Transactions of the American Fisheries Society 129:598–606, 2000
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Effects of Swim Speed and Activity Pattern on Success of Adult Sockeye Salmon Migration through an Area of Difficult Passage

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Abstract.—We used electromyogram telemetry to examine swim speeds and passage success for 12 adult sockeye salmon *Oncorhynchus nerka* migrating through Hell's Gate, a reach in the Fraser River canyon that is notorious for creating conditions that impede salmon migrations. Fishways exist in one segment; however, the approach immediately downstream of the fishways is also very challenging to migration. Average swim speeds (in body lengths per second; BL/s) were slower ($P = 0.017$) and residency times shorter ($P = 0.058$) in the approach for fish that successfully entered the fishways (mean = 1.85 BL/s, SE = 0.71; mean = 34.57 min, SE = 17.39; $n = 7$) compared with those of fish that were unsuccessful (mean = 4.23 BL/s, SE = 0.85; mean = 1,742 min, SE = 1,367; $n = 5$). Migrant-specific swim-speed patterns revealed that fish alternated at different time scales between relatively fast and slow speeds. Continuous swimming at greater than maximum sustained speeds (U_{crit}) never exceeded 3 min in the case of any of the successful migrants, but unsuccessful migrants exhibited one or more periods (each of >10 min duration) of continuous swimming at speeds greater than U_{crit}. Unsuccessful fish disappeared downstream and died without passing Hell's Gate. Hyperactivity seems to have played a significant role in lack of passage success. It is unclear why some fish swam at relatively fast speeds for extended periods of time while others did not. It is possible that unsuccessful migrants swam fast because they used relatively turbulent and fast-flowing migration paths. Some individuals may also be prone to swim at relatively fast speeds regardless of migration path.

Pacific salmon *Oncorhynchus* spp. must rely solely on energy reserves to carry out their upriver migration, to complete their gonad development, and to spawn. Energy-saving behaviors, such as swimming at hydrologic or metabolic optimum speeds (Webb 1995), "burst-then-coast" swimming (Weihs 1974), or the selection of low-velocity or reverse-current paths (Webb 1995; Hinch and Rand 1998), may thus be important migration tactics for these upriver migrants. These behaviors may be particularly crucial at sites of difficult passage, where energetic demands may exceed the migrant's metabolic scope. However, we have a limited understanding of fish swimming activity and behavior at such sites.

Hell's Gate, a reach in the Fraser River canyon that is located 180 km upstream of Vancouver, British Columbia (Figure 1), is notorious for creating conditions that impede salmon migrations (Ricker 1987; MacDonald and Williams 1998). Fishways were constructed in a segment of Hell's Gate in 1946 to mitigate passage problems (Talbot and Jackson 1950), and today several levels of vertical slot structures operate on both sides of the river (Clay 1961). Yet the area immediately downstream of the fishways is still very challenging to migration. The average swimming activity levels of sockeye salmon *Oncorhynchus nerka* passing through Hell's Gate are higher than at any other location in the Fraser Canyon (Hinch et al. 1996; Hinch and Rand 1998), and lactate assays of muscle biopsies from sockeye salmon that migrated through Hell's Gate confirm that anaerobic metabolism is invoked during passage (Hinch et al. 1996). Further, biochemical investigations and bioenergetic modeling of energy use have revealed that Hell's Gate is the most energetically costly reach for Fraser River sockeye salmon stocks (Ballantyne et al. 1996; Rand and Hinch 1998).

Despite the presence of the fishways, sometimes many adult salmon do not successfully pass through Hell's Gate. About one-half of the 1997 Early Stuart run (240,000 out of 500,000 fish) that entered the Fraser River did not reach spawning grounds, and many of these unsuccessful migrants reached but failed to pass Hell's Gate (MacDonald and Williams 1998). Although high river discharge initiated the obstruction, it is uncertain how individual-specific activity levels and behaviors played roles in this massive fish loss. In general, the interplay of behavioral and environmental factors that are associated with passage success has not been adequately explored at sites of difficult passage.

