Mechanisms Influencing the Timing and Success of Reproductive Migration in a Capital Breeding Semelparous Fish Species, the Sockeye Salmon

Glenn T. Crossin[1,*]
Scott G. Hinch[1,2]
Steven J. Cooke[3]
Michael S. Cooperman[1]
David A. Patterson[4]
David W. Welch[5]
Kyle C. Hanson[3]
Ivan Olsson[1]
Karl K. English[6]
Anthony P. Farrell[7]

[1]Centre for Applied Conservation Research, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada; [2]Institute for Resources, Environment and Sustainability, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada; [3]Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada; [4]Fisheries and Oceans Canada, Cooperative Resource Management Institute, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada; [5]Kintama Research Corporation, 10–1850 Northfield Road, Nanaimo, British Columbia V9S 3B3, Canada; [6]LGL Environmental, 9768 Second Street, Sidney, British Columbia V8L 3Y8, Canada; [7]Faculty of Land and Food Systems, University of British Columbia, Vancouver, British Columbia V6T 1Z4, Canada

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ABSTRACT

Two populations of homing sockeye salmon (*Oncorhynchus nerka*; Adams and Chilko) were intercepted in the marine approaches around the northern and southern ends of Vancouver Island (British Columbia, Canada) en route to a natal river. More than 500 salmon were nonlethally biopsied for blood plasma, gill filament tips, and gross somatic energy (GSE) and were released with either acoustic or radio transmitters. At the time of capture, GSE, body length, and circulating testosterone ([T]) differed between populations, differences that reflected known life-history variations. Within-population analyses showed that in Adams sockeye salmon, plasma glucose ([glu]), lactate ([lactate]), and ion concentrations were higher in the northern approach than in the southern approach, suggesting that the former was more stressful. GSE, [T], and gill Na^+,K^+-ATPase activities also differed between the two locales, and each varied significantly with Julian date, suggesting seasonality. Despite these relative geographic differences, the timing of river entry and the ability to reach spawning areas were strongly correlated with energetic, reproductive, and osmoregulatory state. Salmon that delayed river entry and reached spawning areas had relatively high GSE and low [T] and gill ATPase. In contrast, salmon that entered the river directly but that ultimately failed to reach spawning areas had lower GSE and higher [T] and gill ATPase, and they also swam at significantly faster rates (failed fish ~20.0 km d^{-1} vs. successful fish ~15.5 km d^{-1}). Physiologically, salmon that did not enter the river at all but that presumably died in the marine environment exhibited high stress (plasma [glu] and [lactate]) and ionoregulatory measures (plasma [Na^+], [Cl^-], osmolality).

Introduction

Animal migrations are characterized by the directed, predictable movement of large numbers of individuals among habitats. From an evolutionary point of view, migrations usually accompany key life-history transitions and present opportunities for individuals to maximize lifetime fitness. Migrations are also strong selective agents in the evolution of life-history variation (Stearns 1992). When migrations are initiated for the purpose of reproduction, the demands of homeostatic metabolism, growth, and gamete production must all be satisfied (Calow 1985), but with limited energy to parse among these varied processes, trade-offs evolve in the form of physiological and behavioral constraint (Reznick 1992; Rose and Bradley 1998; Zera and Harshman 2001).

For capital breeding animals, which fuel migrations exclusively through endogenous energy reserves (i.e., lipid and protein catabolism), the timing of migration has evolved as a key life-history trait (Burgner 1991; Dingle 1996). Generally, these occur within a narrow window of opportunity when environmental conditions at breeding grounds are optimal for reproduction (Alerstam and Lindström 1990; Dingle 1996; Hodgson and Quinn 2002; Prop et al. 2003). For example, on their return from the high seas, some populations of sockeye salmon (*Oncorhynchus nerka*) spawning in the Fraser River of British Co-

* Corresponding author; e-mail: crossin@interchange.ubc.ca.

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lumbia, Canada, will hold in the estuary for 2–6 wk before initiating river migrations to natal spawning areas. This holding tactic is associated with high river migration success (>80%; Cooke et al. 2004) and has presumably evolved to minimize exposure to peak river temperatures in mid- to late summer (Hodgson and Quinn 2002).

Many studies have described the nature and pattern of animal migrations—most notably in birds, insects, and fish (see Dingle 1996; Dingle and Drake 2007)—and the influence of endogenous energy levels and reproductive hormones on migration timing are well known (reviewed by Dingle [1996]). A key factor influencing migration timing is the seasonal photoperiodic release of gonadotropin-releasing hormone and the subsequent production of sex steroid hormones, and a modulating influence is endogenous energy supply (Dingle 1996). Until recently, however, it has been difficult to test the proximate physiological mechanisms of migratory behavior. Recent studies with Pacific salmon have coupled biopsy with positional telemetry to identify links between migration behavior and underlying physiology (Cooke et al. 2005, 2006*a*, 2006*b*; Young et al. 2006; Crossin et al. 2007, 2008). For example, after holding for several weeks in the estuary, those sockeye salmon that successfully entered the Fraser River were characterized by relatively high gross somatic energy (GSE) densities and low concentrations of circulating reproductive hormones at the time of sampling (Cooke et al. 2006*a*, 2006*b*). Conversely, unsuccessful sockeye salmon were those that did not hold in the estuary and began upriver migration 6–8 wk earlier than historic averages (Cooke et al. 2004). These early-migrating fish had lower migration success (<50%), lower somatic energy densities, and higher reproductive hormone concentrations (Cooke et al. 2008). Because migration timing is adaptive, the higher mortality observed as a result of early migration is perhaps predictable and most certainly has negative effects on fitness. Indeed, so radical a departure from adaptive mean dates of migration is not likely to be favored by directional selection (sensu Grant and Grant 1989).

We therefore examined the hypothesis that behavior and survivorship of homing sockeye salmon are influenced by their relative energetic and reproductive states. Using biotelemetry, we assessed migration rates and survivorship at three spatiotemporal scales and examined functional relationships with their physiology at time of capture in the marine environment. First, we examined the baseline physiology of two populations of sockeye salmon (Adams and Chilko) over a 3-wk period of arrival in coastal areas approximately 250 km from the mouth of a natal river (i.e., the Fraser River). Both are large populations that comigrate in coastal areas, but on arrival at the river mouth, Chilko migrate directly in river (i.e., a summer-run population), whereas Adams usually hold for several weeks before entering (i.e., a late-summer-run population). Recently, though, segments of this latter population have forgone estuarine holding (Cooke et al. 2004). As a result, a wide range of entry dates now exists that facilitates intrapopulation tests of the regulators of river entry behavior. Second, using acoustic and radio biotelemetry, we examined the physiologic correlates of river entry timing, marine and freshwater travel rates, and survival as salmon migrated an approximately 200-km stretch of the southern British Columbia coast and nearly 500 km up the Fraser River to spawning grounds. Finally, we contrasted the physiology of salmon that held in the estuary for 3 wk before entering the river and subsequently survived the migration to natal spawning versus those that entered after holding for only 1 wk and subsequently died in river.

Drawing from the fact that energy levels and reproductive hormone levels tend to work in opposition and are fundamentally important to the initiation of animal migrations (Woodhead 1975; Ueda and Yamauchi 1995)—and especially in salmon (Cooke et al. 2006*a*, 2008; Young et al. 2006; Crossin et al. 2007)—we predicted that (1) Adams sockeye salmon entering the river without estuarine holding and then dying en route to spawning areas would have lower energy densities than those that hold and survive. We also predicted that (2) the former group of sockeye salmon would have correspondingly higher circulating reproductive hormone concentrations. Our final prediction was that (3) sockeye salmon entering the river early and dying would have higher gill Na^+,K^+-ATPase activities. Because this enzyme is the principal agent involved in ionoregulatory function, fish moving from the hyperosmotic marine environment to the hypoosmotic river must downregulate its activity in order to survive (Clarke and Hirano 1995; Shrimpton et al. 2005). Some recent studies suggest that its expression proceeds seasonally and in tandem with hypothalamo-pituitary-gonadal (HPG) axis activation (Wingfield and Sapolsky 2003).

Material and Methods

Capture, Physiological Sampling, and Radio and Acoustic Tagging

In the summer of 2006, a purse-seining vessel was chartered to intercept homing Fraser River sockeye salmon in two marine areas adjacent to Vancouver Island, British Columbia: at the western end of Juan de Fuca Strait (JDFS) and in the southern end of Johnstone Strait (JS; Fig. 1). Fraser River sockeye salmon return from the open ocean predominantly through JDFS, although in recent years most fish have migrated via the northern passage through JS (J. Cave, Pacific Salmon Commission, Vancouver, personal communication). In a given year and for a given population, the proportion migrating through JS and JDFS can change. Sampling began in JDFS on August 6–10, 2006, when the earliest segment of Adams sockeye salmon and comigrating Chilko sockeye salmon were detected by in-season test fisheries administered by the Pacific Salmon Commission. Test fisheries then indicated that the majority of salmon began favoring the northern passage through JS shortly after that, so capture operations were shifted to JS on August 11–12, 2006. Sampling continued in that location from August 16 to 19 and from August 24 to 27, 2006 (see Robichaud and English 2007 for more details).

