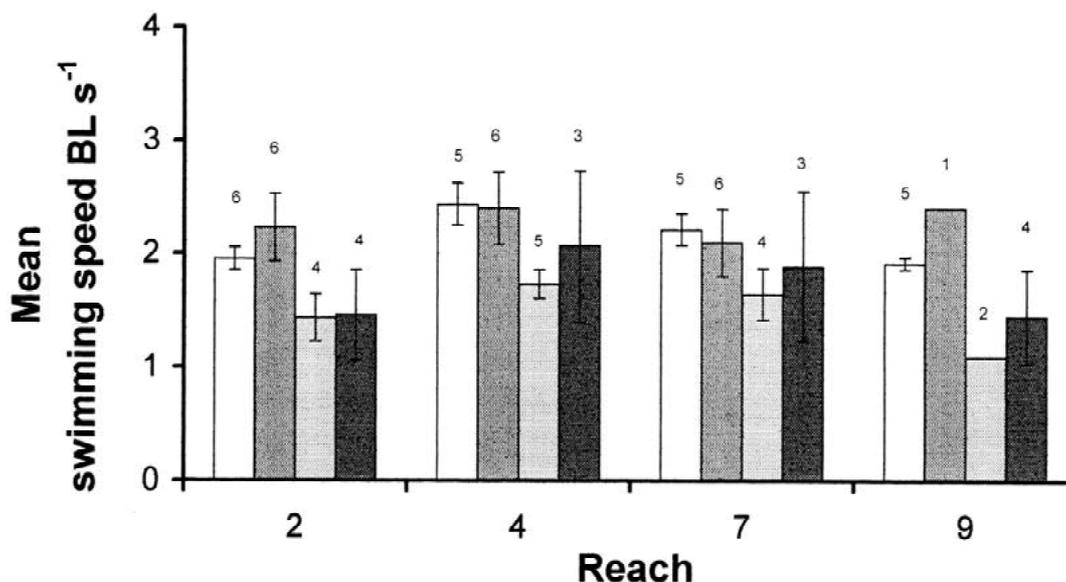


Figure 2. Mean swimming speeds in BL (plus/minus the standard error) for pink salmon females (white bars), pink salmon males (dark grey bars), sockeye salmon females (light grey bars), and sockeye salmon males (black bars). Numbers on bars indicate sample size.

relations for pink salmon at reaches 2 and 4 between mass and proportion of time spent burst swimming ( $r = 0.7388$ ,  $n = 12$ ,  $P = 0.0061$ ;  $r = 0.6521$ ,  $n = 11$ ,  $P = 0.030$ , respectively) and between mass and burst swimming rate ( $r = 0.8469$ ,  $n = 12$ ,  $P = 0.0005$ ;  $r = 0.6215$ ,  $n = 11$ ,  $P = 0.041$ ). We found no other significant correlations for pink salmon and none for sockeye salmon ( $P > 0.05$  in each case).

#### *Qualitative description of migration path behaviours and swimming strategies*

Of the 38 times that pink salmon individuals entered the study reaches, 84% were along north and west banks. In contrast, of the 29 times that sockeye salmon entered the reaches, 83% were along south and east banks. All study animals were released downstream of reach 1 (Fig. 1) at the identical locale on the north-west river bank. At each reach, sockeye salmon consistently exhibited higher levels of bank infidelity than pink salmon (sockeye salmon: among-reach mean 39.5% and range 13–50%; pink salmon: among-reach mean 21.8% and range 0–33%). Sockeye salmon tended to cross reaches (crossings per individual) more often than pink salmon (sockeye salmon: among-reach mean 1.14 and range 0.50–1.75; pink salmon: among-reach mean 0.75 and range 0.20–1.20). There were no clear between-species differences in regards to number of backtrackings per individual

(sockeye salmon: among-reach mean 0.77 and range 0–1.75; pink salmon: among-reach mean 0.84 and range 0–1.44).

To help illustrate the general differences between species that we observed in swimming patterns (Fig. 3) and migration path characteristics, we selected two individuals (a male sockeye salmon and a female pink salmon) for a detailed reach specific presentation of travel paths (Figs 5a and 6a) and of temporal patterns of instantaneous swim speeds (Figs 5b and 6b). Figure 5 illustrates results for a typical sockeye salmon. This male displayed backtracking and crossing in reaches 7 and 9 (Fig. 5a). Bouts of burst swimming were elicited in all reaches but were prevalent in reaches 7 and 9, and through the first half of reach 4 (Fig. 5b). Bursts were frequent in these reaches but usually brief in duration, lasting only a few seconds at a time. Burst speeds were relatively high (often 6–9 BL s<sup>-1</sup>) and were usually immediately followed by periods of low levels of sustained speeds (often 0 to 1 BL s<sup>-1</sup>). Periods of sustained and prolonged swimming did occur in parts of reaches 2 and 4, however, never more than 3 min passed without burst swimming interrupting these slower swimming speeds. Prolonged speeds were not consistently elicited and seemed to result primarily as a transition between burst and sustained speeds. We termed the swimming patterns of sockeye salmon as a ‘burst-coast and burst-sustained’ strategy.