The purpose of our study was to describe patterns of individual-specific swim speeds and be-

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Received August 21, 1998; accepted June 8, 1999

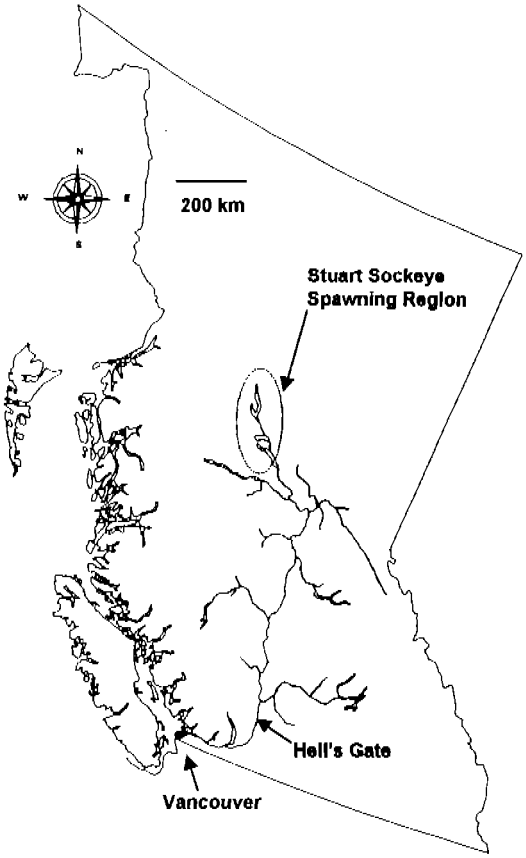

FIGURE 1.—Map of British Columbia showing the position of Hell's Gate on the Fraser River and the Stuart sockeye salmon spawning region.

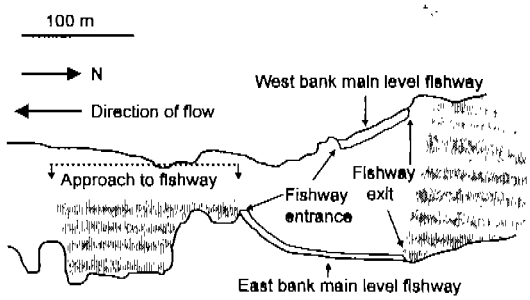

FIGURE 2.—Aerial diagram of the Hell's Gate region, at the discharge levels encountered in this study, showing east and west bank main level fishways and the fishway-approach segment. Although there are several other horizontal levels of fishways at this location, only the main levels are depicted; our study animals did not use other levels. The shaded zones indicate the approximate areas of radio reception by our antenna network.

haviors of upriver-migrating sockeye salmon that were attempting to pass through Hell's Gate and to contrast the swimming strategies associated with successful and unsuccessful passage. In order to address these issues, we used electromyogram (EMG) telemetry information that was previously collected as part of a larger study by Hinch and Rand (1998). This study provided only a brief summary description of average swim speeds by successful sockeye salmon at Hell's Gate and did not report on migration route, behavior, or passage success, nor did this study present any results or interpretation of individual-specific activity levels.

Methods

Study animals.—The study focused on Early Stuart sockeye salmon, which spawn in the Stuart Lake system in British Columbia's central interior (Figure 1). These sockeye salmon are among the longest distance migrants in the Fraser River system (traveling approximately 1,200 km upriver) and are the first sockeye salmon stock to migrate up the Fraser River each year. Typically, the peak of the Early Stuart migration through Hell's Gate occurs in mid to late July, when river discharge is relatively high (Ricker 1987). In July of 1993 and 1995, 11 fish (5 males, 6 females) and 9 fish (8 males, 1 female) (mass, 1.8–3.2 kg; length, 55–63 cm), respectively, were implanted with EMG transmitters. They were released 35 km downstream of Hell's Gate. For details regarding fish capture, refer to Hinch et al. (1996) and to Hinch and Rand (1998).