In each sampling area, the seine vessel served as the platform for fish biopsy, transmitter implantation, and fish release. On

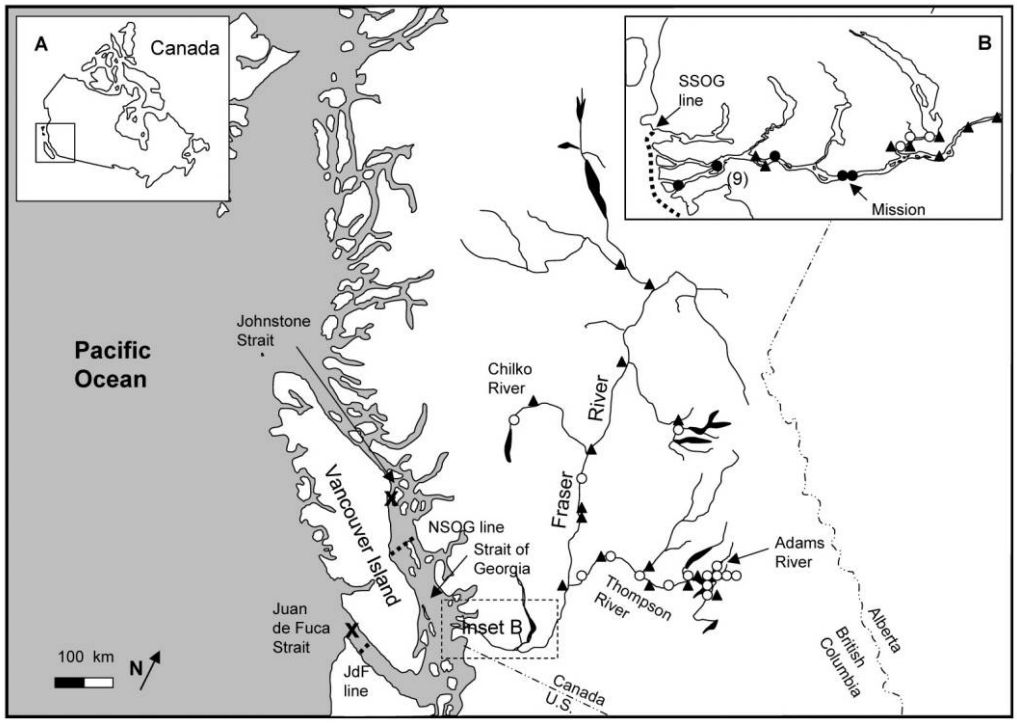

Figure 1. Map of coastal British Columbia and the Fraser River watershed indicating the locations of our capture and sampling efforts on sockeye salmon (*Oncorhynchus nerka*) and the location of acoustic (*circles*) and radio (*triangles*) receivers. Acoustic telemetry arrays positioned in Johnstone Strait and Juan de Fuca (*JdF*) Strait and at the Fraser River mouth are indicated with dotted lines. Insets include a map of Canada highlighting the study location and a blowup of the mouth and lower reaches of the Fraser River. NSOG = northern Strait of Georgia, SSOG = southern Strait of Georgia.

completion of each seine set, the purse seine was brought along the starboard rail of the vessel, and while still in the water, individual salmon were dip netted and transferred to a large flow-through holding tank on the boat's deck. Ten to 20 sockeye salmon were taken from each seine set, and once on board, salmon were individually processed and released as quickly as possible. After biopsy and transmitter insertion, sockeye salmon were held in recovery tanks for a maximum of 15 min (mean 2 min) until they regained equilibrium and then were returned over the side of the boat. Most fish were on board for less than 20 min. In the collection of physiological samples, we used protocols for the nonlethal unanesthetized sampling of sockeye salmon (see Cooke et al. 2005; English et al. 2005), approved by the University of British Columbia Animal Care Committee in accordance with the Canadian Council of Animal Care. An extensive comparison between biopsied and nonbiopsied salmon showed that our sampling protocols exerted no deleterious effects on behavior or survivorship (Cooke et al. 2005).

Details of our handling, biopsy, and tagging procedures can be found in Cooke et al. (2005). Briefly, biopsy protocols were as follows. Salmon were removed from the holding tank and placed in a V-shaped trough provided with continuous fresh seawater. We then measured and collected fork length (FL), an adipose fin clip for DNA, a 1.5-mL blood sample for assessing plasma biochemistry, a 1-cm-deep-by-3-mm muscle biopsy for gene array analyses (not discussed in this article), and a <4-mm clip of gill filament tips (~0.03 g; McCormick 1993) for assessment of gill Na^+,K^+-ATPase activity. Tissues were packaged in cryovials and stored on dry ice until transfer to a −80°C freezer. GSE (MJ kg^{-1}) was determined with a handheld microwave energy meter (Distell Fish FatMeter FM 692; Crossin and Hinch 2005). Either a radio or an acoustic transmitter was then inserted into the fish intragastrically (see Cooke et al. 2004, 2006*a* for details on transmitters). To assess the effects of capture and handling on fish survival, relationships between capture to release time (i.e., total handling time), stress measures, and survival to Mission, British Columbia, were examined with ANOVA and regression models. These analyses focused on Adams sockeye salmon because they had sufficient numbers to provide strong statistical power.

Radio and Acoustic Receiver Arrays

For salmon bearing acoustic tags, the first possible detection of JS-released fish was ~70 km, at the northern Strait of Georgia (NSOG) acoustic receiver line, and for JDFS-released fish, it was ~50 km, at the JDFS line (Fig. 1). Salmon from both release sites were next detected at the southern Strait of Georgia

(SSOG) line, extending in an arc around the river mouth. River entry was assessed as a positive detection ~85 km upriver at Mission at the tidal boundary. Acoustic receivers were then placed at intervals throughout the Fraser River watershed, but the greatest concentration was along the migration path of the Adams River sockeye salmon, which was the dominant run of 2006. Detailed information on the position of acoustic receivers in 2006 is provided by Kintama Research (2007). Acoustic receiver lines and stations were evaluated for their performance in both marine water and freshwater, and detection efficiency was ~100% (Kintama Research 2007).

For salmon bearing radio tags, first detection was at Mission, ~300 km from both the JS and the JDFS release sites (Fig. 1). Several additional receivers were positioned throughout the watershed, and details are provided by Robichaud and English (2007).

Laboratory Assays

We determined population identity for individual sockeye salmon using DNA analyses (Beacham et al. 1995, 2004) that were confirmed in fish successfully reaching spawning areas via telemetry data. DNA assignments in Fraser River sockeye salmon have a 96% accuracy (Beacham et al. 1995, 2004). Plasma testosterone ([T]) and 17β-estradiol ([E_2]) levels were measured by radioimmunoassay (McMaster et al. 1992) and used to assign fish sex because sexual dimorphism was not yet fully expressed at that point of migration. Plasma glucose ([glu]), lactate ([lactate]), osmolality, cortisol ([cortisol]), and ions ([Na^+], [Cl^-]) were quantified by procedures described by Farrell et al. (2001*a*). Gill Na^+,K^+-ATPase activity was determined by kinetic assay (McCormick 1993).

Statistical Analyses

All physiological data were $\log_{10}$ transformed to reduce heteroscedasticity. Individuals from 16 Fraser River sockeye salmon populations were biopsied and telemetered, but we limited our analyses and discussion to the Chilko and Adams populations because these were the only two with sufficient numbers of individuals to permit rigorous statistical analyses. We analyzed fish from JS and JDFS separately because previous studies have shown that salmon sampled in these areas differ physiologically (Miller et al. 2007). Thus, within each capture location, we used MANOVA to explore physiological differences between the sexes at time of capture. Variables examined were plasma [Na^+], [Cl^-], [lactate], [glu], osmolality, and gill Na^+,K^+-ATPase activity. Sex-specific variables—GSE, FL, [T], and [E_2] (females only)—were excluded from this analysis. We next examined multivariate differences by population by incorporating into the MANOVA model plasma [Na^+], [Cl^-], [lactate], [glu], osmolality, and gill Na^+,K^+-ATPase activity. Population differences in GSE, FL, [T], and [E_2] were run for each sex separately (MANOVA).

To identify the relative importance of individual variables underlying significant MANOVA models, we conducted a series of ANCOVAs. Within each capture locale, population was the main effect, and because sampling occurred over a period of approximately 3 wk—during which time fish were running against a biological clock—Julian date of capture was used as a covariate to generate time-corrected least square means. When analyzing the sex-specific variables, population differences were estimated in each capture locale for each sex separately. Interactions between population and Julian day were examined in all models. When interaction terms were nonsignificant, they were removed, and the model was rerun.

To describe population- and sex-specific differences in travel times from each release location (JS and JDFS) to the various receiver locales, ANCOVA was used to generate length-corrected least square means (i.e., FL as the model covariate). Correlation analyses were run to assess population- and sex-specific relationships between travel times and physiological variables. If significant correlations were found, we used linear regression to describe the relationship between the physiological factor (the dependent variable) and the travel time of individuals (the independent variable).