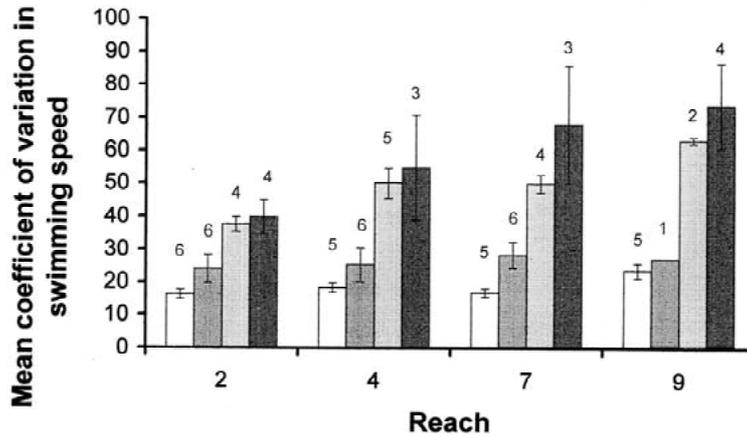


Figure 3. Mean coefficient of variation in swimming speed ( $\pm$  the standard error) for pink salmon females (white bars), pink salmon males (dark grey bars), sockeye salmon females (light grey bars), and sockeye salmon males (black bars). Numbers on bars indicate sample size.

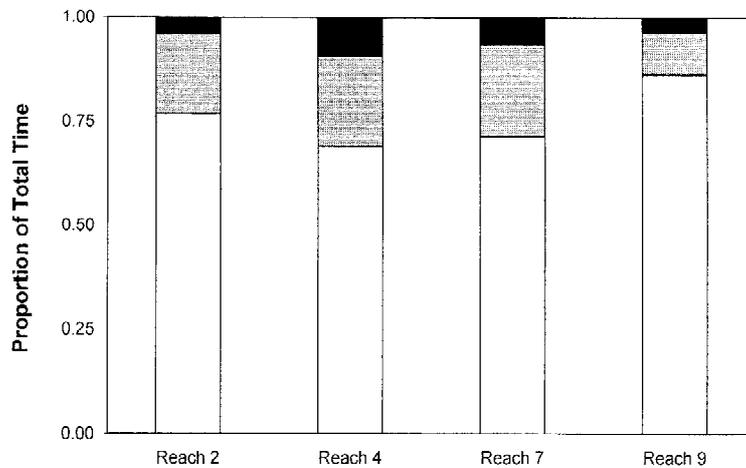


Figure 4. Proportion of time spent swimming with sustained (white), prolonged (grey) and burst (black) speeds at each reach. These values were calculated by averaging proportions of total time spent swimming within each of the three speed categories for individual fish, within each sex-species class, and then averaging these values within reaches.

Figure 6 demonstrates results for a typical pink salmon. This individual exhibited no backtracking and few crossings (Fig. 6a). As with sockeye, burst swimming was elicited in all reaches, however unlike sockeye, burst speeds never exceeded  $4 \text{ BL s}^{-1}$  (Fig. 6b). As with sockeye, speeds oscillated among sustained, prolonged and burst levels but in contrast to sockeye, most speeds were within a relatively narrow range ( $1\text{--}3 \text{ BL s}^{-1}$ ) and only rarely were very slow speeds of  $0\text{--}0.5 \text{ BL s}^{-1}$  elicited. We termed the swimming patterns of pink salmon as a ‘burst-prolonged and sustained-prolonged’ strategy.

