Physiological and energetic correlates of en route mortality for abnormally early migrating adult sockeye salmon (*Oncorhynchus nerka*) in the Thompson River, British Columbia

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Abstract: Since 1995, large segments of the late-run sockeye salmon (*Oncorhynchus nerka*) stock complex from the Fraser River, British Columbia, Canada, have been initiating spawning migrations several weeks earlier than normal. Most aberrant migrants die before spawning. To evaluate the mechanisms underlying the mortality, we intercepted late-run sockeye salmon of the Adams–Shuswap stock complex halfway along their freshwater migration (i.e., in the Thompson River Canyon situated 270 km from the Fraser estuary), nonlethally assessed physiological and energetic status, and tracked individuals using gastrically inserted radio transmitters. Aberrant migrants that resumed their migration but failed to reach the spawning grounds had lower gross somatic energy, higher average migration ground speeds, higher plasma osmolality, and higher levels of plasma reproductive hormones than those that reached the spawning grounds. Fish surgically fitted with electromyogram radio transmitters did not continue their migration and fell downstream. These fish displayed excessive bleeding during transmitter implantation, an unusual phenomenon that likely contributed to the fish's inability to resume migration. Blood clotting time decreased steadily throughout the migration period. Collectively, these data implicate a combination of energy depletion, premature reproductive development, and blood loss from wounds as potential contributors to mortality in early migrating late-run sockeye.

Résumé : Depuis 1995, des fractions importantes du complexe de stocks à migration tardive du saumon rouge (*Oncorhynchus nerka*) du Fraser, Colombie-Britannique, Canada, se sont mises à commencer leur migration de fraye plusieurs semaines en avance de la période normale. La plupart des migrateurs aberrants meurent avant de frayer. Afin d'élucider les mécanismes qui expliquent cette mortalité, nous avons intercepté des saumons rouges à migration tardive du complexe de stocks Adams–Shuswap (c.-à-d., dans le canyon de la rivière Thompson à 270 km en aval de l'estuaire du Fraser) au milieu de leur migration d'eau douce; nous avons évalué leurs statuts physiologique et énergétique au moyen de méthodes non létales et suivi des individus à l'aide d'émetteurs radio introduits dans l'estomac. Les migrateurs aberrants qui reprennent leur migration mais qui n'atteignent pas les sites de fraye ont une énergie somatique brute plus faible que ceux qui les atteignent; ils ont aussi une vitesse au sol moyenne de migration plus grande, une osmolalité plasmatique plus élevée et des concentrations plasmatiques d'hormones reproductives plus fortes. Les poissons munis par chirurgie d'émetteurs radio à électromyogrammes n'ont pas poursuivi leur migration et ont dérivé vers l'aval. Ces poissons subissent une hémorragie excessive au moment de l'implantation de l'émetteur, un phénomène inhabituel qui a sans doute contribué à leur incapacité à reprendre la migration. Le temps requis pour la coagulation

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du sang diminue constamment durant la période de migration. Dans leur ensemble, ces données font intervenir une combinaison d'épuisement énergétique, de développement reproductif prématuré et de perte de sang par les blessures comme causes possibles de la mortalité chez les saumons précoces du groupe de migration tardive.

[Traduit par la Rédaction]

Introduction

The spawning migrations of Pacific salmon (*Oncorhynchus* spp.) are physiologically challenging, using limited energy reserves to adjust osmoregulation from salt water to fresh water, migrate upstream, develop gonads, and spawn (Brett 1995). Despite having a general understanding of migration rates, movement patterns, and survival for some species and stocks during migrations (Groot and Margolis 1991; Quinn 2005), there is little information on how the physiological state of migrants affects their ability to reach spawning grounds. This knowledge gap may hinder the explanation of year-to-year variation in spawning abundance and subsequent juvenile production.

A recent alteration in river migration behaviour and mortality in Fraser River (British Columbia, Canada) sockeye salmon (*Oncorhynchus nerka*) permitted an examination of the role of physiological state in migration success. Though over 150 distinct spawning sites are used by sockeye salmon in the Fraser River system, fisheries managers identify four broad run timing groups based on entry timing of maturing adults into fresh water: early stuart, early summer, summer, and late (Woodey 1987). Sockeye enter the Fraser River between June and October. The late-run timing group is the last to enter and unlike the other timing aggregates, typically holds in the outer estuary for several weeks prior to starting river migration. This estuarine delay occurs despite arrival time near the river mouth at approximately the same time as early summer and summer stocks, which enter the river immediately upon arrival. Since 1995, large segments of late-run sockeye salmon have ceased their holding behaviour and have entered fresh water 3–6 weeks earlier than historically observed (Cooke et al. 2004*a*; Lapointe et al. 2004). However, these aberrant migrants have experienced high rates of mortality prior to spawning, which in some years exceeded 90% (Cooke et al. 2004*a*; Lapointe et al. 2004). In contrast, prior to 1995 and aberrant migration, mortality during river migration rarely exceeded 20% in any year for late-run Fraser River sockeye salmon (Macdonald and Williams 1998).

