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RESEARCH ARTICLE

Behaviour and physiology of sockeye salmon homing through coastal waters to a natal river

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Abstract Adult sockeye salmon (*Oncorhynchus nerka*, $N = 179$) from six Fraser River populations (British Columbia) were intercepted in continental shelf waters ~215 km from the Fraser River mouth, gastrically implanted with acoustic transmitters, non-lethally biopsied for blood biochemistry, gill Na^+,K^+-ATPase activity and somatic energy density and then released. Migration behaviour and travel times to the river mouth and into the river were monitored by underwater telemetry receivers positioned at the river mouth and in the river. Post-release survival of salmon was excellent, with 84% ($N = 150$) of fish reaching the furthest receiving station ~85 km upriver. Fish from Late-summer run populations (Adams and Weaver Creek) averaged a migration rate of ~20 km day^{-1} through the marine area and held at the river mouth and adjacent areas for 7–9 days before entering the river. Summer-run populations (Birkenhead, Chilko, Horsefly and Stellako) had a migration rate ~33 km day^{-1} and held for only 1–3 days. Once in river, similar patterns were observed: Late-run populations migrated at ~28 km day^{-1} and Summer-run populations at ~40 km day^{-1}. From point of release to the river mouth, males migrated faster than females, but once in river migration rates did not differ between sexes. Among all females, a correlation was discovered between levels of circulating testosterone and river entry timing. This correlation was not observed among males. Plasma K^+, Cl^-, glucose, lactate and osmolality were also correlated with entry timing in both sexes.

Introduction

The seasonal migrations of adult Pacific salmon (*Oncorhynchus* spp.) from the North Pacific Ocean to distant freshwater spawning locales rank among the most dramatic displays of behaviour in the animal kingdom. Yet, despite years of study, our understanding of the cues and mechanisms guiding ocean

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salmon to natal rivers is rudimentary (reviewed by Hinch et al. 2006). The key stimulus initiating homeward migration and maturation appears to be a change in photoperiod that is perceived by salmon and which activates the hypothalamic-pituitary-gonadal axis, thus setting reproductive development in motion (Ueda and Yamauchi 1995; Ueda et al. 2000). Additional endocrine, visual, and chemosensory systems likely assist them in navigating coastal margins to the mouths of natal rivers (Quinn 1980; Quinn et al. 1989).

Upon arrival at the natal river mouth, the timing of river entry is an important life-history decision made by salmon that is both species and population (or stock) specific. Ultimately, entry timing affects when fish arrive on the spawning grounds and dates of spawning, as well as subsequent rates of embryonic and fry development (Burgner 1991). Timing is also influenced by river temperatures and discharge rates, the distance to and elevation of spawning grounds, and the physical characteristics of the spawning environment (Gilhoussen 1990; Brett 1995; Hodgson and Quinn et al. 2002; Lee et al. 2003). For any given salmon species, and population within species, interannual variations in entry timing are usually small. For example, timing by populations of sockeye salmon (*Oncorhynchus nerka*) rarely deviate by more than a week interannually (Cooke et al. 2004), though there has been a recent, unprecedented change in entry timing of some populations returning to the Fraser River in British Columbia which has pushed entry dates far beyond baseline levels of variation.

Since 1995, as many as 60–90% of the individuals from populations entering the Fraser River in late summer (classified as the 'Late-run stock group' by fisheries managers) have advanced their entry date by as much as 8 weeks from historic averages. Given the highly adaptive nature of migration timing by homing salmon, and to migrant animals in general, such behaviour is highly anomalous and negative fitness consequences are expected (Dingle 1996; Bêty et al. 2004; Cooke et al. 2004). Indeed, over four million Late-run sockeye have perished en route to spawning grounds since changes in river-entry timing were first detected over a decade ago, thus constituting a conservation crisis. By migrating early, sockeye enter the Fraser River at a time when temperatures are generally warmer than those historically encountered by the population and to which various phenotypes have adapted (Lee et al. 2003). Such exposures exert physiologic stress and accelerate rates of parasite disease development, which can alter performance and place salmon at considerable risk (G. T. Crossin et al., in review).

Efforts to characterize the physiological mechanisms underlying this recent change in entry timing require information gleaned from individual homing fish. We have developed protocols for the non-lethal biopsy of salmon which, when coupled with telemetry, provide mechanistic insights to migration behaviour. Despite recent evaluations that have characterized potential mechanisms of mortality in river-migrating sockeye (Cooke et al. 2006, 2007; Young et al. 2006), the endogenous mechanisms affecting their behaviour in coastal areas and the timing of river entry remain poorly understood (Hinch et al. 2006). Therefore, we examined whether energetic condition, reproductive state, and osmoregulatory preparedness were key factors affecting the decision of homing sockeye to leave the marine environment and initiate upriver migrations.

For Pacific salmon, which are semelparous animals relying on fixed endogenous energy reserves to power migration and reproduction, time and energy are of fundamental importance to the successful completion of upriver migration and thus are key to fitness (Brett 1995; Hendry and Berg 1999; Hendry et al. 2004; Crossin et al. 2004). There is a wide body of literature addressing the adaptive significance of somatic energy to homing salmon (Brett 1995; Hendry and Berg 1999; Kinnison et al. 2001; Crossin et al. 2004). There is also the recognition of a broad, direct relationship between migration timing and seasonal increases in circulating sex steroids in migrant animals (Dingle 1996). Previous work has shown that senescing sockeye with low somatic energy and high levels of circulating sex steroids tend to initiate upriver migrations earlier than less reproductively mature individuals, and often die en route to spawning grounds as a result (Cooke et al. 2006; Young et al. 2006). Building from these studies, we used telemetric and physiological techniques to examine the mechanisms underlying individual behaviours and entry timing.

Homing salmon were intercepted from six major spawning populations ~215 km from the mouth to the Fraser River and non-lethally sampled to assess their energetic and osmoregulatory states, and blood biochemistry (see Cooke et al. 2005). Salmon were then fitted with acoustic transmitters and released, allowing us to monitor individual and population specific behaviours as fish homed through the coastal marine environment and into the Fraser River. We examined correlations between these physiologic variables and observed behaviours (migratory path and timing), and predicted that salmon entering the river early would (1) have lower somatic energy levels, and (2) higher circulating levels of reproductive steroid hormones relative to individuals entering later. Because homing salmon must remodel their gill architecture to maintain ionic balance when moving from salt to freshwater, we also predicted that early entering individuals have (3) lower gill Na^+, K^+-ATPase levels.

Materials and methods

Biopsy and tagging techniques

On August 20–22 and August 26–27 of 2003, sockeye salmon ($N = 178$) were captured by a 55 ft purse seine vessel

near Brown's Bay, at the southern end of Johnstone Strait, British Columbia (Fig. 1), following methods detailed in Cooke et al. (2006). This vessel also served as the platform for fish biopsy and acoustic transmitter implantation. Surface water temperatures at time of capture and release were 10–13°C. Upon 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 dipnetted and transferred to a large flow-through holding tank on the boat's deck. Approximately 10–12 fish were taken from each seine set, and once onboard, were processed sequentially and released as quickly as possible (ranging from 5 to 50 min). In the collection of physiological samples, we used protocols for the non-lethal, unanaesthetized sampling of sockeye salmon (see Cooke et al. 2005) that were pre-approved by the University of British Columbia Animal Care Committee in accordance with the Canadian Council of Animal Care.