### Discussion

This study details the swimming behaviours of two species of salmon migrating through the same reaches in the Fraser River. We found that mean swimming speeds did not differ between pink and sockeye salmon, nor did they differ between sexes within species. Further, ground speeds did not differ between sexes and species. One might conclude from this that migration swimming strategies are relatively conservative. However, the level of variability in swimming speeds, the patterns of this variability, and a consideration of migration pathways, revealed clear differences in swimming behaviours and strategies between species. Relative to pink salmon, sockeye salmon had

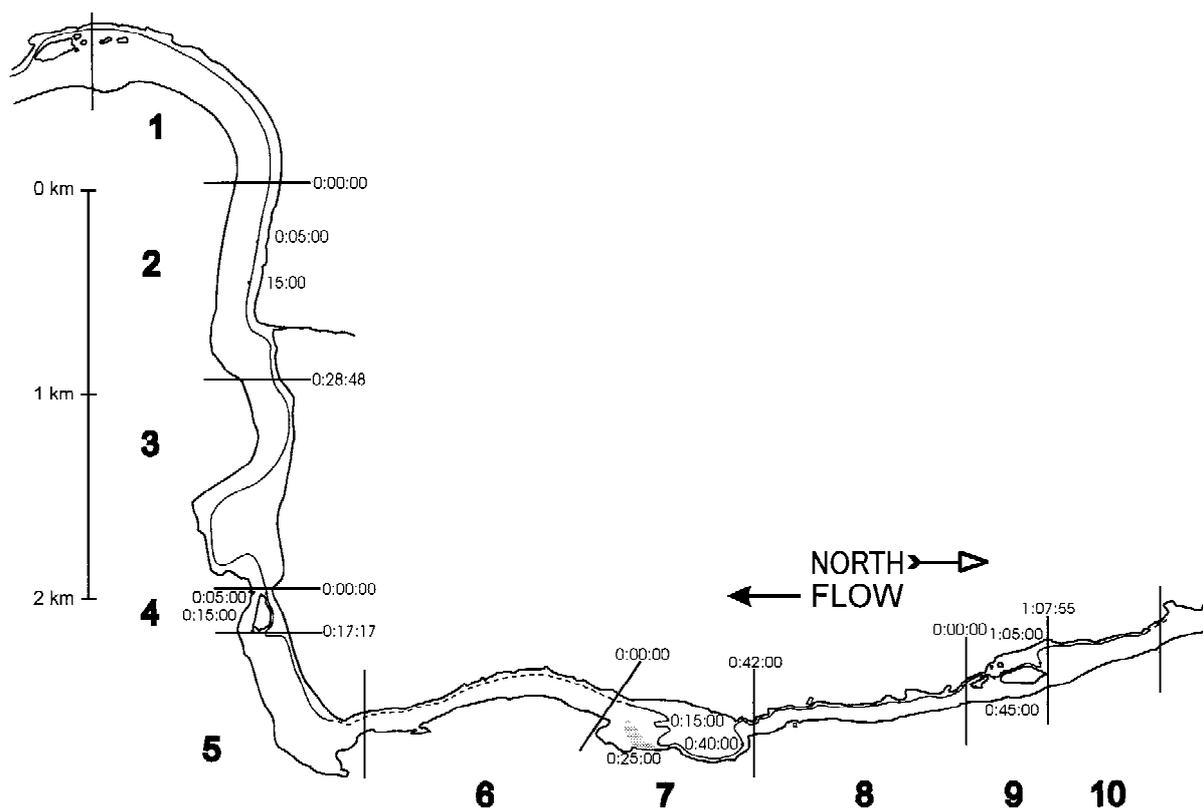


Figure 5a. Map of the study area showing the upstream migratory path of a male sockeye salmon (thin line). Times of entry, exit and intermediary points are indicated for each of the four study reaches.

highly variable swimming speeds and changed migration paths frequently. We suspect that sockeye explore alternative migration paths more frequently than pink salmon and in the process, encounter much higher variability in head currents. Using hydroacoustics at one locale in the lower Fraser River, Xie et al. (1997) found that sockeye salmon tended to migrate farther from shore in deeper water and in much looser aggregations than pink salmon, the latter supporting the notion that sockeye may utilize more diverse migration paths. Adult sockeye salmon, being larger than adult pink salmon (in our study 58% heavier, 13% longer), should be able to generate more power for a given tailbeat and thus could make forward progress against faster and more diverse currents than pink salmon. Thus, we might expect sockeye to roam more freely. However, the role of size is not clear – sockeye females are the same size as pink males yet their respective swimming patterns are different based on our CV analysis. The two species were studied in different years, yet the differences in temperature and discharge between study periods were quite small, particularly

in light of the extensive natural among-year variability that exists in hydrological conditions in the Fraser River (Macdonald et al., 2000). Thus, it is likely that river conditions did not play a strong role in causing the observed interspecific differences.