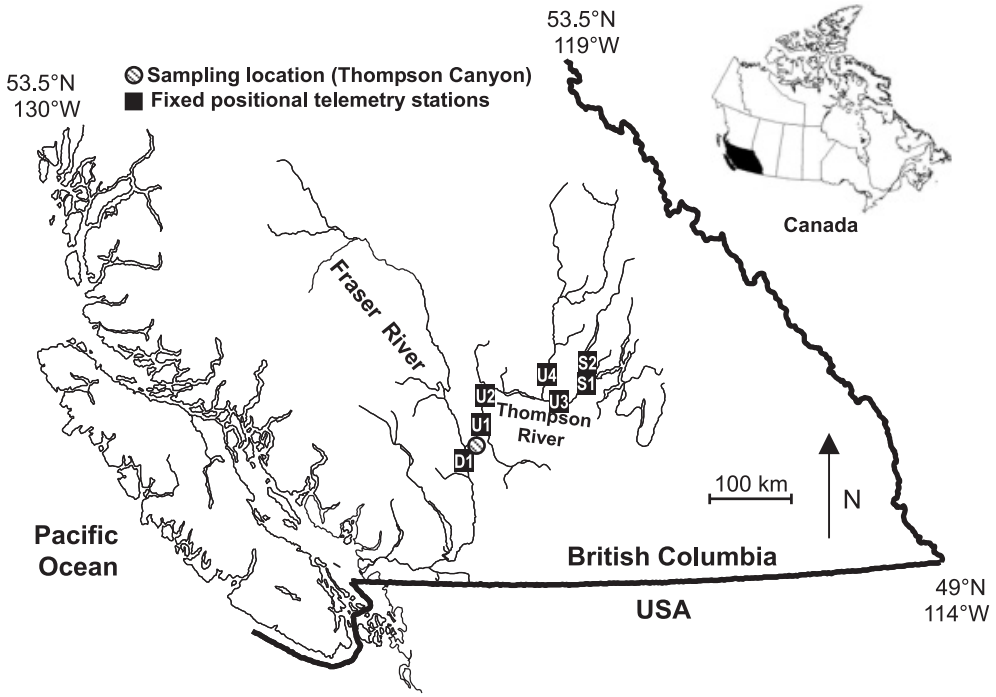
To date, there has been no direct study of the underlying causes of the high mortality associated with the aberrant early migration of late-run sockeye salmon. However, most proposed hypotheses suggest that certain physiological systems are malfunctioning during freshwater migration (Cooke et al. 2004*a*). One hypothesis is based on the observed association between depletion of somatic energy reserves and mortality in migrating adult sockeye salmon (Rand and Hinch 1998). Migrating adult salmon are in a catabolic state, having ceased feeding prior to river entry; in fact Fraser River sockeye salmon have stopped feeding at least 200–400 km from the river mouth (Hinch et al. 2005). Thus, late-run sockeye salmon depend on a fixed energy reserve for migration, reproductive development, and spawning. By entering the Fraser River early, late-run sockeye salmon are more likely to encounter higher water temperatures and flows than they would normally experience in the fall. Increased flow and water temperatures increase transport costs and would accelerate the depletion of fixed energy reserves. Further, when salmon encounter higher flows, we might expect to see erratic swimming patterns and considerable burst swimming (Macdonald 2000), leading to elevated levels of plasma lactate, glucose, and cortisol (Fagerlund 1967; Farrell et al. 2000; Barton 2002). High levels of lactate and the associated metabolic acidosis have long been associated with post-exercise mortality (Black 1958). Related studies have shown that a freshwater myxosporan parasite (*Parvicapsula minibicornis*) contributes to mortality and reduced exercise capacity in adult late-run salmon if they accumulate more than approximately 450 degree-days in fresh water (Wagner et al. 2005). Although individuals in this study were captured at a location that would traditionally be encountered by migrating adults prior to accumulating 450 degree-days, elevated temperatures and flow along with early freshwater entry may allow development of the parasite to an extent that it affects individuals prior to or at the location of capture for this study.

A second hypothesis is based on the notion that reproductive hormone concentrations involved in the initiation of spawning migrations (Ueda et al. 1998; Munakata et al. 2001) can influence migration behaviour and mortality (Høgåsen and Prunet 1997; Ueda et al. 1998). Early river entry and en route mortality could be associated with advanced reproductive development. Secondary sexual characteristics and egg production typically develop during the freshwater migration (Hendry and Berg 1999). Premature maturation may reduce energy stores required for migration or compromise swimming efficiency. Reproductive maturation is also closely linked with rapid senescence and tissue degeneration in Pacific salmon (Dickhoff 1989; Finch 1990; Hendry and Berg 1999).

Materials and methods

We intercepted adult late-run sockeye salmon of the Adams–Shuswap stock complex in the Thompson River Canyon, approximately halfway along their freshwater migration, and used radiotelemetry coupled with biological sampling to link the fate of individual fish with their behaviour and physiological condition. We focused on sockeye salmon that spawn in or near Shuswap Lake because of their importance to fisheries, their relative abundance during the year of sampling, and their relatively long freshwater migration (~485 km, the furthest of all late-run stocks) and the associate need of high energy. Gross somatic energy (GSE) was measured, and blood samples were taken prior to implanting either a conventional or electromyogram (EMG)

Fig. 1. Map of study system with insert showing relative location within Canada. Fish were implanted with transmitters and biologically sampled in the Thompson River 10 km upstream of the junction of the Thompson River and Fraser River (denoted by a hatched circle: 50.3°N, 121.4°W). Fixed radiotelemetry receivers (solid squares) were positioned downstream of the release location (D1), upstream and en route to spawning grounds (U1, U2, U3), at the junction to the North Thompson River to assist with stock complex identification (U4), and at spawning grounds (S1, S2).



radio transmitter. We examined whether (*i*) energy use, associated with inefficient swimming and elevated stress, or (*ii*) premature reproductive development was associated with mortality in sockeye salmon with aberrant early migration.