Key to our analysis of migration timing was the calculation of estuarine holding time before river entry. We defined this as the time lapse between release in JS/JDFS to first detection at Mission, ~85 km up the Fraser River (Fig. 1). We chose Mission as the definitive point of river entry because it represents the tidal boundary and because it is the first location on the migratory route where both acoustic- and radio-tagged fish could be jointly detected (radio-tag transmissions attenuate in saltwater). To differentiate between holding and nonholding tactics, we divided holding times into the twenty-fifth and seventy-fifth percentiles in order to contrast extreme differences. The twenty-fifth percentile represented salmon that entered the Fraser River in <10 d and classified as nonholding. The seventy-fifth percentile represented salmon that entered >20 d and classified as holding. We focused our analysis on Adams sockeye salmon released in JS simply because (*a*) the number of fish in the twenty-fifth and seventy-fifth percentiles were sufficient for analysis; (*b*) it allowed us to compare results with those of Cooke et al. (2008), who used a similar approach; and (*c*) there were too few fish released in JDFS to enable this analysis. The physiology underlying the different behavior/fate differences was compared with ANCOVA, and Julian date was used as a covariate.

All analyses were conduced using JMP 4.0 (SAS Institute, Cary, NC). Because of multiple comparisons, we conducted Bonferroni corrections to minimize the potential for Type II errors. We designated statistical significance at $\alpha = 0.05$ and made Bonferroni corrections to minimize the possibility of false positives. Because of the high conservatism of Bonferroni corrections (Cabin and Mitchell 2000), we also indicate significance at $\alpha = 0.05$ and $\alpha = 0.01$, thus allowing readers to define for themselves the levels that are most biologically meaningful (Cabin and Mitchell 2000).

Results

Tagging Summary, Baseline Physiology of Salmon Intercepted in the Marine Environment, and Handling Effects

In total, 797 sockeye salmon from 16 Fraser River populations were captured, biopsied, and tagged (see Hinch et al. 2009 for complete tagging summary). For this study, 409 Adams and 96 Chilko sockeye salmon were analyzed to provide contrasts between the most abundant late-summer-run and summer-run timing populations. Table 1 summarizes information about the number of salmon captured in each marine sampling location, the number and types of transmitters deployed, and an abridged detection summary of receivers positioned throughout the study area (Fig. 1). A detailed summary of all fish captured in 2006 is presented by Hinch et al. (2009).

Multivariate analysis of the physiological variables (i.e., GSE, plasma $[Na^+]$, $[Cl^-]$, [glu], [lactate], [cortisol], osmolality, and gill Na^+,K^+-ATPase activity) revealed a significant difference between males and females at each marine location (MANOVA: JS, $P < 0.001$, $N = 400$; JDFS, $P < 0.005$, $N = 105$). Models examining sex differences with Julian day of capture as a covariate indicated that the variables driving the significant MANOVA were GSE (ANCOVA: JS, $P < 0.001$, $N = 389$; JDFS, $P < 0.026$, $N = 103$) and plasma [glu] (ANCOVA: JS, $P < 0.001$, $N = 390$; JDFS, $P < 0.001$, $N = 105$). We thus removed GSE and glucose from the model and reclassified them as sex-specific variables. When the MANOVA was rerun, no differences between sexes were found in plasma $[Na^+]$, $[Cl^-]$, [lactate], [cortisol], osmolality, and gill Na^+,K^+-ATPase activities (JS, $P = 0.588$, $N = 400$; JDFS, $P = 0.312$, $N = 105$). Males and females were thus pooled for these variables when univariate analyses were run.

MANOVA models examining population differences in physiology (i.e., $[Na^+]$, $[Cl^-]$, [lactate], osmolality, gill Na^+,K^+-ATPase) at capture were significant in JS ($P < 0.003$, $N = 400$) but not in JDFS ($P = 0.079$, $N = 105$). ANCOVA using Julian day of capture as a covariate revealed that the population differences driving the significant MANOVA model in JS were [lactate] ($P < 0.002$) and $[Cl^-]$ ($P = 0.013$; see Table 2). When the sex-specific variables were analyzed, the MANOVA model was significant for both males and females (JS, both $P < 0.001$, male $N = 195$, female $N = 202$; JDFS, both $P < 0.001$, male $N = 48$, female $N = 58$). ANCOVA showed that the population-level variables that were significantly different were male FL ($P < 0.001$) and female [T] ($P = 0.022$; Table 2).

Handling effects that lead to fish mortality are expected to occur within 2 d after release (English et al. 2005). Analyses of handling effects are presented by Hinch et al. (2009), but to summarize, no relationships with survival were found with set duration and abundance or the time on board the vessel. Of those acoustic-tagged Adams sockeye salmon released in JS, 23% were undetected on the NSOG line approximately 2 d swim from JS, but all Chilko sockeye salmon were detected. Similarly, all Adams and Chilko sockeye salmon released in JDFS were detected on the JDFS line 1–2 d away from the release site. After accounting for variation in handling time before biopsy (i.e., capture and prebiopsy holding times), there were no significant differences between plasma cortisol con-

Table 1: Numbers of acoustic- and radio-tagged sockeye salmon (*Oncorhynchus nerka*) released in Johnstone Strait (JS) and Juan de Fuca Strait (JDFS) and the numbers that were subsequently detected on the first marine acoustic line after the point of release

Release Area, Population Type, and Transmitter Type	Total Released	Detected on First Line	Detected on First and SSOG Lines	Detected in Fraser River (Mission, BC)	Detected at Spawning Areas[a]
JS:					
Adams:					
Acoustic	68	52	45	36 (52%)	21 (31%)
Radio	275	NA	NA	122 (44%)	98 (36%)
Chilko:					
Acoustic	7	7	7	6 (75%)	NA
Radio	41	NA	NA	15 (37%)	NA
JDFS:					
Adams:					
Acoustic	11	11	7	4 (36%)	2 (18%)
Radio	55	NA	NA	25 (46%)	13 (24%)
Chilko:					
Acoustic	5	5	2	1 (20%)	NA
Radio	43	NA	NA	18 (42%)	NA

Note. First marine acoustic lines were the Northern Strait of Georgia acoustic receiver line for JS-released fish, and the Juan de Fuca line for those released in JDFS. Also listed are the numbers of fish detected at the Fraser River mouth on the Southern Strait of Georgia (SSOG) acoustic line and those detected in river at Mission, British Columbia (see Fig. 1). NA indicates the inability to detect radio tags in saltwater.

[a] Detection of Chilko sockeye salmon at terminal areas could not be assessed with confidence because the position of terminal receivers was upstream of where some sockeye salmon are know to spawn. Thus, fish may have been successful in reaching spawning areas but may not have been detected.

Table 2: Comparison of the biological attributes of two populations of sockeye salmon (*Oncorhynchus nerka*) intercepted and sampled in Johnstone Strait (JS) and Juan de Fuca Strait (JDFS)

Variable and Population by Sex	JS (*N*)	JDFS (*N*)	Marine Area *P*	Julian Day (Covariate) *P*
Gross somatic energy (MJ kg^{-1}):				
Adams ♀	8.8 ± .03 (182)	8.7 ± .10 (35)	.632	**.001**
Adams ♂	8.6 ± .05 (160)	8.6 ± .16 (27)	.465	**<.001**
Chilko ♀	9.1 ± .16 (25)	9.1 ± .15 (31)	.933	.045*
Chilko ♂	8.8 ± .17 (24)	8.7 ± .20 (19)	.619	.118
Nose to fork length (cm):				
Adams ♀	58.6 ± .19 (182)	58.7 ± .59 (35)	.894	.627
Adams ♂	60.6 ± .21 (160)	61.4 ± .63 (27)	.299	.506
Chilko ♀	57.6 ± .68 (25)	58.2 ± .66 (31)	.644	.911
Chilko ♂	58.9 ± .88 (24)	60.4 ± 1.05 (19)	.386	.996
Plasma [glu] (mmol L^{-1}):				
Adams ♀	6.5 ± .08 (182)	4.9 ± .25 (35)	**<.001**	**<.001**
Adams ♂	7.2 ± .08 (160)	5.6 ± .24 (27)	**<.001**	**<.001**
Chilko ♀	7.1 ± .31 (25)	5.2 ± .30 (31)	**.002**	**.004**
Chilko ♂	7.6 ± .23 (24)	5.8 ± .28 (19)	**<.001**	.065
Plasma [lact] (mmol L^{-1}):				
Adams pooled	10.4 ± .23 (342)	7.1 ± .68 (62)	**<.001**	.089
Chilko pooled	9.4 ± .71 (49)	8.2 ± .75 (50)	.251	.425
Plasma [Na^+] (mmol L^{-1}):				
Adams pooled	179.5 ± .64 (342)	172.9 ± 1.86 (62)	**<.001**	**<.001**
Chilko pooled	178.2 ± 1.97 (49)	175.5 ± 2.10 (50)	.424	.703
Plasma [Cl^-] (mmol L^{-1}):				
Adams pooled	153.5 ± .29 (342)	151.2 ± .83 (62)	.012*	.295
Chilko pooled	151.4 ± .94 (49)	150.0 ± 1.00 (50)	.406	.558
Plasma osmolality (mOsm kg^{-1}):				
Adams pooled	373.3 ± .98 (342)	370.5 ± 2.83 (62)	.412	.425
Chilko pooled	370.7 ± 2.98 (49)	370.7 ± 3.17 (50)	.999	.993
Gill Na^+,K^+-ATPase (μmol ADP mg^{-1} protein h^{-1}):				
Adams pooled	3.4 ± .10 (342)	3.7 ± .29 (62)	.861	**<.001**
Chilko pooled	4.1 ± .40 (49)	4.1 ± .42 (50)	.905	.045*
Plasma [cortisol] (ng mL^{-1}):				
Adams pooled	400.7 ± 7.8 (342)	430.0 ± 25.2 (62)	.297	.059
Chilko pooled	414.9 ± 18.6 (49)	432.8 ± 22.5 (50)	.608	.996
Plasma [T] (ng mL^{-1}):				
Adams ♀	38.5 ± 1.99 (182)	40.8 ± 6.21 (35)	.683	**<.001**
Adams ♂	25.8 ± 1.42 (160)	26.4 ± 4.32 (27)	.151	**<.001**
Chilko ♀	31.3 ± 6.53 (25)	42.2 ± 6.34 (31)	.828	**.004**
Chilko ♂	17.3 ± 3.97 (24)	25.3 ± 4.71 (19)	.416	.006**
Plasma [E_2] (ng mL^{-1}):				
Adams ♀	7.9 ± .49 (182)	13.6 ± 1.44 (35)	**<.001**	**<.001**
Chilko ♀	4.5 ± 1.74 (25)	11.6 ± 1.60 (31)	.074	.009**