Individual salmon were removed from the holding tank and placed ventral side up in a padded V-shaped trough that was provided with a continuous supply of ambient seawater from a tube positioned near the salmon's head. Two people restrained the salmon while a third collected the biopsy. Typically, fish were confined to the trough for <3 min during which time fork length (FL, cm) was measured, tissues were biopsied and an acoustic transmitter inserted. Biopsies included the removal of (a) a 0.5 g clip of adipose fin for DNA stock identification, (b) a 3 ml blood sample from the caudal vein (using a 1.5″, 21 gauge vacutainer syringe; Houston 1990) for assessing plasma chemistry and (c) a <4 mm clip of 6–8 gill filament tips (~0.03 g) along the first gill arch (McCormick 1993) for assessing gill Na^+,K^+-ATPase activity. Gill tissue and centrifuged plasma samples were stored on dry ice for several hours to days until transfer to a −86°C freezer. A hand-held micro-wave energy meter (Distell Fish Fatmeter model 692, Distell Inc., West Lothian, Scotland, UK) was placed on the left side of the fish in two locations to quantify gross somatic energy levels (GSE, MJ kg^{-1}) (Crossin and Hinch 2005). Vemco V16-H3 acoustic transmitters (16 mm diameter, 51 mm length, 25.0 g in air; Vemco Inc., Shad Bay, NS, Canada) were pushed down the esophagus into the stomach with a plastic applicator. Fish were immediately returned over the side of the boat and monitored until they swam away. Fish were on-board for <1 h. The release site was ~215 km from the mouth of the Fraser River.

Laboratory assays

Population identity was determined for individual fish using both DNA and scale analyses (Beacham et al. 1995, 2004). DNA can correctly assigned baseline populations to lake of origin about 80% of the time (Beacham et al. 2004). A radio telemetry study conducted in 2003 conducted in parallel to the present study found that DNA correctly classified fish to the Stuart, Stellako, Chilko/Quesnel and

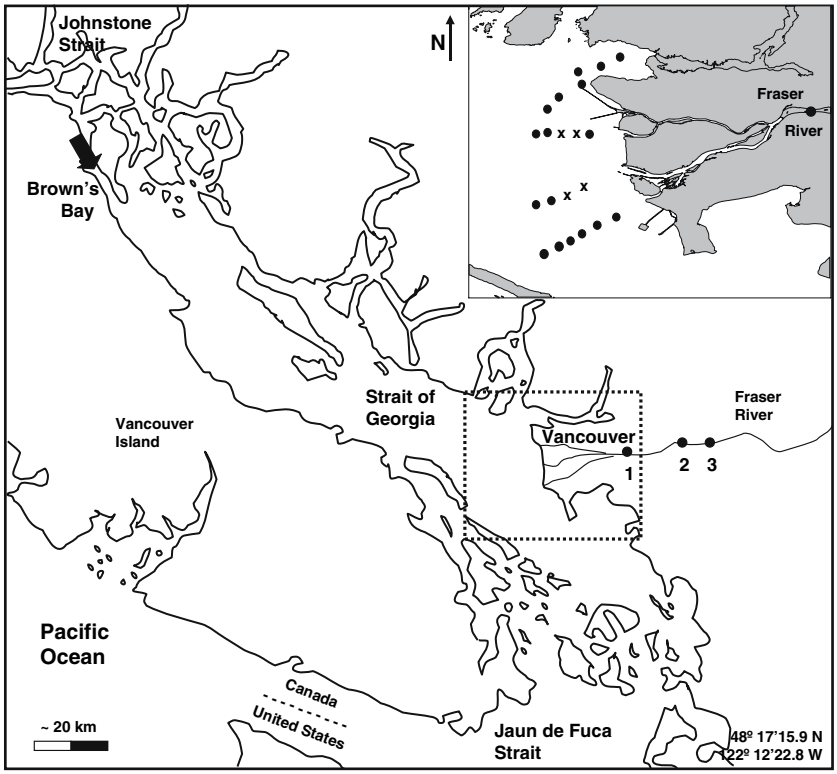

Fig. 1 Map of southwestern coastal British Columbia and Vancouver Island with an inset of the Fraser River delta showing the position of the acoustic receiver array at the river mouth. Salmon were captured by purse-seine at Brown's Bay, biopsied for physiological samples, and fitted with acoustic transmitters. Fish were then released and eventually detected in the array (*black circles*) and at receiver stations in the Fraser River at the confluence with the Pitt River (1), at Albion (2), and at Mission (3) (*numbered black circles*). Acoustic receivers that were deployed but not recovered are indicated with '*x*'

Late-run stock groups about 94% of the time based on where radio tagged fish were last detected (English et al. 2004). Numbers of tagged fish and tagging details for the present study are presented in Table 1.

Plasma testosterone (T) and 17β-estradiol (E_2) levels were measured by radioimmunoassay (McMaster et al. 1992) and used to assign fish sex as secondary sexual characteristic were not fully expressed at that point of migration. Sex was assigned by plotting T against E_2 which generated two distinct clusters. Plasma ions (K^+, Cl^- and Na^+), glucose, lactate and osmolality were quantified by procedures described by Farrell et al. (2001). Gill tissue Na^+,K^+-ATPase activity was determined by kinetic assay (McCormick 1993).

Acoustic receiver array and transmitters

Acoustic receivers were placed in an array on the seabed of the Strait of Georgia (SOG) on 11–13 August 2003 (see Welch et al. 2006). In total, 21 Vemco VR-2 receivers were deployed in four lines extending off the mouth of Fraser River (Fig. 1). VR-2 receivers are internally recording data loggers, which record the tag ID code (serial number) and the date and time that an acoustic tag is detected. The array of receivers extended north to south 36 km, and each line extended 7–9 km out into the Strait from the nearshore, creating a rough grid of ~250 km^2. The receiver lines were positioned to cover the four main entrances to the Fraser River. Three additional VR-2s were positioned at the Pitt River confluence, Albion and Mission, BC, which are 43, 65 and 83 km, respectively, upriver from the mouth. The later most receivers at Mission lie at the tidal boundary; thus fish moving beyond this move into fully fresh and non-tidally influenced river water. With the tags used in this study, the VR-2s could detect a fish passing within ~1 km under ideal circumstances, though the achieved range varies with environmental conditions.

