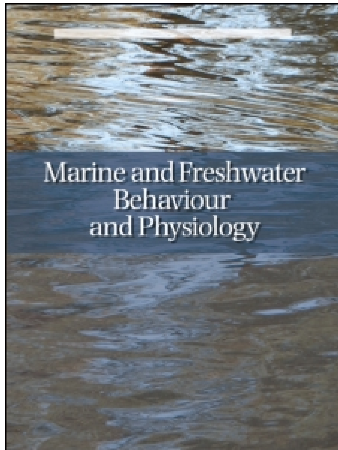
This article was downloaded by: *[Canadian Research Knowledge Network]*
On: *18 February 2010*
Access details: *Access Details: [subscription number 918588849]*
Publisher *Taylor & Francis*
Informa Ltd Registered in England and Wales Registered Number: 1072954 Registered office: Mortimer House, 37-41 Mortimer Street, London W1T 3JH, UK



Marine and Freshwater Behaviour and Physiology
Publication details, including instructions for authors and subscription information:
http://www.informaworld.com/smpp/title~content=t713644420

Physiological profiles of sockeye salmon in the Northeastern Pacific Ocean and the effects of exogenous GnRH and testosterone on rates of homeward migration

Glenn T. Crossin [a]; Scott G. Hinch [ab]; David W. Welch [c]; Steven J. Cooke [d]; David A. Patterson [e]; Jayme A. Hills [e]; Yonathon Zohar [f]; Ulrike Klenke [f]; Melinda C. Jacobs [c]; Lucas B. Pon [a]; Paul M. Winchell [c]; Anthony P. Farrell [g]
[a] Centre for Applied Conservation Research, Department of Forest Sciences, University of British Columbia, Vancouver, BC V6T 1Z4, Canada [b] Institute for Resources, Environment and Sustainability, University of British Columbia, Vancouver, BC V6T 1Z4, Canada [c] Kintama Research Corp., Nanaimo, BC V9S 3B3, Canada [d] Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada [e] Fisheries and Oceans Canada, Cooperative Resource Management Institute, Simon Fraser University, Burnaby, BC V5A 1S6, Canada [f] Center of Marine Biotechnology, University of Maryland Biotechnology Institute, Baltimore, MD 21202, USA [g] Department of Zoology and Faculty of Land and Food Systems, University of British Columbia, Vancouver, BC V6T 1Z4, Canada

To cite this Article Crossin, Glenn T., Hinch, Scott G., Welch, David W., Cooke, Steven J., Patterson, David A., Hills, Jayme A., Zohar, Yonathon, Klenke, Ulrike, Jacobs, Melinda C., Pon, Lucas B., Winchell, Paul M. and Farrell, Anthony P.(2009) 'Physiological profiles of sockeye salmon in the Northeastern Pacific Ocean and the effects of exogenous GnRH and testosterone on rates of homeward migration', Marine and Freshwater Behaviour and Physiology, 42: 2, 89 — 108
To link to this Article: DOI: 10.1080/10236240902846770
URL: http://dx.doi.org/10.1080/10236240902846770

PLEASE SCROLL DOWN FOR ARTICLE

Full terms and conditions of use: http://www.informaworld.com/terms-and-conditions-of-access.pdf

This article may be used for research, teaching and private study purposes. Any substantial or systematic reproduction, re-distribution, re-selling, loan or sub-licensing, systematic supply or distribution in any form to anyone is expressly forbidden.

The publisher does not give any warranty express or implied or make any representation that the contents will be complete or accurate or up to date. The accuracy of any instructions, formulae and drug doses should be independently verified with primary sources. The publisher shall not be liable for any loss, actions, claims, proceedings, demand or costs or damages whatsoever or howsoever caused arising directly or indirectly in connection with or arising out of the use of this material.

