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Physiological correlates of coastal arrival and river entry timing in late summer Fraser River sockeye salmon (*Oncorhynchus nerka*)

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Animal migrations typically occur within a predictable time frame and sequence, but little is known about the triggers that initiate migration, despite their importance in animal ecology and for resource management. The migration of adult sockeye salmon (*Oncorhynchus nerka*) in the Fraser River, British Columbia, Canada, is an excellent model to study such triggers because for nearly a decade a segment of the late summer stocks has been proceeding into the river as much as 6 weeks earlier than the historic norm. In this study, late-run sockeye salmon ($N = 146$) were intercepted about 215 km from the mouth of the Fraser River and implanted with radio transmitters. These fish were biopsied, which included drawing blood from the caudal vessels, removing some gill filament tips, and quantifying energetic status using a microwave energy meter. Fish that entered the river without delaying in the estuary were in a more advanced state of reproductive maturation, as evidenced by hormone and energy levels. Indicators of osmoregulatory preparedness (i.e., plasma ions and gill Na^+/K^+-ATPase activity) provided little insight into migration timing aside from greater variation in Na^+/K^+-ATPase activity in fish that entered early relative to those that held in the ocean. Given the dissimilar reproductive hormone profiles for early arrival into the estuary and early entry into the Fraser River, it appears that only a subset of the population are early migrants and triggers for early migration may be related to a relatively advanced reproductive development and higher energetic status. These findings provide the first assessment of the physiological correlates of migration timing and provide a mechanistic understanding of the proximate factors associated with abnormal migration timing in late-run sockeye salmon. *Key words:* cues, energetics, migration behavior, timing. *[Behav Ecol 19:747–758 (2008)]*

Migration is a widespread phenomenon exhibited by most animal taxa, with scale and extent differing by many orders of magnitude (Dingle 1996). Characteristically, migration is a directed movement between at least 2 separated and distinctive habitats (e.g., from feeding areas to reproductive habitats). The evolutionary basis for animal migration is that the fitness benefits and costs associated with residing in a particular habitat change with the life-history stages of an individual such that fitness benefits are derived from the migration (Baker 1978; Dingle 1980; Gross 1987). Although the specific purpose can differ, migration is often linked to reproduction (Sinclair 1983; Dingle 1996) such as the well-known upriver migration of adult Pacific salmon (*Oncorhynchus* spp.; Groot and Margolis 1991; Hinch et al. 2005), which is the culmination of a several thousand kilometer migration from rich ocean feeding grounds to natal streams for reproduction and death.

An important characteristic of migrations is that they occur within a reasonably predictable time frame and sequence (Dingle 1996). In fact, long-term averages (more than 50 years) in timing of coastal arrival, migration initiation (i.e., freshwater entry), and spawning of Pacific salmon rarely deviate from average timing by more than 1 week (Hamilton 1985; Woodey 1987). Furthermore, so predictable is the timing of their river entry that different stocks of Fraser River sockeye salmon (*Oncorhynchus nerka*) are grouped by the timing of their river migration (e.g., early Stuarts, early summers, summers, late summers; Killick 1955; Woodey 1987). Despite considerable study on the interplay of behavior, physiology, and environment in the context of migration, little is known about the

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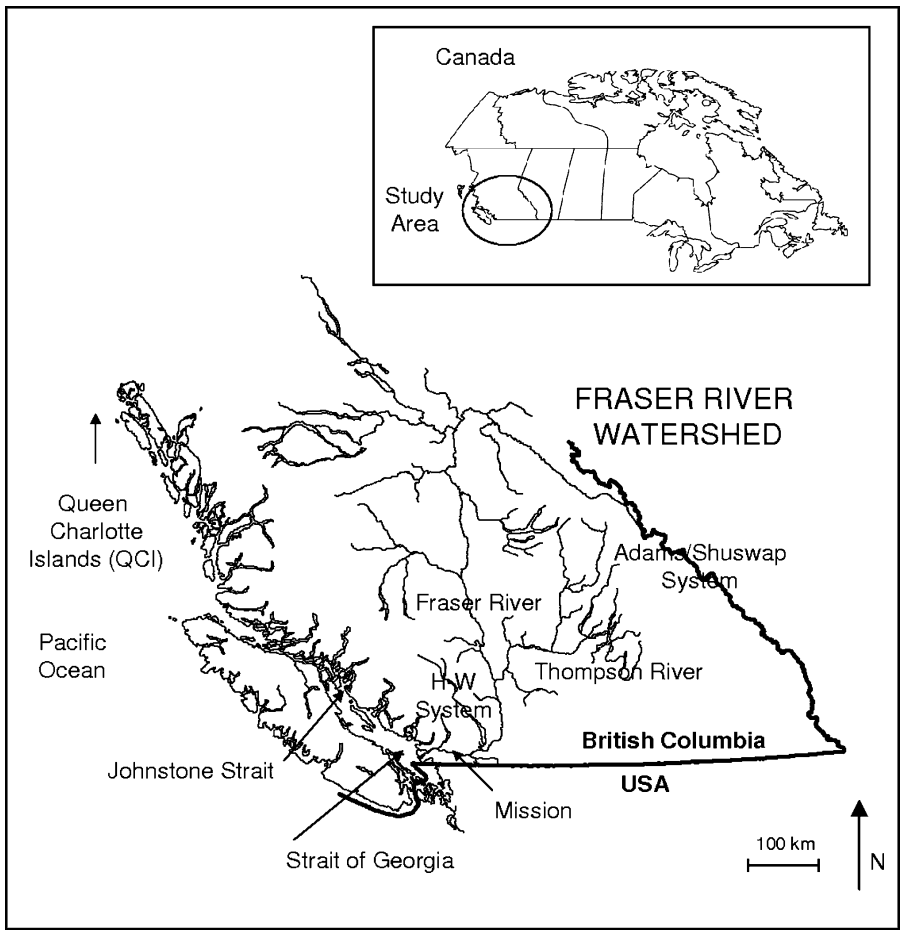

Figure 1
Map of study system inset within Canada and the Fraser River watershed of British Columbia. Fish were implanted with transmitters and biosampled in Johnstone Strait, a coastal area where fish begin to encounter estuarine conditions. Late-run sockeye salmon typically delay in the Strait of Georgia for several weeks prior to entering the river. A radiotelemetry receiver array was deployed at Mission, British Columbia, to monitor Fraser River entry. This analysis focused on late-run sockeye salmon from the Harrison-Weaver (H-W) or Adams-Shuswap stock complexes. Sockeye salmon first enter coastal areas at Queen Charlotte Islands, some 500 km from the mouth of the Fraser River.

factors that trigger the initiation of migrations for Pacific salmon (Hinch et al. 2005) or other animals (Gauthreaux 1980; Dingle 1996). It is generally understood that the endocrine system, coupled with environmental cues, and endogenous timing mechanisms play a role in migration timing and initiation (Gauthreaux 1980). Here, we use sockeye salmon as a model to explore the potential role of physiological and energetic status on triggering the return migration into freshwater. Furthermore, we take advantage of a particular stock complex, the late summer run from the Fraser River, British Columbia (Figure 1), which has been exhibiting an aberrant migration behavior; significant portions of the stock complex have been deviating from the historic normal river entry time by up to 6 weeks for almost a decade.

