Influence of river speed on path selection by migrating adult sockeye salmon (*Oncorhynchus nerka*)

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Abstract: We applied stereovideographic techniques to investigate path selection, ground speed, and swimming speed in adult sockeye salmon (*Oncorhynchus nerka*) ascending the Seton River, British Columbia. We tracked three-dimensional trajectories of salmon through 10 reaches and characterized the current profile at each site. At sites with relatively slow currents, the encountered river current speeds along the fish's trajectory were significantly lower than the mean current speed of the site. However, at higher current speed sites, fish experienced current speeds at or above the average current speed of the site and increased their ground speed through these sites. Observed in situ swimming speeds were 1.4–76.0 times greater than swimming speeds expected based on tailbeat frequency – swimming speed predictive relationships established in flume studies. We conclude that (*i*) at sites with relatively slow or moderate current speeds, fish minimize exposure to high-speed currents to minimize energy expenditure, (*ii*) at sites with high-speed currents, fish may change their migration strategy, minimizing time spent searching for low current speed pathways and increasing their ground speed to expedite passage, and (*iii*) laboratory-derived predictive equations may only be appropriate for predicting in situ swimming costs at sites with moderate and linearly flowing currents.

Résumé : Nous avons utilisé des techniques de vidéographie stéréo pour étudier le choix des voies de passage, la vitesse au sol et la vitesse de nage chez des saumons rouges (*Oncorhynchus nerka*) adultes qui remontent la rivière Seton, en Colombie-Britannique. Nous avons suivi les trajectoires tridimensionnelles des saumons à travers 10 sections du cours d'eau et avons décrit les profils des courants à chaque site. Aux sites de courants relativement lents, la trajectoire des poissons traverse des vitesses de courant significativement plus faibles que la vitesse de courant moyenne de la rivière à ce site. Cependant, aux sites de courants plus forts, les poissons rencontrent des vitesses de courant égales ou supérieures à la vitesse de courant moyenne du site et augmentent leur vitesse au sol en traversant ces sites. Les vitesses de nage observées dans le milieu sont 1,4–76,0 fois plus élevées que celles qui sont attendues d'après les relations prédictives entre la fréquence de battement de la queue et la vitesse de nage établies en canal expérimental. Nous concluons que (*i*) aux sites de vitesses de courant relativement lentes ou moyennes, les poissons minimisent leur exposition aux courants rapides afin de réduire leurs dépenses énergétiques au minimum, (*ii*) aux sites de forts courants, les poissons changent probablement de stratégie de migration en réduisant le temps consacré à la recherche de voies à faibles courants et en accélérant leur vitesse au sol de manière à réduire leur temps de traversée et (*iii*) les équations prédictives obtenues en laboratoire ne semblent pouvoir servir à évaluer les coûts de la nage in situ qu'aux sites de courants modérés à flux linéaire.

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Introduction

Most anadromous adult fish cease feeding upon starting spawning migrations and must complete the upriver journey and spawn using reserve energy. Body constituent analyses of fish sampled at the start and at the end of the migration have revealed that these migrations can be energetically demanding (e.g., 50–70% of initial energy may be used; Brett 1995; Jonsson et al. 1997; Leonard and McCormick 1999).

Migrants may use several different behavioural tactics to conserve energy including selecting low-speed current paths, burst-and-coast swimming, or swimming steadily at metabolic optimal speeds, defined as the speed that minimizes energy expenditure per metre traveled (reviewed in Webb 1995).

In addition, migrants may choose areas of reduced flow. This hypothesis to minimize energy consumption during migration was first postulated decades ago (Osborne 1961).

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Past studies of salmon migration behaviour based on visual observations and split-beam echosounders have shown that salmon swim linearly along the banks and bottom of river systems (Ellis 1966*a*; Xie et al. 1997). In a report on the migration behaviour of salmon, Ellis (1966*a*) showed salmon to migrate preferentially in nearshore and deeper water with marked lower current speeds. Fretwell (1981) has also shown adult fish to migrate near shore in current speeds below that of the average river flow. These observations suggest that salmon are able to distinguish between high- and low-speed flow fields on a large (entire river) scale. Salmon have also been shown to initiate upriver migration on incoming tides presumably taking advantage of the decrease in downstream river flow when possible (reviewed in Groot and Margolis 1991). As a result, salmon appear to preferentially migrate in lower speed flow areas within large river systems.