For analytical purposes, we divided the movements of fish from Brown's Bay to Mission into three distinct migratory segments and examined travel or holding times in each. Specifically, we determined three population-specific travel times: (1) travel time from Brown's Bay to first detection on the SOG array at the Fraser River mouth (segment 1), (2) holding time (first to last detection) in the SOG array (segment 2) and (3) travel time from the Pitt River confluence to Mission, BC (segment 3) (see Figs. 1, 3). Using segment distances we calculated migration travel rates. By examining the number and temporal sequence of VR-2 receivers visited by homing sockeye, we estimated the migration trajectories of all fish through the SOG array so that we could better visualize movement patterns. Graphic representation of these patterns were generated for individuals from two Late-run (Adams and Weaver) and two Summer-run (Chilko and Horsefly) populations (Fig. 5). These four individuals were deemed representative in that the number of VR-2s that each visited was similar to the mean number visited by their population.

Table 1 Number of acoustic transmitters deployed, the number of physiologically sampled sockeye salmon, and the number of tagged individuals detected in the ocean and in the Fraser River in 2003

Tagging summary	Late-run		Summer-run				Other populations	Total
Population	Adams	Weaver	Birkenhead	Chilko	Horsefly	Stellako		
Number tagged	36	18	31	47	28	10	8	178
Number that were biopsied (females, males)	16 (6, 10)	12 (6, 6)	19 (8, 11)	22 (11, 11)	10 (5, 5)	6 (3, 3)	3 (1, 2)	88 (40, 48)
Number detected in ocean (biopsied versus unbiopsied)	30 (14, 16)	15 (10, 5)	23 (13, 10)	37 (19, 18)	20 (5, 15)	10 (6, 4)	6 (2, 4)	141 (69, 72)
Percentage of total released	83%	83%	74%	79%	71%	100%	75%	79%
Number detected in river (biopsied versus unbiopsied)	30 (13, 17)	15 (10, 5)	27 (17, 11)	40 (21, 18)	22 (7, 15)	10 (6, 4)	6 (1, 5)	150 (75, 75)
Percentage of total released	83%	83%	87%	85%	79%	100%	75%	84%
Number failing to enter river (% of total released)	6	3	4	7	6	0	2	28 (16%)
Number detected in ocean but not in river	2	0	1	3	2	0	1	9 (5%)
Number unaccounted	4	3	3	4	4	0	1	19 (11%)

Numbers are reported by population. After release, fish were subsequently detected in the receiver array at the Fraser River mouth (ocean detections), and (or) in the river at the Pitt River confluence, Albion and Mission receiver stations. Fish not detected anywhere are classified as 'unaccounted' individuals

Statistical analyses

All physiological data were log(10)-transformed to reduce heteroscedasticity. As only half of the fish in this study were physiologically biopsied, we assessed whether our physiological sampling methodology exerted any deleterious affects on salmon behaviour and survival by contrasting travel times and survivourship (measured as a detection at the last in-river VR-2 station at Mission) from the point of release to Mission, between biopsied and non-biopsied fish using analysis of variance (ANOVA) and a chi-square contingency table analysis, respectively. We also used chi-square to examine whether the number of ocean losses was distributed evenly across the six main populations, or whether particular populations were more heavily impacted. We examined for any broad physiologic differences (variables: GSE, Na^+, K^+, Cl^-, osmolality, lactate, glucose and gill Na^+,K^+-ATPase) between survivors and ocean losses using multivariate analysis of variance (MANOVA). Sexes were pooled for these analyses.

To explore physiological differences among populations at time of capture, MANOVAs were conducted on sex-specific data. Variables included in the models were: GSE, FL, Na^+, K^+, Cl^-, osmolality, lactate, glucose, gill Na^+, K^+-ATPase, T and, for females only, E_2. To identify the relative importance of individual variables underlying multivariate relationships, we conducted a series of two-way ANOVAs with population and sex as main effects, and their interaction. Three variables were sex-specific (female plasma 17β-estradiol, male plasma testosterone and female plasma testosterone) so only one-way ANOVAs could be used for those. A posteriori tests were used to identify populations that differed when the ANOVA model was significant. To assess sex- and population-specific relationships between travel times (from point of release to specific locations) and physiological variables, we conducted a series of correlation analyses. Where correlations were significant, we used linear regression to describe relationships between the physiological factor (the dependent variable) and travel time of individuals (the independent variable) and used analysis of covariance (ANCOVA) to assess whether these relationships differed between sexes or among populations (the class variables).

All analyses were conduced using JMP 4.0 (SAS Institute, Cary, NC, USA). Because of multiple comparisons, we conducted Bonferroni corrections to minimize the potential for Type-II errors (Rice 1989). We designated statistical significance at $\propto = 0.05$. However, due to the high conservatism of Bonferroni corrections (see Cabin and Mitchell 2000), we indicate significance at the $\alpha = 0.05$, $\alpha = 0.01$ and $\alpha = 0.001$ levels (see Tables 1, 2), thus allowing readers to define for themselves which levels are most biologically meaningful (as per Cabin and Mitchell 2000).

Results

Six major Fraser River populations were identified from DNA analyses: Chilko, Horsefly, Stellako, Adams, Weaver and Birkenhead. Chilko, Horsefly and Stellako enter the Fraser River immediately after arrival from early August through September and are classified as 'Summer-run' populations (or stocks) by management agencies (M. Lapointe, Pacific Salmon Commission, personal communication). Adams and Weaver delay entry for up to 6 weeks after arriving at the estuary (holding), entering in September and October, and are classified as 'Late-run' populations. Birkenhead behave somewhat intermediate and arrive in coastal areas with the Late-run Adams and Weaver populations, but migrate immediately into the Fraser River with Summer-run populations. For convenience, we grouped Birkenhead sockeye with the Summer-run populations. A summary of population identities, acoustic tag deployments, number of detections and the total number and sex of biopsied individuals is presented in Table 1.

Salmon abundances at date of passage through the marine area tagging site at Brown's Bay, and past a hydroacoustic counting facility in the lower Fraser River (at Mission, BC) are presented in Fig. 2. Data were collected from DFO and PSC test fisheries, and from the PSC hydroacoustic facility at Mission, BC (M. Lapointe, Pacific Salmon Commission, personal communication). Late- and Summer-run populations overlapped during passage through Johnstone Strait, though the peak of abundance was slightly earlier for Summer-run fish (Fig. 2a). In contrast, Fraser River entry was bi-modal, with Summer-run fish entering earlier than Late-run fish, though some Late-run fish entered at the same time as Summer-run fish (Fig. 2b).