The late-run sockeye salmon stocks, which are very important economically to the commercial fishery and culturally to First Nations (i.e., aboriginals), represent 1 of 4 stock complexes in the Fraser River watershed distinguished by the timing of freshwater entry and the location of spawning (Killick 1955; Woodey 1987). They arrive in August near the mouth of the Fraser River, in the Strait of Georgia (Figure 1), where they normally remain for 3–6 weeks, prior to initiating upriver migration. However, since 1995, segments of the population have initiated upriver migration up to 6 weeks earlier and therefore have reduced or eliminated their estuarine delay behavior (Lapointe et al. 2003; Cooke, Hinch, Farrell, et al. 2004; Figure 2). Early migration does not confer an earlier spawning date but instead is associated with high mortality rates, in some years exceeding 90% for several stocks (Lapointe et al. 2003; Cooke, Hinch, Farrell, et al. 2004). To provide mechanistic insights into how freshwater migration may be triggered, as well as to better understand the potential causes (by evaluating correlates) of the aberrant migratory behavior of late-run sockeye salmon, we compared the physiology of adult salmon that entered the Fraser River early with those with normal entry time. Unlike the majority of past research on salmon migrations that have examined population-scale behavioral and physiological patterns, we focused on individual variation using telemetry and nonlethal biopsies.

A new frontier of modern ecology focuses on individual variation in animal behavior and linking such variation to physiological and energetic conditions (Goldstein and Pinshow 2002; Altmann SA and Altmann J 2003). However, linking individual behavior and physiology presents major practical challenges (Bennett 1987; Costa and Sinervo 2004), particularly with respect to migration (Webster et al. 2002), because of our current inability to provide real-time data on physiological or energetic status (e.g., Cooke, Hinch, Wikelski, et al. 2004). Nevertheless, by coupling nonlethal tissue biopsy with individual positional telemetry, we monitored individual fish prior to migration into freshwater. We then compared physiological and energetic status of fish that displayed abnormal early river entry with those that displayed a normal delay behavior in the Strait of Georgia. This approach allowed us to test the hypothesis that individual migration behavior is influenced by a combination of physiological and energetic preparedness for the upriver journey. In addition, we were able to assess migration timing in 3 ways. First, we assessed the timing of arrival in the coastal estuarine environment (arrival in the estuary) some 215 km from the river mouth for a 3-week period. Second, we assessed the status of individual fish that exhibited normal estuarine delay behavior relative to those

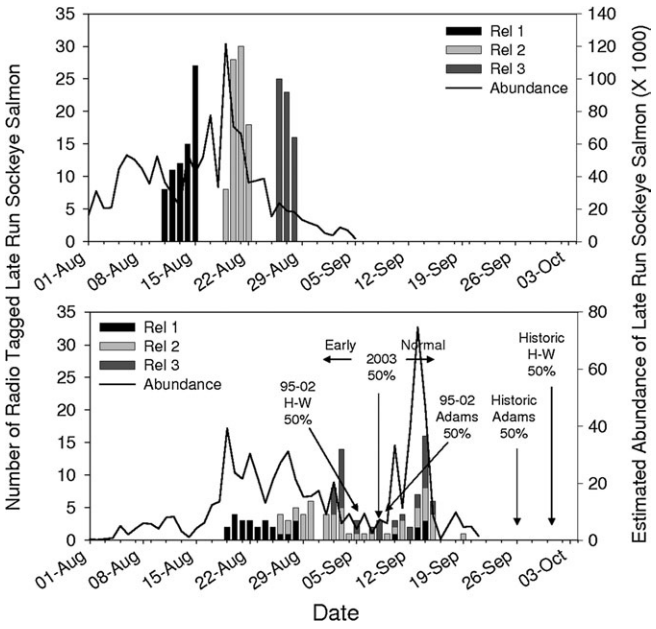

Figure 2
Schematic of the composite 2003 late-run migration timing (lines) at both Johnstone Straight and Mission relative to telemetered late-run fish (vertical bars). Data at Johnstone Straight were generated using test fisheries, and data at Mission were generated using a hydroacoustic counting facility and test fisheries (see Benneheka et al. 1995). Key timing elements are indicated on the figure including the delineation between "early" and "normal" for 2003, as well as historical 50% migration dates for context. Rel 1, 2, and 3 indicate the 3 release periods for telemetered fish.

that did not. Finally, we assessed the timing of individual river entry relative to the migration timing of the entire late-run complex, as provided by traditional stock estimates by fisheries managers. We recognize that a fundamental limitation of our approach is that our analysis can only yield correlation and not causation. Nonetheless, such an approach is needed prior to embarking on a more experimental study that would involve large-scale manipulations.

We developed 3 predictions about individual timing behavior, primarily focused on entry timing (delay), but equally applicable to arrival in the coastal estuary. First, we predicted that early-entry fish should have lower energy than those that delay and enter later in the season. This prediction was based on the idea that the sockeye salmon have limited energy to complete the migration and spawn (Brett 1995; Crossin et al. 2003, 2004) and that individual fish with lower energy stores may need to enter the river early to prevent energy stores from being exhausted prior to spawning. Adult sockeye salmon can perish if their river migration is delayed significantly (Rand and Hinch 1998), probably because the energy stores become depleted. Second, we predicted that early-entry fish would be in an advanced state of osmoregulatory preparedness for life in freshwater. This prediction is based on the fact that salmonids require major physiological alterations as they switch during their migration from hypoosmotic to hyperosmotic (Clarke and Hirano 1995; Shrimpton et al. 2005). Here we assayed gill Na^+K^+-ATPase and plasma ionic status with the expectation that early entrants would show a premature shift toward freshwater residency (Wood and Shuttleworth 1995). Finally, we predicted that early-entry fish should be in a more advanced state of maturation as indicated by reproductive hormone profiles in their plasma. We reasoned that individual fish with advanced reproductive development should proceed toward spawning grounds before those fish that are less reproductively advanced, considering the critical role for the endocrine system in migration and maturation (Woodhead 1975; Ueda and Yamauchi 1995).

MATERIALS AND METHODS

Overall approach

We used protocols to biopsy unanesthetized sockeye salmon without compromising fish survival or behavior. These protocols were validated in a parallel study, in which 3 independent assessments were used to demonstrate that it was possible to biopsy sockeye salmon and implant radio transmitters without causing deleterious effects to behavior or survival (Cooke et al. 2005).

The present investigation was part of a larger telemetry study in which (N = 559) sockeye salmon (see English et al. 2004 for detail on fish meristics and a summary of the behavior of fish excluding all physiological information) were intercepted near the southern end of Johnstone Strait (Figure 1), approximately 215 km from the mouth of the Fraser River. The region where fish were captured is influenced by the Fraser River and is therefore considered estuarine from an oceanographic perspective, although the depth of freshwater influence in Johnstone Strait is considerably less than in areas closer to the mouth of the Fraser River (Thomson 1981). Because sockeye salmon normally migrate directly through Johnstone Strait, we used this sampling to provide an index of the fish's physiological status on arrival in the Strait of Georgia, which adjoins to the mouth of the Fraser River. Fish were collected using a large purse seine net deployed from a commercial fishing vessel, which also served as the platform for biopsy, radiotagging, and fish release. Fish were sampled, tagged, and released for a 3-week period: August 11–15 (Release 1), August 19–22 (Release 2), and August 26–28 (Release 3). Surface water temperatures were 10–13 °C. Fish arrival to the Fraser River was monitored approximately 300 km from the release site by 2 radio telemetry stations, located 85 km upstream from the mouth of the river at Mission, British Columbia (Figure 1), and beyond tidal influences. These stations were deployed on opposite banks, each consisting of 2 antennas and a data logging radio receiver (SRX_400, Lotek Engineering Inc., Newmarket, Ontario). Details on the receiving system are provided in English et al. (2004). Our estimate of the time the fish delayed migration by holding in the Strait of Georgia was calculated as the difference between the fish release date and its arrival at Mission. The normal (pre-1995) behavior of late-run sockeye salmon is to migrate toward the Fraser River but delay in marine conditions of the Strait of Georgia adjacent to the river mouth (Figure 1) for up to several weeks (Cooke, Hinch, Farrell, et al. 2004).