More recent studies using physiological telemetry on upriver-migrating adult Pacific salmon (*Oncorhynchus* spp.) have demonstrated that current speed and flow turbulence are important environmental features affecting energy use (Hinch and Rand 1998; Standen 2001; Standen et al. 2002). These studies have suggested that differences among species, sexes, or reaches in relative energy use are largely attributed to differences in behaviour (e.g., swim speeds, migratory paths). Within these studies, fish were also found to migrate close to shore and to the bottom, suggesting that fish are avoiding high current speed, energetically expensive areas within the river. These telemetry studies provide measures of behaviour at relatively coarse scales over reaches of 50–1000 m in length. The objective of the present study was to determine if migrants can take advantage of finer scale speed current variations within a reach towards improving our understanding of how swimming behaviours may affect energy utilization or conservation during migration.

Underwater stereovideography was recently employed to explore the behavioural tactics used by upriver-migrating adult sockeye salmon (*Oncorhynchus nerka*) to conserve energy on a fine scale (Hinch and Rand 2000). This study concluded that salmon minimized energy costs per metre traveled when encountered currents were slow (i.e., <0.25 m·s^{-1}). It also suggested that at this fine scale, salmon might actively select low-speed or reverse-flow current pathways as additional means of conserving energy (Osborne 1961). However, there were significant limitations to the methodological approach of Hinch and Rand (2000). Their camera calibration technique limited data collection only to those individuals that swam along a plane within the field of view. Therefore, it was not possible to fully explore the hypotheses that salmon were choosing certain pathways (e.g., low current speed or reverse-flow areas) over others. Consequently, energy cost estimations that were based on laboratory-derived metabolic rates for rectilinear swimming ignore fish taking more circuitous paths. While Pacific salmon do exhibit "line swimming" behaviour, with relatively straight trajectories within nearshore areas of reduced flow in large, fast flowing rivers (Ellis 1966*a*), migrations are less directed and they display higher levels of meandering in small rivers and streams. Thus, the "planar" observational approach that Hinch and Rand (2000) relied on in their video methodology may not be appropriate for studying migration behaviours of many stocks and locations of anadromous fish.

The present study examines behaviours of fish exhibiting both linear and nonlinear migration pathways within chosen reduced flow areas by employing a three-dimensional stereovideographic approach (Hughes and Kelly 1996). We follow actual trajectories through the water to determine swimming speed and speed over the ground of adult sockeye salmon during segments of their upriver migration. Using bioenergetic equations found in the literature, we also compare observed swimming speeds (U_{obs}) with theoretical optimal swimming speeds (U_{opt}) in an attempt to describe fish migration behaviour in situ and improve upon previously published description techniques.
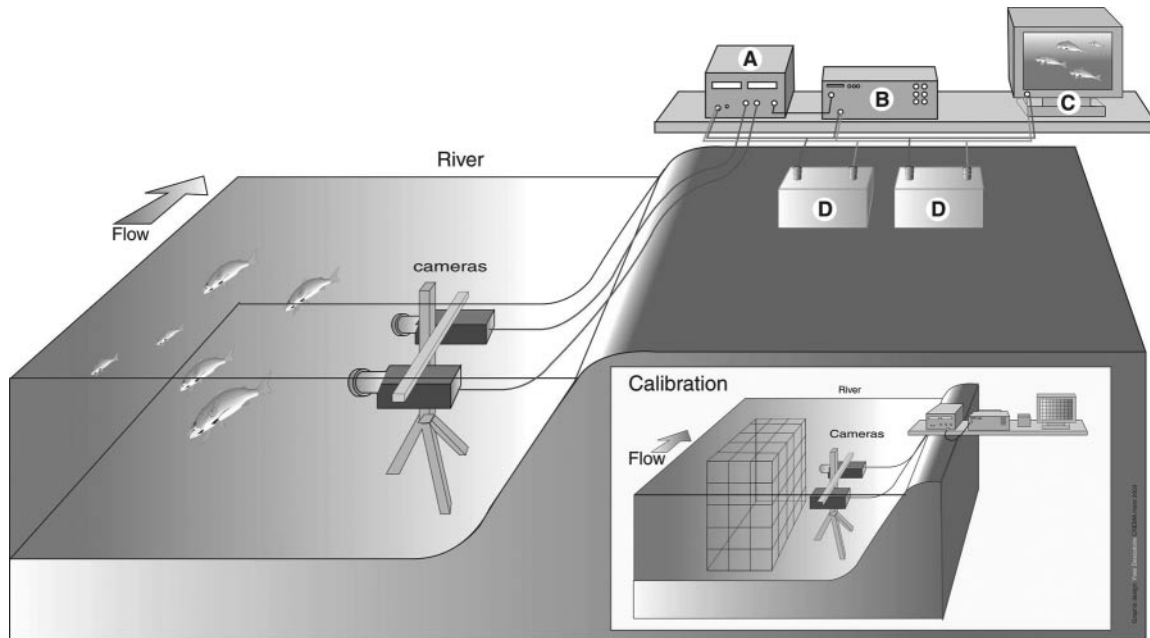
Methods