Marine and Freshwater Behaviour and Physiology
Vol. 42, No. 2, March 2009, 89–108

Taylor & Francis
Taylor & Francis Group

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Physiological profiles of sockeye salmon in the Northeastern Pacific Ocean and the effects of exogenous GnRH and testosterone on rates of homeward migration

Glenn T. Crossin[a*], Scott G. Hinch[a,b], David W. Welch[c], Steven J. Cooke[d], David A. Patterson[e], Jayme A. Hills[e], Yonathon Zohar[f], Ulrike Klenke[f], Melinda C. Jacobs[c], Lucas B. Pon[a], Paul M. Winchell[c] and Anthony P. Farrell[g]

[a]*Centre for Applied Conservation Research, Department of Forest Sciences, University of British Columbia, Vancouver, BC V6T 1Z4, Canada;* [b]*Institute for Resources, Environment and Sustainability, University of British Columbia, Vancouver, BC V6T 1Z4, Canada;* [c]*Kintama Research Corp., 10-1850 Northfield Rd., Nanaimo, BC V9S 3B3 Canada;* [d]*Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada;* [e]*Fisheries and Oceans Canada, Cooperative Resource Management Institute, Simon Fraser University, Burnaby, BC V5A 1S6, Canada;* [f]*Center of Marine Biotechnology, University of Maryland Biotechnology Institute, 701 E. Pratt, Baltimore, MD 21202, USA;* [g]*Department of Zoology and Faculty of Land and Food Systems, University of British Columbia, Vancouver, BC V6T 1Z4, Canada*

(*Received 19 August 2008; final version received 24 February 2009*)

We captured 196 adult Fraser River sockeye salmon (*Oncorhynchus nerka*) in the Gulf of Alaska and collected blood and tissue samples to describe their energetics and physiology at an early stage of homeward migration. Somatic energy concentrations differed significantly among population (run-timing) groups, with the earliest entering group (the Early Summer-runs) possessing less energy than Summer-run and Late Summer-run sockeye. Conversely, Early Summer-run fish had invested significantly more in testicular development relative to the other run-timing groups (76.1 ± 9.8 g vs. 47.0 ± 8.0 g and 39.0 ± 5.4 g). Egg production followed a similar trend but was only marginally significant. Plasma testosterone was also nearly twice as high in Early Summer sockeye relative to Late Summer-run sockeye (89.01 ± 13.12 ng mL^{-1} vs. 38.69 ± 5.61 ng mL^{-1}). To test the pleiotropic effect of reproductive hormones on migratory behaviour, we implanted these same 196 sockeye with gonadotropin-releasing hormone and/or testosterone and examined travel times via acoustic telemetry. Relative to controls, there was no significant relationship between hormonal treatment and travel times, which suggests that exogenous treatment had little effect though sample size was small ($N = 13$). Nonetheless, pre-treatment levels of testosterone correlated significantly with travel times ($r = -0.813$), irrespective of treatment.

Keywords: Fraser River; migration; *Oncorhynchus nerka*; Pacific salmon; pleiotropy; reproductive hormones

*Corresponding author. Email: crossin@interchange.ubc.ca

ISSN 1023–6244 print/ISSN 1029–0362 online
© 2009 Taylor & Francis
DOI: 10.1080/10236240902846770
http://www.informaworld.com