Study site

Fish were captured, biologically sampled, and released at one site in the Thompson River Canyon, British Columbia. The site was located 10 km upstream of the confluence of the Fraser and Thompson rivers, 270 km upstream of the ocean, and about halfway along the approximately 480 km freshwater migration route of the Adams River and Shuswap Lake sockeye salmon stocks (Fig. 1). Downstream of this confluence, the Fraser River presents migration obstacles in the form of high loads of suspended sediment (Macdonald 2000), areas of high flow velocities (Hinch and Rand 1998), and gillnet fisheries. The Thompson River has lower discharge rates and suspended sediment loads than the Fraser River, but the first 20 km of the Thompson River from the mouth contains areas of constricted bedrock channels with large steps along the bed, where currents are complex and fast. Previous research using EMG telemetry in the Fraser River (e.g., Hinch and Rand 1998; Hinch et al. 2002; Standen et al. 2002) indicated that sockeye salmon are most physically challenged during upstream migration through these types of habitats.

Fish capture and biological sampling

Sockeye salmon were collected between mid-August and early October 2003, a period that spanned the entire migration period for late-run sockeye salmon through the Thompson River. During the sampling period, average river temperature at our site displayed a seasonal decline from 19.5 to 16.0 °C. Fish were captured within 0.5 m of the shore by dip nets lowered to a maximum depth of 1 m. Successful fishing locations were associated with areas of constricted flow and where fish were observed to travel primarily along this edge area, presumably avoiding areas of higher flow near the middle of the river channels. Fish capture methods were consistent throughout the sampling period. Within 30 s of capture, single fish were placed ventral side up in a foam-lined, V-shaped trough, which supplied flowing river water to the mouth of the fish, submerging the entire head. Individual fish were restrained by one or two people, while another person collected a blood sample via a caudal puncture (Houston 1990) using a syringe (1.5 inch (1 in = 2.5 cm), 21 gauge) and vacutainer (3 mL), which was immediately stored in an ice-water slurry. Pressure was applied to the puncture site to facilitate blood clotting. If blood was not drawn within 1 min, the fish was excluded from the study and immediately sacrificed by cerebral percussion. A portion of the adipose fin was collected and stored in ethanol for DNA analysis and a fork length measurement was made. A microwave energy meter (Distell fish fatmeter, model 692; Distell Inc., West Lothian, Scotland, UK) was used to assess somatic energy levels following the methods in Crossin and Hinch (2005). While in the trough, the left side of the fish was partially lifted out of water to permit the energy meter to be placed on two locations of the body wall near the dorsal fin. Gender was assessed using external secondary sexual

characteristics or with the aid of reproductive hormones (see below). Blood samples were centrifuged within 10 min of storage on ice and two 0.5 mL plasma aliquots were immediately removed, stored on dry ice in the field, and transferred to –80 °C upon return to the lab. Of 60 late-run sockeye salmon gastrically implanted with radio transmitters, GSE was assessed on 54 and blood collected from 36. The sampling approach described has been shown to have no detrimental effects to sockeye salmon migration rates or survival (Cooke et al. 2005).

Radiotelemetry

Fish were gastrically implanted with positional radio transmitters (model MCFT-3A, Lotek Wireless Inc., Newmarket, Ontario) via the mouth using a plastic tag applicator (Ramstad and Woody 2003; English et al. 2004). Transmitters were implanted either immediately after capture (n = 24) or immediately after blood sampling (n = 36). No anaesthesia was used on fish released with a positional radio transmitter. Transmitters weighed 16.1 g in air and 6.2 g in water and measured 16 mm in diameter and 51 mm in length. The antenna trailed out of the mouth of the fish, and 30 mm of tubing from a Floy anchor tag was affixed to the end of the antenna. The tagging and sampling procedures were terminated if either the procedure took longer than 150 s or the fish escaped from the trough. Fish were released immediately after tagging into a deep pool with a back eddy, slightly downstream of the capture location.

Six receiver stations (Lotek Inc. receiver models SRX400 or SRX400A) capable of logging information from the positional transmitters were installed at locations along the Thompson River migratory route upstream of our site (Fig. 1). Each station was composed of up to three antennas (three- to four-element Yagi). Two receivers were positioned upstream of the release site on the Thompson River (U1 and U2, 22 and 47 km from release site, respectively), and two receivers were positioned at late-run spawning streams (199 km and 205 km from release site). One receiver was positioned on the North Thompson River (U4, 134 km from release site), which enabled detection of early-summer-run fish that comigrate with aberrantly early-timed, late-run fish and which may have been inadvertently sampled and tagged. To detect fish that headed downstream after release, one station was positioned 10 km downstream of the release site at the confluence of the Thompson and Fraser rivers (D1). Receivers collected data from 25 August until the last transmitter detection on 24 October 2003 (English et al. 2004). Fish were classified as casualty if they were detected at an upstream detection station but not at a spawning ground detection station, survivor if they were detected at a spawning ground detection station, or dropout if they were not detected at a fixed station upstream of the release location.

Following biological sampling (same approaches as described above), fish destined for EMG transmitter implantation were transferred to a net-pen (~1.5 m × 1.5 m × 1.5 m) constructed from polyvinyl chloride (PVC) pipe and plastic fencing placed in the river. Only females were used for EMG telemetry to limit interindividual variability. Within 48 h of capture, fish were anaesthesized (buffered tricaine methanesulfonate, MS-222; 40–50 $mg \cdot L^{-1}$), implanted with an EMG transmitter, and released after a short recovery period (15–60 min). We began EMG surgery on 29 fish. Surgeries on 11 fish were halted before transmitter insertion because of excessive bleeding from the surgical incision. Of the 18 fish implanted with transmitters, 14 also displayed unusual bleeding from the incision, which was deemed excessive for four fish. As a result, we released only 10 fish with EMG transmitters. After release, fish were tracked by hand using a mobile radio receiver (Lotek Inc. model SRX400) and single three-element Yagi antenna. EMG transmitters measure activity of main swimming muscles that can be used to estimate swimming speed and energy expenditure (Standen et al. 2002; Cooke et al. 2004*b*). Full details on the EMG pulse interval transmitter and surgical procedures for sockeye salmon are found in Hinch et al. (1996), with more generic detail in Cooke et al. (2004*b*).