Study site and animals

We focused our study on Gates Creek sockeye salmon, a relatively abundant Fraser River stock. In July and August of each year, mature adults migrate nearly 600 km, gaining 300 m in elevation, from the Fraser River mouth to spawning grounds. In 2000, we selected 10 sites in the upper and lower Seton River for video observations. The Seton River is a relatively small river with a maximum width of 20 m, a depth between 0.5 and 3 m, and a gradient ranging from 0.1% to 0.8%. Sites were selected to include the full range of average current speeds. All were easily accessible and had excellent water clarity. We videotaped migrating fish (average length = 64.4 cm, SD = 13.5 cm) from 27 July to 8 August.

Video system

We used four black and white charged couple device cameras. Two were Panasonic WV-BP312 with 570 lines of horizontal resolution and two were Cohu model 2100 with 570 lines of horizontal resolution and were fitted with a spherical high-speed aperture lens (Panasonic WV-LA408C3 with 4.5-mm focal length and Cosmicar/Pentax with 3.7-mm focal length, respectively). Each pair of cameras was oriented in parallel (optical axis separation of 11.3 and 8.2 cm, respectively) and fixed to a stand located 1–5 m away from the subject. Each camera was enclosed in a cylindrical anodized aluminum housing fitted with flat Plexiglas ports. Video signals were sent to a multiplexer-quad unit (Panasonic WJ-420) and then to a VHS time-lapse recorder (Panasonic AG-6124) where images from all cameras were recorded simultaneously on the same video frame at 60 frames·s^{-1}. Thus, the recorded video image was a composite of four independent, time-synched images, one for each camera. A black and white LCD monitor (1024 × 768 pixels) (OmniVision Inc., Sunnyvale, Calif.) was used to assist with focus, calibration, camera orientation, and determination of water and fish speeds. All components of the system were powered by two 12-V deep-cycle batteries. At all sites, cameras were positioned underwater facing the centre of the river, with their optical axis parallel to the surface of the water. Cameras were able to clearly record images of fish at up to 10 m into the river within which most of the migrating fish were located.

Fig. 1. Diagram of the underwater video setup. Cameras situated underwater sent video signals through cables to a multiplexer-quad unit (A) and then to a VHS time-lapse recorder (B) where all signals were recorded simultaneously on the same video frame. Images were viewed on a television monitor (C). All components were powered by two 12-V deep-cycle batteries (D). Inset: the video image was calibrated using an aluminum cube placed momentarily in the field of view of the cameras and digitized to provide a scaled grid from which to measure all other distances. River velocity was also measured in a 27-point grid within the field of view of the cameras.