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Introduction

The long-distance migrations of animals have long fascinated ecologists, and the spawning migrations of Pacific salmon (*Oncorhynchus* spp.) are amongst the longest known, traversing large swathes of the north Pacific Ocean and extending vast distances into natal watersheds. Though migrations can be viewed as population-level processes, analysis of individual movements can provide insights to the behavioural and physiological mechanisms that underlie migrations. Direct observations of individual migratory behaviours have been gleaned from positional telemetry in which salmon were tracked whilst homing through coastal waters to natal rivers (Døving et al. 1985; Quinn et al. 1989; Tanaka et al. 2000; Cooke et al. 2005, 2006a, b, 2008; Crossin et al. 2007), and efforts to characterize the physiological mechanisms that underlie migratory behaviours have benefited from the collection of physiological biopsies at the time of transmitter implantation (Cooke et al. 2005, 2006a, b, 2008; Crossin et al. 2007, 2009a). Descriptive studies with Pacific salmon have shown that the shift from ocean foraging to homeward migration in Pacific salmon is tied to the photoperiodic activation of the Hypothalamo-Pituitary-Gonadal axis (HPG; Ueda and Yamauchi 1995; Onuma et al. 2009). Indeed, the initiation of reproductive migrations in general has been linked to seasonal surges in Gonadotropin-Releasing Hormone (GnRH) and testosterone, a pattern observable in a wide range of animal taxa (birds, reptiles and fish, reviewed by Dingle 1996). Experimental work with lake-dwelling sockeye salmon (or 'kokanee' salmon, the potamodromous form of *Oncorhynchus nerka*) has shown that exogenous implantation of GnRH results in the cessation of active foraging in an open lake environment, increases in circulating testosterone and a premature migration to a natal inlet stream for spawning (Sato et al. 1997; Kitahashi et al. 1998). Exogenous GnRH also led to increases in the number of times that adult sockeye would attempt to leap over a waterfall after shifting from salt to freshwater (Plate et al. 1999), and to increases in the rate and speed of upstream migration in homing sockeye (Sato et al. 1997). It is thus clear that a principal driver of migratory rate and pattern, at least in freshwater contexts, is the seasonal surge of reproductive hormones.

Other studies with salmon have shown that endogenous energy supply, which for homing salmon is finite, and the activity of gill Na^{+},K^{+}-ATPase, an enzyme that enables salmon to maintain homeostasis whilst traversing salinity gradients, are strong correlates of migratory timing into natal rivers. Adult Pacific salmon (*Oncorhynchus* spp.) stop feeding during homeward coastal migrations and must fuel subsequent freshwater migrations to natal areas, gamete production and spawning activities with stored somatic energy (Hinch et al. 2006). Upon arrival at the river mouth, adults exhibit population-specific patterns of energy allocation, morphology and behaviour, which are best explained by life-history theory (Hendry and Berg 1999; Crossin et al. 2004). For example, populations with long and arduous upriver migrations divert less energy to gonad development, are more fusiform and swim more efficiently – characteristics conducive to energy conservation (Brett 1995; Hendry and Berg 1999; Kinnison et al. 2001, 2003; Crossin et al. 2004). Recent studies with biopsy telemetry have begun to characterize the physiological mechanisms underlying variation in homing behaviour (e.g. Cooke et al. 2005).

Individuals that are more reproductively advanced (i.e. have higher circulating testosterone) and have lower somatic reserve energy tend to migrate faster and more directly towards spawning areas than those that are less reproductively advanced and have more somatic energy (Cooke et al. 2006a, b, 2008; Young et al. 2006; Crossin et al. 2007). Osmoregulatory preparedness is also an important factor affecting migratory behaviour in estuarine areas (Hinch et al. 2006). The activity of gill Na^{+},K^{+}-ATPase, and plasma ion concentrations are variables that have shown correlations with rates of migration into natal rivers (Cooke et al. 2006b; Hinch et al. 2007).

While all these observations have provided fascinating details about the behaviour of homing salmon, especially as they pertain to river-entry timing, most of these studies have focused on salmon at the marine-to-freshwater interface (Cooke et al. 2005, 2006a, b, 2008; Crossin et al. 2007) or exclusively in freshwater (Young et al. 2006). In these studies, salmon had already begun the programmed catabolism of their digestive tract that so characterizes their semelparous, capital breeding life-history, and were exhibiting life-history variation in somatic energy supply and reproductive development (i.e. trade-offs; Kinnison et al. 2001, 2003; Crossin et al. 2004). However, the initiation of homeward migration begins months earlier when salmon are on the high seas and still actively foraging (Onuma et al. 2009). Very few studies have examined the energetics, physiology and reproductive trade-offs (if present) in salmon far at sea, mostly due to the difficulty of capturing them. As such, our current understanding of their ocean life-history is limited (Hinch et al. 2006). Is the life-history variation that we observe at the onset of upriver migration detectable in ocean salmon free from energetic constraint? What is the relationship between somatic energy, reproductive investment and migratory behaviour at this early stage of migration?