We investigated the unusual bleeding phenomenon by measuring blood clotting time in an additional 62 sockeye salmon captured at our site between 7 September and 7 October 2003. Blood clotting time was determined immediately after termination by cerebral percussion by cutting the gill arch and dripping 10 drops of fresh blood on a clean, shade-stored, glass slide within 1 min of fish death. With a stopwatch, we measured the time for the blood sample to form into a singular, gelled mass while keeping the slide out of direct sunlight. This method proved to be relatively precise by repetition and was applied over relatively consistent air temperatures. Other methods, including filling a haematocrit tube with blood and timing the formation of a connected string of clotted blood between broken sections of the tube, proved inaccurate and difficult to repeat.

Stock and timing group classification

Stock identification of individual fish was determined by microsatellite DNA variation (Beacham et al. 1995). DNA analyses revealed that of all fish captured for radio transmitter implantation, 17 fish were early-summer-run, and 60 fish were late-run. Late-run sockeye salmon captured before 16 September 2003 were classified as aberrant, and those captured after this date were classified as normal. This delineation date was used because (*i*) two peaks in abundance occurred at the location of sampling that were clearly separated by this date, and (*ii*) periods after 16 September represent the traditional arrival time of late-run sockeye salmon at the sampling location in the Thompson River, as determined from long-term average passage times of late-run sockeye salmon at a downstream location (August 29 at Mission, B.C.; English et al. 2004) and average migration travel times from this location to the sampling location (18 days; D.A. Patterson, unpublished data). Although DNA analysis was not conducted on the group of fish used for blood clotting measurements, this test was limited to fish captured after 7 September. The late sampling dates occured after the majority of identified early-summer-run fish passed our site, suggesting that the majority were late-run fish.

Plasma analyses

Plasma ion, cortisol, and osmolality measurements followed the procedures described by Farrell et al. (2000). The measurements were repeated if there was disagreement between duplicates >2.5 $mequiv. \cdot L^{-1}$. Concentrations of plasma Na^+ and K^+ were measured using a model 510 Turner flame

photometer. Plasma aliquots (5 μL) were diluted 1:200 with a prepared 15 mequiv. lithium·L^{-1} solution. The photometer was calibrated prior to use and checked against a standard approximately every five samples. Measurements were repeated if the disagreement between duplicates was >2%. Plasma lactate and glucose concentrations were measured using a YSI 2300 StatPlus lactate–glucose analyzer (Yellow Springs Instruments Co., Yellow Springs, Ohio). Plasma osmolality was measured in duplicate on 10 μL samples using a model 5500 Wescor vapour pressure osmometer (Wescor Inc., Logan, Utah). Measurements were repeated if the disagreement between duplicates was >3%. Plasma cortisol concentrations were measured in duplicate using 96-well enzyme-linked immunosorbent assay (ELISA) kits (Neogen Corp., Lexington, Kentucky). Testosterone (T), 17β-estradiol (E2), and 11-ketotestosterone (11-KT) were measured by radioimmunoassay (Van Der Kraak and Chang 1990; McMaster et al. 1992). The interassay variabilities for the T, E2, and 11-KT radioimmunoassays were 6.6%, 11.6%, and 8.8%, respectively. We regressed plasma E2 values against T values to assign gender to fish, which resulted in two distinct clusters of the data corresponding to male and female fish.

Data analysis

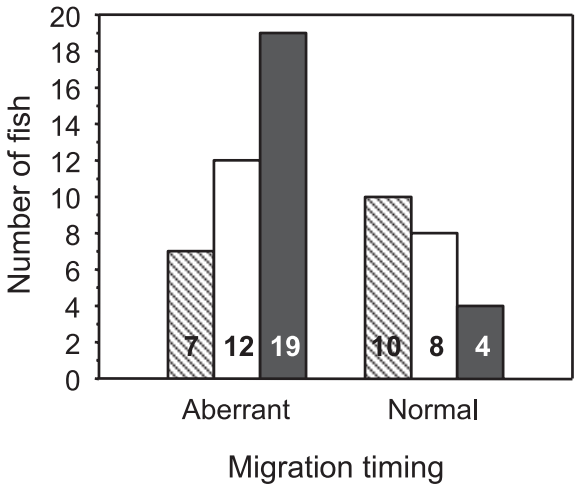
A series of factorial two-way analysis of variance (ANOVA) tests were used to examine for differences in GSE, plasma metabolites, and plasma ions between aberrant and normal migrants and among survivors, casualties, and dropouts. An all pairwise multiple comparisons a posteriori procedure was used (Tukey's test) to evaluate those groups that contributed to main effects. We estimated individual fish ground speeds using distances, time of travel between telemetry receiver stations, and fish body length (BL). Migration ground speeds were compared between aberrant (both casualties and survivors) and normal migrants using two-way ANOVA and Tukey's post hoc tests to evaluate significant effects (all analyses were assessed for significance at $\alpha = 0.05$). Plasma cortisol required $\log_{10}$ transformation to meet statistical normality and equal variance requirements. The segregation of reproductive hormone results by migration timing, migration fate, and gender created sample sizes too small for comprehensive analyses. To specifically evaluate the potential role of reproductive development on mortality in aberrant migrants, select *t* tests were used comparing female plasma reproductive hormone levels between aberrant survivors and casualties. We used linear regression and a *t* test to compare blood clotting time with date of capture. A χ^2 test was used to compare survival between fish that were released with a radio transmitter as well as blood sampled and those that were not. All analyses were conducted using SigmaStat 2.03 (SPSS Inc., Chicago, Illinois).