We classified the telemetered fish into one of several 'fate' categories (Table 1). Fish detected on at least one SOG receiver were termed 'ocean-detected' (79% of total releases) and fish detected on at least one river receiver were termed 'river-detected' (84% of total releases). The higher percentage of river-detected fish than ocean-detected fish indicates that about 6% of fish entering the river went undetected in the ocean, probably because four SOG receivers near the main entrance to the Fraser River were lost and never recovered (Fig. 1). Fish that were detected in the ocean but not subsequently in the river were termed 'failed river entrants' (5% of total releases) and fish that were never detected on any receiver after release were termed 'unaccounted' (11% of total releases). By using three sets of paired receivers, our ability to detect fish once they entered the river was very high. In fact, of the 150 fish

Table 2 Comparison of the physiological attributes of sockeye salmon (*Oncorhynchus nerka*) upon capture at Brown's Bay by population and sex

Variables	Populations	Mean capture values and SEMs	Total *N*	Population	Sex	Interaction
Gross somatic energy (MJ kg^{-1})	Adams	9.00 ± 0.22^{a}	85	***F* = 7.88, *P* < 0.001**	$F = 3.70$, $P = 0.06$	$F = 0.92$, $P = 0.48$
	Weaver	7.82 ± 0.25^{c}				
	Birkenhead	7.78 ± 0.20^{c}				
	Chilko	9.01 ± 0.18^{a}				
	Horsefly	8.16 ± 0.27^{b}				
	Stellako	9.40 ± 0.35^{a}				
Plasma Na^{+} (mmol L^{-1})	Adams	179.60 ± 1.97	84	$F = 1.61$, $P = 0.17$	$F = 0.22$, $P = 0.64$	$F = 1.59$, $P = 0.17$
	Weaver	184.17 ± 2.26				
	Birkenhead	182.16 ± 1.80				
	Chilko	177.40 ± 1.71				
	Horsefly	179.24 ± 2.47				
	Stellako	178.27 ± 3.19				
Plasma K^{+} (mmol L^{-1})	Adams	0.76 ± 0.21	84	$F = 0.64$, $P = 0.67$	$F = 0.12$, $P = 0.73$	$F = 0.22$, $P = 0.95$
	Weaver	1.00 ± 0.24				
	Birkenhead	1.28 ± 0.19				
	Chilko	1.08 ± 0.18				
	Horsefly	0.84 ± 0.26				
	Stellako	1.07 ± 0.34				
Plasma Cl^{-} (mmol L^{-1})	Adams	146.22 ± 1.10	85	$F = 1.03$, $P = 0.41$	$F = 7.35$, $P < 0.01$ ** females > males	$F = 0.20$, $P = 0.96$
	Weaver	148.73 ± 1.26				
	Birkenhead	145.08 ± 1.00				
	Chilko	146.08 ± 0.93				
	Horsefly	146.25 ± 1.38				
	Stellako	145.20 ± 1.78				
Plasma osmolality (mOsm kg^{-1})	Adams	353.69 ± 3.79	85	$F = 0.54$, $P = 0.75$	$F = 0.02$, $P = 0.90$	$F = 0.43$, $P = 0.83$
	Weaver	358.38 ± 4.35				
	Birkenhead	351.88 ± 3.47				
	Chilko	350.31 ± 3.22				
	Horsefly	353.40 ± 4.77				
	Stellako	357.17 ± 6.16				
Plasma glucose (mmol L^{-1})	Adams	7.37 ± 0.26	85	$F = 1.05$, $P = 0.40$	$F = 2.95$, $P = 0.09$	$F = 0.69$, $P = 0.64$
	Weaver	6.97 ± 0.30				
	Birkenhead	7.05 ± 0.24				
	Chilko	6.68 ± 0.22				
	Horsefly	6.70 ± 0.32				
	Stellako	7.28 ± 0.42				
Plasma lactate (mmol L^{-1})	Adams	9.40 ± 0.80	85	$F = 1.01$, $P = 0.42$	$F = 0.04$, $P = 0.84$	$F = 0.85$, $P = 0.52$
	Weaver	10.58 ± 0.92				
	Birkenhead	9.70 ± 0.73				
	Chilko	8.23 ± 0.68				
	Horsefly	9.17 ± 1.01				
	Stellako	8.99 ± 1.30				
Gill Na^{+},K^{+}-ATPase (μmol ADP mg^{-1} protein h^{-1})	Adams	1.71 ± 0.14	85	$F = 0.62$, $P = 0.69$	$F = 0.12$, $P = 0.73$	$F = 2.24$, $P = 0.06$
	Weaver	1.62 ± 0.16				
	Birkenhead	1.63 ± 0.13				
	Chilko	1.81 ± 0.12				
	Horsefly	1.62 ± 0.18				
	Stellako	2.09 ± 0.23				

Table 2 continued

Variables	Populations	Mean capture values and SEMs	Total *N*	Population	Sex	Interaction
Male plasma testosterone (pg ml^{-1})	Adams	7,470 ± 1,418	39	$F = 0.86$, $P = 0.52$	n/a	n/a
	Weaver	6,125 ± 1,419				
	Birkenhead	8,532 ± 1,228				
	Chilko	6,504 ± 1,047				
	Horsefly	6,079 ± 1,553				
	Stellako	4,297 ± 2,005				
Female plasma testosterone (pg ml^{-1})	Adams	5,052 ± 603[a]	46	**$F = 5.59$, $P < 0.001$**	n/a	n/a
	Weaver	4,908 ± 779[a]				
	Birkenhead	7,925 ± 575[c]				
	Chilko	5,812 ± 575[b]				
	Horsefly	7,554 ± 853[c]				
	Stellako	4,422 ± 1,101[a]				
Female plasma 17β-estradiol (pg ml^{-1})	Adams	4,090 ± 949	46	$F = 1.46$, $P = 0.23$	n/a	n/a
	Weaver	5,197 ± 1,226				
	Birkenhead	5,197 ± 905				
	Chilko	5,533 ± 905				
	Horsefly	4,048 ± 1,343				
	Stellako	2,547 ± 1,733				

Analyses were conducted using ANOVA with population and sex as main effects, and their interaction. All variables were log(10) transformed prior to analysis

Significant correlations are $*P < 0.05$, $**P < 0.01$

Bold faced values indicate significance at Bonferroni corrected $\alpha = 0.005$ for females, 0.006 for males

Superscript letters indicate Tukey's test population differences in significant ANOVA models

detected in river, 135 (or 90%) were detected at all three receiver stations, 13 (or <9%) were detected at two of the three stations, and only two (or >1%) were detected at a single river station. The raw detection files downloaded from the receivers indicate that each fish was detected multiple times as it made its way past a receiver, and once detected, was never detected again at a later date, suggesting directed upriver movement.

Of the fish that reached the last up-river receiver station, we found no difference between those biopsied ($N = 74$) and not biopsied ($N = 76$) in either their travel time (ANOVA, $P = 0.091$) or their survivourship (chi-square, $P = 0.726$); ultimately, 83% of biopsied and 85% of non-biopsied fish were detected at Mission. These results suggest that our biosampling procedure exerted no deleterious effects on salmon behaviour, survival and travel times, which is consistent with our previous studies (Cooke et al. 2005, 2006). We also found no difference between the proportion of fish that survived to Mission versus the number of ocean losses within each of the six main populations (chi-square test, $P = 0.756$), suggesting that the small percentage of mortality observed was distributed evenly across populations.