Study site.—The average daily river discharge during July was similar for 1993 and 1995 (3,640 and 4,030 m/s, respectively; obtained from Water Survey of Canada station 45 km downstream of Hell's Gate). River stage height during the study periods corresponded to the height of the main level fishways at Hell's Gate. Surface water velocities at Hell's Gate approximated 6 m/s in the middle of the river, based on estimates from stage height–water velocity relationships in Talbot and Jackson (1950). Water temperatures during the study periods ranged from 16°C to 18°C. The Fraser River width is approximately 40 m at the entrance of the east bank fishways and about 100 m approximately 70 m upstream and downstream of the fishway exit and entrance (Figure 2). Our study area was 280 m long and was composed of two consecutive segments: a 150-m approach to the east bank fishway and the 130-m east bank fishway (Figure 2). The approach was constrained by sheer cliff walls and was characterized by two large peninsular outcroppings and several deeply incised

fissures. The fishways are made of concrete and are designed with vertical slot baffles, which create a series of pools (5.4 m apart, 6 m wide, and up to 13.5 m deep). The average velocity of water flowing between pools is about 2.4 m/s (Clay 1961). Additional details of the Hell's Gate fishways are provided in Talbot and Jackson (1950) and in Clay (1961). The reach immediately upstream of the exit of the fishways was not constrained by cliffs but rather was characterized by a slope of large boulders and rocks along the bank and by relatively slow-moving water at the river's edge.

Telemetry details.—Four-element Yagi antennas were installed 5–15 m above the river to monitor fish passage through discrete portions of the study area. The approach and entrance to the east bank fishway was monitored by four antennas, whose coverage extended approximately from the riverbank to the river center line, in a section extending from the large peninsular outcropping situated 150 m downstream of the fishway entrance to the fishway entrance (Figure 2). When possible, individuals were also tracked by hand from shore using a three-element antenna to augment coverage. In 1993, three four-element antennas monitored the west bank fishway approach, entrance, and exit (Figure 2), but because no Early Stuart sockeye salmon were recorded using this migration route, the west bank approach and fishway were not monitored in 1995. However, in both years, two four-element antennas monitored the entire width of the river upstream of the fishways (Figure 2). Radio signal–strength information obtained via these particular antennas enabled us to determine whether fish exited from the upstream end of the west or east bank fishways.

Remote signal data-logging receivers (model SRX_400; Lotek Engineering, Newmarket, Ontario) monitored areas on a frequency-priority sequence. The downstream receiver monitored the entry, passage, and exit of the approach and the entry of the east bank fishway. The upstream receiver monitored the exit of that fishway. Twice per week both receivers were programmed with the transmitter frequencies (149–152 MHz) appropriate for the fish that were approaching Hell's Gate. Once a fish had exited the fishway, its frequency was removed from the downstream receiver. Frequencies were not removed from the upstream receiver, which enabled us to determine whether any fish had passed through our study area undetected by our downstream receiver and whether any fish had dropped back through the study area after successful upstream passage out of the study area. Receivers scanned for about 5 s for each transmitter frequency. Once a frequency was detected, the receiver logged the EMG pulse interval signal alternately with scanning for any remaining frequencies. Electromyogram pulse interval signals were transmitted (on average) every 5 s; however, transmissions from any given fish were usually recorded on longer time scales (i.e., up to 15 s) as a result of the scanning and recording time for all other frequencies. The downstream receiver was usually scanning for two to three frequencies at any given time. Also, transmissions to the recorder were periodically interrupted when fish were situated behind or under rock outcroppings and when fish moved downstream and out of the study area. Electromyogram pulse intervals, radio-signal strength (a unitless index), antenna identification, and temperatures were stored in real time by the receivers. Data were downloaded from receivers at least twice per week.