Results

Positional radiotelemetry

Of the 60 late-run fish implanted with a positional radio transmitter, 63% (38 fish) were captured before September 16 and classified as aberrant and 37% (22 fish) were captured after this date and classified as normal (Fig. 2). Of the aberrant migrants, 50% (19 fish) were survivors, having reached spawning grounds, 32% (12 fish) were casualties, detected upstream but not at spawning grounds, and 18% (7 fish) were dropouts, detected downstream but never upstream of release. Of normal migrants, 18% (4 fish) were survivors, 36% (8 fish) were casualties, and 46% (10 fish) were dropouts. There was no difference in migration fate between fish that were sampled for blood ($n = 36$) and those that were not ($n = 24$; $\chi^2 = 2.658$, $P = 0.265$).

Fig. 2. Number of aberrant and normal late-run sockeye salmon (*Oncorhynchus nerka*) grouped by migration fate as determined by positional radiotelemetry detections (hatched bars, dropout (i.e., fell downstream after release and never detected upstream); open bars, casualty (i.e., detected upstream but not at spawning grounds); solid bars, survivor (i.e., detected at spawning grounds)). Sample sizes (*n*) are shown within each bar.



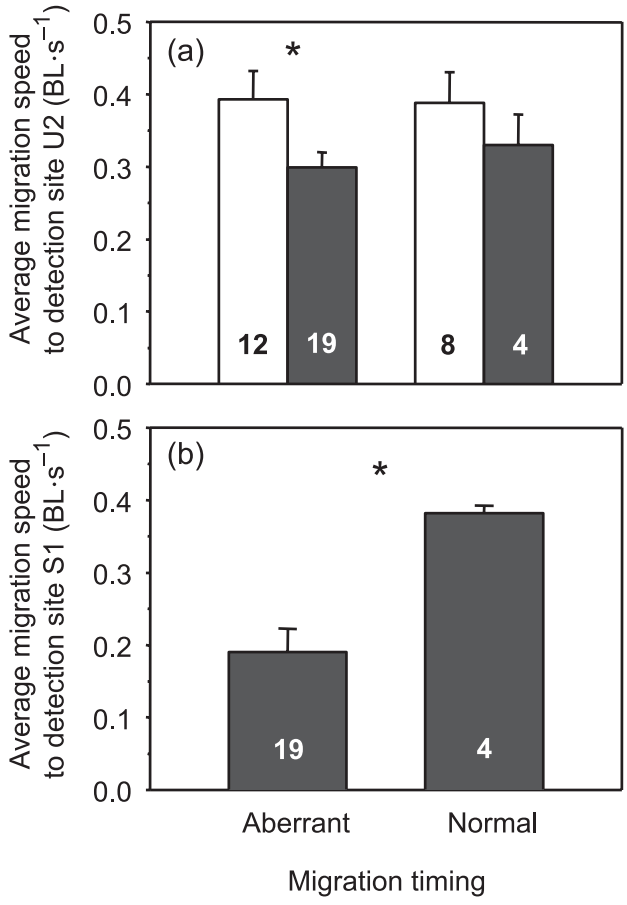
Average ground speed from the release site to the second upstream detection station (U2) did not differ by migration timing ($F = 0.109$, $P = 0.743$) but did differ by migration fate, with higher ground speeds in aberrant casualties than in survivors ($F = 3.544$, $P = 0.030$; Fig. 3*a*). Migration ground speed from release to spawning grounds was higher in aberrant than in normal migrants ($t = 82$, $P = 0.007$; Fig. 3*b*).

Physiological and energetic analyses

GSE differed by migration timing and fate (Table 1), with lower GSE in aberrant casualties than in both aberrant survivors ($P < 0.001$) and dropouts ($P = 0.004$) and higher GSE in aberrant compared with normal survivors ($P = 0.005$), casualties ($P = 0.005$), and dropouts ($P = 0.007$). Plasma lactate differed by migration fate (Table 1), with higher lactate in aberrant casualties than in dropouts ($P = 0.020$). Plasma glucose also differed by migration fate, with lower glucose in casualties than in dropouts for both timing groups combined (Table 1). Plasma cortisol did not differ by migration fate or timing (Table 1).

Plasma osmolality differed by migration timing (Table 1), with higher osmolality in aberrant casualties than in survivors ($P = 0.021$) and higher osmolality in aberrant than in normal dropouts ($P = 0.002$) and casualties ($P = 0.003$). More generally, plasma K^+ differed by migration timing, with higher K^+ in aberrant migrants across all migration

Fig. 3. Mean + standard error of (*a*) average migration ground speed (body length (BL)·s^{-1}) estimated from travel between release and upstream detection site U2 (47 km upstream) for casualties (open bars) and survivors (solid bars) and (*b*) average swimming speed (BL·s^{-1}) estimated from travel between U2 and spawning grounds (detection station S1, 163 km upstream). Sample sizes (*n*) are shown within each bar. Statistically significant (α = 0.05) differences indicated by asterisk (*).



fates combined (Table 1). Other plasma ions (Na^+ and Cl^-) did not differ by migration timing or fate.

Reproductive hormones

Plasma T, 11-KT, and E2 were compared only between aberrant female survivors and casualties because of low sample sizes. However, significant differences were observed for T and 11-KT, with higher reproductive hormone levels in aberrant casualties than in survivors (Table 2).