Camera calibration and data collection

Camera calibration was conducted according to methods developed by Hughes and Kelly (1996) and is described below. Cameras were calibrated using a 0.3 m × 0.5 m × 0.5 m aluminum quadrat. The quadrat resembled a cage with horizontal and vertical aluminum bars (each 1 cm in diameter) at 10-cm intervals (hereafter referred to as nodes). Each pair of cameras was set up and secured so that they were immobile during the observations. The quadrat was placed in the field of view of each pair of cameras (see example in Fig. 1 inset) to ensure that at least nine nodes from both the near and far face of the quadrat were visible in both cameras. To reduce calibration error, the quadrat was placed within the path of the majority of fish as seen from shore (Fig. 1 inset). After the quadrat's image was recorded, it was removed from the water. In the laboratory, video images were replayed and a single frame video image of the quadrat was captured and digitized. The nodes of the near and far face were digitized for each camera to get two sets of x,y coordinates of the quadrat. The x,y coordinates were then analyzed using algorithms in Hughes and Kelly (1996), which allowed us to take two-dimensional stereo images and calculate three-dimensional x,y,z real-world coordinates. We found error (estimated by determining error of locating corner nodes on the quadrat) in determining positional fixes to be low (≤2 cm).

Current speed within the field of view was measured using a CMC-2 current meter with a number 3 propeller of size 50 mm × 0.025 m (Hydrological Services Ltd., Sydney, Australia). Current speeds were assessed in a three-dimensional grid pattern within the field of view of the camera. Each site location consisted of about 2.5 m^3 of water

(1.3 m × 1.3 m × 1.5 m) within which 27 current speed measurements were taken; the average distance between adjacent measurements was 25.7 cm (SD = 17.4). Average site velocity is calculated as the average of the 27 current speed measurements. Current speed measurements were made at the end of each site recording session and water heights were measured multiple times daily to ensure that water discharge was constant throughout the data collection process. The net direction of flow at each site was always in the downriver direction. Depth was also recorded at each position where speeds were measured. These depth measurements were used to compute mean water depth at each of our sites. The propeller of the current meter was videotaped and digitized to determine the three-dimensional location of the measured current points. These current values, as well as their location, were then interpolated (Matlab, version 5.3.0.14912a(R11)) (The Mathworks, Inc., Natick, Mass.) based on distance averaging with a linear smoothing factor to predict current speeds between measured points. In this manner, current speed at any point within 50 cm of the measured calibration points in the camera field of view could be calculated.

Cameras recorded fish migrations for 2–8 h, during daylight, at each site. The range in recording times depended on the frequency of fish passage at a particular site. Fish were selected from video images based on their visual clarity. Generally, fish positioned within 3 m of the cameras produced the clearest images and were thus used. To decrease error, fish that were greater than 50 cm from the nearest quadrat or current measurement point were not used. At least 30 fish were recorded swimming by the cameras at each site, 20 of which were randomly selected and digitized

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Table 1. Theoretical optimal swimming speed (U_{opt}) and observed swimming speed (U_{obs}) for each video site.

Site	Encountered velocity (cm·s^{-1} ± SE)	U_{opt} (cm·s^{-1} ± SE)	U_{obs} (cm·s^{-1} ± SE)	P
SD12	4.46±0.08	54.46±0.08	125.24±8.16	<0.001*
SD34	9.61±0.83	59.61±0.83	92.53±3.26	<0.001*
B12	10.73±2.03	60.73±2.03	77.42±13.59	0.301
E34	34.54±1.91	84.53±1.91	71.40±3.83	<0.001*
E12	41.55±0.58	91.55±0.58	86.25±3.38	0.160
J34	43.76±0.75	93.76±0.75	95.91±4.77	0.635
J12	57.19±0.78	107.19±0.78	123.71±3.56	<0.001*
O12	61.11±1.01	111.11±1.01	120.43±3.67	0.025*
D212	70.60±1.31	120.60±1.31	142.13±4.41	<0.001*
V34	140.56±1.12	190.56±1.12	291.95±6.52	<0.001*

Note: P values from paired t tests are listed with an asterisk denoting significant differences between U_{opt} and U_{obs} for given sites.

for analysis following the same methods described above for the quadrat. If the digitized fish were within the minimal error range of the calibration cube, they were included in the analysis. Migration pathway was digitized based on rostrum tip location at the point of first entry into the camera field of view and first exit out of the field of view as well as every one quarter of a second in between. Using the interpolation program described above, the current speed that each fish encountered (hereafter referred to as encountered current speed) was estimated at each digitized location along the fish pathway as well as at all midpoints between digitized locations. Speed over the ground for each fish was determined by measuring the distance that the fish traveled over 15 video frames (frame rate was 1/60th of a second). Fish not only make headway through the water, but as the water flows downstream, they must also make headway over the ground. Therefore, U_{obs} for each fish was calculated as the sum of the encountered current speed and the speed over the ground.