The area of coverage by each fixed antenna was examined throughout the study using a transmitter that was suspended in fixed locations in the river. Antenna positions were adjusted in accordance with changes in river height to ensure minimum overlap of radio-signal reception by sequential antennas. This was accomplished by raising, lowering, or reangling the antennas by hand. We determined that transmitter horizontal position could be identified to within plus or minus 15 m using four-element antennas that were fixed on stands and to within plus or minus 5 m using hand-held three-element antennas.

Data collection and analysis.—A description of the EMG pulse interval radio transmitters and specific details about their surgical implantation are outlined in Hinch et al. (1996). By studying volitionally swimming adult sockeye salmon containing EMG transmitters (in the laboratory), Hinch and Rand (1998) showed that EMG pulse interval signals were strongly correlated to tailbeat frequency, and they developed predictive relationships between EMG pulse intervals and instantaneous swim speeds (in body lengths per second; BL/s). We used these relationships to estimate a swim speed that was associated with every EMG pulse interval that we recorded for each fish in the field. For each fish, we calculated residency time (in the approach and in the fishway) and mean, maximum, and minimum swim speed in the approach. Residency time was calculated as the difference between the times at which fish entered consecutive segments. If after entering a segment

a fish moved back downstream and then re-entered that segment, we used the first time of entry into the segment. We grouped individual fish by passage outcome through the approach; the fish either successfully left this segment and entered the fishway or the fish was unsuccessful at entering the fishway. We used one-way analyses of variance to identify general differences in residency time and mean, maximum, or minimum swim speeds between successful and unsuccessful fish. Each migrant acted as a replicate for these analyses. Because of low sample size, individuals were pooled between years and sexes.

We evaluated the role of swim-speed pattern as a determinant of passage outcome by generating time series plots of instantaneous swim-speed values for each individual fish that entered the approach and by qualitatively compared patterns between successful and unsuccessful migrants. For each individual, we noted the duration of continuous swimming that exceeded the fish's maximum sustained speed (also called the critical swimming speed, or U_{crit}), which is 2.3 BL/s for adult sockeye salmon in water of equivalent temperature to that in our study (Brett and Glass 1973). We hand-tracked three individuals to obtain additional details on migration paths.

Results

Eight of 11 fish in 1993 and 7 of 9 fish in 1995 passed through the east bank fishway. Fish did not pass through the west bank fishway in either year. We were able to collect EMG pulse interval information in the approach on all of the migrants that were not successful at entering the east bank fishway. Because of problems with radio reception, EMG pulse interval data from the approach for eight of the successful fish were not collected. We thus have EMG pulse interval data on passage through the approach for seven individuals that successfully migrated into the fishway and for five that did not successfully enter the fishway. After their failed attempts at entering the fishway, the five unsuccessful fish disappeared from the Hell's Gate area. Daily searches conducted with hand-tracking equipment over the next several weeks (through an area extending 35 km downstream of Hell's Gate) failed to locate these individuals (with the exception of one fish that was located 10 km downstream of Hell's Gate; details provided below). Successful individuals did not return downstream into the Hell's Gate area after ascending and exiting the fishway.

Average swim speeds through the approach were slower ($P = 0.017$) for individuals that successfully entered the fishway (mean = 1.85 BL/s, SE = 0.71; $n = 7$) compared with those of unsuccessful fish (mean = 4.23 BL/s, SE = 0.85; $n = 5$). In addition, successful passage through the approach was characterized by lower maximum and minimum swim speeds ($P = 0.008$ and 0.023, respectively). The average maximum speed for successful migrants was 5.81 BL/s (SE = 1.41; $n = 7$), whereas for unsuccessful migrants, this speed was 11.49 BL/s (SE = 0.49; $n = 5$). Successful migrants had average minimum speeds of 0.07 BL/s (SE = 0.03; $n = 7$), and unsuccessful migrants had average minimum swim speeds of 1.22 BL/s (SE = 0.52; $n = 5$). Average time spent in the approach was shorter ($P = 0.058$) for migrants that successfully entered the fishway (mean = 34.57 min, SE = 17.39; $n = 7$) than for those that were unsuccessful (mean = 1,742 min, SE = 1,367; $n = 5$).