EMG telemetry

Only one fish released with an EMG transmitter successfully resumed its upstream migration, and DNA analysis confirmed that it was an early-summer-run fish. The remaining nine EMG tagged and released late-run fish dropped out and were never detected near or upstream of the release location during the entire sampling period. These fish typically and gradually moved downstream to the confluence of the Thompson and Fraser rivers over a 48–72 h period and remained downstream or were not detected for the rest of the sampling period. We collected intermittent EMG data on these fish during their fall back. EMG pulse intervals for each fish were converted to instantaneous swimming speeds using equations from Healey et al. (2003). Swimming speeds in excess of 1.5 BL·s^{-1} were common, and average speeds among individuals ranged from 0.48 to 0.52 BL·s^{-1} (detailed EMG and swimming speed data are not shown). These data indicate that fish were not passively carried downstream but were likely alive and actively swimming.

Excessive bleeding was observed in 14 of 18 fish subjected to surgery. Of the five fish that did not bleed excessively during surgery, one was the early-summer-run fish that we successfully tracked, two were aberrant late-run fish, and two were normal late-run fish. Necropsies on eight fish that bled excessively but were not released revealed that bleeding was not due to damage to internal viscera or organs nor by severing large blood vessels during surgery. The time required for blood to clot increased over the sampling period (R^2 = 0.215, P < 0.001; Fig. 4), with higher blood clotting time in aberrant (133 ± 13 s, n = 37) than normal (77 ± 5 s, n = 61) migrants (t = 3.393, P = 0.001).

Discussion

We evaluated potential linkages between energetic and physiological variables and mortality during the spawning migration of late-run Fraser River sockeye salmon. When intercepted halfway through their freshwater migration, aberrant late-run migrants had higher energy levels than normal late-run migrants. This result refutes the hypothesis that lower energy reserves are contributing to early entry behaviour, but still permits the possibility of a low energy mechanism for mortality in aberrant migrants. Other work by our group (S.J. Cooke, unpublished data) indicated a similar pattern of energy density when these fish first enter the Fraser River from the ocean, with lower energy in normal migrants. These results suggest that the marine holding behaviour of normal late-run salmon contributes to this energy differential through both routine metabolism and reduced feeding prior to freshwater entry. Feeding has greatly slowed during the coastal migration and has largely ceased about 200 km from the river mouth (Hinch et al. 2005). Hendry et al. (2004) suggests a genetic link between migration and energetic–reproductive state, with high somatic energy and small ovaries characterizing the earliest arriving and spawning females within a sockeye salmon population.

An important new finding in the present study was that casualties that were aberrantly timed had lower energy reserves prior to release and faster ground speeds through the first 47 km of upstream migration than did aberrant survivors. Several mechanisms could account for these differences. First, faster ground speeds likely imply faster swimming speeds, which would contribute to increased metabolic costs. Aberrant survivors had lower migration ground speeds than aberrant casualties and normal survivors. Given that sockeye salmon have a minimum cost of transport at a swimming speed of approximately 1 BL·s^{-1} (Lee et al. 2003), it is possible that unless aberrant fish properly pace upstream migration, they may not reach spawning grounds because of energetic exhaustion. Second, aberrant female casualties had higher reproductive hormones than aberrant survivors; thus, the former likely diverted more energy to

Table 1. Comparison of biological variables between late-run sockeye salmon (*Oncorhynchus nerka*) that exhibited aberrant or normal migrations and reached spawning grounds (survivor), were detected upstream of release but not at spawning grounds (casualty), or fell downstream after release and were never detected upstream of release (dropout).

						ANOVA output		
Physiological variable	Migration fate	Aberrant timing	*n*	Normal timing	*n*	Timing	Fate	Interaction
Gross somatic energy ($MJ \cdot kg^{-1}$)	Survivor	7.92±0.20ax	17	6.56±0.42y	4	F = **25.168**, P **<0.001**	F = **9.831**, P **<0.001**	F = 0.100, P = 0.905
	Casualty	6.61±0.25bx	11	5.45±0.30y	8			
	Dropout	7.97±0.42ax	4	6.39±0.27y	10			
Plasma lactate ($mmol \cdot L^{-1}$)	Survivor	5.19±0.85ab	6	4.50±1.04	4	F = 1.384, P = 0.249	F = **3.609**, P = **0.040**	F = 1.972, P = 0.158
	Casualty	7.78±0.79a	7	5.03±0.85	6			
	Dropout	3.67±1.12b	3	4.46±0.73	8			
Plasma cortisol* ($ng \cdot mL^{-1}$)	Survivor	133±71	6	56±101	3	F = 1.276, P = 0.269	F = 0.521, P = 0.600	F = 0.035, P = 0.966
	Casualty	185±66	7	152±78	5			
	Dropout	149±101	3	133±58	8			
Plasma glucose ($mmol \cdot L^{-1}$)	Survivor	4.43±0.20	6	4.68±0.24	4	F = 0.085, P = 0.772	F = **3.453**, P = **0.046**†	F = 0.980, P = 0.388
	Casualty	4.37±0.18	7	4.40±0.20	6			
	Dropout	5.14±0.28	3	4.74±0.17	8			
Plasma osmolality ($mosmol \cdot L^{-1}$)	Survivor	329±8a	6	321±10	4	F = **17.962**, P **<0.001**	F = 2.236, P = 0.126	F = 2.434, P = 0.106
	Casualty	360±7bx	7	325±8y	6			
	Dropout	356±11abx	3	309±7y	8			
Plasma K^+ ($mequiv. \cdot L^{-1}$)	Survivor	2.54±0.43	7	1.08±0.57	4	F = **7.249**, P = **0.011**‡	F = 0.624, P = 0.543	F = 0.409, P = 0.668
	Casualty	2.87±0.43	7	1.78±0.47	6			
	Dropout	2.18±0.57	4	1.60±0.40	8			
Plasma Cl^- ($mequiv. \cdot L^{-1}$)	Survivor	130.6±1.1	7	128.8±2.0	2	F = 0.007, P = 0.933	F = 0.268, P = 0.768	F = 1.849, P = 0.185
	Casualty	129.1±1.1	7	132.6±2.0	2			
	Dropout	131.1±1.4	4	129.1±1.7	3			
Plasma Na^+ ($mequiv. \cdot L^{-1}$)	Survivor	161.6±2.4	7	166.6±3.2	4	F = 1.097, P = 0.303	F = 3.177, P = 0.382	F = 3.177, P = 0.056
	Casualty	163.6±2.4	7	160.8±2.6	6			
	Dropout	164.8±3.2	4	155.6±2.3	8			