We also calculated U_{opt} at each site using the sockeye salmon bioenergetics model used in Hinch and Rand (1998) to define the cost of transport curve from which U_{opt} is calculated (Table 1) (see Videler (1993) for a theoretical explanation of the calculation of U_{opt}). We then compared U_{obs} at each site with the U_{opt} calculated from the bioenergetics equation to facilitate discussion of observed migration behaviour.

We viewed the tapes in slow motion and determined the tailbeat frequency (TBF) (one complete oscillation of the caudal peduncle was considered one tailbeat) of each fish as it passed through a site. We then estimated the speed expected at the measured TBF, which we defined as tailbeat swimming speed, from a previously published laboratory-derived relationship between TBF and rectilinear swimming speed (Brett 1995). This approach for estimating swimming speed had been used in recent field examinations of salmon migrations (Hinch and Rand 1998; Standen et al. 2002). However, this approach may underestimate costs of migration because of this rectilinear assumption. We will compare this previous approach with our more realistic three-dimensional one.

Data analysis

To determine if fish were using low-speed current fields for migration, we conducted paired t tests to compare fish encountered current speeds with average site current speed at each site. Paired t tests were also used to compare U_{obs} of the fish with U_{opt} calculated from the bioenergetics model and again with tailbeat swimming speed. Analysis of variance, with least squared means as the a posteriori method, was used to compare speed over the ground, U_{obs} and tailbeat swimming speed among sites. All statistical tests were based on $P \leq 0.05$, and Bonferroni's correction was made to control for Type I errors when making multiple comparisons. If error variance heteroscedasticity was present in the raw data, variables were log transformed prior to analysis.

Results

Average site current velocities calculated from flow velocity measurements ranged from 6.2 to 119.9 cm·s^{-1} among sites (grand mean = 52.7 cm·s^{-1}, SE = 9.9, total n = 10) (Fig. 2). Among sites, the mean encountered current speeds ranged from 4.5 to 140.6 cm·s^{-1} (grand mean = 47.4 cm·s^{-1}, SE = 12.6, total n = 10) (Fig. 2). Encountered current speeds were lower than average site current speeds at sites E34 (P = 0.0213), J12 (P = 0.0427), J34 (P = 0.0004), SD12 (P = 0.0025), and SD34 (P = 0.0010) (Fig. 2). There were no differences between encountered current speed and average site current speed at sites B12 (P = 0.0530), D212 (P = 0.0572), E12 (P = 0.1302), and O12 (P = 0.7270) (Fig. 2). Encountered current speed was greater than average site current speed at site V34 (P = 0.0069) (Fig. 2). It may be prudent to note that site B12 and site D212 both have near significant P values, suggesting a trend in the data that is evident in Fig. 2. Specifically, average encountered speeds appear to be lower than average site speeds at low and moderate current sites but equal to or potentially higher at high current speed sites.

Speeds over the ground were normalized by log transformation. Speeds over the ground varied among some sites ($F_{[9,138]}$ = 60.30, P = 0.0001) (Fig. 3). Comparisons of least square means revealed that fish exhibited fastest speeds over