Of the seven fish that entered the fishway, all successfully ascended. The average residency time in the fishway was 19.05 min (SE = 6.99). The average migration speed (e.g., ground speed) to pass through the fishway (mean = 11.37 cm/s, SE = 4.04) did not differ ($P > 0.05$) from the average migration speed for these same individuals as they passed through the approach (mean = 7.23 cm/s, SE = 3.52).

We determined that fish 8 and 12 reached the fishway entrance but failed to enter, whereas fish 9, 10, and 11 never passed by the peninsular rock outcropping situated 25 m downstream of the fishway entrance (see Figure 2). Fish 9 and 11 spent several hours (approximately 80 and 15 h, respectively) transmitting swim-speed information. Radio-signal transmissions of several of the unsuccessful migrants were periodically blocked (Figure 3), which indicated that fish were under rock ledges, behind peninsular rock outcroppings, or temporarily situated downstream of the approach (Figure 2).

Patterns of individual-specific swim speeds revealed that fish did not swim at constant speeds; instead they tended to alternate, at different time scales, between relatively fast and slow speeds. However, exact levels of fast and slow varied among individuals (Figure 3), and successful fish tended to elicit bouts of relatively fast speeds very infrequently. The U_{crit} value, which is 2.3 BL/s, was attained and surpassed by all but one successful individual (Figure 3). However, continuous swimming at speeds greater than U_{crit} never exceeded 3 min for any of these individuals.