Synopsis of biopsy and tagging techniques

After capture, fish were individually netted from the purse at the side of the vessel and held in large flow through totes on deck. Fish were individually removed from the tote, placed ventral side up in a V-shaped trough lined with foam and provided with continuous gill irrigation with seawater. Fish were manually restrained in the trough for less than 3 min, while tissues were biopsied and a radio transmitter was inserted using the methods outlined in Cooke et al. (2005). The biopsy procedure involved 1) removing a small piece (0.5 g) of the adipose fin for DNA stock identification, 2) removing one scale for ageing, 3) removing 1.5 ml of blood from the caudal vessel (Houston 1990) for assessing plasma chemistry, and

4) removing <4 mm from the tips of 6–8 filaments (0.3 g) from the first gill arch (McCormick 1993; Schrock et al. 1994) for assessing gill enzyme activity. Gill tissue and centrifuged plasma samples were stored on dry ice for several days prior to being held in a −80 °C freezer until analysis. A handheld microwave energy meter (Distell Fish Fatmeter model 692, Distell Inc., West Lothian, Scotland, UK) was placed on the left side of the fish in 2 locations to quantify somatic energy levels (see approach in Crossin and Hinch 2005). Radio transmitters, which measured 16 mm in diameter and 51 mm in length and weighed 16.1 g in air and 6.2 g in water (MCFT-3A, Lotek Engineering Inc.), were inserted into the stomach using a plastic applicator (Ramstad and Woody 2003). Fish were returned to the holding tote to recover for <1 h after this procedure. All fish in the tote were released as a group in an attempt to minimize predation by marine mammals.

Assays

We focused on fish from the 2 largest late-run stocks: the Harrison-Weaver and the Adams-Thompson-Shuswap (Figure 1). Of 559 fish sampled and released, 188 fish were identified as late run and 371 fish were summer run. Stock origin was ascribed to individual fish by a combination of DNA analyses (see Beacham et al. 1995), scale analysis (see Cook and Guthrie 1987), and the recovery of radio transmitters at terminal spawning grounds. Tissue biopsies and energy measurements were taken on 117 late run fish; an additional 29 fish had only energy measurements before release.

Plasma testosterone (T), 17β-estradiol (E_2), and 11-ketotestosterone (11-KT) levels were measured by radioimmunoassay (Van Der Kraak and Chang 1990; McMaster et al. 1992). The interassay variabilities for the T, E_2, and 11-KT radioimmunoassays were 6.6%, 11.6%, and 8.8%, respectively. At time of capture, sex could not be confidently assigned using external features; therefore, we regressed plasma E_2 values against T values, which resulted in 2 distinct clusters of the data corresponding to male and female fish. Plasma ion, cortisol, lactate, glucose, and osmolality measurements followed the same procedures described by Farrell et al. (2000, 2001). Gill tissue Na^+/K^+-ATPase activity was determined with a kinetic assay run in 96-well microplates at 25 °C and read at a wavelength of 340 nm for 10 min (McCormick 1993; Shrimpton et al. 2005) with the ATPase activity measurement expressed as μmol ADP/mg protein/h.

Statistical analysis

Multivariate analysis of variance (MANOVA) was used to examine for differences between sexes for the suite of physiological variables, with the exception of reproductive hormones, which are clearly sex specific. No other variables were determined to be sex specific. MANOVA was then used to examine for differences between stock groupings (Harrison-Weaver and Adams-Shuswap). Only energy differed among stocks and was thus analyzed separately. All other samples were pooled for subsequent analyses. MANOVA was then be used to examine for general differences among sockeye salmon grouped according to 1) date of capture, 2) date of river migration initiation, and 3) duration of delay in the Strait of Georgia after capture. Canonical variates analysis (CVA) was used a posteriori to identify differences among the multivariate centroids in instances where the MANOVA was significant (i.e., CVA was used to identify specific variables that contributed to differences among categories, as well as how the variables were interrelated; McGarigal et al. 2000). All multivariate analyses were conducted on $\log_{10}$-transformed data (McGarigal et al. 2000).

Correlation analysis was used to identify relationships between timing variables and physiological variables. Data determined to be normal, using Shapiro–Wilks tests, were analyzed using Pearson coefficients whereas Spearman rho coefficients were used for nonnormal data (Zar 1996). To analyze 2 sample data, we used *t*-tests when data were normal (assessed by Shapiro-Wilks test) and exhibited homogeneous variances (assessed using the Levene's test; Zar 1996). Otherwise, we used Wilcoxon rank tests. All analyses were conduced using JMP 4.0 (SAS Institute, Raleigh, NC) and were assessed for significance at $\propto = 0.05$.

RESULTS

Status of fish intercepted in Johnstone Strait

Sockeye salmon that were intercepted in Johnstone Strait displayed temporal changes in their physiology and energy status for the 18-day sampling period. Fish exhibited decreasing levels of gross somatic energy as the sampling period progressed (Figure 3a,b; Table 1). In contrast, plasma concentrations of certain reproductive hormones increased during the sampling period. In particular, males exhibited a positive relationship between arrival time in the Strait of Georgia and 11-KT (Figure 3g), whereas females exhibited a positive relationship between arrival time and 17β-E_2 (Figure 3h). No other significant correlations were found between either reproductive hormones and arrival time or osmoregulatory indicators (Na^+/K^+-ATPase, Cl^-, Na^+, and osmolality) and arrival time in Johnstone Strait (Table 1). There were significant negative relationships between arrival time in Johnstone Strait and all the stress parameters (K^+, cortisol, plasma lactate, and plasma glucose; Figure 3c–f, respectively).

MANOVA revealed no differences between sex or stock groups (both $P < 0.05$); therefore data were pooled; all subsequent multivariate analyses included gross somatic energy, osmolality, ions, Na^+/K^+-ATPase, cortisol, and metabolites. We identified differences among the 3 sampling periods (MANOVA, $F_{18,146} = 4.612$, $P < 0.001$). The first canonical axis explained 61% of the variation (Table 2). All sampling periods differed (CVA, P's < 0.05), with the variation driven largely by cortisol, lactate, and glucose, an observation consistent with the notion that our handling of fish improved over time.

Delay between fish release and river entry

Travel times for tagged fish from Johnstone Strait until they were first recorded at Mission ranged from 6 to 32 days. Fish must travel 215 km from Johnstone Strait to the mouth of the Fraser River, which they can do in approximately 5 days (averaging more than 40 km/day; Quinn and terHart 1987) with an additional day to reach Mission. Therefore, 6 days is the minimum travel time from tagging to detection at Mission, assuming no delay. We subtracted the minimum travel time of 6 days from the travel time to Mission to conservatively estimate the fish's delay time in the Strait of Georgia. Delays ranged between 0 and 26 days and displayed a bimodal distribution, with modes at 2 and 12 days. Therefore, fish that arrived at Mission in less than 8 days were classified as ones that did not delay in the Strait of Georgia, whereas those that arrived on or after 9 days were considered to have delayed. Among all the biological variables examined, there were few significant relationships with duration of delay (Table 3). Females with shorter ocean delays had higher 11-KT and 17β-E_2 levels than those with longer delays (Figure 4c,d; Table 3). Though marginally nonsignificant, Adams fish with low energy appeared to delay for shorter durations than those with higher energy (Figure 4b;