River reach was also an important determinant of swimming patterns. The four reaches spanned a gradient in river hydraulic features from reach 2 with no constrictions, a single channel and unidirectional currents to reach 9 with multiple constrictions, several distinct channels and multidirectional currents. Reaches 4 and 7 were intermediate in their hydraulic character, both had constrictions and multidirectional currents, but the former had two channels whereas the latter had only one. We found a general relationship between hydraulic complexity and swimming speed variation; the CV was lowest at reach 2, intermediate for reaches 4 and 7, and highest at reach 9. We also observed that, compared to reach 2, the number of river crossings were 2–3 times higher at reaches 4, 7 and 9 (pers. obs.). High levels of crossings and increased swimming speed variability at sites of mul-

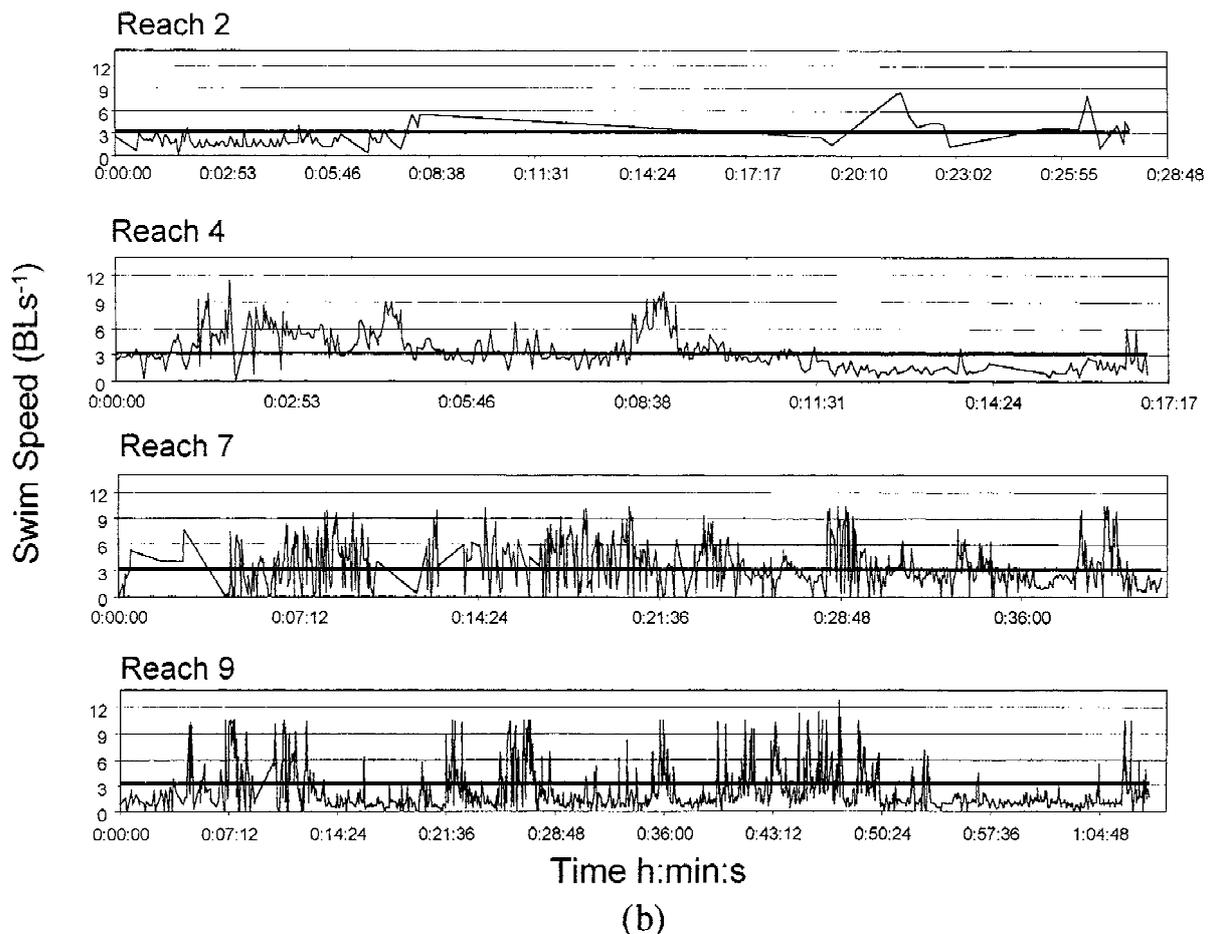


Figure 5b. Time-series plots of instantaneous swimming speeds for the male sockeye in Figure 5(a) from time of reach entry to exit for each of the four reaches. The solid lines represent  $U_{crit}$ .

tidirectional currents and multiple channels suggests that individuals had difficulty locating appropriate migration paths, possibly because these sites generated confusing migration cues (Hinch et al., 1996; Hinch & Bratty, 2000). The reach with the fastest surface currents (reach 4) required the highest mean swimming speeds, and the highest proportion of time swimming at burst levels, for passage. Interestingly, reach 4 also had the lowest bank infidelity out of all reaches (pers. obs.). Taken together, these results suggest that salmon can readily locate migration paths in fast water; but elevated swimming speeds are required to overcome the encountered currents.