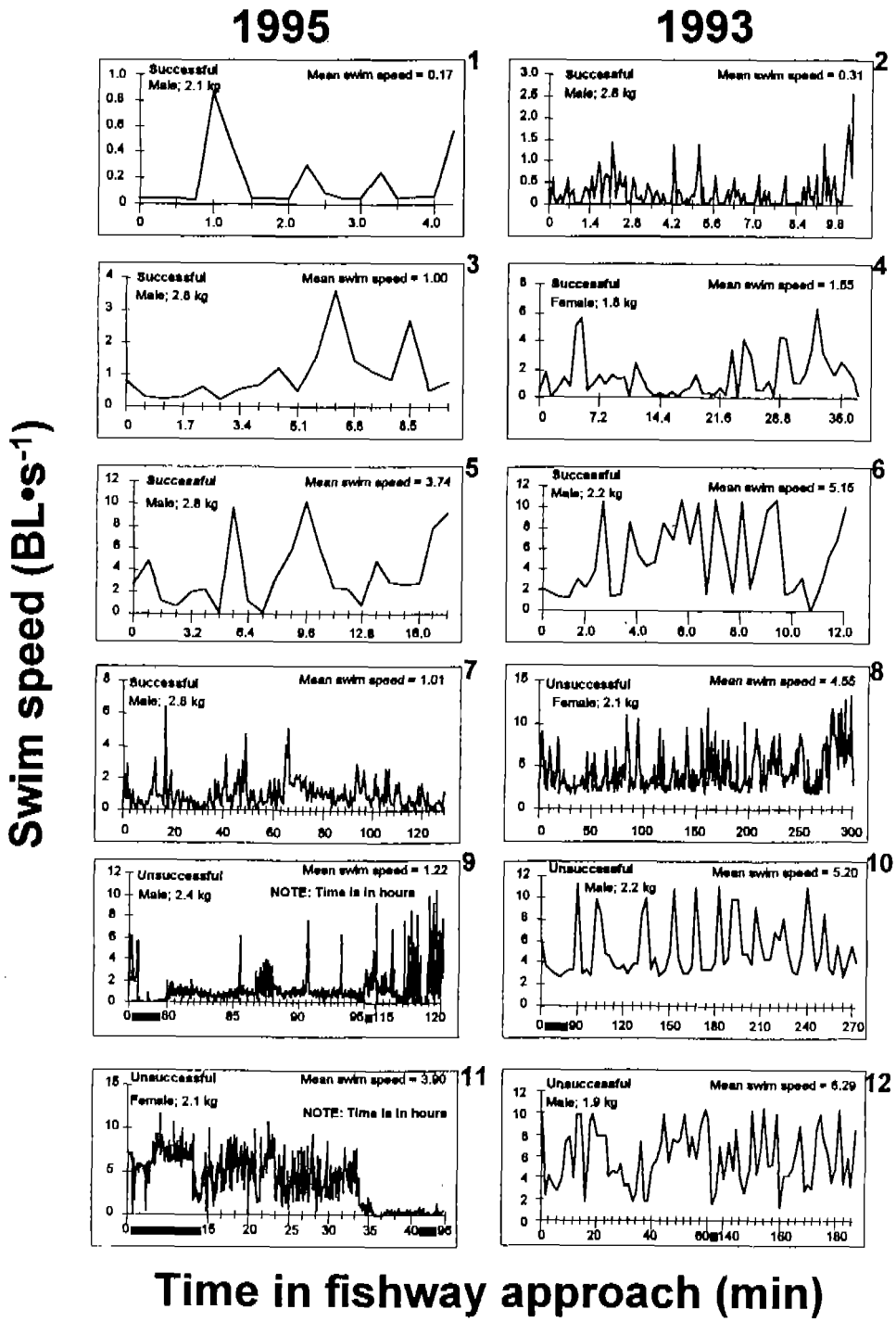

FIGURE 3.—Time series plots of swim speeds, in body lengths (BL) per second, for 12 individual sockeye salmon migrating in the approach over a 2-year period. The year of collection, fish identification number, passage outcome (successful or unsuccessful), sex, mass, and mean swim speed are indicated for each migrant. Note: the axis scales are different for each individual; periods of noncontinuously recorded swim speeds are indicated by black bars along the time axis and by no axis tick marks; times for fish 9 and 11 are in hours.

Very different swim-speed patterns were observed for the unsuccessful migrants. For instance, the minimum speeds of fish 10 exceeded U_{crit} for its entire time in the approach (over 270 min). Minimum speeds of fish 8 and 12 only occasionally dropped below U_{crit}, and periods of continuous swimming above U_{crit} of up to 20 min in duration were observed for both. Fish 9 exhibited bouts of swim speeds (>10 min each) that exceeded U_{crit} during the last 5 h that the fish was in the approach. Fish 11 speeds were in excess of U_{crit} for at least three separate continuous periods of greater than 60 min (each) in duration. By hour 35, fish 11 stopped swimming for the ensuing several days that it spent in the approach.

Three of the 12 fish were hand-tracked through the approach. Both fish 2 and 6 moved through the approach within 5 m of the river's edge, occupying the consecutive small pools that are associated with fissures in the canyon wall. They both spent about 12 min in the approach before entering the fishway. In contrast, fish 8 migrated upstream in the approach for 280 min in a path that was at least 15 m from the canyon wall, away from the pools and fissures that the other two fish had encountered. It reached the pool at the fishway entrance at minute 280 and remained there, swimming at 5–10 BL/s for the subsequent 20 min before disappearing downstream out of the approach. We located this fish 5 h later, when it was holding a position 10 km downstream of Hell's Gate; however, this fish could not be located during subsequent daily searches.