Note. Sockeye salmon known to be captured in fisheries were removed from the analysis. When necessary, means were adjusted to account for covariation with Julian day of sampling (ANCOVA). All variables were $\log_{10}$ transformed before analysis. Boldface indicates significance at Bonferroni-corrected α values: 0.005 for females, 0.006 for males.

* $\alpha < 0.05$.

** $\alpha < 0.01$.

centrations between JS-released Adams sockeye salmon that successfully entered the river and those that did not (survivor [cortisol] = 404.8 ± 9.7 ng mL^{-1}, mortality [cortisol] = 407.7 ± 8.9 ng mL^{-1}; ANCOVA, fate $P = 0.825$, prebiopsy time $P < 0.001$, $N = 366$). However, there was a significant difference in [lactate] between groups (survivor [lactate] = 9.17 ± 0.28 mmol L^{-1}, mortality [lactate] = 10.50 ± 0.25 mmol L^{-1}; ANCOVA, fate $P < 0.001$, prebiopsy time $P < 0.001$, $N = 417$; Fig. 2).

Physiological Correlates of Survival to River Entry

In salmon released in JS, comparisons between Adams sockeye salmon that failed to reach Mission and those that succeeded showed significant differences between plasma [glu] (males only, $P = 0.032$), [lactate] ($P = 0.009$), [Na^+] ($P = 0.022$), [Cl^-] ($P < 0.001$), and osmolality ($P = 0.003$; Table 3). No physiological differences were found between JS-released Chilko sockeye salmon (Table 3). In JDFS-released sockeye salmon, the only significant difference between failed and successful fish was in the FL of male Adams sockeye salmon: failed fish were significantly smaller than successful fish ($P = 0.021$).

Marine Migration Rates

Rates of migration through the marine environment could be assessed only in fish bearing acoustic transmitters. Within-population, length-adjusted travel times by males and females to each marine location did not differ (ANCOVA, all $P > 0.05$), so the sexes were pooled. From JS, Adams sockeye salmon took 2.6 ± 0.1 d (~24.2 km d^{-1}) to reach the NSOG line, approximately 63 km away, while Chilko sockeye salmon took only 1.4 ± 0.4 d (~45.0 km d^{-1}; Fig. 3*A*). These differences were statistically significant (ANCOVA, $P = 0.002$, $N = 53$). For JS to the SSOG line, approximately 183 km from the capture site, Adams sockeye salmon took 5.2 ± 0.2 d (~35.2 km d^{-1}), and Chilko took 3.4 ± 0.4 d (~53.8 km d^{-1}; ANOVA, $P < 0.001$, $N = 53$). Thus, on release in JS, Chilko sockeye salmon swam at nearly twice the rate of Adams sockeye salmon through the Strait of Georgia.

From JDFS, Adams sockeye salmon ($N = 11$) took 3.1 ± 0.4 d (~16.1 km d^{-1}) to reach the JDFS acoustic receiver line approximately 50 km away, while Chilko sockeye salmon ($N = 5$) took 2.6 ± 0.5 d (~19.2 km d^{-1}; Fig. 3*B*). These population-specific rates were not significantly different (ANCOVA, $P = 0.534$, $N = 16$). Travel rates from JDFS to the SSOG receiver line positioned approximately 200 km from the capture site 7.0 ± 0.5 d (~28.6 km d^{-1}) for Adams sockeye salmon ($N = 7$) and 7.3 ± 0.9 d (~27.4 km d^{-1}) for Chilko sockeye salmon ($N = 3$). These rates were not significantly different (ANCOVA, $P = 0.770$, $N = 9$).

Within population and release area, travel times to Mission did not differ between radio-tagged and acoustically tagged fish (Chilko, $P > 0.05$; Adams, $P > 0.05$). However, between populations, rates of travel differed from both areas. From JS, Adams sockeye salmon took 12.9 ± 0.3 d to reach Mission (~21.5 km d^{-1}), and Chilko took 7.0 ± 0.9 d (~39.6 km d^{-1}; ANCOVA, $P < 0.001$, $N = 185$). From JDFS, Adams took 14.9 ± 1.0 d (~19.0 km d^{-1}), and Chilko took 9.5 ± 1.5 d (~29.8 km d^{-1}; $P < 0.005$, $N = 43$). Thus, despite the similar speeds at which Chilko and Adams fish migrated through JDFS to the river mouth, Adams fish entered the river after holding for ~6 d, while Chilko fish entered after a day (travel from SSOG to Mission is ~1 d).

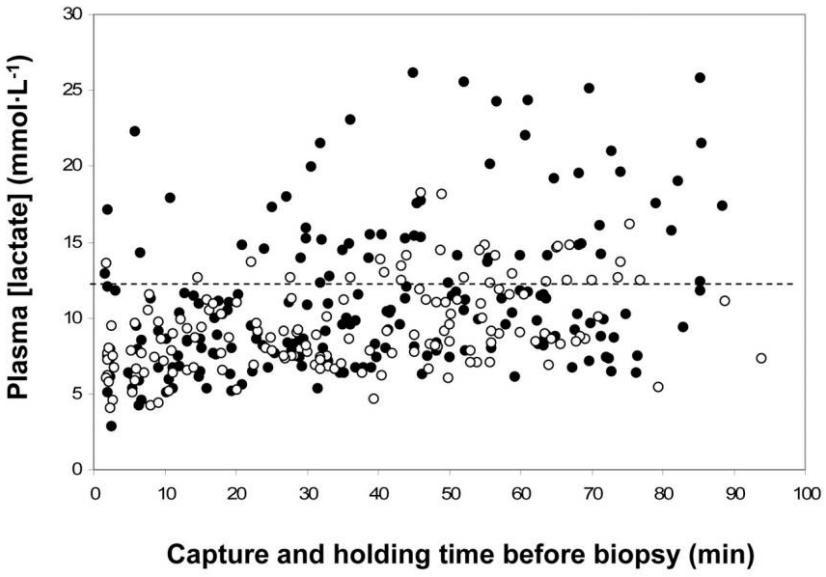

Figure 2. Relationship between plasma [lactate] and cumulative capture and prebiopsy holding times in sockeye salmon captured and released in Johnstone Strait. Filled circles represent sockeye salmon that failed to enter the Fraser River; open circles represent those that did so successfully. The dashed line indicates the threshold above which salmon have difficulty recovering from anaerobic stress (~12 mmol L^{-1}; Jain and Farrell 2003).

Table 3: Comparison of biological attributes of sockeye salmon (*Oncorhynchus nerka*) that disappeared en route to the Fraser River while homing from Johnstone Strait (JS) and Juan de Fuca Strait (JDFS) with those that survived to enter the river