We combined 'failed river entrants' with 'unaccounted' into a category of 'ocean-losses' ($N = 14$), and used this new group to compare the physiology of those that disappeared in the ocean with those that successfully reached Mission ($N = 74$). We found no differences in plasma ions, metabolites, somatic energy and gill Na^+,K^+-ATPase between ocean loss fish and successful migrants (MANOVA, $F = 0.667$, $P = 0.274$, $N = 86$). Because the MANOVA was non-significant, we did not run subsequent ANOVAs for each individual variable. We caution, however, that the lack of statistical significance may have been a result of a low sample size in the ocean-losses category. Results from a parallel telemetry study which occurred at the same time, on the same populations of co-migrating sockeye, using the same tagging platforms and using similar biopsy protocols as the present study, but which had more than twice the sample size as the present, found that fish that disappeared during migration (i.e. ocean loses) were characterized by statistically higher plasma Na^+, osmolality and lactate levels than surviving fish (Cooke et al. 2006).

Sex-specific MANOVAs indicated a significant population-level physiological difference among females (Wilks Lambda $P < 0.002$, $N = 46$), but not among males (Wilks Lambda $P = 0.217$, $N = 40$). Table 2 lists population means and standard errors for all of the physiological variables measured. Two-way ANOVAs revealed significant population level differences in GSE levels (Table 2: $F = 7.88$,

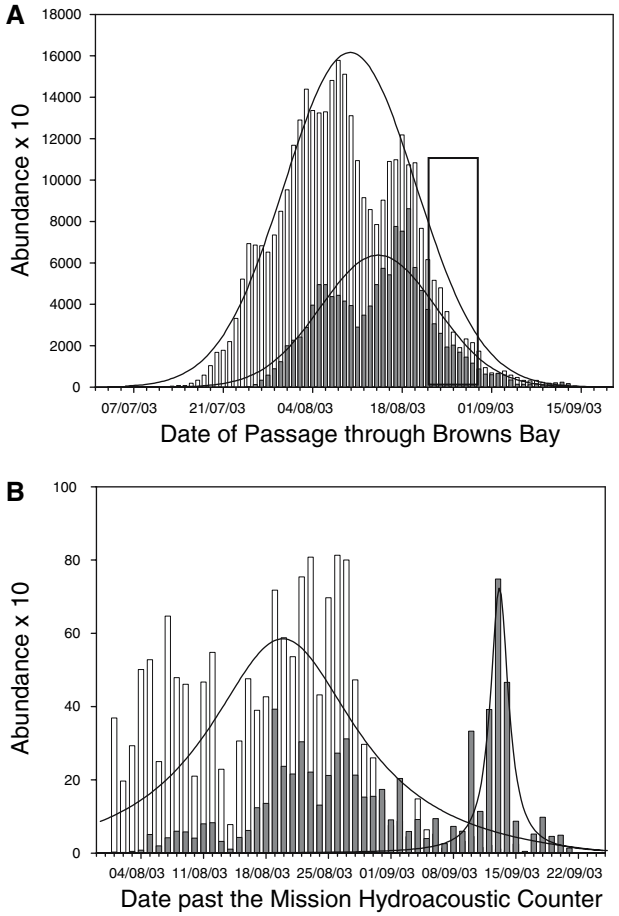

Fig. 2 Abundances of sockeye salmon and dates of passage through the marine area collection site in Johnstone Strait (**a**), and past a hydroacoustic enumeration facility ~80 km upriver from the Fraser River mouth (**b**). *Dark bars* are Late-run abundances, and *light bars* are Summer-run abundances. *Rectangle* in panel a indicates the dates during which fish from this study were sampled. Data from M. Lapointe, Pacific Salmon Commission, unpublished data

$P < 0.01$, $N = 85$), and significant population differences in plasma testosterone concentrations among females (Table 2, $F = 5.59$, $P < 0.01$, $N = 46$). Tukey's tests revealed that GSE was greatest in Adams and Chilko fish, lowest in Weaver, Birkenhead and Stellako fish and moderate in Horsefly fish. Female testosterone was greatest in Birkenhead and Horsefly, lowest in Adams, Weaver and Stellako and moderate in Chilko. No population differences were observed for the remaining variables (plasma Na^+, K^+, Cl^-, glucose, lactate, T, E_2 and gill Na^+, K^+-ATPase). A significant effect of sex was observed in plasma Cl^- concentrations (Table 2, $F = 7.35$, $P < 0.01$, $N = 85$) with values higher in females (147.7 ± 0.68 mmol L^{-1}) than in males (144.8 ± 0.73). None of the interaction terms in any of the two-way ANOVAs were significant (all $P > 0.06$).

We calculated population-specific rates of travel and (or) holding times through the four segments of the homing migration. Through segment 1, populations differed in travel time (population $P = 0.025$, $N = 66$; Fig. 3a), and males migrated faster than females (sex $P = 0.017$, $N = 66$; 4.53 ± 0.3 for males versus 5.53 ± 0.3 days for females). However, through all other segments, populations differed in travel times but males and females did not (segment 2, population $P < 0.001$, sex $P = 0.655$, $N = 66$; segment 3, population $P = 0.020$, sex $P = 0.959$, $N = 62$; segment 4, population $P < 0.001$, sex $P = 0.552$, $N = 67$; Fig. 3b–c). The Late-run Adams and Weaver populations spent significantly more time holding at the river mouth (segment 2) and migrated at slower rates over an ~40 km stretch of the Fraser River (segment 3) than the four Summer-run populations (Birkenhead, Chilko, Horsefly and Stellako). By dividing the distance travelled through segments 1–2 by travel time for each individual, the estimated coastal migrations rates were ~20.9 km day^{-1} for Late-run populations

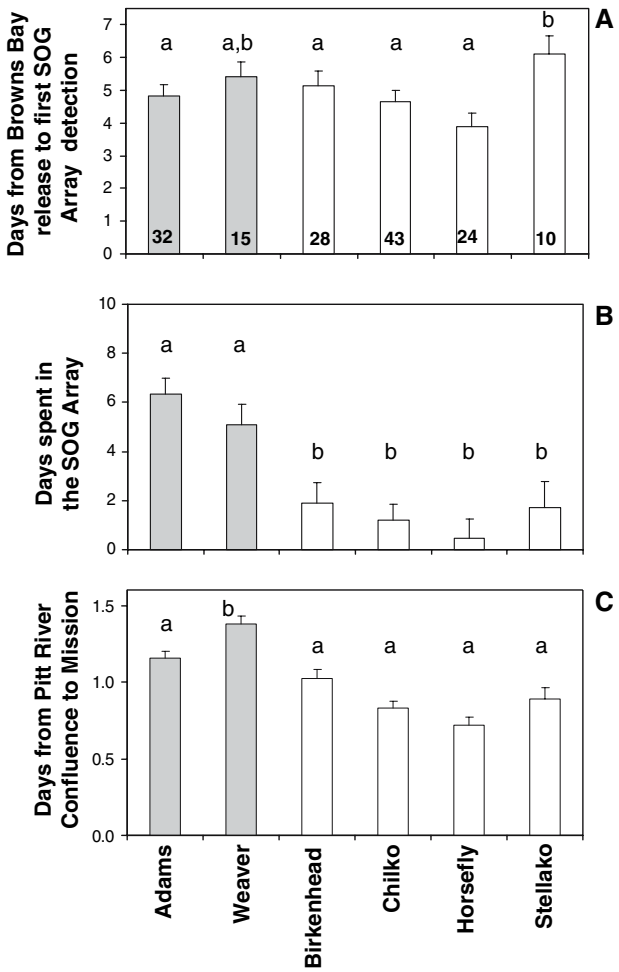

Fig. 3 Mean travel time from point of release at Brown's Bay to first SOG array detection (**a**), mean holding time in the SOG array (**b**), and mean travel time from the Fraser-Pitt Rivers confluence to Mission B.C. (**c**). *Dark bars* are Late-run populations, and *light bars* are Summer-run populations. Sample sizes (numbers of fish) are indicated at base of *bars* in panel A. *Error bars* signify ±1 SEM. *Different letters* indicate significance at $P < 0.05$

and ~33.2 km day^{-1} for Summer-run populations. River migration rates (segment 3) were ~27.7 km day^{-1} for Late-run populations and ~40.1 km day^{-1} for Summer-run populations.