Note: Two-way analyses of variance (ANOVA) were conducted with fate as the main effect. Data are shown as mean ± SE. Statistical output in bold indicates significant models ($\alpha = 0.05$). For analyses exhibiting significant main effects, multiple comparisons were evaluated using a Tukey's test ($\alpha = 0.05$). Dissimilar letters indicates significant differences between migration fates within timing groups (a, b, c) and between migration timing within fate groups (x, y).

*$\log_{10}$-transformed for analysis.

†Dropout greater than casualty for both timing groups combined.

‡Aberrant greater than normal timing for all fate groups combined.

Table 2. Comparison of female plasma reproductive hormone concentrations between late-run sockeye salmon (*Oncorhynchus nerka*) that exhibited aberrant migrations and either reached spawning grounds (survivor) or were detected upstream of release but not at spawning grounds (casualty).

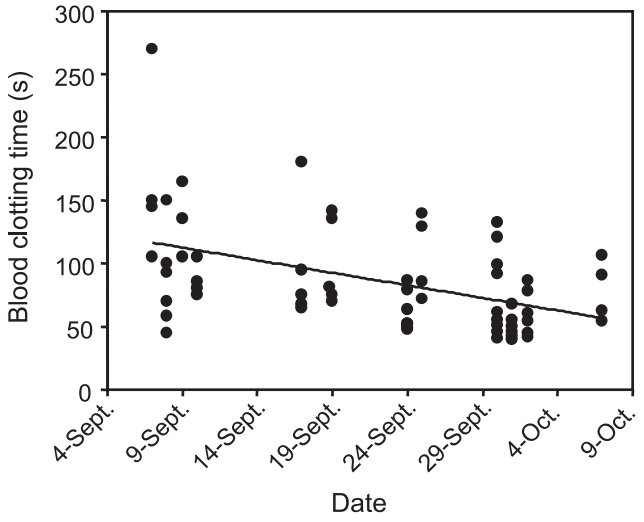
	Aberrant survivor		Aberrant casualty				
Female reproductive hormone	Mean	*n*	Mean	*n*	*t*	Power	*P*
Testosterone ($pg \cdot mL^{-1}$)	16 080±3 880	4	30 550±3 570	5	–2.738	0.592	**0.029**
11-Ketotestosterone ($pg \cdot mL^{-1}$)	953±218	4	1745±183	5	–2.807	0.617	**0.026**
17β-Estradiol ($pg \cdot mL^{-1}$)	3398±656	4	4589±464	5	–1.526	0.163	0.171

Note: Data are shown as mean ± SE. Analyses were conducted using *t* tests. Statistical output in bold indicates significant models ($\alpha = 0.05$).

gonads, potentially leaving them energetically deficient for the swimming challenges that remained. These ideas are discussed below.

Fraser River sockeye salmon reach spawning grounds with barely enough energy to ripen gonads, perform courtship, and spawn (Crossin et al. 2004*a*). Normal Adams River sockeye salmon (a major component of the late-run stock group that migrates through the Thompson River) begin the freshwater migration with about 8 $MJ \cdot kg^{-1}$ of somatic energy and complete the migration with about 5 $MJ \cdot kg^{-1}$, approximately 4 $MJ \cdot kg^{-1}$ of which is required to sustain their life throughout spawning; thus, they have only a 1 $MJ \cdot kg^{-1}$ energy buffer (Crossin et al. 2004*a*). For female sockeye salmon, swimming metabolism and gonad development utilize similar amounts of energy (~1.5 $MJ \cdot kg^{-1}$ each) (Crossin et al. 2004*b*). Thus, only modest increases in

Fig. 4. Time required for blood to clot for sockeye salmon (*Oncorhynchus nerka*) captured between 7 September and 7 October 2003. Linear regression line is shown ($R^2 = 0.215$, $P < 0.001$).



energy demands for either of these processes could conceivably exhaust energy reserves by depleting the 1 $MJ \cdot kg^{-1}$ buffer.

Upriver migration can be triggered by injection of T and 11-KT in precocious, castrated, male cherry salmon (*Oncorhynchus masou masou*) and by T, 11-KT, and E2 in immature parr (Munakata et al. 2001). T and 11-KT concentrations also increase during river migration of salmonids (Tveiten et al. 1998; Munakata et al. 2001; Leonard et al. 2002). Based on physiological samples from fish from the marine environment several hundreds of kilometres from the mouth of the Fraser River, it has been suggested that the early migration phenomenon in late-run sockeye salmon may be linked with an acceleration of reproductive development (Cooke et al. 2004*a*). Our results suggest that this accelerated reproductive development may also play a role in the abnormally high level of en route mortality. We found aberrant late-run sockeye salmon that died en route to spawning grounds had higher levels of T in females and higher levels of 11-KT in both sexes. Furthermore, elevated levels of reproductive hormones are believed to be partially responsible for tissue degradation and senescence during and after spawning by Pacific salmon (Dickhoff 1989). Thus, more advanced reproductive development during the migration could have reduced the energy available for swimming or compromised migration ability in another way, such as affecting tissue degradation, migration behaviour, or swimming ability as a result of premature development of secondary sexual characteristics.