	Marine Fate			
Variables by Release Area and Population by Sex	Disappeared before Entering River (*N*)	Successfully Entered River (*N*)	Fate (within Population) *P*	Julian Day (Covariate) *P*
JS gross somatic energy (MJ kg^{-1}):				
Adams ♀	8.8 ± .04 (103)	8.8 ± .05 (79)	.697	**.002**
Chilko ♀	8.8 ± .23 (17)	8.9 ± .23 (8)	.883	.083
Adams ♂	8.4 ± .07 (88)	8.5 ± .08 (72)	.342	**<.001**
Chilko ♂	8.6 ± .11 (16)	8.8 ± .15 (8)	.223	**.004**
Nose to fork length (cm):				
Adams ♀	58.3 ± .24 (103)	58.9 ± .27 (79)	.082	.435
Chilko ♀	57.3 ± .40 (17)	58.4 ± .61 (8)	.171	.721
Adams ♂	60.5 ± .26 (88)	61.1 ± .29 (72)	.119	.516
Chilko ♂	58.5 ± .89 (16)	58.9 ± 1.27 (8)	.786	.990
Plasma [glu] (mmol L^{-1}):				
Adams ♀	6.3 ± .10 (103)	6.6 ± .12 (79)	.032*	**<.001**
Chilko ♀	6.2 ± .32 (17)	6.7 ± .48 (8)	.531	.013*
Adams ♂	7.1 ± .10 (88)	7.0 ± .11 (72)	.559	**<.001**
Chilko ♂	7.2 ± .20 (16)	7.1 ± .28 (8)	.684	.014*
Plasma [lact] (mmol L^{-1}):				
Adams	10.8 ± .30 (191)	9.4 ± .33 (151)	.009**	.189
Chilko	9.4 ± .60 (33)	7.4 ± .90 (16)	.089	.505
Plasma [Na^+] (mmol L^{-1}):				
Adams	180.2 ± .81 (191)	177.4 ± .91 (151)	.022*	.164
Chilko	180.2 ± 1.71 (33)	175.7 ± 2.54 (16)	.163	.392
Plasma [Cl^-] (mmol L^{-1}):				
Adams	154.2 ± .34 (191)	152.4 ± .38 (151)	**<.001**	.392
Chilko	152.1 ± .82 (33)	151.0 ± 1.22 (16)	.489	.545
Plasma osmolality (mOsm kg^{-1}):				
Adams	375.4 ± 1.20 (191)	369.9 ± 1.35 (151)	**.003**	.815
Chilko	371.8 ± 2.57 (33)	368.6 ± 3.82 (16)	.498	.615
Gill Na^+,K^+-ATPase (μmol ADP mg^{-1} protein h^{-1}):				
Adams	3.3 ± .11 (191)	3.3 ± .13 (151)	.846	**<.001**
Chilko	3.4 ± .32 (33)	3.7 ± .47 (16)	.583	.035*
Plasma [cortisol] (ng mL^{-1}):				
Adams	415.4 ± 10.4 (37)	394.7 ± 11.2 (29)	.179	.035*
Chilko	419.0 ± 23.5 (35)	409.9 ± 26.4 (12)	.804	.851
Plasma [T] (ng mL^{-1}):				
Adams ♀	43.3 ± 2.67 (103)	42.5 ± 3.06 (79)	.919	**<.001**
Chilko ♀	52.6 ± 7.58 (17)	47.7 ± 11.38 (8)	.805	**.002**
Adams ♂	29.2 ± 1.92 (88)	27.9 ± 2.14 (72)	.679	**<.001**
Chilko ♂	23.7 ± 4.49 (16)	30.4 ± 6.41 (8)	.440	<.009**
Plasma [E_2] (ng mL^{-1}):				
Adams ♀	9.7 ± .63 (103)	8.6 ± .72 (79)	.126	**<.001**
Chilko ♀	9.8 ± 1.57 (17)	8.2 ± 2.36 (8)	.487	.015*
JDFS gross somatic energy (MJ kg^{-1}):				
Adams ♀	9.0 ± .09 (21)	9.0 ± .12 (14)	.918	.303
Chilko ♀	9.4 ± .11 (21)	9.0 ± .20 (6)	.101	.809
Adams ♂	9.0 ± .11 (16)	9.2 ± .12 (15)	.277	.486
Chilko ♂	8.9 ± .26 (13)	8.9 ± .39 (6)	.838	.432

Table 3 (*Continued*)

Variables by Release Area and Population by Sex	Marine Fate: Disappeared before Entering River (*N*)	Marine Fate: Successfully Entered River (*N*)	Fate (within Population) *P*	Julian Day (Covariate) *P*
Nose to fork length (cm):				
Adams ♀	58.5 ± .53 (21)	59.5 ± .70 (14)	.295	.747
Chilko ♀	58.1 ± .67 (21)	58.0 ± 1.23 (6)	.775	.785
Adams ♂	60.2 ± .54 (16)	62.1 ± .60 (15)	.024*	.673
Chilko ♂	59.8 ± 1.13 (13)	61.4 ± 1.69 (6)	.468	.936
Plasma [glu] (mmol L^{-1}):				
Adams ♀	5.6 ± .18 (21)	5.5 ± .23 (14)	.586	.014*
Chilko ♀	5.9 ± .18 (21)	6.0 ± .32 (6)	.724	.552
Adams ♂	6.4 ± .28 (16)	6.5 ± .32 (15)	.872	.248
Chilko ♂	6.3 ± .33 (13)	6.1 ± .50 (6)	.975	.753
Plasma [lactate] (mmol L^{-1}):				
Adams	8.3 ± .57 (37)	7.6 ± .66 (29)	.591	.082
Chilko	8.4 ± .64 (35)	10.4 ± 1.19 (12)	.221	.607
Plasma [Na^+] (mmol L^{-1}):				
Adams	176.7 ± 1.64 (37)	174.8 ± 1.88 (29)	.564	.044*
Chilko	174.1 ± 1.77 (35)	177.7 ± 3.31 (12)	.384	.942
Plasma [Cl^-] (mmol L^{-1}):				
Adams	151.9 ± .98 (37)	151.5 ± 1.12 (29)	.669	.092
Chilko	149.4 ± .85 (35)	150.1 ± 1.60 (12)	.571	.349
Plasma osmolality (mOsm kg^{-1}):				
Adams	373.9 ± 2.70 (37)	369.9 ± 3.10 (29)	.446	.078
Chilko	368.7 ± 2.67 (35)	378.0 ± 5.00 (12)	.236	.356
Gill Na^+,K^+-ATPase (μmol ADP mg^{-1} protein h^{-1}):				
Adams	4.9 ± .37 (37)	4.5 ± .42 (29)	.260	.668
Chilko	4.4 ± .38 (35)	5.8 ± .71 (12)	.097	.432
Plasma [cortisol] (ng mL^{-1}):				
Adams	391.9 ± 20.2 (37)	404.8 ± 22.4 (29)	.672	.484
Chilko	427.0 ± 16.4 (35)	440.6 ± 19.5 (12)	.599	.441
Plasma [T] (ng mL^{-1}):				
Adams ♀	13.2 ± 1.85 (21)	15.1 ± 2.44 (14)	.418	.007**
Chilko ♀	25.3 ± 2.80 (21)	16.5 ± 5.14 (6)	.115	.750
Adams ♂	11.4 ± 2.43 (16)	8.4 ± 2.72 (15)	.996	.280
Chilko ♂	14.7 ± 3.04 (13)	12.6 ± 4.52 (6)	.617	.412
Plasma [E_2] (ng mL^{-1}):				
Adams ♀	6.7 ± 1.12 (21)	6.0 ± 1.37 (14)	.473	.059
Chilko ♀	7.0 ± 1.23 (21)	8.9 ± 2.36 (6)	.876	.441

Note. Sockeye salmon known to be captured in fisheries were removed from the analysis. When necessary, means were adjusted to account for covariation with Julian day of sampling (ANCOVA). All variables were $\log_{10}$ transformed before analysis. Boldface indicates significance at Bonferroni-corrected α values: 0.005 for females, 0.006 for males.

* $\alpha < 0.05$.

** $\alpha < 0.01$.

River Migration Success in Adams Sockeye Salmon as a Function of Estuarine Holding Tactic, Fate, and Physiology

We were able to ascribe a river migration fate for the Adams fish by examining detection data at in-river and terminal-area receiver stations (see Fig. 1). Fish were thus classified into four groups based on estuarine holding tactic and fate: (i) held in estuary and failed to reach spawning areas (hold/fail; $N = 0$), (ii) held in estuary before entering river and successfully reached terminal spawning areas (hold/succeed; $N = 13$), (iii) did not hold in estuary and failed to reach spawning areas (no-hold/fail; $N = 24$), or (iv) did not hold in estuary and successfully reached spawning areas (no-hold/succeed; $N = 13$). The numbers of fish in each classification deviated significantly from the null hypothesis, which predicts equal numbers of fish in each (χ^2, $P < 0.001$).