Females allocate significantly more energy to gonad development during migration than do males (reviewed in Brett, 1995). As energy reserves to complete migration are limited and females are relatively smaller than males, it has been suggested that energy

saving swimming behaviours should be more strongly selected for in females than in males (Hinch & Rand, 1998). This should be especially true for long distance migrating stocks (Bernatchez & Dodson, 1987) such as those in our study. Although we found no general differences between male and female swimming behaviours at all reaches, we did find that at the reaches with complex hydraulics where passage is presumably most difficult, females exhibited some energy conserving behaviours. For instance, at reach 9, female sockeye salmon exhibited disproportionately high levels of sustained swimming and as a result, very low average swimming speeds. At reach 4, female pink salmon exhibited extremely high levels of prolonged swimming. Females of both species exhibited low burst rates, whereas sockeye salmon males exhibited disproportionately high burst rates (2–10 times higher) at the reaches with complex hydraulics.

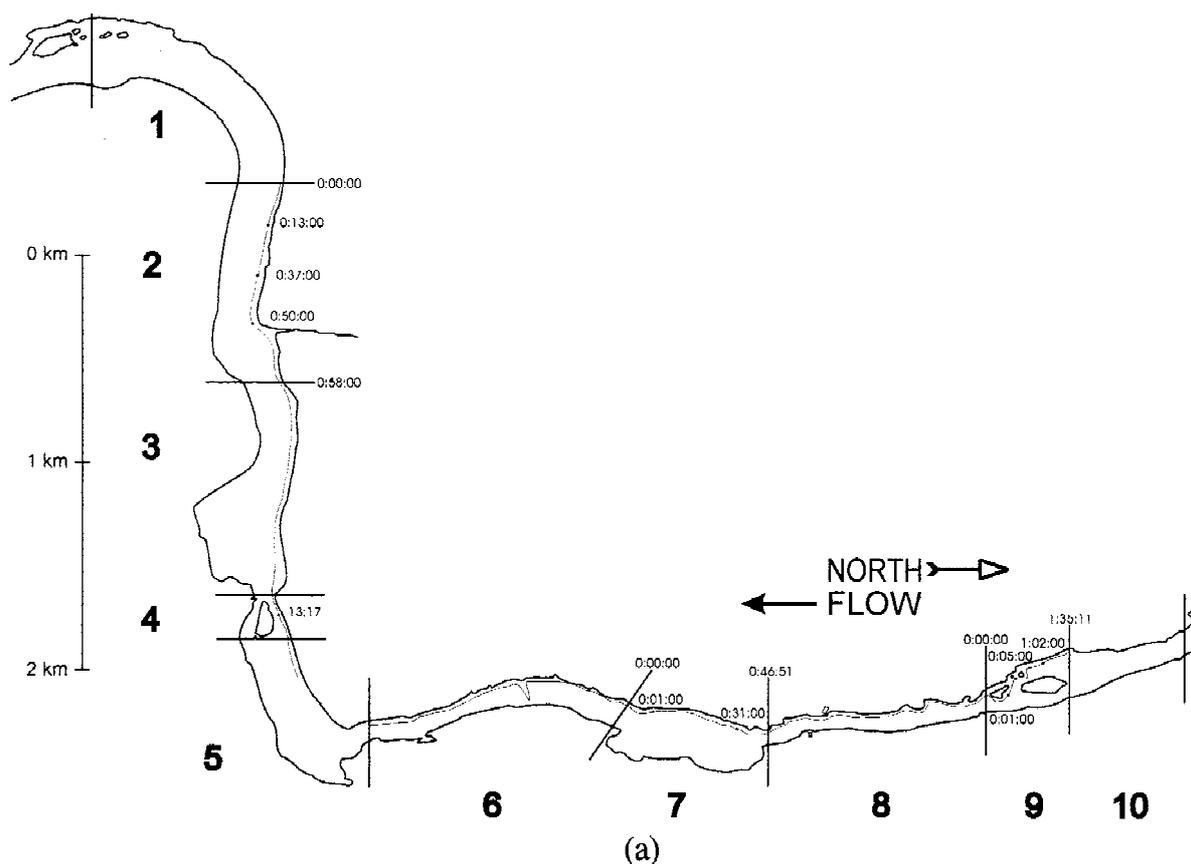


Figure 6a. Map of the study area showing the upstream migratory path of a female pink salmon (thin line). See Figure 5 for details.