Our study involved the capture of maturing oceanic sockeye salmon as they made continental landfall near the Queen Charlotte Islands in the northeast Pacific Ocean (coastal British Columbia, Canada), over 850 km from the mouth of their natal Fraser River. We captured fish from the three main Fraser River population collectives or 'run-timing' groups over a span of 6 days. Despite a short window of co-migration past the Queen Charlotte Islands, these groups will eventually enter the Fraser River in a general sequence over an extended 3-month period (FRAP 1995). Upon capture, salmon were non-lethally biopsied for energetic condition, blood plasma and gill tissues, and were then implanted with GnRH or with GnRH in combination with testosterone, or received a sham injection (saline) or no injection (control). Salmon were then surgically implanted with acoustic transmitters and released to resume migration. Migratory behaviour was monitored as they swam across several acoustic telemetry receiving lines positioned at intervals along the homeward trajectory.

We had two principal objectives. The first was to examine whether energetic condition, reproductive state and osmoregulatory preparedness varied among populations in open-ocean environments as they are known to once upriver migrations have begun (i.e. in estuaries and rivers; Crossin et al. 2004, 2009a). Because populations that initiate upriver migrations into the Fraser River in early summer encounter more energetically demanding in-river conditions (i.e. greater freshwater distances and higher river discharges), and because they spawn earlier

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

than salmon that initiate upriver migrations in Late Summer, we predicted that fish from Early Summer-runs would (1) have higher somatic energy reserves, (2) be more reproductively advanced and (3) be more osmoregulatorily 'prepared' for freshwater entry than later Summer-runs. Our second objective was to test the hypothesis that circulating reproductive hormone concentrations are key factors affecting rates of migration from open ocean environments to the natal river. We predicted that fish receiving exogenous hormones would (4) exhibit faster rates of homeward migration relative to controls.

Methods and materials

Fish capture and sampling protocols

After about 1 year as coastal ocean residents, post-smolt sockeye move off the continental shelf into the open ocean. For Fraser River sockeye, whose ocean distributions have been examined (French et al. 1976; Burgner 1991), a transition into the Gulf of Alaska is dependent on current patterns and temperature and their subsequent open ocean migration is dominated by the direction and strength of the Alaskan Gyre (Healey 2000). When homeward migrations are initiated, Fraser River sockeye swim eastward to the coast where they historically have made continental landfall at latitudes near the northwest coast of British Columbia, Canada (Thomson et al. 1992). Fraser River sockeye are comprised of over 150 populations which are classified into four broad run-timing groups based on long-term observations of Fraser River entry dates (FRAP 1995). Runs begin entering the Fraser River in late June and finish by the end of October. We studied individuals within the three largest run-timing groups with historical peak migrations into the Fraser River during mid to late July (Early Summer-runs), early to mid-August (Summer-runs) and late August to late September (Late Summer-runs) (FRAP 1995). There is some overlap of upriver migration of Summer-runs with the other two groups but Early Summer- and Late Summer-runs generally do not overlap. However, segments of all groups co-migrate in open ocean and coastal areas en route to the Fraser River (Cooke et al. 2006a, b).