Fig. 2. Mean (+1 SE) encountered current speed (open bars) and site current speed (solid bars) for each site. Sites are arranged in increasing mean encountered current speed along the horizontal axis. Stars represent significant differences ($P \leq 0.05$) between mean encountered current speed and mean site current speed. The first row along the horizontal axis gives site name codes, the second row gives mean site depths, and the third row gives average river gradients for each site. Sample size is noted by numbers above each bar.
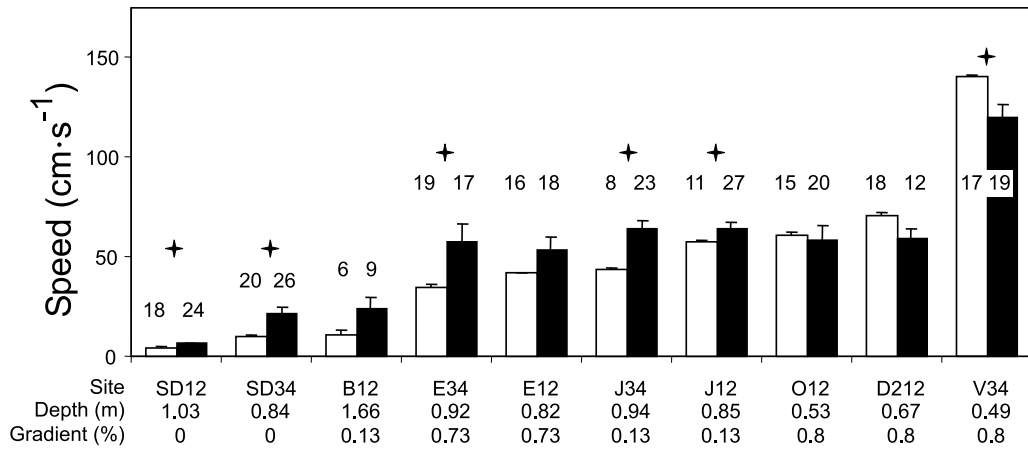
Fig. 3. Mean tailbeat swimming speed (TBFss ± SE; shaded bars), mean observed swimming speed (U_{obs} ± 95% CI; open bars), and mean speed over the ground (GS ± 95% CI; solid bars) for each site. Significant differences between sites for tailbeat swimming speed, mean observed swimming speed, and mean speed over the ground are listed along the x axis; within each variable, corresponding letters represent no significant differences between sites. Sites are arranged in increasing mean encountered current speed along the x axis.
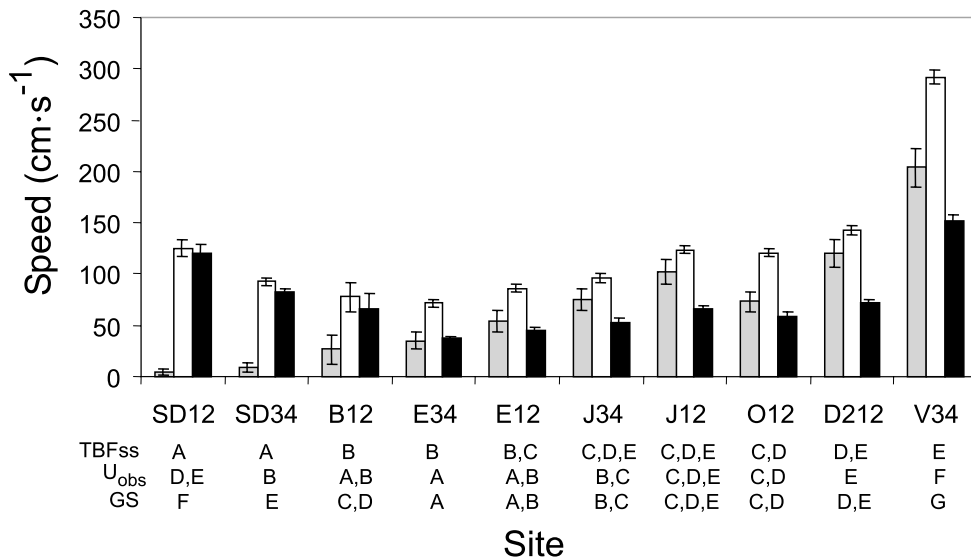
the ground at sites SD12 and V34 compared with all other sites ($P \leq 0.0001$ for all contrasts) and the slowest speeds in site E34 compared with the other sites ($P \leq 0.0003$ for all contrasts), although site E12 did not differ from site E34. Significant differences ($P \leq 0.005$) in speeds over the ground among the remainder of the sites can be found in Fig. 3. The U_{obs} also varied among some sites ($F_{[9,138]}$ = 151.29, $P = 0.0001$) (Fig. 3). Least square means comparisons revealed that U_{obs} values were fastest at site V34 relative to all other sites ($P = 0.0001$ for all contrasts) and slowest at site E34 relative to all other sites. Significant differences ($P \leq 0.005$) in U_{obs} among the remaining sites can be found in Fig. 3. When compared using a simple t test, U_{obs} values were higher than U_{opt} for sites SD12, SD34, J12,

O12, D212, and V34 ($P \leq 0.0001$ for all contrasts). The U_{obs} was lower than U_{opt} at site E34 ($P \leq 0.025$) and did not differ significantly from that at all other sites (Table 1).