Bioenergetics modelling has shown that these types of elevated rates of swimming speeds by male sockeye make them energetically less efficient migrants than females (Hinch & Rand, 1998).

Consistently, individual fish explained significant amounts of variation in swimming speed behaviours. Was variation in fish size a contributing factor? Based on body constituent analyses of upriver migrating Atlantic salmon (*Salmo salar* L., Jonsson et al., 1997) and American shad (*Alosa sapidissima* Wilson, Leonard et al., 1999), within-sex, large fish used more energy than small fish. We found that at reaches 2 and 7, large pink salmon exhibited higher proportions of burst swimming and higher burst rates, and like the examples above, presumably had higher energetic costs than small pink salmon. However, we could not detect any other size-related relationships thus our results provide only weak evidence to support a size-based explanation for observed levels of individual variability. Regardless of weight, sex or species, there could also be a genetic propensity for certain swim-

ming behaviours in some individuals. Hinch & Bratty (2000) could find no clear explanation for why some individual upstream sockeye migrants elicited hyperactive swimming patterns. The causes of individual variability in swimming patterns requires much further study.

Our interpretations of EMG data from migrating fish will only be as good as 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, maturation stage, and transmitter-specific factors (reviewed in Thorstad et al., 2000). Indeed we recognize this and have developed our relationships using fish at the same stages of maturation as those released into the field, and with size and sex as co-variates in the models. In terms of transmitter-specific factors, EMG information can vary with the muscle insertion position of the sensing electrodes and