Using a commercial purse seine vessel chartered for this study, capture efforts began on 28 July 2006 and continued until 3 August 2006 along the northwest coast of the Queen Charlotte Islands (Figure 1). Sampling dates were targeted to capture salmon at the peak of the 2006 migration past the Queen Charlotte Island (Mike Lapointe, Pacific Salmon Commission, Vancouver, BC, Canada, personal communication). Though we captured fish over a relatively small time frame, inter-population variation in somatic energy and physiological parameters were similar to those observed in other studies of Fraser River sockeye when sampled over a longer period of time (Cooke et al. 2005, 2006a, b, 2008). Though there is some degree of temporal variation in somatic energy and physiological profiles within a population of migrant animals depending on when sampling occurs (i.e. during the leading, peak or tail end of a run), differences between populations of Fraser River sockeye are usually large enough to avoid any biases imposed by sampling date.

Seining was conducted in a manner to minimize capture stress and handling, and several of the tagging methods were similar to those used in previous ocean-capture studies with adult sockeye (Cooke et al. 2006a, b, 2008; Crossin et al. 2007). Upon the completion of a seine set, the net was brought alongside the rail of the vessel and

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

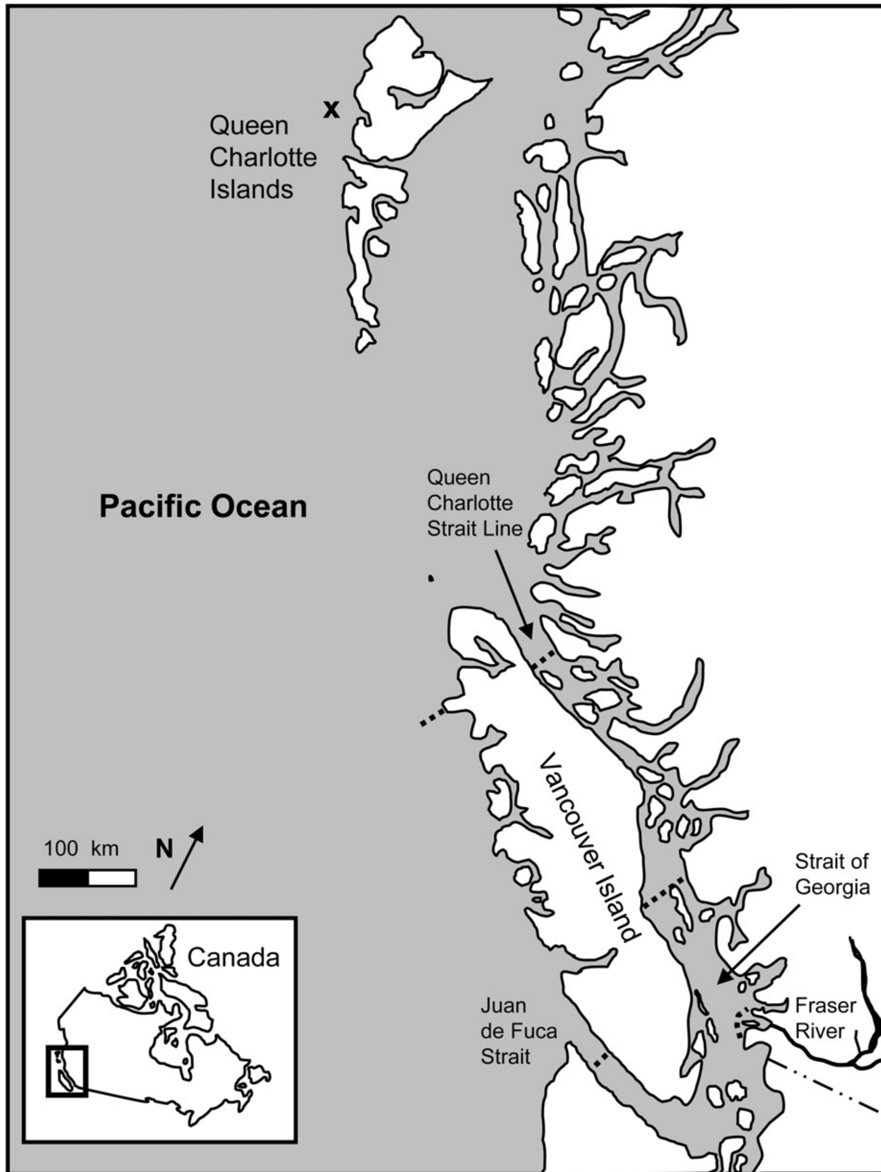


Figure 1. Map of the northeast Pacific Ocean and coastal British Columbia with an inset of Canada. The location where homing sockeye salmon were captured by purse seine in Rennell Sound, Queen Charlotte Islands, is marked with an 'x'. After capture, sockeye were then biopsied, tagged, hormonally implanted, and released. Also shown are the locations of acoustic receiver arrays (dashed lines) where a homing salmon could be detected whilst homing toward and into the Fraser River.

kept in the water as a single, large 'bag'. Individual fish were then dip-netted from the bag and transferred swiftly to a large tank on the quarter deck containing a continuous supply of fresh, ambient seawater. Ten to fifteen salmon were dip-netted from each set and all other salmon were promptly released.

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