TBF swimming speeds also were normalized using a log transformation. Tailbeat swimming speed varied between some sites ($F_{[9,138]}$ = 42.7, $P = 0.0001$) (Fig. 3). Least square means comparisons revealed that tailbeat swimming speeds were slowest at sites SD12 and SD34 compared with all other sites ($P \leq 0.0013$ for all contrasts). Tailbeat swimming speed did not differ among sites B12, E34, and E12 ($P \geq 0.0474$ for all contrasts), sites E12, O12, J34, and J12 ($P \geq 0.0154$ for all contrasts), or sites O12, J34, J12, and D212 ($P \geq 0.1509$ for all contrasts). Tailbeat swimming speed was higher at site V34 than at all other sites ($P \leq 0.0029$) with

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the exception of sites J34 ($P = 0.0191$), J12 ($P = 0.0756$), and D212 ($P = 0.0937$). When compared using a simple t test, tailbeat swimming speed was lower than U_{obs} at all sites ($P \leq 0.0289$ for all contrasts) with the exception of sites J34 ($P = 0.0897$), J12 ($P = 0.1256$), and D212 ($P = 0.1372$).

Discussion

Active selection of low-flow pathways during migration to reduce exposure to higher speed river currents has been hypothesized by a number of researchers who have studied adult salmon migration over coarse spatial scales (Osborne 1961; Brett 1995; Hinch and Rand 1998). Hydroacoustic surveys (Xie et al. 1997) and visual observations and telemetry (Ellis 1966*b*; Fretwell 1981; Hinch et al. 2002) show that swimming paths of salmon tend to be closely associated with river banks and bottom features in fast rivers where current speeds are usually lower than the mean speed of the river (Henderson 1966). In addition, the hydraulic complexity (turbulence and vorticity) of a river is associated with river topography creating complex flow features around obstacles associated with the banks and bottom of the river. This study selected sites on the general migratory paths of salmon, close to the banks and bottom of the river. Within these lower current speed areas, fish preferentially swam in even lower speed current pathways. However, we found that at higher current speed sites, fish did not use lower speed pathways, instead encountering current speeds at or above the average speed for the immediate vicinity. This behaviour is counterintuitive. High-speed sites represent the most expensive areas for upriver migration where one might assume that fish seeking low current speed would achieve the greatest benefit. In addition, we found that in sites with high current speeds, fish actually increase their speed over the ground.

We propose that fish change their migratory strategy from one of energy conservation to that of time conservation, increasing ground speed above the energetic optimal when encountering high-speed currents to minimize the amount of time spent in these high-speed areas. To test this idea, we have taken a general cost of swimming model presented by Videler (1993) and commonly used to produce species specific bioenergetic models and calculated minimal energy costs to traverse a given ground distance against currents of different speeds. We have taken parameters from Beauchamp et al. (1989) to make the general model specific to sockeye salmon. Within this sockeye specific cost of transport curve, U_{opt} for still water is the tangent to the curve that passes through the origin (see Videler 1993). Following the same mathematical principles, one can change the *x*-intercept of the tangent to the curve, which in turn changes the point at which the tangent meets the curve. As in the still water example, the *x*-intercept of the tangent represents the speed of the current in which the fish is swimming and the point of the tangent line represents the U_{opt} at that specific encountered velocity. For example, the tangent of the line passing through point (10,0) represents the U_{opt} for a fish swimming against a velocity of 10 cm·s^{-1}. This exercise shows us that in order for a fish to minimize the cost of transport as it encounters faster current speeds, it must increase its swimming speed to maintain its speed over the ground.