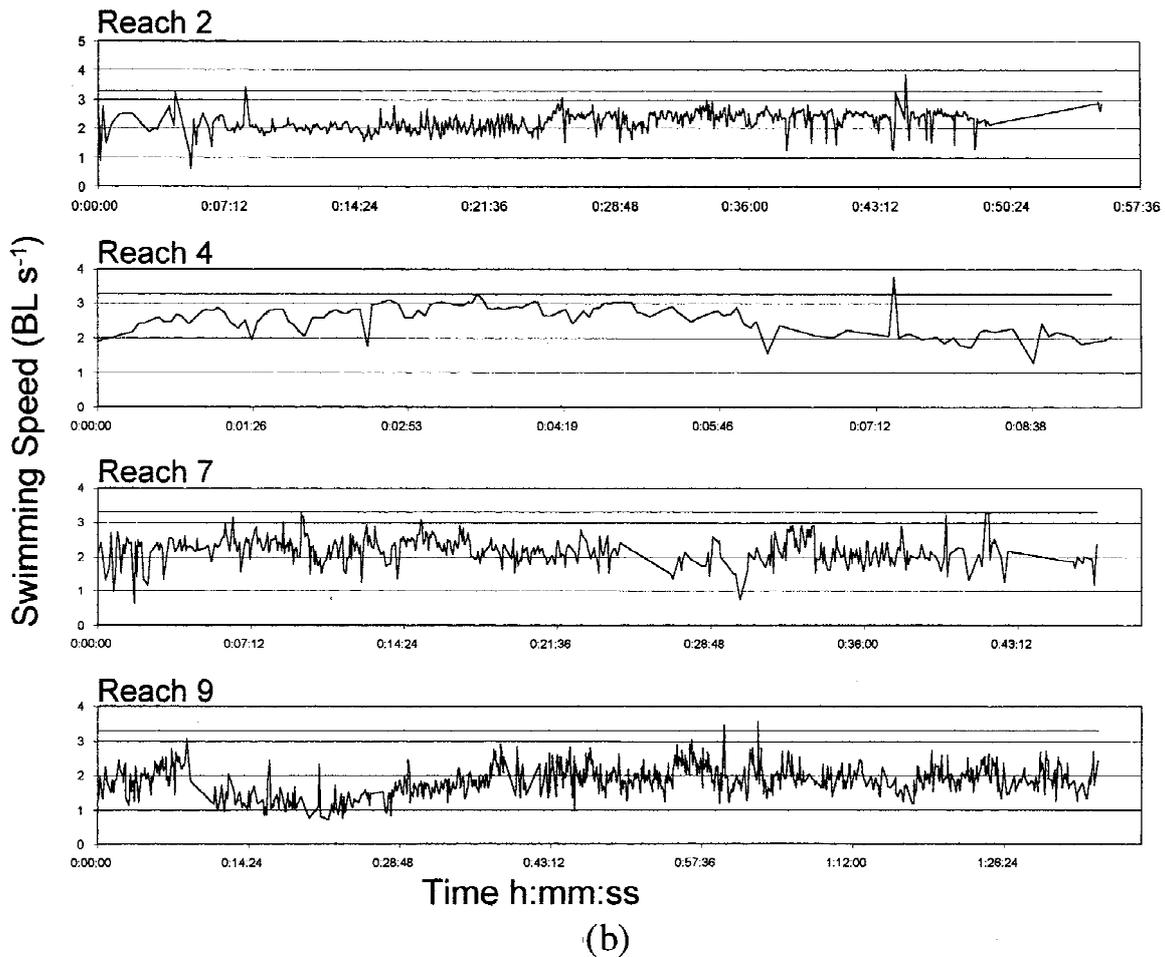


Figure 6b. Time-series plots of instantaneous swimming speeds for the female pink salmon in Figure 6(a) from time of reach entry to exit for each of the four reaches. See Figure 5 for details.

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 and species in EMG patterns indicates just how influential the variables reach and species are in the face of these other potential sources of variation. Ideally, one should develop EMG–swimming speed

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*). We have found that this is not possible with mature Pacific salmon who are very near death – fish do not seem able to fully recover from laboratory performance experiments and successfully complete their migration.

In conclusion, sockeye salmon and pink salmon ‘solve’ their migration challenges by swimming with very different strategies. Although mean swimming speeds were not different, sockeye salmon were much more variable in swimming speeds than pink salmon, a point that was clearly illustrated in Figures 5 and 6 where we identified the sockeye swimming pattern as ‘burst-coast and burst-sustained’ and the pink swimming pattern as ‘burst-prolonged and sustained-prolonged’. Interestingly, there were no broad differ-

ences between species in terms of proportions of total time spent at sustained, prolonged or burst speeds implying that both species used aerobic and anaerobic metabolic pathways approximately the same amounts of time. There is some evidence that male sockeye salmon have higher burst rates at constricted reaches. The relative frequency of burst swimming in sockeye salmon was surprising. In some constricted reaches, over 50% of the time was spent bursting. However, it should be pointed out that constricted reaches (e.g., reaches 4, 7 and 9) are not the 'norm' and that reach 2 is probably the dominant type of reach encountered during the migration. Nonetheless, the extensiveness and magnitudes of bursts and burst rates in migrating salmon are intriguing and could mean that we need to re-evaluate our thinking about energetics and performance in migrating fish. Furthermore, as the criteria defining swimming speed categories are developed in confined laboratory respirometer tunnels under steady swimming conditions, conclusions about the actual amounts of aerobic vs anaerobic costs in field studies such as ours must be made cautiously until such criteria can be assessed under more natural swimming conditions.