There were few significant correlations between travel rates and holding times and the physiological and energetic variables. Correlations between individual travel and holding time estimates and physiology are summarized for each sex in Table 3. The strongest correlations were between female testosterone levels and holding time in segment 2 ($r = -0.485$, $P < 0.01$, $N = 36$) and travel time through segment 3 ($r = -0.524$, $P < 0.01$, $N = 34$), both of which were significant after Bonferroni correction. Female testosterone levels were also correlated with time from Pitt River confluence to Mission ($r = -0.324$, $P < 0.02$, $N = 48$). These data suggest that entry timing and migration speed were related to testosterone levels in females. Indeed, both Late- and Summer-run females showed the same negative relationship between entry date and testosterone levels (Fig. 4). Neither the intercepts nor the slopes of these linear regression relationships differed (ANCOVA, $P = 0.587$). The pooled regression equation is $y = -132.93x + 5 \times 10^6$, $r^2 = 0.288$, $N = 39$. Other significant correlations in females at $\alpha = 0.05$ were identified between travel time and plasma K^+, osmolality and glucose. In males, no Bonferroni significant correlations were observed, but correlations were observed at $\alpha = 0.05$ between travel time and plasma Cl^-, osmolality, glucose and lactate (Table 3).

Males and females showed similar migratory patterns through the SOG array, and the movements of four representative fish are presented in Fig. 5. The two Summer-run individuals (a male and a female, Fig. 5a, b) covered a much smaller area than the two Late-run individuals (also a male and a female, Fig. 5c, d) who were detected over a much broader area. These patterns are consistent with the travel and holding times presented in Fig. 3 and indicate that the Summer-run fish entered the river quickly relative to the Late-run fish that held for a much longer time before entering the river.

Table 3 Sex-specific correlations coefficients and *P*-values relating sockeye salmon gross somatic energy, body size and plasma biochemistry to travel and holding times determined through acoustic telemetry

Sex	Variables	Time from Brown's Bay to SOG array	N	Holding time in SOG array	N	Time from last SOG array detection to Pitt River confluence	N	Time from Pitt River confluence to mission	N
Females	Gross somatic energy (MJ kg^{-1})	0.080 (0.65)	36	0.010 (0.56)	36	0.171 (0.34)	34	0.033 (0.83)	48
	Nose to fork length (cm)	0.004 (0.98)	36	−0.101 (0.56)	36	−0.221 (0.21)	34	−0.054 (0.72)	48
	Plasma Na^+ (mmol L^{-1})	0.321 (0.06)	35	0.292 (0.09)	35	−0.108 (0.55)	33	0.018 (0.91)	47
	Plasma K^+ (mmol L^{-1})	0.157 (0.37)	35	0.046 (0.79)	35	−0.371 (<0.03)*	33	−0.089 (0.55)	47
	Plasma Cl^- (mmol L^{-1})	0.071 (0.68)	36	0.209 (0.22)	36	−0.113 (0.52)	34	−0.023 (0.88)	48
	Plasma osmolality (mOsm kg^{-1})	0.212 (0.22)	36	0.359 (0.03)*	36	−0.093 (0.60)	34	−0.001 (0.99)	48
	Plasma glucose (mmol L^{-1})	0.342 (0.04)*	36	0.336 (<0.05)*	36	−0.024 (0.89)	34	0.34 (0.019)	48
	Plasma lactate (mmol L^{-1})	0.165 (0.34)	36	0.302 (0.07)	36	−0.182 (0.30)	34	0.099 (0.50)	48
	Plasma testosterone (pg ml^{-1})	−0.193 (0.26)	36	**−0.485 (<0.001)**	36	**−0.402 (<0.001)**	34	−0.325 (<0.02)*	48
	Plasma 17β estradiol (pg ml^{-1})	0.062 (0.72)	36	−0.010 (0.95)	36	−0.048 (0.79)	34	0.059 (0.69)	48
	Gill Na^+/K^+ ATP-ase (μmol ADP mg^{-1} protein h^{-1})	−0.087 (0.62)	35	−0.160 (0.36)	35	−0.110 (0.50)	39	0.140 (0.35)	47
Males	Gross somatic energy (MJ kg^{-1})	−0.205 (0.26)	32	−0.324 (0.07)	32	−0.350 (0.06)	29	−0.176 (0.35)	30
	Nose to fork length (cm)	0.007 (0.97)	32	0.108 (0.56)	32	0.435 (<0.01)**	29	0.182 (0.34)	30
	Plasma Na^+ (mmol L^{-1})	0.281 (0.12)	32	0.283 (0.12)	32	0.255 (0.18)	29	0.083 (0.66)	30
	Plasma K^+ (mmol L^{-1})	0.208 (0.26)	32	−0.048 (0.80)	32	0.030 (0.88)	29	−0.174 (0.36)	30
	Plasma Cl^- (mmol L^{-1})	0.471 (<0.01)**	32	0.425 (<0.02)*	32	0.127 (0.51)	29	−0.004 (0.98)	30
	Plasma osmolality (mOsm kg^{-1})	0.478 (<0.01)**	32	0.351 (<0.05)*	32	0.195 (0.31)	29	−0.087 (0.65)	30
	Plasma glucose (mmol L^{-1})	0.192 (0.29)	32	0.366 (<0.04)*	32	0.046 (0.81)	29	0.117 (0.54)	30
	Plasma lactate (mmol L^{-1})	0.494 (<0.01)**	32	0.480 (<0.01)**	32	0.230 (0.23)	29	0.147 (0.44)	30
	Plasma testosterone (pg ml^{-1})	−0.129 (0.48)	32	0.277 (0.13)	32	0.322 (0.09)	29	0.084 (0.66)	30
	Gill Na^+/K^+ ATP-ase (μmol ADP mg^{-1} protein h^{-1})	0.138 (0.45)	32	−0.212 (0.24)	32	−0.309 (0.10)	29	−0.155 (0.41)	30

* Signify statistical significance at $\alpha = 0.05$

** Signify significance at $\alpha = 0.01$. Bold faced values signify significance at Bonferroni corrected $\alpha = 0.0033$ for females (11 variables), 0.0035 for males (10 variables)