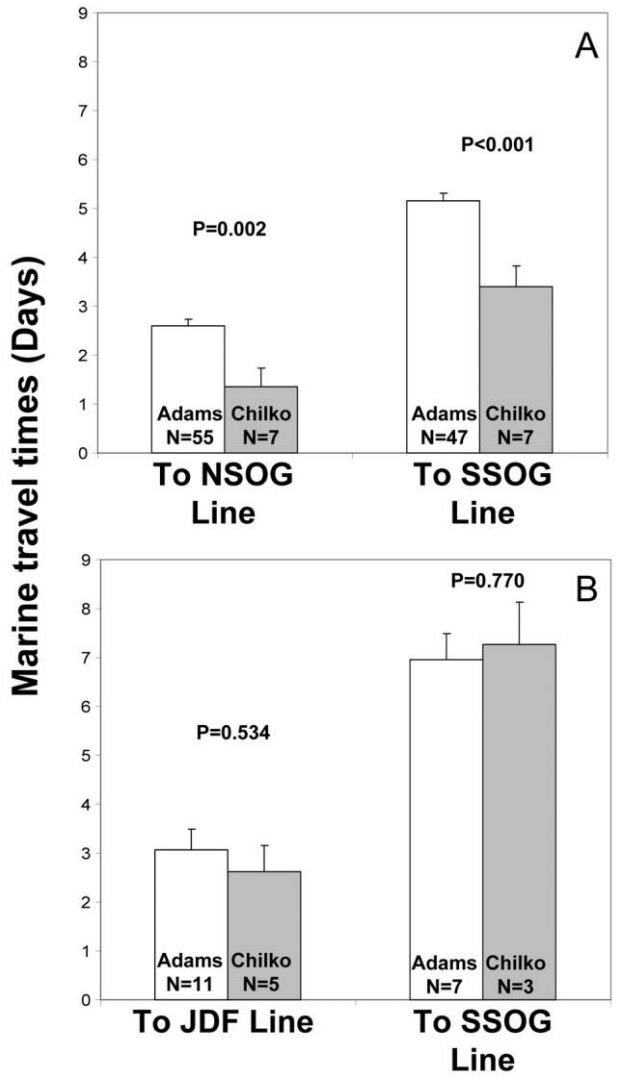

Figure 3. Mean travel times by Adams and Chilko sockeye salmon from Johnstone Strait (JS; *A*) and Juan de Fuca Strait (JDFS; *B*) to acoustic receiver lines positioned in the marine environment en route to the Fraser River. The distances from point of release to each receiver line in *A* are ~64 and 183 km, respectively, and in *B* are ~50 and 200 km, respectively. Fewer sockeye salmon were captured and released in JDFS because capture operations were moved to JS after 1 wk because of higher diversion through JS as the season progressed (see "Material and Methods"). Sexes were pooled. Travel times were corrected to account for variation in body length. Error bars are ±SEM. NSOG = northern Strait of Georgia, SSOG = southern Strait of Georgia.

For each of the four behavior/fate categories, we calculated upriver travel rates between Mission and the Thompson River confluence. Individuals of the hold/succeed group were the slowest swimmers, taking 11.3 ± 0.84 d (~15.5 km d^{-1}) to swim the 172-km stretch of river to the Thompson confluence. The no-hold/fail and no-hold/succeed salmon were significantly faster swimmers, taking 7.8 ± 0.71 and 8.9 ± 0.80 d, respectively (~22.6 and ~19.2 km d^{-1}), to cover the same distance (Fig. 4).

Physiological Correlates of Estuarine Holding Tactic and River Migration Fate

Physiological comparisons were made between the four hold-tactic-fate groups homing from JS (Table 4). River entry behaviors occurred ~5–8 d after biopsies were taken, and fate was assessed upward of 20 d after biopsy. Female sockeye salmon that did not hold and subsequently failed to reach spawning areas had GSE significantly lower (8.4 ± 0.13 MJ kg^{-1}) than that of holding fish that were both successful and unsuccessful (8.9 ± 0.17 and 8.8 ± 0.14 MJ kg^{-1}, respectively; ANCOVA, $P = 0.009$, $N = 22$). Additionally, female sockeye salmon that held and were successful had circulating [T] significantly lower (17.5 ± 11.28 ng mL^{-1}) than that of both nonholding groups (60.3 ± 8.62 and 61.2 ± 9.73 ng mL^{-1}; ANCOVA, $P = 0.010$, $N = 22$). Gill Na^+,K^+-ATPase activities were significantly lower in male and female sockeye salmon that held and were successful (2.2 ± 0.37 μmol ADP mg^{-1} protein h^{-1}) than in the nonholding groups (3.8 ± 0.27 and 3.9 ± 0.35 μmol ADP mg^{-1} protein h^{-1}; Table 4). Thus, female salmon that delayed river entry by holding in the estuary and were successful upriver migrants were less mature, had a higher GSE, and were more prepared for freshwater entry than salmon that did not delay, independent of their river migration fate. Salmon that did not hold and eventually died in river were more reproductively advanced and had lower GSE and [T]. In male salmon, GSE and [T] were not significantly related to river entry tactic and fate, but the trend was similar to that observed in females (Table 4).

Correlations were examined between the time it took indi-

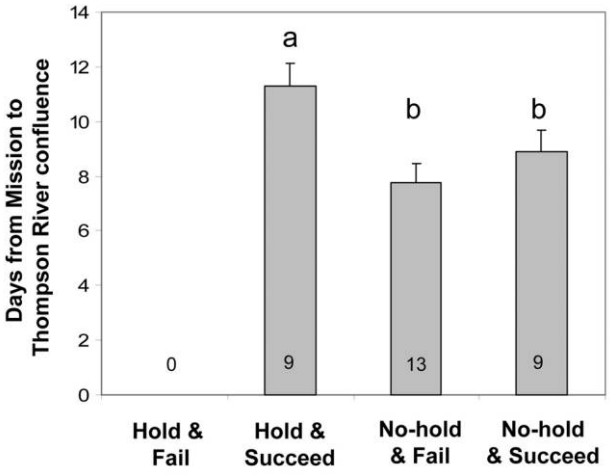

Figure 4. Travel times by Adams sockeye salmon, released in Johnstone Strait, over an ~172-km stretch of the Fraser River between Mission and the Thompson River confluence. Travel times are presented as a function of estuarine holding behavior and fate: fish held at the river mouth and subsequently survived river migration to spawning areas, entered the river directly without holding and died in river, or entered without holding and survived. No fish that held died in river. Travel times were corrected to account for variation in Julian day, which would include variation in temperature and flow regimes. Error bars are ±SEM.

Table 4: Comparison of biological attributes of Adams sockeye salmon (*Oncorhynchus nerka*) homing from Johnstone Strait that held in the estuary and survived to spawning areas versus those that did not hold in the estuary and disappeared

Variables and Sex	Migratory Tactic and Fate			Migratory Tactic and Fate *P*	Julian Day (Covariate) *P*
	Held and Survived (*N*)	Did Not Hold and Disappeared (*N*)	Did Not Hold and Survived		
Gross somatic energy (MJ kg^{-1}):					
♀	8.9 ± .17 (6)	8.4 ± .13 (9)	8.8 ± .14 (7)	.009**	.186
♂	9.1 ± .47 (7)	8.0 ± .30 (15)	8.7 ± .46 (6)	.208	.026*
Nose to fork length (cm):					
♀	57.6 ± .95 (6)	58.8 ± .72 (9)	59.2 ± .82 (7)	.483	.196
♂	61.5 ± .98 (7)	62.3 ± .61 (15)	61.6 ± .95 (6)	.980	.211
Plasma [glu] (mmol L^{-1}):					
♀	6.8 ± .48 (6)	6.9 ± .37 (9)	6.8 ± .42 (7)	.996	.017*
♂	6.9 ± .26 (7)	7.0 ± .16 (15)	7.2 ± .25 (6)	.764	**<.001**
Plasma [lactate] (mmol L^{-1}):					
Pooled	9.6 ± 1.00 (13)	11.2 ± .75 (24)	8.5 ± 1.0 (13)	.097	.891
Plasma [Na^+] (mmol L^{-1}):					
Pooled	178.2 ± 4.68 (13)	176.8 ± 3.51 (24)	178.2 ± 4.50 (13)	.735	.116
Plasma [Cl^-] (mmol L^{-1}):					
Pooled	151.7 ± 1.23 (13)	152.6 ± .92 (24)	151.5 ± 1.19 (13)	.731	.580
Plasma osmolality (mOsm kg^{-1}):					
Pooled	373.0 ± 4.72 (13)	374.6 ± 3.54 (24)	368.3 ± 4.53 (13)	.549	.455
Gill Na^+,K^+-ATPase (μmol ADP mg^{-1} protein h^{-1}):					
Pooled	2.2 ± .37 (13)	3.8 ± .27 (24)	3.9 ± .35 (13)	**<.001**	.045*
Plasma [cortisol] (ng mL^{-1}):					
Pooled	436.0 ± 26.1 (13)	368.5 ± 24.3 (24)	392.4 ± 27.6 (13)	.172	.959
Plasma [T] (ng mL^{-1}):					
♀	17.5 ± 11.28 (6)	60.3 ± 8.62 (9)	61.2 ± 9.73 (7)	.010**	**<.001**
♂	21.5 ± 6.64 (7)	31.8 ± 4.15 (15)	36.1 ± 6.48 (6)	.216	**.005**
Plasma [E_2] (ng mL^{-1}):					
♀	10.3 ± 3.19 (6)	12.5 ± 2.44 (9)	7.65 ± 2.75 (7)	.208	.007**
♂	NA	NA	NA	NA	NA

Note. Sockeye salmon known to be captured in fisheries were removed from the analysis. When necessary, means were adjusted to account for covariation with Julian day of sampling (ANCOVA). All variables were $\log_{10}$ transformed before analysis. Boldface indicates significance at Bonferroni-corrected α values: 0.005 for females, 0.006 for males. NA = not available.

* $\alpha < 0.05$.

** $\alpha < 0.01$.

vidual Adams sockeye salmon to enter the Fraser River and their physiological profile at time of release, independent of holding behavior. Correlations were drawn for two groups of salmon: those that died in the Fraser River en route to spawning areas ($N = 35$) and those that successfully reached spawning areas ($N = 114$; Table 5). In successful migrants, gill Na^+,K^+-ATPase activities in both sexes ($r = -0.316$, $P < 0.001$) and plasma [T] in females ($r = -0.340$, $P = 0.008$) were negatively correlated with travel times to Mission (Table 5). None of the other physiological variables was significantly correlated with travel times to Mission in fish that subsequently died in river (Table 5). Mean travel times to Mission, corrected for variation in FL, clearly show that the successful fish were those that held in the estuary (14.1 ± 0.39 d), while those that entered the Fraser more quickly with little estuarine holding (11.4 ± 0.64 d; ANCOVA, $P < 0.001$, $N = 178$) died in river.