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### References

- Beamish, F. W. H., 1978. Swimming capacity. In Hoar, W. S., & D. J. Randall (eds.), *Fish Physiology*, Vol. 7. Academic Press, New York, NY: 101–186.
- Bernatchez, L. & J. J. Dodson, 1987. Relationship between bioenergetics and behaviour in anadromous fish migrations. *Can. J. Fish. aquat. Sci.* 44: 399–407.
- Brett, J. R., 1967. Swimming performance of sockeye salmon (*Oncorhynchus nerka*) in relation to fatigue time and temperature. *J. Fish. Res. Bd Can.* 24: 1732–1741.
- Brett, J. R. & N. R. Glass, 1973. Metabolic rates and critical swimming speeds of sockeye salmon (*Oncorhynchus nerka*) in relation to size and temperature. *J. Fish. Res. Bd Can.* 30: 379–387.
- Brett, R. J., 1995. Energetics. In Groot, C., L. Margolis & W. C. Clarke (eds), *Physiological Ecology of Pacific Salmon*. UBC Press, Vancouver, BC: 1–68.
- Burgetz, I. J., A. Rojas-Vargas, S. G. Hinch & D. J. Randall, 1998. Initial recruitment of anaerobic metabolism during sub-maximal swimming in rainbow trout (*Oncorhynchus mykiss*). *J. exp. Biol.* 201: 2711–2721.
- Gilhousen, P., 1980. Energy sources and expenditures in Fraser River sockeye salmon during their spawning migration. *Bull. Int. Pacific Salmon Fish. Comm.* XXII.
- Groot, C. & L. Margolis, 1991. *Pacific Salmon Life Histories*. UBC Press, Vancouver, BC.: 564.
- Hinch, S. G. & J. Bratty, 2000. Effects of swim speed and activity pattern on success of adult sockeye salmon migration through an area of difficult passage. *Trans. am. Fish. Soc.* 129: 598–606.
- Hinch, S. G. & P. S. Rand, 1998. Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): role of local environment and fish characteristics. *Can. J. Fish. aquat. Sci.* 55: 1821–1831.
- Hinch, S. G., R. E. Diewert, T. J. Lissimore, A. M. J. Prince, M. C. Healey & M. A. Henderson, 1996. Use of electromyogram telemetry to assess difficult passage areas for river-migrating adult sockeye salmon. *Trans. am. Fish. Soc.* 125: 253–260.
- Jonsson, N., B. Jonsson & L. P. Hansen, 1997. Changes in proximate composition and estimates of energetic costs during upstream migration and spawning in Atlantic salmon. *J. Animal Ecol.* 66: 425–436.
- Kuchl, R. O., 1994. *Statistical Principles of Research Design and Analysis*. Daxbury Press, Belmont, CA.
- Leonard, J. B. K. & S. D. McCormick, 1999. Effects of migration distance on whole-body and tissue-specific energy use in American shad (*Alosa sapidissima*). *Can. J. Fish. aquat. Sci.* 56: 1159–1171.
- Macdonald, J. S., 2000. Mortality during the migration of Fraser River sockeye salmon (*Oncorhynchus nerka*): a study of the effect of ocean and river environmental conditions in 1997. *Can. Tech. Rep. Fish. aquat. Sci.* #2315.
- Macdonald, J. S., and eleven others, 2000. The influence of extreme water temperatures on migrating Fraser River sockeye salmon (*Oncorhynchus nerka*) during the 1998 spawning season. *Can. Tech. Rep. Fish. Aquat. Sci.* #2326.
- McKinley, R. S. & G. Power. 1992. Measurement of activity and oxygen consumption for adult lake sturgeon (*Acipenser fulvescens*) in the wild using radio-transmitted EMG signals. In Priede, I. G. & S. M. Swift (eds), *Wildlife Telemetry: Remote Monitoring and Tracking of Animals*. Ellis Horwood, West Sussex, UK: 307–318.
- Northcote, T. G. & M. D. Burwash, 1991. Fish and fish habitats of the Fraser River Basin. In Dorcey, A. H. J. (ed.), *Water in Sustainable Development: Exploring our Common Future in the Fraser River Basin*. Westwater Research Center, University of British Columbia, Vancouver, BC: 117–144.
- Økland, F., B. Finstad, R. S. McKinley, E. B. Thorstad & R. K. Booth, 1997. Radio-transmitted electromyogram signals as indicators of physical activity in Atlantic salmon. *J. Fish Biol.* 51: 476–488.
- Rand, P. S. & S. G. Hinch, 1998. Swim speeds and energy use of up-river migrating sockeye salmon: simulating metabolic power and assessing risk of energy depletion. *Can. J. Fish. aquat. Sci.* 55: 1832–1841.
- SAS Institute, 1988. *SAS/STAT User's Guide*, Release 6.03 Edition. SAS Institute Inc., SAS Campus Drive, Cary NC 27513, USA.

- Standen, E. M., S. G. Hinch, M. C. Healey & A. P. Farrell. In press. Energetic costs of migration through the Fraser River canyon, British Columbia, in adult pink (*Oncorhynchus gorbuscha*) and sockeye (*O. nerka*) salmon as assessed by EMG telemetry. *Can. J. Fish. aquat. Sci.*
- Thorstad, E. B., F. Økland, A. Koed, & R. S. McKinley, 2000. Radio-transmitted electromyogram signals as indicators of swimming speed in lake trout and brown trout. *J. Fish Biol.* 57: 547–561.
- Williams, I. V. & J. R. Brett, 1987. Critical swimming speed of Fraser and Thompson River pink salmon (*Oncorhynchus gorbuscha*). *Can. J. Fish. aquat. Sci.* 44: 348–356.
- Xie, Y., G. Cronkite, & T. J. Mulligan, 1997. A split-beam echosounder perspective on migratory salmon in the Fraser River: A progress report on the split-beam experiment at Mission, B.C., in 1995. Pacific Salmon Commission Technical Report 8: 1–32.