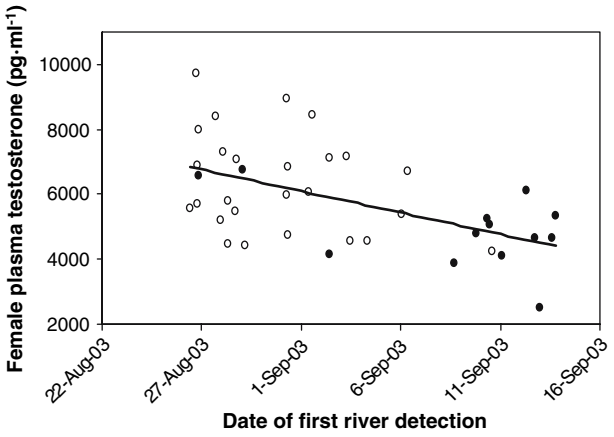

Fig. 4 Relationship between dates of river entry and plasma testosterone concentrations in female sockeye salmon. Fish were released at Brown's Bay, 215 km from the mouth of the Fraser River and river entry date was determined by telemetry. *Open circles* represent Summer-run populations, *dark circles* represent Late-run populations. The line is the best linear fit for the pooled data: $P < 0.001$, $r^2 = 0.288$

Discussion

Although the timings of sockeye salmon migrations into freshwater are largely population-specific adaptations to environmental factors (river temperature and discharge rates), we found that within a population's particular window of river entry, individual variation in timing by female sockeye was associated with circulating testosterone levels, but not with somatic energy levels or measures of osmoregulatory preparedness. Both Late- and Summer-run females with high testosterone levels entered the river significantly faster than those with lower levels, which supports our prediction and is consistent with results from a parallel study in which the holding time at the river mouth prior to entry was inversely related to female 11-keto testosterone and 17β estradiol levels (Cooke, et al. 2007). Our results show that Late-run females entering directly, thus forgoing the 2–6 weeks period in the SOG that is typical for Late-run fish, have hormone levels that resemble Summer-run females which do not hold. Furthermore, our results provide support for the idea that the recent migration of Late-run salmon into the Fraser River far in advance of adaptive norms, and their consequent high mortality (Cooke et al. 2006; Young et al. 2006), is related in part to an advance of the reproductive schedule of females. However, neither Late- nor Summer-run males show correlations between testosterone and entry timing, despite having circulating levels those were in most cases higher than that of females. This raises fundamental questions about their

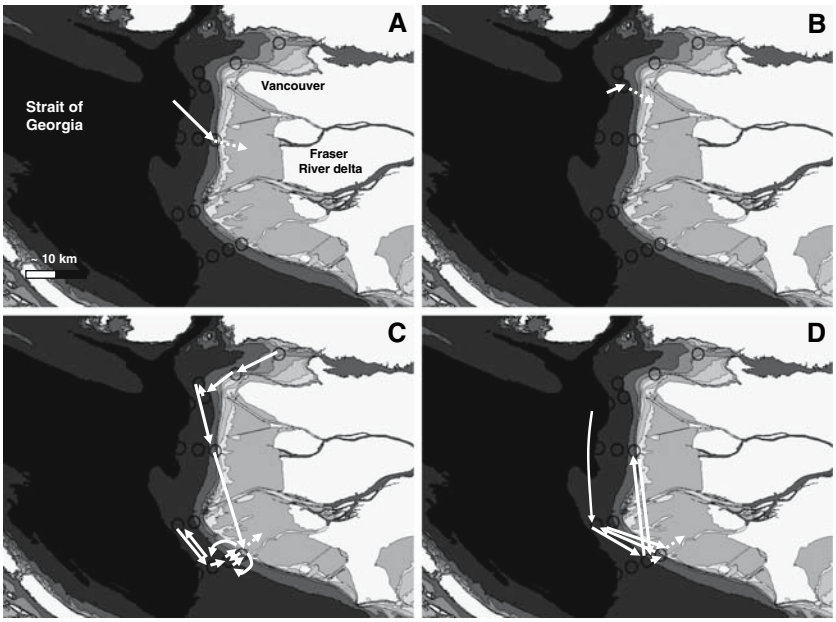

Fig. 5 Representative movements of sockeye salmon homing through marine waters to the Fraser River: **a** Summer-run Chilko male, first entered the array at 1956 hours, August 25 and was last detected at 2307 hours, August 26 for a total of 0.13 days. The fish was detected upriver 0.89 days later at Mission. **b** Summer-run Horsefly female, first entered the array at 1913 hours, August 25 and was last detected at 0242 hours, August 26 for a total of 0.51 days. The fish was detected upriver 0.72 days later at Mission. **c** Late-run Adams female, first entered the array at 1116 hours, August 27 and was last detected at 1021 hours, September 8 for a total of 11.96 days. The fish was detected upriver 5.37 days later at Mission. **d** Late-run Weaver male, first entered the array at 1812 hours, August 28 and was last detected at 1053 hours, September 8 for a total of 10.70 days. The fish was detected upriver 4.15 days later at Mission. *Solid lines* indicate the linear sequence of VR-2s visited by each fish and are not proportional to time. *Dashed lines* are projected directions of river entry. Land is presented in *white*. Water depth is indicated by *grey-scale* gradations, with deepest water in *darkest grey*. Position of acoustic receivers are indicated in the inset of Fig. 1

behavioural ecology and about the cues initiating freshwater entry which will be addressed below. Predictions about somatic energy and osmoregulatory state as drivers of freshwater entry were not strongly supported by the data for either sex.

Homing sockeye salmon exhibit a considerable degree of life-history variation. At the mouths of natal rivers, somatic energy densities, size at maturity, ovary mass and egg number and the expression of secondary sexual characteristics all vary by population in response to the distances fish must swim upriver to spawning grounds (Brett 1995; Hendry and Berg 1999; Kinnison et al. 2001; Crossin et al. 2004). Presumably, these patterns have evolved, in part, as a means to optimize the partitioning of finite somatic energy reserves between the competing demands of active and standard metabolism, and reproductive development. Additionally, the behaviour of homing salmon varies at the mouths of natal rivers. Variation in river entry dates can be inferred from the variation in spawning dates observed among populations. And indeed, records kept by fisheries managers clearly indicate differences in run-timing and in holding time at the river mouth, though at present this variation cannot be ascribed to specific populations. Summer-run populations travelling furthest up the Fraser River (i.e. Chilko, Horsefly and Stellako), and the Birkenhead population tend to initiate migration in early summer, ahead of the summer peak in river temperatures. Those travelling shorter distances (Late-run Adams and Weaver populations) avoid peak river temperatures by holding for up to 6 weeks in estuarine waters at the river mouth. Interestingly, both behavioural tactics ensure that salmon migrate into the river when temperatures are near adaptive performance optima (i.e. oxygen consumption rates; Lee et al. 2003).