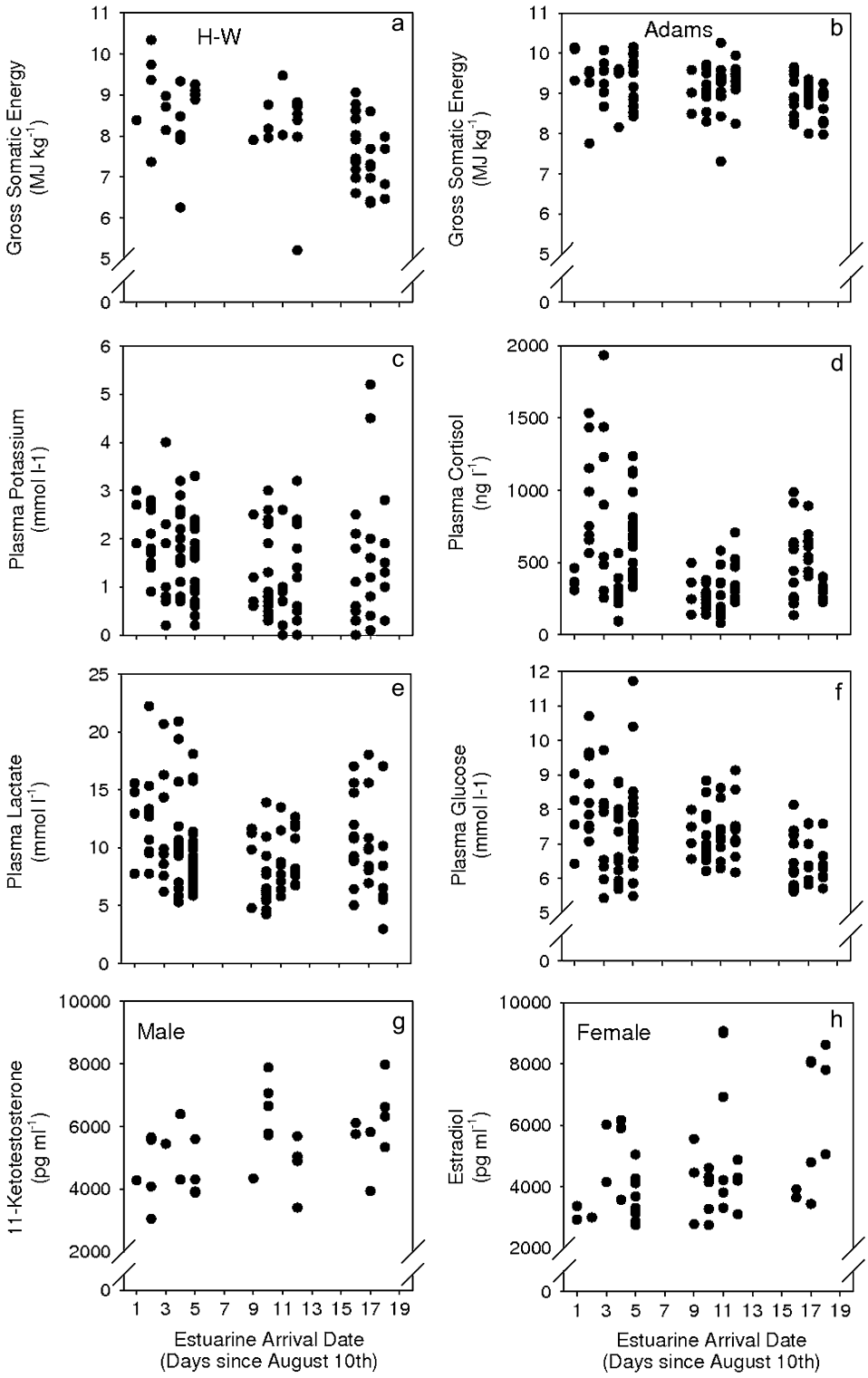

Figure 3
Relationship between estuarine arrival timing (date fish captured and released in the Johnstone Strait) and biological variables. Statistical details for each panel are presented in Table 1. Gross somatic energy is analyzed separately for different stock groupings (H-W, Harrison-Weaver, and Adams, Adams-Shuswap) and reproductive hormones analyzed separately for the 2 sexes. All other analyses represent all late-run sockeye salmon for which bio-sampled data were collected. Statistical details are reported in Table 1.

Table 3) consistent with our prediction. However, this pattern was not evident among the Harrison-Weaver fish (Figure 4a; Table 3). Multivariate analysis did not reveal any differences in physiological measures among fish that delayed or did not delay (MANOVA, $F_{9,58} = 0.834$, $P = 0.588$).

Our classification of fish into those that delayed and those that did not based on an 8-day criterion may have resulted in too coarse of a classification. Therefore, we reclassified fish into those that delayed for the longest periods (i.e., >13 days; 75th percentile) and those that delayed for the shortest periods (i.e., <2 days; 25th percentile). Fish from the Adams stock that delayed for long periods had higher energy than those that did not delay (Figure 5b). A similar pattern was observed for fish from the Harrison-Weaver system (Figure 5a), although with a smaller sample size the difference was not significant ($P = 0.121$). There were no differences associated with ionic status, metabolites, or stress indicators (Table 4), though Na^+/K^+-ATPase values were significantly more variable for fish that did

Table 1

Relationship between estuarine arrival timing (date fish captured and released in the Johnstone Strait) and biological variables

	Johnstone Strait arrival timing		
Variable	Sample size	Correlation coefficient	*P* value
Gross somatic energy (H–W)	53	*r*, −0.497	<0.001
Gross somatic energy (Adams)	103	*r*, −0.380	<0.001
Plasma Na^+	126	r_s, −0.030	0.741
Plasma K^+	126	*r*, −0.303	<0.001
Plasma Cl^-	121	r_s, 0.130	0.143
Plasma osmolality	127	*r*, −0.056	0.531
Plasma cortisol	126	r_s, −0.282	0.002
Plasma lactate	127	*r*, −0.198	0.026
Plasma glucose	127	*r*, −0.404	<0.001
Na^+/K^+-ATPase	93	*r*, −0.060	0.587
T (male)	30	*r*, 0.122	0.520
T (female)	45	r_s, 0.246	0.103
11-KT (male)	30	*r*, 0.414	0.023
11-KT (female)	45	*r*, 0.187	0.220
17β-E_2 (male)	30	*r*, −0.219	0.245
17β-E_2 (female)	45	*r*, 0.422	0.004

Type of correlation coefficients are indicated prior to the actual value (*r*, Pearson coefficient; r_s, Spearman coefficient). Gross somatic energy is analyzed separately for different stock groupings and reproductive hormones analyzed separately for the 2 sexes. All other analyses represent all late-run sockeye salmon sampled in Johnstone Strait.