Physiological stress can accelerate energy use and impair swimming performance in migrating salmon (Farrell et al. 1998; Wagner et al. 2003). Stress can also reduce a fish's ability to maintain blood ion concentrations (Eddy 1981; Ackerman et al. 2000). We thus evaluated osmoregulatory status but found no consistent patterns among plasma ion levels linking osmoregulatory dysfunction with en route mortality. We did, however, find that plasma osmolality was higher in aberrant casualties than in survivors and higher plasma K^+ in aberrant than in normal migrants. These differences could be associated with the normal decline in plasma ion concentrations that occurs after entry into fresh water or during maturation and senescence. Adult chum salmon (*Oncorhynchus keta*) exhibited reduced but stable ion concentrations in fresh water following transfer from salt water (Morisawa et al. 1979; Hasegawa et al. 1987). Higher osmolality in aberrant casualties than in survivors could indicate that the former had spent less time in fresh water prior to capture. This result is consistent with the migration ground speed differences discussed above, suggesting that aberrant casualties are moving upstream more quickly, possibly resulting in energetic exhaustion. However, the lack of difference in plasma ions that most strongly contribute to osmolality (e.g., Na^+ and Cl^-) may suggest other causes for this difference, which we are unable to identify.

The occurrence of excessive bleeding during EMG transmitter implantation surgeries was unexpected. Dozens of studies have used EMG transmitter implantation techniques similar to that used in this study to examine river migrations of adult sockeye (e.g., Hinch et al. 1996; Hinch and Bratty 2000), pink (*Oncorhynchus gorbuscha*) (Standen et al. 2002), Chinook (*Oncorhynchus tshawytscha*) (Brown and Geist 2002), and Atlantic salmon (*Salmo salar*) (Økland et al. 2000). However, none have reported excessive bleeding. Excessive bleeding may have been related to an impaired blood clotting mechanism, since the time required for blood to clot increased over the period of sampling, such that blood from normal migrants clotted in approximately half the time of aberrant migrants. The time required for blood to clot generally declines when healthy Pacific salmon become diseased or stressed and the number of circulating thrombocytes increases (Casillas and Smith 1977). A naturally occurring parasite (*Parvicapsula minibicornis*) that affects kidney function is contracted in the estuary by all homeward-migrating sockeye salmon (St-Hilaire et al. 2002). This parasite can lead to disease and kidney malfunction if water temperatures are relatively high as can be experienced by early migrating late-run sockeye salmon (Wagner et al. 2005). However, we do not know whether this or other parasite infections could influence blood clotting.

Although we cannot assign a mechanism to poor blood clotting and excessive bleeding from wounds, it is clear that any level of physical rupture of the fish's exterior surface (skin and gills) could provide an additional mechanism for mortality. All but one of the fish implanted with EMG transmitters either could not be released or fell back. The EMG-tagged fish that fell back after release did not have a relatively low energy reserves nor did EMG data indicate that these fish were exhibiting constant burst swimming, which would have rapidly drained their energy reserves. Sockeye salmon typically encounter rocky bed conditions in both the Fraser and Thompson canyons, a gauntlet of gill nets, and intraspecific interactions from encounters with thousands of conspecifics and congenerics (i.e., migrating pink salmon) during their upstream migration, all of which could cause abrasions or lesions leading to excessive bleeding or more rapid infections in early migrants. Unusual bleeding from injuries received during migration could provide an additional mechanism for mortality during migration. Further investiga-

tion is required to determine the cause of reduced blood clotting times and to confirm relationships among physical injury, excessive bleeding, and mortality in aberrant migrants.

It is unlikely that physiologically sampling these fish contributed unduly to en route mortality because migration fate for telemetered fish was similar for fish that were sampled for blood or not. Although 28% of fish released with a radio transmitter failed to move 22 km upstream, our reported levels of plasma lactate were lower than the threshold (<15.0 $mmol \cdot L^{-1}$) suggested by Jain et al. (1998) for detecting impaired critical swimming ability for mature sockeye salmon. Delayed mortality as a result of handling effects is generally restricted to 24 h and rarely more than 48 h (Wertheimer 1988; Farrell et al. 2000). Fish were classified as en route mortality only if they reached the second upstream detection station, which was 47 km from the release site. Travel times to this location averaged more than 60 h.

In summary, by individually tracking fish after physiological sampling, we investigated a complex phenomenon affecting the migration success of Fraser River sockeye salmon. Furthermore, by linking physiology during mid-migration with fate, this study has revealed potentially important roles of energetic status and reproductive development in influencing the en route mortality associated with an aberrant migration behaviour. Aberrant migrants that died en route to spawning grounds had lower energy stores and faster migration ground speeds than aberrant migrants that reached their spawning grounds. Concurrently, aberrant migrants that died en route had higher levels of reproductive hormones, suggesting that advanced maturation may have contributed to reduced migratory ability and death prior to spawning. Sockeye salmon that fell back downstream after being released did not exhibit higher stress, impaired osmoregulatory function, low energy stores, or energetic exhaustion. Excessive bleeding during EMG transmitter implantation surgery suggests a possible injury mechanism that could also contribute to high en route mortality. Further studies evaluating this bleeding phenomenon are necessary to refine this hypothesis.

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