The fundamental importance of somatic energy to successful upriver migration was the basis for the prediction that variation in river entry timing would depend in part on the availability of reserve energy. GSE reserves did differ significantly among populations (Table 2), but were not significantly correlated with timing at any segment of the migratory route. Although ultimately a constraint to successful migration, somatic energy did not appear to constrain the entry timing of sockeye in this study. The spread of somatic energy levels observed in this study are within the normal range of values observed in Fraser sockeye salmon (Crossin et al. 2004).

We had also predicted that river entry timing and behaviour would reflect a degree of osmoregulatory preparedness, but gill Na^+,K^+-ATPase activities did not differ among populations and also did not significantly correlate with entry timing. All fish sampled at Brown's Bay had enzyme activities that were at a level similar to those reported earlier by Shrimpton et al. (2005) for homing sockeye at the same location. All fish sampled at Brown's Bay thus appeared physiologically prepared for the ionic challenges associated with freshwater entry. Despite this however, some individuals entered the river directly (i.e. within hours of first detection at the river mouth) while others held for more than a week before entering. Plasma osmolality was correlated with a longer travel time in males to the river mouth, and longer holding times in males and females, suggesting that gill ATPase activity at the salt-to-freshwater interface does not necessarily reflect subtle differences in an individual's internal osmotic composition. Alternatively, high-osmolality may reflect a differential effect of handling stress.

Plasma glucose and lactate levels at capture were not significantly different among the six populations, suggesting that our handling of fish during tagging and sampling was consistent. Average glucose and lactate levels (6.5–7.5 and 8.5–10.5 mmol L^{-1}, respectively), were both above baselines values, suggesting some handling stress, but lactate was below a critical threshold level (>12 mmol L^{-1} lactate; Jain and Farrell 2003) above which rapid recovery in rainbow trout is inhibited. Furthermore, plasma glucose in males and females, and lactate in males, were positively correlated with travel times to, and holding times at, the river mouth. As these variables are commonly used to assess the stress response of fish, it is possible that the stress associated with purse-seine capture and handling at Brown's Bay affected swim performance en route to the river mouth and resulted in a potential delay across the six populations under study. Research on the same populations had earlier shown that high plasma lactate and cortisol levels were characteristic of sockeye that failed to enter the Fraser River (Cooke et al. 2006). While we can implicate stress with a delay in ocean migration, we cannot attribute ocean losses to stress, though we caution low numbers of ocean losses may have precluded statistical resolution of such an effect.

Stress related increases in plasma cortisol, glucose and lactate can have a depressive effect on circulating sex steroid levels in fish (Pankhurst and Van Der Kraak 1997; Kubokawa et al. 1999). However, we did not see unusually low-hormone titres. Furthermore, we did not see a significant correlation between female plasma testosterone and travel time from Brown's Bay to the SOG array, but we might have expected a longer travel time associated with lower hormone levels. Nevertheless, testosterone was a key correlate of holding time and river entry timing in females.

The final stages of ovarian maturation in salmonids is associated with pronounced changes in steroid hormone biosynthesis (Van Der Kraak et al. 1989; Devlin and Nagahama 2002; Nakamura et al. 2005). In late vitellogenic follicles, there is a marked reduction in the expression of aromatase which is responsible for the conversion of testosterone and androstendione to 17β-estradiol and estrone,

respectively. Consequently, circulating androgen levels rise. There are also increases in the activity of other enzymes, most notably those involved in the synthesis of progestins that are involved in the maturation of oocytes. Thus, the observation that female fish with the highest testosterone levels were the first to initiate upriver migration is consistent with our prediction, and suggests strongly that those fish were in an advanced reproductive state relative to fish entering later. Interestingly, though hormone levels were somewhat higher in summer-run females (Fig. 5), both Summer- and Late-run females showed the same inverse relationship between testosterone and entry timing.

In males, testosterone levels were generally higher than in females but were not significantly correlated with timing behaviour at any stage. In fact, we did not detect any clear physiological indicator of freshwater entry in males. Unfortunately, we did not measure 11-keto testosterone in this study, which is a derivative of testosterone and a powerful androgen with strong affects on behaviour. However, in a parallel study conducted with the same populations of fish at the same time and place as this study, 11-keto testosterone levels did not correlate with holding behaviour or river entry in males (Cooke et al. 2007). Entry may thus be affected by some endogenous variable (or variables) that we did not measure in this study, or by some other exogenous factor. One interesting hypothesis to test is that males synchronize and initiate freshwater entry and upriver migration in response to the entry schedules of females. Evolutionary theory predicts that female animals will time reproduction to coincide with optimal environmental conditions for the rearing of offspring (Lack 1954), and our results lend support to this idea. Accordingly, male sockeye should synchronize river entry to reflect the migratory schedules of females. Male sockeye, and indeed all male Pacific salmon, are known to arrive on spawning grounds before females (termed protandrous reproduction, or 'protandry') in order to position themselves optimally for access to females (Morbey 2000), a tactic common among species in which competition for females during courtship is fierce (Myers 1981; Oring and Lank 1982). If male sockeye are timing their entry to that of co-migrant females, then they should swim faster than females to arrive on spawning grounds first. Telemetry studies on upriver migrating sockeye support this prediction (Hinch and Rand 1998; Standen et al. 2002) though it is most obvious in relatively fast and turbulent reaches (Hinch and Bratty 2000).

Additional support for the idea that males time their migration to that of females comes from pheromone studies in spawning salmon. F-type prostaglandins released in the urine of vitellogenic female rainbow trout (*O. mykiss*) act as releaser-type pheromones which positively influence male courtship behaviour, milt volume and circulating testosterone and 17,20-dihydroxyprenenone levels (Olsén and Liley 1993). As females commonly enter the river in a vitellogenic state, our results suggest the possibility that females could be emitting a chemical cue that influences the entry timing of males, though certainly dilution factors are much larger in the marine area than in spawning systems. However, Døving and Stabell (2003) have proposed that the return to natal rivers by ocean homing salmon is facilitated by a conspecific recognition of animo acids, bile salts, steroid hormones and prostaglandins, all of which salmon can detect at very low concentrations (Døving et al. 1980). Collectively, these compounds constitute what is known as the 'home stream olfactory bouquet' (Carruth et al. 2002) and may be key to guiding salmon into and up natal rivers, but at present this hypothesis has not been tested.

In summary, from the point of release at Brown's Bay, male sockeye were faster than females when homing through nearly 200 km of the SOG, where tides and currents are strong and variable. Upon arrival at the river mouth, clear differences in behaviour were detected among Late- and Summer-run populations, which is consistent with fishery records and which are likely tactics shaped by the mean temperature regimes encountered historically en route to spawning areas. Late-run sockeye milled about by the river mouth, covering a greater area and visiting more acoustic receivers than Summer-run sockeye, and resided longer before heading upriver. The sexes did not differ in these patterns, nor did they in migration travel times in the lower, tidally affected reaches of the Fraser River. The key physiological variable related to freshwater entry of females was plasma testosterone. None of the physiological variables were correlated with river-entry timing in males, and in neither sex were energetic condition or osmoregulatory state strongly correlated with entry timing.

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