Discussion

The Hell's Gate area is the most energetically demanding single point of passage on the Fraser River for migrating adult salmon (Ballantyne et al. 1996). However, there have been no studies that have examined, on an individual-fish basis, how many sockeye salmon are unsuccessful at passage and what the behavioral characteristics of unsuccessful and successful migrants are. The Early Stuart stock, because it migrates early in the summer—when discharge is relatively high—encounters the most difficult passage at Hell's Gate. Visual observations of Early Stuart sockeye salmon that are milling at Hell's Gate suggest that large fractions of the stock (e.g., 50–100%) can be impeded for several days in the approach segment during periods of high discharge (MacDonald and Williams 1998; A. C. Cooper and K. A. Henry, International Pacific Salmon Fisheries Commission, unpublished data). Following their upstream blockage at Hell's Gate in early July 1997, a result of extremely high discharge (average daily July discharge was approximately 7,530 m/s), many of the milling migrants dropped downstream, where they remained until their death (MacDonald and Williams 1998). Our telemetry results confirm these types of visual observations and indicate that this phenomenon may also occur, to a lesser degree, in Early Stuart sockeye salmon in years of relatively low discharge (e.g., 1993 and 1995). However, because our sample sizes were so low, caution should be used when extrapolating our rate of passage success (75%; 15 out of 20 fish) to that of the entire stock in those years.

Although we cannot evaluate what, if any, effect our transmitters and their implantation had on passage success, Hinch et al. (1996) tracked Early Stuart sockeye salmon in 1994 (using conventional radio transmitters) through the Fraser Canyon to Hell's Gate. They found no differences in migration rates between fish carrying esophageally implanted transmitters (no anesthesia and less than 30 s handling time) and fish carrying abdominally implanted transmitters (a surgical approach similar to that used for EMG transmitter implantation). Moreover, although not reported, seven out of the eight fish (87.5%) in their study successfully passed through the fishway (S. G. Hinch, University of British Columbia, unpublished data)—a passage success rate similar to that in the present study.

Individuals that were successful at passage into and through the east bank fishway shared several characteristics. In particular, they had relatively short residency times and relatively slow mean, maximum, and minimum swim speeds in the approach. Thus, successful migrants were able to swim upstream relatively slowly, yet they were still able to make rapid forward progress. One way to pass through a highly turbulent and fast flow reach like Hell's Gate would be to use pathways of low and reverse flow. Our limited hand-tracking suggested that successful fish migrated near shore (an area where currents were relatively slow) and, in many instances, were moving upstream as a result of eddies formed by the fissures in the canyon wall. There is evidence that adult sockeye salmon take advantage of reverse-flow paths associated with riverbanks. Hinch and Rand (1998) tracked adult Early Stuart sockeye salmon with EMG telemetry as they migrated upriver through a wide, unconstricted reach of the Nechako River in central British Columbia and found that many fish had ground speeds that equaled or exceeded

their swim speeds, which implied the use of reverse-flow pathways.

Weihs (1974) demonstrated with nonsalmonid fishes that exhibit "burst-then-coast" swimming could reduce transport costs by 60%. Although some of our successful migrants never attained "burst" speeds, they all nonetheless generally exhibited an "accelerate-then-coast" swimming pattern. This pattern may reflect a behavioral tactic, similar to that described by Weihs, for saving energy and reducing physiological stress (Webb 1995). In contrast, unsuccessful fish exhibited (with the exception of portions of the time that fish 9 and 11 spent in the approach; Figure 3) a "burst-then-sustained speed" pattern, in which fish seemed to frequently alternate between burst and maximum sustained speeds.

Migrants that were unsuccessful at entering the fishway had longer residency in the approach than did successful migrants. The one unsuccessful fish that we hand-tracked was migrating relatively far offshore in an area with very fast, turbulent, and multidirectional flow patterns. If unsuccessful fish tended to use these offshore migration paths (even only periodically), then the erratic flow conditions could confuse and slow migrants, thereby increasing their residency times. Hinch and Rand (1998) suggested that sockeye salmon migrating through reaches in the lower Fraser Canyon that contained islands had relatively long migration times because of complex flow conditions. Further, convoluted hydrodynamics at the start of the fish ladder at the Well's Dam on the Columbia River appeared to cause confusion in migrating sockeye salmon, resulting in delays of 30 h at the start of their ascent (Swan et al. 1994; Stuehrenberg et al. 1995). Others have noted that high water velocity and turbulence alter migrant behavior and diminish success in locating and passing through fishways (Barry and Kynard 1986; Rainey 1991; Kynard 1993).