Table 3

Relationship between delay prior to river entry (elapsed time in days between release in Johnstone Strait and first detection at Mission) and biological variables

	Delay prior to river entry		
Variable	Sample size	Correlation coefficient	*P* value
Gross somatic energy (H-W)	27	*r*, 0.293	0.137
Gross somatic energy (Adams)	66	*r*, 0.230	0.062
Plasma Na^+	74	r_s, 0.096	0.415
Plasma K^+	74	*r*, 0.105	0.372
Plasma Cl^-	71	*r*, 0.098	0.414
Plasma osmolality	75	*r*, 0.024	0.837
Plasma cortisol	75	r_s, −0.093	0.426
Plasma lactate	75	r_s, −0.032	0.780
Plasma glucose	75	*r*, 0.086	0.462
Na^+/K^+-ATPase	74	r_s, 0.025	0.831
T (male)	30	r_s, −0.266	0.156
T (female)	45	*r*, −0.237	0.117
11-KT (male)	30	*r*, −0.257	0.171
11-KT (female)	45	*r*, −0.394	0.008
17β-E_2 (male)	30	*r*, −0.171	0.365
17β-E_2 (female)	45	*r*, −0.326	0.029

Type of correlation coefficients are indicated prior to the actual value (*r*, Pearson coefficient; r_s, Spearman coefficient). Gross somatic energy is analyzed separately for different stock groupings and reproductive hormones analyzed separately by sex. Other analyses represent all late-run sockeye salmon that passed Mission. H-W, Harrison-Weaver.

not delay (Table 4; Figure 5c). There were no differences in reproductive hormones attributable to the delaying behavior of male sockeye salmon. For females, however, all the reproductive hormones (Table 4; Figure 5d,e) were elevated (although T was not significant, $P = 0.095$; Figure 5f) in fish that did not delay relative to those that delayed for a long period. Multivariate analysis did not find any differences in biological variables between fish categorized as long delays versus those that did not delay (MANOVA, $F_{9,17} = 1.769$, $P = 0.149$).

Timing of river entry

Some fish from all 3 sampling groups were able to reach Mission in 6 days (English et al. 2004), dispelling the possibility that the improvement in fish handling biased the results. Telemetered fish were first documented reaching Mission on August 19th, and the last fish reached Mission on September 19th, 32 days after tagging started. The arrival time of telemetered fish at Mission displayed a bimodal distribution with one group arriving between August 19 and September 3 and another between September 10 and 15 (English et al. 2004). As a result, September 7th represented the date of 50% passage of late-run sockeye salmon. Therefore, fish arriving at Mission before that date were considered early migrating and those arriving after that date were considered normal migrating (see Figure 2). Among all the biological variables examined by univariate analyses, there were no significant relationships with date of river entry (i.e., days from August 15th; Table 5). None of the biological variables that we examined differed among entry time when fish were categorized as early or normal (MANOVA, $F_{9,58} = 0.690$, $P = 0.715$).

A potential limitation of the early and late classification is that the fish we sampled did not include the extremes of the migration behavior because untagged fish were documented entering the river as early as August 1st and as late as September 20th (Figure 2). In fact, these dates are likely conservative because hydroacoustic techniques used to estimate passage at Mission are not robust when few fish are present (Figure 2). It is possible that our categorization of migrants into early and normal groups based on a simple September 7th criterion may have resulted in too coarse of a classification. Therefore, we restricted some analyses to the 25th and 75th percentiles, thereby reclassifying early fish as those that entered the river extremely early (i.e., before August 29th) versus those that entered at later normal periods (i.e., after September 13th; dates based on 25th and 75th percentiles) and redid the analyses. This approach enabled us to assess fish in the 2 modes. Again, no significant differences existed between early and normal migrants for ionic status, metabolites, stress indicators, energetics, and reproductive hormones with univariate (Table 6) and multivariate (MANOVA, $F_{9,34} = 0.886$, $P = 0.547$) analyses.

Table 2

Total standardized canonical coefficients for the first 2 axes (CAN 1 and CAN 2) from CVAs for an assessment of differences among the 3 sampling periods indicating different condition on arrival to the estuary

Variable	CAN 1	CAN 2
Gross somatic energy	−1.019	1.423
Plasma Na^+	−1.844	−0.349
Plasma K^+	0.034	0.042
Plasma Cl^-	−4.399	−4.161
Plasma osmolality	3.779	1.156
Plasma cortisol	0.306	−0.001
Plasma lactate	0.245	0.079
Plasma glucose	−0.934	0.905
Na^+/K^+-ATPase	0.246	0.002
Explained variance (%)	61	39

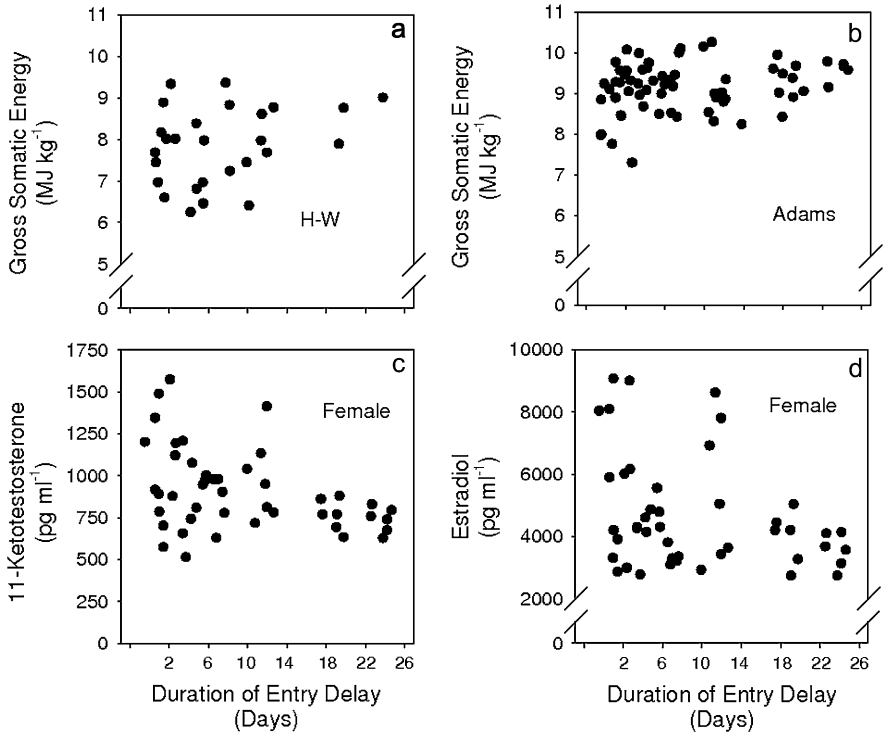

Figure 4
Relationship between delay prior to river entry (elapsed time in days between release in Johnstone Strait and first detection at Mission) and biological variables. Statistical details for each panel are presented in Table 3. Gross somatic energy is analyzed separately for different stock groupings (H-W, Harrison-Weaver, and Adams, Adams-Shuswap) and reproductive hormones analyzed separately for the 2 sexes. All other analyses represent all late-run sockeye salmon for which biosampled data were collected. Statistical details are reported in Table 3.

DISCUSSION

We used sockeye salmon as a model to understand the role of physiological and energetic status as triggers of freshwater spawning migrations. We hypothesized that variation among individuals in timing of upriver migration is related to their physiological and energetic state and specifically that abnormally early migrating late-run Fraser sockeye salmon have endogenous characteristics that enhance their migration preparedness. Because of expense, fish telemetry studies have rarely involved hundreds of fish, and, moreover, telemetry with any organism has rarely used biopsy techniques. Thus, our study represents the first of this scale to evaluate the behavioral physiology of the initiation of an animal migration.

Migration timing was assessed at 3 distinct time periods, arrival in the coastal environment, estuarine delay behavior related to holding in the Strait of Georgia, and river entry. Below, we discuss each of these periods. We also recognize that there are different stages of migration related to life history and that understanding initiation factors for a particular migration must be thought of in context of the previous migration and its initiation factors (i.e., sockeye salmon's migration from the open ocean to the coast that precedes the upriver migration). As such, where possible, we discuss the state of physiological and energetic variables relative to fish sampled from the Queen Charlotte Islands approximately 500 km from the river mouth (Hinch et al. 2005), indicative of fish several weeks prior to their arrival to the Fraser River mouth (Figure 2).