Discussion

We examined the behavior of 505 sockeye salmon with acoustic and radio telemetry as salmon migrated through two different coastal approaches to the mouth of a natal river and then onward to spawning areas, a total distance of more than 650 km. We are aware of no other study that has contrasted salmon behavior and physiology relative to the direction of their marine approach to a natal river—in this case from either the northern or the southern passages around Vancouver Island en route to the Fraser River. Through both inter- and intrapopulation anal-

Table 5: Correlation coefficients and *P* values relating time to enter Fraser River with physiological profile at time of release

Variables and Sex	Disappeared in River (*P*)	*N*	Survived to Spawning Areas (*P*)	*N*
Gross somatic energy (MJ kg^{-1}):				
♀	.115 (.660)	17	.104 (.424)	61
♂	−.210 (.404)	18	.133 (.341)	53
Nose to fork length (cm):				
♀	.114 (.581)	17	−.147 (.257)	61
♂	−.346 (.159)	18	.129 (.351)	54
Plasma [glu] (mmol L^{-1}):				
♀	−.267 (.300)	17	−.028 (.829)	60
♂	−.046 (.856)	18	.019 (.894)	54
Plasma [lactate] (mmol L^{-1}):				
Pooled	−.108 (.538)	35	.118 (.210)	114
Plasma [Na^+] (mmol L^{-1}):				
Pooled	−.125 (.488)	35	.090 (.343)	114
Plasma [Cl^-] (mmol L^{-1}):				
Pooled	.075 (.667)	35	.040 (.675)	114
Plasma osmolality (mOsm kg^{-1}):				
Pooled	.015 (.932)	35	.110 (.244)	114
Gill Na^+,K^+-ATPase (μmol ADP mg^{-1} protein h^{-1}):				
Pooled	−.126 (.472)	35	−.316 (**<.001**)	114
Plasma [cortisol] (ng mL^{-1}):				
Pooled	.035 (.941)	7	.129 (.126)	114
Plasma [T] (ng mL^{-1})				
♀	−.115 (.662)	17	−.340 (.008*)	60
♂	.156 (.537)	18	−.184 (.186)	53
Plasma [E_2] (ng mL^{-1}):				
♀	.95 (.716)	17	.17 (.896)	61
♂	NA		NA	

Note. Correlations are drawn for fish that disappeared in the Fraser River en route to spawning areas and for fish that successfully reached spawning areas. Sockeye salmon known to be captured in fisheries were removed from the analysis. All variables were $\log_{10}$ transformed before analysis. Boldface indicates significance at Bonferroni-corrected α values: 0.005 for females, 0.006 for males. NA = not available.

* $\alpha < 0.01$.

yses, we found support for the hypothesis that the timing and success of spawning migrations are influenced by contrasting energetic and reproductive processes, a finding that is consistent with previous studies (Cooke et al. 2006*a*, 2006*b*, 2008; Crossin et al. 2007). For example, we found that advanced reproductive development, as indicated by high plasma [T] and correspondingly low GSE, was significantly related to early river entry timing and failed migration to spawning areas (i.e., en route mortality). A novel discovery was that GSE, in addition to its importance to migration timing, was vitally important for buffering the negative effects of senescence once upriver migrations had begun. Irrespective of entry timing, individuals with relatively higher GSE were more likely to survive migration to spawning areas. Novel too was that only in females were these processes significantly detected, a finding that lends support to the theory that male sockeye salmon initiate upriver migrations in response to the schedules of females (i.e., protandrous migrations; Crossin et al. 2007) and that their own energetic and reproductive processes affect entry timing to a lesser degree. Finally, we also discovered a key influence of gill Na^+,K^+-ATPase activities on river entry timing and river migration success in both sexes, something that we had long hypothesized (Cooke et al. 2004, 2006*a*, 2006*b*) but for which we lacked empirical support. Critical to establishing these linkages was a statistical accounting for variation in Julian date of sampling (fish were captured during an ~3-wk period), which is something that we had not done in earlier studies.

Initial Physiology, Behavioral Tactics, and Survival to Spawning Grounds

A model of migration behavior and survivorship was put forth by Cooke et al. (2006*b*) in which the survival probability of late-summer runs of Fraser River sockeye salmon (e.g., Adams)

was best in salmon that held at the river mouth before entering the river and poorest in those that entered directly without holding. Our results are consistent with this model. However, when we contrasted the different migratory behaviors and fates of Adams sockeye salmon, we observed nearly equal numbers of males and females in each behavior/fate category, but it was only in females that we found significant associations between physiology and behavior/fate. Consistent with our first prediction, high GSE and low [T] were found in female salmon that held before entering the river and subsequently survived to spawning areas. In contrast, females with low GSE and high [T] entered the river quickly but died before reaching spawning areas, a tactic bestowing zero lifetime fitness to these semelparous animals. Not surprisingly, it is the former behavioral tactic that has been most commonly observed in Adams sockeye salmon and is believed to be adaptive (Burgner 1991). In male sockeye salmon, the relationships between energy, reproductive hormone concentrations, and behavior/fate were not significant, but they mirrored the patterns observed in females. This suggests that males have more flexibility around entry timing, and perhaps because they invest comparatively less energy in gamete production during upriver migration than females, they may take their entry cues from females, who are under greater developmental constraint (Morbey and Ydenberg 2001; Crossin et al. 2007). This idea remains to be tested.

Notwithstanding the general relationship between migration timing and fate, some individuals entered the river early without estuarine holding but nevertheless survived to spawning grounds. These fish had higher GSE than those that also entered without holding but died in river (significantly so in females, trending in males). GSE in the "no-hold and surviving" fish was nearly equal to that in fish that "held and survived" (i.e., the adaptive tactic). Thus, in salmon straddling the line between advanced maturity and senescence, somatic energy may provide an important buffer against migration failure when fish migrate directly into the river without holding, but this is not necessarily a trigger for upriver migration. It is important to note that we defined migratory success in this study as a fish's positive detection at spawning areas, but we did not actually monitor spawning (reproduction), which is the true measure of success. It should be noted, however, that previous studies have shown that most no-holding sockeye salmon reaching spawning areas ultimately fail to spawn (Wagner et al. 2005). Thus, while high somatic energy may buffer these migrants against migration failure, they will probably fail to reproduce successfully (i.e., prespawning rather than en route mortality; Cooke et al. 2004; Wagner et al. 2005).

Survival to spawning areas was significantly related to processes tied to biological circannual clocks, specifically maturation (Fostier and Jalabert 1986; Kobayashi et al. 1997; Norberg et al. 2004) and osmoregulation (Arendt 1998; Kulczykowska 2002). As mentioned previously, for those salmon that held in the estuary and successfully reached spawning areas, river entry timing was significantly and negatively correlated with [T] (in females) and gill Na^+,K^+-ATPase activities (in both sexes). Values for both variables were significantly higher in salmon that did not hold before river entry and failed during river migration. Thus, a synchronicity of maturational and osmoregulatory processes at the saltwater to freshwater interface appears to be vitally important to migratory survival by homing sockeye salmon, observations that support our second and third predictions.

Osmoregulatory physiology is mediated in part by cortisol secretion (McCormick 1993), and there is some evidence of seasonally rhythmic secretion in salmonids, but results are equivocal, varying by species and study (see Shrimpton et al. 2000). We did not see an effect of Julian date on [cortisol], but the stress of purse-seine capture may have masked our ability to detect this. However, in smolting salmon (i.e., young salmon transitioning from freshwater to saltwater) there is a seasonal responsiveness of the interrenal tissue and cortisol secretion (Carey and McCormick 1998), and the direct role that cortisol plays in gill Na^+,K^+-ATPase regulation is well established (McCormick 1993). We found that the downregulation of gill ATPase was significantly influenced by Julian date.

Seasonality

During homeward migration through coastal areas, salmon encountering areas of low salinity presumably downregulate gill Na^+,K^+-ATPase activities in anticipation of river entry (Hinch et al. 2006). Consistent with this idea, we observed lower gill ATPase activities in JS than in JDFS, where surface salinities were ~10 to <30‰ in the former and >30‰ in the latter (Institute for Ocean Sciences, Fisheries and Oceans Canada, Sidney, British Columbia, http://www.pac.dfo-mpo.gc.ca/sci/osap/data/searchtools/searchlighthouse_e.htm). However, when we accounted for variation in Julian date of sampling, geographic differences in ATPase activity vanished, suggesting that gill ATPase activity is expressed along a temporal trajectory during migration. This is consistent with studies showing links between the seasonal-induced and the photoperiodically induced secretions of prolactin and cortisol in homing salmon, hormonal processes that directly influence gill Na^+,K^+-ATPase expression and total osmoregulatory capacity (Hirano et al. 1990; McCormick 2001; Manzon 2002).