Unsuccessful migrants swam for prolonged periods at speeds above their U_{crit}, and in some instances, they swam at certain speeds for durations that can cause exhaustion and the cessation of swimming, according to results from past laboratory swimming-performance experiments. For example, at river temperatures in our study, sockeye salmon should fatigue if speeds of 2.8 BL/s are exceeded for 20 min, if speeds of 3.0 BL/s are exceeded for 10 min, or if speeds of 3.5 BL/s are exceeded for 3 min (values from relationships in Brett 1967 and Beamish 1978). Each of our unsuccessful fish often swam several times at speeds and for periods of time that surpassed these laboratory criteria. This observation suggests that these fish were likely experiencing levels of fatigue and stress during their passage at Hell's Gate. Furthermore, it suggests that swimming-performance criteria established by swimming fish at constant speeds (in laboratory swim tunnels) until exhaustion may underestimate maximum levels of performance in field situations in which upriver migrants do not swim at constant speeds but instead alternate between fast and slow speeds.

It is not possible to determine with certainty the causes of fish disappearance from the approach. We are, however, certain that unsuccessful migrants died without passing Hell's Gate, and hyperactivity appears to have played an important role in preventing these fish from entering the fishway. One possibility is that extended periods of swimming at fast speeds could deplete much of the fish's limited energy reserves, leaving little energy for additional upriver progress (Rand and Hinch 1998). It is also possible that the sustained and repeated bouts of anaerobic activity (e.g., swimming at prolonged speeds above U_{crit}) could lead to mortality by causing lethal levels of blood lactate to accumulate, thereby resulting in metabolic acidosis (Black 1958; Wood et al. 1983; Wood and Perry 1985; Tufts et al. 1991). This phenomenon would be exacerbated by moderate levels of hypoxia (Farrell et al. 1998), which could develop in-river within the large schools of fish that often mill about immediately downstream of the fishway entrance (S. G. Hinch, personal observation).

The reasons why some fish swam at such fast speeds for extended periods of time and why others did not are not clear. One factor may be the choice of migration path; unsuccessful migrants may have swam relatively fast as a response to encountering turbulent, fast offshore flows. Another factor is that some individual fish intrinsically swim at relatively fast speeds. Hinch and Rand (1998) found that some Early Stuart migrants swam consistently at individual-specific speeds through segments within the lower Fraser River canyon. If some individuals are prone to swim at relatively fast speeds, then they may be at a higher risk than others for passage failure. Natural selection likely favors individuals from long-distance migrating stocks that adopt energy-saving behaviors during their homeward migration (Bernatchez and Dodson 1987). Thus, points of difficult passage, such as Hell's Gate, may serve as a strong force se-

lecting for the adoption of energetically efficient migration tactics.

Acknowledgments

We thank Ron Diewert for helping design and implement the field program, and we appreciate the field assistance of Angela Prince, Tim Lissimore, Susan Low, Chris Bobiński, Dave Priekshot, Randy Lake, Ingrid Burgetz, Kari Long, Andrew Lotto, and Pier van Dishoeck. We also thank Cam Grant, Herman Ensenhofer, Dennis Martens, Bob Gordon, Roy McGechaen, and the Cultus Lake Laboratory for logistic support. We especially thank Mike Healey and Peter Rand for their insights and discussions. Comments from Steve Cooke, Scott McKinley, Ted Castro-Santos, Jim Winter, and an anonymous reviewer improved the manuscript. This project was supported by the Fraser River Action Plan through Canada's Green Plan and by an NSERC Research grant to S. G. Hinch.

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