Sampling strategy

Using telemetry coupled with nonlethal physiological and energetic sampling, we were able to document the mechanisms underlying individual variation in behavior. To our knowledge, this represents the first time that such an experiment has been conducted on this scale in any animal (Altmann SA and Altmann J 2003). Although the technique was extremely successful, the short-term stress indicators were not overly useful for interpreting variation in behavior. Because fish were all captured in a purse seine and held for variable periods, sometimes under high densities, fish were stressed, as has been documented by a variety of capture techniques (e.g., Farrell et al. 2000, 2001). There was a gradation of stress observed across sampling periods, with stress generally highest during the first sampling period where the most fish were handled. Although this makes it difficult to interpret these stress indices, it is unlikely that this level of stress was sufficient to alter the other physiological variables (e.g., reproductive hormones, Na^+/K^+-ATPase) in the time period between capture and sampling or to alter behavior on release. Other experiments that have involved capturing migrating individuals and then terminally sampling them also have recognized that capture- and handling-induced stress could represent a problem (e.g., Comeau et al. 2002; Leonard et al. 2002). We are confident that our observations for osmoregulatory and hormonal indicators represent natural patterns but that our short-term stress indicators are not overly informative given some level of capture- and handling-related stress (Cooke et al. 2005) and are thus not discussed in detail.

A drawback with our sampling effort was that the normal migration run through Johnstone Strait extends over a much longer time period than we were able to study. Although our sampling was spread for a 3-week period, late-run fish began to arrive in the coastal environment some 2 weeks earlier than when we began sampling and continued for a further approximately 10 days (English et al. 2004; Pacific Salmon Commission, unpublished data; Figure 2). Sampling during earlier periods was avoided to optimize the number of late-run fish sampled due to large abundances of comigrating stocks during the early periods, as well as conservation concerns regarding some stocks. Perhaps, if we had sampled the very earliest arrivals, we would have detected additional trends. Nonetheless, nearly equal proportions of tagged late-run sockeye salmon entered the river before and after the 50% migration date (September 7th) for the entire run timing group, enabling us to differentiate between these groups (Figure 2).

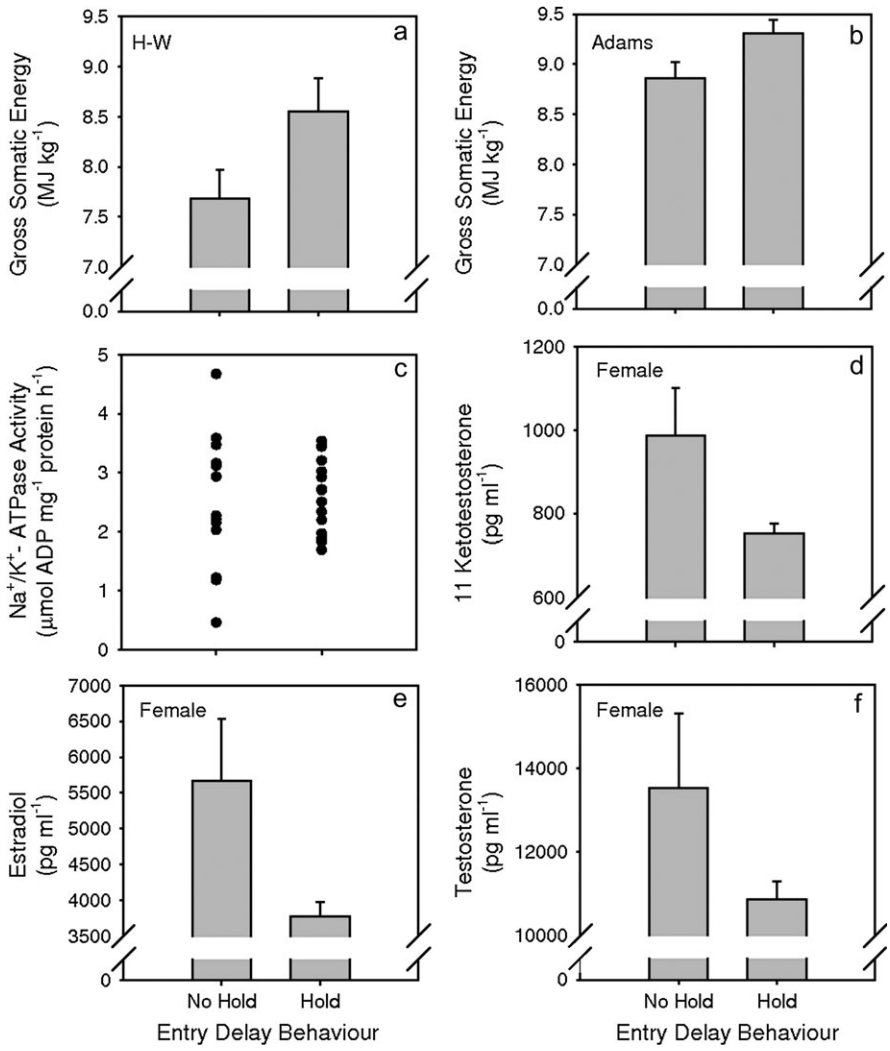

Figure 5
Comparison of biological variables between late-run sockeye salmon that delayed in the Strait of Georgia for less than 2 days prior to migrating upriver (no delay) and those that delayed for longer than 13 days (delay). The delay period was determined by subtracting the minimum travel time of 6 days from the elapsed time in days between release in Johnstone Strait and first detection at Mission. Statistical details for each panel are presented in Table 4. In panel c, data are visualized as a scatter plot to illustrate the different levels of variance among the 2 delay behaviors. All other data are means ± standard errors. Gross somatic energy is analyzed separately for different stock groupings (H-W, Harrison-Weaver, and Adams, Adams-Shuswap) and reproductive hormones analyzed separately for the 2 sexes. All other analyses represent all late-run sockeye salmon that passed Mission and that were encompassed by our data categories. Statistical details are reported in Table 4.

Similar breakdowns were possible for delay behavior, with the distribution being bimodal (English et al. 2004). Also, by focusing on the "extremes" (by analyzing the earliest and latest fish or most extreme delay periods), we were able to maximize our ability to detect timing differences.

Status of sockeye salmon intercepted in Johnstone Strait

We predicted that there would be a gradation of energetic status and physiological condition associated with arrival into estuarine waters (i.e., Johnstone Strait) with earlier arrivals having lower energy and advanced osmoregulatory and reproductive hormonal preparedness relative to later timed migrants. Across our 2.5-week sampling period, we rarely observed these patterns. Sockeye salmon passing through Johnstone Strait were not all at the same reproductive or energetic status but were more homogeneous in terms of their osmoregulatory status. Both reproductive and energetic status of sockeye salmon intercepted in Johnstone Strait were found to be time dependent, even within a 2.5-week migratory window, highlighting the fact that fish do not arrive in the same state. Fish sampled early had significantly higher energy than later timed migrants. Also, the energy status of fish in the Johnstone Strait was lower than fish captured several weeks earlier in the Queen Charlotte Islands (Hinch et al. 2005), suggesting that sockeye salmon are in a state of declining energy even before their arrival in the estuary. The decline in energy status over time could be due to the fact that fish arriving in Johnstone Strait are in a catabolic state having already reduced or stopped feeding. This contention is supported by the absence of gut contents that we observed when gastrically tagging fish. Therefore, those fish arriving at a later time would have a lower energy status simply because they had been in a catabolic state for a longer period of time (Gilhousen 1980; French et al. 1983). Alternatively, fish arriving early are in better condition in terms of energy stores because of better feeding opportunities in the open ocean (Davis et al. 1998; Rand 2002) or perhaps an easier migration journey from the open ocean. Also, fish arriving later are further on in maturation process, as evidenced by elevated hormone levels, and thus, more energy may have been mobilized and allocated to increased gonadal development (Kiessling et al. 2004). At present, however, it is unknown if the reproductive clock is driving the catabolic state.