As with gill ATPase activity, [T] did not differ between capture locales when Julian date was accounted for, suggesting that reproductive development also advances along a fixed trajectory, an observation supported by a vast body of literature on seasonality in birds, mammals, reptiles, amphibians, and other fish (Dawson et al. 2001; review in Dingle 1996). Interestingly, [E_2] in Adams females was higher in JDFS relative to JS, even after variation in Julian date was removed. Chilko females followed a similar trend. These differences may be indicative of an acute physiological stress because plasma [lactate], [glu], [Na^+], and [Cl^-] were all higher in JS than in JDFS (McDonald and Milligan 1997). Stress is known to have inhibitory effects on the HPG axis and the synthesis of T and E_2 (for reviews see Sapolsky 2002; Wingfield and Sapolsky 2003; for sockeye salmon, see Hinch et al. 2006). The lower [E_2] in JS raises the possibility of a stress inhibition of aromatase activity in ovarian

follicles. Inhibition of E_2 has been documented in the brains of chronically stressed mammals and birds (reviewed by Balthazart and Ball [1998]), but whether this occurs in regions other than the brain, and whether this response occurs in chronically stressed salmonids, remains to be tested. It is not clear why females at JS would have been more stressed than those at JDFS.

Rates of Migration

While homing from JS to the Fraser River mouth, Chilko sockeye salmon swam at nearly twice the rate of Adams sockeye salmon (~53.8 vs. ~35.2 km d^{-1}). However, this was not the case in JDFS-released sockeye salmon, where the two populations swam at similar rates (~27.4 and 28.6 km d^{-1}). We do not have an explanation for these regional or population differences, although speeds in both locales were similar to those observed in previous studies (Quinn and terHart 1987; Quinn et al. 1989). We found that Adams sockeye salmon had higher stress levels in JS relative to JDFS, but the comparatively slower migration speeds observed in JS are what we would normally anticipate from homing sockeye salmon. Previous studies of homing Fraser sockeye salmon have estimated average migration rates of 20–25 km d^{-1}, with periods of strongly directed and rapid swimming interspersed with slower wandering behaviors (Quinn and terHart 1987; Quinn et al. 1989). Similarly, fisheries' managers commonly note that Adams and other late-run populations swim at slower rates in coastal areas and take longer to enter the river compared with summer-run populations (see Crossin et al. 2004). Thus, we would not attribute the regional differences in migration speeds by Adams sockeye salmon to the effects of stress.

Once in river, we examined rates of travel among Adams sockeye salmon from each of the various timing and fate combinations. Fish that held in the estuary and successfully reached spawning areas swam upriver at ~15.5 km d^{-1} through an approximately 172-km stretch of the lower Fraser River. In contrast, fish that did not hold in the estuary swam at faster rates (~19.2–22.6 km d^{-1}). River temperatures and discharge rates have well-documented effects on fish swim speeds (Lee et al. 2003; MacNutt et al. 2006; Hanson et al. 2008). Because of the timing of river entry, the salmon that did not hold in the estuary and entered the river early would probably have encountered higher midsummer river temperatures and flows than those that held and entered weeks later in autumn. We had expected the early no-hold fish to swim at slower speeds, but this is not what we observed. This was probably due to the higher circulating concentrations of testosterone in salmon that did not hold before entering, which has known stimulatory effects on migratory behavior (Munakata et al. 2001; Cooke et al. 2006*a*, 2006*b*, 2008; Crossin et al. 2007).

Despite the evidence of circannual biological rhythms in animals (most extensively studied in birds; for review, see Wingfield et al. 1990; Ramenofsky and Wingfield 2007) and the synchronizing effect of seasonally predictable events such as changing photoperiods, there have been few studies examining the role of hormones in the regulation of migratory behavior (reviewed by Ramenofsky and Wingfield [2007]). Our study and other recent studies point to a consistent role of testosterone and its derivatives in the coordination of river entry timing by migratory Pacific salmon (Munakata et al. 2001; Cooke et al. 2006*a*, 2006*b*, 2008; Young et al. 2006; Crossin et al. 2007). However, experimental tests of hormonal regulation of migration timing at this and other scales are needed.

The Influence of Stress during Homeward Migration

Plasma lactate, Na^+, Cl^-, and osmolality were all significantly higher in male Adams salmon that failed to enter the river while homing from JS than in successful fish, suggesting that the former failed because of the combined effects of stress and ionoregulatory imbalance. Increased stress is likely to diminish a fish's capacity to overcome the ionic gradient at the saltwater to freshwater interface. Thus, river entry may be a strong selective agent, although other agents are certainly possible (i.e., predation). We recognize, however, that the absolute differences that we measured in sodium and chloride concentrations and in plasma osmolality are small. Nevertheless, that all three were significantly higher in failed fish suggests some collective, pathological link to failure. In Chilko sockeye salmon, however, there were no physiological associations with survival to river entry, nor were there any for Adams and Chilko fish migrating through JDFS. This finding suggests that there is something inherently more stressful to Adams sockeye salmon when migrating through though JS. The path that homing sockeye salmon choose around Vancouver Island and its links to their physiology is an interesting topic about which little is known (but see Blackbourn 1987; McKinnell et al. 1999).

Two stress-related issues are generally unavoidable when studying wild homing salmon: fisheries' harvests and fish handling. Fortunately, commercial harvest in NSOG and SSOG was virtually zero when we conducted our study (M. Lapointe, Pacific Salmon Commission, Vancouver, personal communication), but it was somewhat higher in JDFS, at ~30% d^{-1}. Despite the possibility of a cash reward (indicated in print on the transmitters), very few of our transmitters were returned, which suggests that fisheries' harvests were indeed low or that tags were overlooked when fish were captured and processed. If salmon succumbed to the stress of handling, either directly through a systems-related failure or indirectly by an increased susceptibility to predation, we would have expected to see it within the first 1–2 d after release (as per Robichaud and English 2007), which corresponds to the NSOG line for JS-released salmon and the JDFS line for JDFS-released salmon. Only for Adams sockeye salmon released in JS was there indication of this possibility (23% loss before NSOG line). But for Adams sockeye salmon in JDFS and Chilko sockeye salmon in both JS and JDFS, there were no losses before the first acoustic lines.

Studies have shown that high concentrations of plasma lactate following exhaustive exercise can lead to delayed mortality in fish. Resting lactate concentrations in salmon can be <2 mmol mL^{-1} (McDonald and Milligan 1992; Wagner et al. 2006).

The cumulative time of capture and tank holding before biopsy had varied effects at the individual level, raising lactate by as little as 2 or as much as 20 mmol mL^{-1} from laboratory resting values. The subsequent biopsies presumably contributed an additional lactate load. Not surprisingly, the telemetry data allowed us to identify a significant association between lactate and survival to the Fraser River. It is impossible to know whether individual lactate concentrations increased further or whether they began falling on release from the boat. Whatever the case, our data suggest that in order to survive to the river, a threshold concentration of ~18–20 mmol L^{-1} must not be breached. Furthermore, our data suggest that the likelihood of further increases appears to decline after ~40–60 min from the initial capture (as per Fig. 2).

Studies with salmon and trout have shown that metabolic recovery after exhaustive exercise is prolonged by postexercise inactivity (Milligan et al. 2000) and that high postexercise lactate concentration (i.e., lactacidosis) underlies delayed mortality (Farrell et al. 2001*a*, 2001*b*). The key to reducing lactacidosis after exercise—or in this case after the stress of capture, holding, and biopsy—and to preventing additional increases in cortisol is exposure to a light aerobic exercise regime before release (~0.9 body lengths s^{-1}; Milligan et al. 2000; Farrell et al. 2001*a*, 2001*b*). The aerobic increase in cardiac output and ventilation rate from such a regime promotes the oxidation of plasma lactate, the clearance of glycolytically produced CO_2, and the return of blood pH to normal levels. In our study, fish were held for 2–15 min in a large fish box. Although they were provided with an adequate supply of well-oxygenated water, the design of this box was not optimal for promoting aerobic exercise. In future studies, a Fraser box or an equivalent design should be used for recovery to reduce the risk of postrelease mortality.

Conclusion

We have provided new insights into the behavior and fate of a migratory fish species. We have also expanded our understanding of the physiological determinants of migration timing and survivorship by describing the relationship between somatic energy concentrations and sexual maturity (Cook et al. 2006*a*, 2006*b*, 2008; Young et al. 2006; Crossin et al. 2007). Furthermore, we have strengthened previous observations of behavioral physiology by accounting for temporal variation in somatic energy concentrations, reproductive hormone secretions, and osmoregulatory preparedness. These results raise some interesting comparative questions. For example, in homing salmon we found that both reproductive and osmoregulatory systems develop in concert, processes that are mediated by two different endocrine axes, the HPG and the hypothalamo-pituitary-adrenal (HPA, or, in fish, the hypothalamo-pituitary-interrenal [HPI] homologue), which in most birds, mammals, and other animals usually work in opposition (i.e., the HPA/HPI axis has antigonadotropic effects; Sapolsky 2002) but which in salmon do not (Donaldson 1970; Wingfield and Sapolsky 2003). How are salmon able to produce gametes and breed when adreno/interrenal-cortical functions (leading to high cortisol expression and gill ATPase activity) are so active? Testing the effects of sexual maturation and osmoregulation as proximate triggers of migration timing is required to expand our knowledge of migration beyond simple correlative associations, and testing the combined effects could yield interesting insights to cross-axis stimulations and/or inhibitions as drivers of migration behavior.

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