The fact that our data show that fish increase their ground speed to above the predicted optimal through both very low and high velocity current speeds supports the idea that fish may change their migratory strategies from energy conservation to time conservation when encountering river currents that permit them to gain large distances over the ground quickly (very low speed current areas) as well as river currents that would cause them long delays in time if they were to swim at an optimal speed (very high speed current areas). In both cases, fish are deviating from U_{opt} and decreasing time in transit to navigate a given area. From our data, this decrease in time appears to be the result of both increasing ground speed and decreasing effort in choosing low current speed pathways. These results are supported by Hinch and Rand (2000), who came to similar conclusions using more primitive video methodologies and algorithms for calculating optimality.

A recent study using free-swimming smallmouth bass (*Micropterus dolomieu*) may help explain why fish are increasing ground speed and, in turn, not spending time looking for low-speed pathways. Similar to the results of this study, Peake (2002) found that bass increased their ground speed when encountering high-speed current velocities as well as increasing swimming speed by using unsteady swimming (anaerobic metabolism). These fish when tested for muscle lactate, plasma lactate, and oxygen consumption had only marginally different mean metabolite concentrations from animals that swam at more moderate speeds for twice as long (Peake 2002). These findings suggest that fish may have physiological mechanisms that allow them to increase exercise intensity for a decrease in duration of exercise with no significant rise in energetic costs compared with longer duration steady swimming. It may be that the disadvantage of experiencing higher velocities for a shorter period is less than the disadvantage of spending extra time to seek out moderately lower velocity pathways at a given site. The fish in our study may then be gaining an energetic advantage by swimming faster for a shorter period of time.

In addition to defining path choices of fish, we compared U_{obs} with swimming speed estimated from TBF. We found that tailbeat swimming speeds were significantly lower than U_{obs} at the majority of sites. Clearly, this shows that swimming speed – TBF relationships determined in flumes and swimming tunnels should be used with caution when extrapolating to field settings. Under natural conditions, flow is more turbulent than in experimental water tunnels and flumes. It might be expected that this would require additional forces to stabilize posture and swimming trajectories, resulting in higher TBF speeds than U_{obs}.

Recent laboratory experiments have shown that fish placed in a trail of staggered, counter-rotating vortices (a von Karman trail) are capable of changing their body movement to match the encountered vortices, minimizing muscle activity while maintaining position in a net downstream current (Liao et al. 2001). In addition, vortices shed from a fish's own fins or body (Muller et al. 2000; Drucker and Lauder 2001; Muller et al. 2001) or from neighbouring members of a school (Abrahams and Colgan 1985, 1987; Herskin and Steffensen 1998) may interact with caudal fin vortices potentially increasing thrust for a given tailbeat. Such interactions with fine-scale flow features would result

in tailbeat swimming speeds lower than U_{obs}, as demonstrated by our results and postulated by Hinch and Rand (2000). Therefore, our results suggest that fish can sense and respond to local fine-scale flow variation in such a way that they achieve higher actual speeds than expected based on the TBF.

Our results underscore the need to conduct research into two areas. First, we feel that it is important to develop alternative means to characterize the complex, small-scale turbulent features through which these fish commonly swim. New methods may allow us to better characterize the flow complexity and allow us to place the observed swimming path choice in better context to flow features common in natural channels. There has been some important advancement in recent years in three-dimensional flow visualization and measurement. Particle imaging velocimetry methods involving suspended neutrally buoyant glass beads and sheets of laser light have enabled investigators to visualize flow structure around swimming fish in laboratory situations (e.g., Nauen and Lauder 2001). An application of this method to a more natural stream channel could help in understanding how fish may be taking advantage of hydraulic conditions during their migration. Others have applied acoustic Doppler current profilers to map three-dimensional current patterns in rivers (Nikora and Goring 1998, 2000) that could be used to better link environmental conditions to animal behaviour in situ.

Second, we need to work toward developing better methods of estimating true transport costs through complex river flow features. This may be achieved by conducting a comprehensive study of muscle recruitment involving electromyograms to more accurately estimate power requirements of different gaits adopted by adult migrating salmon through complex hydraulic conditions encountered in situ. This approach has been used with success at a coarse spatial scale (Hinch and Rand 1998; Standen et al. 2002), but we are not aware of any studies done at the fine time and space scales examined in the present study.

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