Also inconsistent with our predictions was that there were no clear relationships between osmoregulatory or ionoregulatory variables and estuarine arrival times. Interestingly, sockeye salmon sampled in Johnstone Strait had lower Na^+/K^+-ATPase and ion concentrations relative to sockeye salmon sampled a few weeks earlier in the season near the Queen Charlotte Islands (located ca. 385 km north of Johnstone

Table 4

Comparison of biological variables between late-run sockeye salmon that delayed in the Strait of Georgia for less than 2 days prior to migrating upriver (no delay) and those that delayed for longer than 13 days (delay)

Variables	No delay	*N*	Delay	*N*	Test statistic	*P* value
Gross somatic energy (H-W) (MJ/kg)	7.686 ± 0.29	7	8.55 ± 0.33	3	*t*, −1.74	0.121
Gross somatic energy (Adams) (MJ/kg)	8.86 ± 0.16	15	9.31 ± 0.13	15	*t*, −2.17	0.039
Plasma Na^+ (mmol/l)	186.6 ± 2.1	15	190.5 ± 2.3	16	*t*, −1.22	0.232
Plasma K^+ (mmol/l)	1.29 ± 0.20	15	1.53 ± 0.26	16	*t*, −0.70	0.487
Plasma Cl^- (mmol/l)	146.0 ± 1.4	15	149.0 ± 1.4	14	*t*, −1.54	0.135
Plasma osmolality (mOsmo/kg)	344.6 ± 3.9	15	344.3 ± 4.1	16	*t*, 0.06	0.956
Plasma cortisol (ng/ml)	553.1 ± 94.2	15	415.4 ± 49.2	16	*t*, 1.32	0.197
Plasma lactate (mmol/l)	8.99 ± 0.97	15	8.43 ± 1.0	16	*t*, 0.39	0.699
Plasma glucose (mmol/l)	6.81 ± 0.35	15	7.33 ± 0.23	16	*t*, −1.26	0.217
Na^+/K^+-ATPase (μmol ADP/mg protein/h)	2.59 ± 0.28	15	2.62 ± 0.16	15	z, −0.20	0.819
T (male) (pg/ml)	11 819 ± 939	7	10 229 ± 1308	4	*t*, 1.00	0.342
T (female) (pg/ml)	13 545 ± 1767	8	10 866 ± 437	12	*t*, 1.76	0.095
11-KT (male) (pg/ml)	5944.3 ± 632.2	7	4785.5 ± 562.6	4	*t*, 1.22	0.253
11-KT (female) (pg/ml)	987.9 ± 114.5	8	752.3 ± 23.9	12	*t*, 2.44	0.026
17β-E_2 (male) (pg/ml)	483.0 ± 119.4	7	395.1 ± 41.3	4	*t*, 0.54	0.605
17β-E_2 (female) (pg/ml)	5672 ± 862	8	3774 ± 203	12	*t*, 2.57	0.019

The delay period was determined by subtracting the minimum travel time of 6 days from the total elapsed time in days between release in Johnstone Strait and first detection at Mission. Analyses were conducted using *t*-tests when data were normal and met the homogeneity of variance assumption. Gross somatic energy is analyzed separately for different stock groupings and reproductive hormones analyzed separately for the 2 sexes. All other analyses represent all late-run sockeye salmon that passed Mission. H-W, Harrison-Weaver.

Strait) where they would have recently ended their ocean migration and started coastal migration toward the Fraser River (Hinch et al. 2005). These physiological changes may be reflective of fish encountering lower salinity surface waters in Johnstone Strait. In fact, the Na^+/K^+-ATPase and ion concentrations in Johnstone Strait were comparable to those from sockeye salmon captured in the lower Fraser River (Shrimpton et al. 2005). Therefore, physiological changes preparing fish for freshwater entry were likely initiated well before arrival in Johnstone Strait.

Delay in the Strait of Georgia before river entry

Fraser River late-run sockeye salmon typically delay in the estuary prior to entering the river for periods of 30+ days. Although this behavior is unusual among Pacific salmonids in general, it is an important element of late-run sockeye salmon life history (Burgner 1991). Interestingly, we observed very few differences among fish that delayed (i.e., ≥9 days holding in the Strait) or those that did not. Sockeye salmon that delayed for extreme periods (i.e., >13 days) tended to have higher energy than those that did not delay at all, although this was only statistically significant for Adams fish. This result is not surprising as we would expect energy to be more limiting for Adams fish due to greater in-river migration difficulty relative to the Weaver/Harrison sockeye salmon, which face a much shorter and less challenging river migration (Crossin et al. 2004). Thus, energetics do play a role in determining the timing of migration, though it was not strong and widespread among stocks as we had anticipated, and a characteristic of fish that are capable of delaying in the ocean for the lengthiest periods is a high energy level. This pattern is consistent with the prediction that earlier timed migrants, particularly those which will undertake long and arduous freshwater migrations, are facing an energetic limitation that requires them to reach spawning grounds more rapidly.

A broader finding from the multistock telemetry study of which ours was a component of (i.e., English et al. 2004) was that fish that had not delayed in the ocean had delayed instead in lakes near terminal spawning areas before entering spawning grounds. While in these lakes, fish accumulated enough thermal units (i.e., degree days; Wagner et al. 2005) to enable a thermally sensitive kidney parasite (*Parvicapsula minibicornis*; Raverty et al. 2000), contracted in the river (St-Hilaire et al. 2002; Jones et al. 2003), to accelerate development and lead to high mortality among early timed migrants. Thus, the reduced energy in early migrants may represent a trigger for upriver migration but does not necessarily reflect a reproductive state advanced further on in the

Table 5

Relationship between date of river entry (as assessed by first detection at Mission, BC) and biological variables

	River entry timing		
Variable	Sample size	Correlation coefficient	*P* value
Gross somatic energy (H-W)	27	*r*, −0.119	0.555
Gross somatic energy (Adams)	66	*r*, −0.022	0.860
Plasma Na^+	74	r_s, 0.037	0.754
Plasma K^+	74	*r*, 0.092	0.434
Plasma Cl^-	71	*r*, 0.125	0.299
Plasma osmolality	75	*r*, −0.111	0.342
Plasma cortisol	75	r_s, −0.186	0.109
Plasma lactate	75	r_s, −0.194	0.095
Plasma glucose	75	*r*, −0.185	0.112
Na^+/K^+-ATPase	74	r_s, −0.008	0.947
T (male)	30	*r*, −0.053	0.779
T (female)	45	*r*, −0.070	0.647
11-KT (male)	30	*r*, 0.087	0.646
11-KT (female)	45	*r*, −0.239	0.113
17β-E_2 (male)	30	*r*, −0.239	0.203
17β-E_2 (female)	45	*r*, −0.048	0.755

Type of correlation coefficients are indicated prior to the actual value (*r*, Pearson coefficient; r_s, Spearman coefficient). Gross somatic energy is analyzed separately for different stock groupings and reproductive hormones analyzed separately for the 2 sexes. All other analyses represent all late-run sockeye salmon that passed Mission. H-W, Harrison-Weaver.

Table 6

Comparison of biological variables between late-run sockeye salmon that entered the Fraser River before August 29 (early extreme timing) and those that entered after September 13 (later normal timing)

Variables	Early	*N*	Normal	*N*	Test statistic	*P* value
Gross somatic energy (H-W) (MJ/kg)	8.40 ± 0.58	5	8.06 ± 0.27	9	*t*, 0.60	0.557
Gross somatic energy (Adams) (MJ/kg)	9.31 ± 0.16	18	9.14 ± 0.10	22	*t*, 0.94	0.354
Plasma Na^+ (mmol/l)	186.3 ± 1.6	25	188.0 ± 1.9	24	*t*, −0.69	0.494
Plasma K^+ (mmol l^{-1})	1.51 ± 0.16	25	1.82 ± 0.27	24	*t*, −0.99	0.329
Plasma Cl^- (mmol l^{-1})	147.3 ± 1.2	25	148.9 ± 1.0	22	*t*, −1.08	0.286
Plasma osmolality (mOsmo/kg)	348.2 ± 3.8	26	344.2 ± 3.0	24	*t*, 0.81	0.420
Plasma cortisol (ng/ml)	553.1 ± 94.2	15	415.4 ± 49.2	16	*t*, 1.75	0.086
Plasma lactate (mmol/l)	9.39 ± 0.59	26	8.75 ± 0.79	24	*t*, 0.66	0.515
Plasma glucose (mmol/l)	7.44 ± 0.22	26	7.07 ± 0.21	24	*t*, 1.19	0.238
Na^+/K^+-ATPase (μmol ADP/mg protein/h)	2.86 ± 0.22	26	2.74 ± 0.16	23	*t*, 0.45	0.653
T (male) (pg/ml)	10 429 ± 655	13	10 421 ± 682	8	*t*, 0.01	0.994
T (female) (pg/ml)	12 174 ± 947	13	11 674 ± 640	16	*t*, 0.45	0.656
11-KT (male) (pg/ml)	4947.9 ± 358.8	13	4997.5 ± 339.5	8	*t*, −0.09	0.927
11-KT (female) (pg/ml)	980.9 ± 81.9	13	827.4 ± 49.9	16	*t*, 1.66	0.107
17β-E_2 (male) (pg/ml)	405.7 ± 73.5	13	333.1 ± 43.4	8	*t*, 0.72	0.478
17β-E_2 (female) (pg/ml)	4494.7 ± 505.4	13	4299.1 ± 412.8	16	*t*, 0.30	0.764

The peak of migration was September 7 for reference. Analyses were conducted using *t*-tests because data were normal and met the homogeneity of variance assumption. Gross somatic energy is analyzed separately for different stock groupings and reproductive hormones analyzed separately for the 2 sexes. All other analyses represent all late-run sockeye salmon that passed Mission. H-W, Harrison-Weaver.

maturation process, as these fish still delay in freshwater lakes. Even so, female sockeye salmon that did not delay had higher reproductive hormone levels than those that delayed for longer periods. Thus, although reproductive maturation rates (i.e., as reflected in gonadal somatic index) appear to be fixed (Patterson et al. 2004), reproductive hormonal patterns may not. It is possible that earlier hormonal alterations may trigger upriver migration and could impose increased costs that may account for differences in energy between fish that delay and those that do not. At present, however, these ideas are largely hypothetical and require testing.

Fish that entered the river without delay had highly variable Na^+/K^+-ATPase values versus those that delayed entry. One of our predictions was based on the notion that fish entering the river earlier would need to be in an advanced state of osmoregulatory preparedness. The increased variability suggests that some individuals that did not delay (ones with very low gill enzyme levels) are clearly ready for freshwater entry well before reaching the river mouth. It is possible that these individuals may function as "lead" fish that initiate migrations into the river and are followed by other individuals that are less prepared for osmoregulation in freshwater. We have observed this sort of leader–follower behavior during in-river fish migrations (Hinch SG, personal observation). Salinity levels are spatially highly variable in the Johnstone Strait/Strait of Georgia area, and fish would be expected to exhibit different levels of Na^+/K^+-ATPase based on exposure to freshwater or lower salinity regions and subsequent downregulation of this enzyme. However, it has been suggested that in the past decade some parts of this coastal area have had a higher than normal freshwater retention (Thomson R, Institute for Ocean Sciences, unpublished data), which may contribute to the high variability we found. Recent work on brown trout (i.e., Nielsen et al. 2004) suggests that Na^+/K^+-ATPase activity can be used to predict downstream migratory behavior thus supporting our hypothesis that osmoregulatory preparedness is involved with initiation of migration. Interestingly, Nielsen et al. (2004) were only able to detect these changes in fish 2 weeks prior to migration and not 2 months before migration. The timing of sampling Na^+/K^+-ATPase is therefore important in being able to predict migratory behavior (Shrimpton et al. 2005).

Timing of river entry

River entry timing is a key component of upriver spawning migrations. Within a given population, there is typically remarkable consistency among years with regard to river entry (Killick 1955). Late-run sockeye salmon in the Fraser River have been entering the river earlier than normal (Cooke, Hinch, Farrell, et al. 2004). Interestingly, results from this study suggest that none of the variables that we examined varied with respect to timing of river entry or when fish were categorized into "early" or "normal" timed migrants. Similarly, analyses of extremes in terms of entry timing (i.e., earliest early's and latest normals) yielded no obvious trends. We had predicted that early-entry fish would have lower energy and be in advanced stages of osmoregulatory and reproductive preparedness. These findings are contrary to our predictions that there would be clear patterns of preparedness evident across this range of entry dates. One possible explanation for the apparent absence of correlation between early entry timing and fish condition/physiology may have to deal with the fact that we did not biosample or tag the very earliest migrants that passed Mission beginning on August 1 (based on DNA sampling from test fisheries). Another important consideration is that entry timing alone does not account for whether late-run sockeye salmon exhibited the characteristic delay behavior. Indeed, during later periods of migration, individuals passing Mission may have delayed for 24+ days or may not have delayed at all. Based on the above findings, there appears to be no predictive capability for determining the actual timing of river entry.

Contribution to understanding migration initiation

Our results enhance our understanding of the relationship between fish condition/physiology and migration behavior, particularly with respect to arrival in the estuary and delay behavior. In addition to providing basic information on migration biology, we were also able to provide insight into more applied issues such as the premature migration phenomenon of late-run sockeye salmon (e.g., Cooke, Hinch, Farrell, et al. 2004). Our study did not reveal a single physiological or energetic variable, or combination thereof, that explained the

majority of variation in migration behavior. This study did help with the refinement of hypotheses regarding both triggers to migration and premature migration. We now know that energetic status and reproductive hormones may be used to differentiate between fish that will delay and those that will not, potentially providing some predictive capability to fisheries managers and thus reducing uncertainty. Earlier analyses evaluated the physiological and energetic correlates of fate including premature mortality enroute to the spawning grounds and successful spawning (Cooke et al. 2006). When coupled with this behavioral assessment, it may be possible to develop a generalized model to explain the phenomenon that can then be tested using manipulative experiments (e.g., implanting fish with hormone pellets, artificially exhausting energy resources). Beyond sockeye salmon, and Pacific salmon, these findings provide important advances for migration biology in general. Energy is an important variable in the migration of many organisms in terms of providing constraints. Our findings suggest that energetic status may explain individual variation in behavior, including elements associated with timing of critical migration phases. Similarly, the endocrine system also appears to play a role in timing and may serve as the proximate trigger for migration initiation although until tested in an experimental framework this is speculative. We also must emphasize the important role of a number of environmental and endogenous cues (reviewed in Smith 1985) that were not studied here but that ultimately underlie the more proximate patterns of physiology and behavior on which we focused in this study. The inclusion of multivariate approaches also enabled us to evaluate a number of variables simultaneously, searching for variation between specified groups. This powerful approach has rarely been applied to studies of migration biology, yet due to the clearly complicated interplay among a number of variables it has much to offer.

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