The biopsy and tagging procedure reported in Cooke et al. (2005) was followed. All biopsies were conducted on unanaesthetized fish to make results comparable with past studies (e.g. Cooke et al. 2006a, b, 2008; Young et al. 2006). 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 less than 3 min during which time fork length (FL, cm) was measured, tissues were biopsied and an external dorsal tag affixed. Biopsies included the removal of (1) a 0.5 g clip of adipose fin for DNA stock identification, (2) a 3 mL blood sample from the caudal vein (using a 1.5″, 21 gauge vacutainer syringe; Houston 1990) for assessing plasma chemistry and (3) a $<$4 mm clip of six to eight gill filament tips ($\sim$0.03 g) along the first gill arch (McCormick 1993) for assessing gill Na^+,K^+-ATPase activity. Gill tissue and centrifuged plasma samples were stored in liquid nitrogen for several days until transfer to a –86°C freezer. A hand-held microwave energy meter (Distell Fish Fatmeter model 692, Distell Inc, West Lothian, Scotland, UK) was to be used to quantify Gross Somatic Energy (GSE) concentrations as we have done in previous studies (e.g. Crossin and Hinch 2005; Crossin et al. 2007), however the meter malfunctioned on the first day of sampling and could not be used. A group of co-migrating sockeye salmon ($N = 36$) were collected on a single day during the middle of our sampling period for the examination of GSE and gonad masses. These 'proxy' fish were sacrificed upon capture and had their gonads removed. Gonads and carcasses were frozen for transport to the laboratory.

We have previously sampled Fraser River sockeye along the west coast of the Queen Charlotte Islands and found that feeding and energy accrual had not yet ceased, suggesting that sockeye were at a very early stage of homeward migration (Hinch et al. 2006). Therefore, so as not to inhibit feeding capacity, we decided that transmitters must be surgically inserted into the abdominal cavity rather than inserted gastrically as we have done in other recent biopsy telemetry studies (e.g. Crossin et al. 2007). Upon completion of biopsy, sockeye were transferred to an anesthetic bath of MS222 (50 mg L^{-1}) for 1–2 min prior to surgery to place sockeye into stage 3 anesthesia. During the 1–2 min surgery to implant the transmitter, sockeye were bathed in a dilute solution of MS222 (20 mg L^{-1}). Transmitters were inserted via a small incision in the abdominal cavity which was closed with 2–3 sutures (see KRC 2007 for implantation specifications). After surgery, individual sockeye received one of four treatments: 150 μg kg^{-1} injection of a GnRH analog (GnRHa; see Mylonas et al. 1995; Mylonas and Zohar 2001), 150 μg kg^{-1} of GnRH plus 4 mg kg^{-1} testosterone (T) injection, sham injection (saline), or no injection (control). Injections were delivered with a 1 cc syringe fitted with a 21 gauge needle into the dorsal sinus between the epaxial musculature, just posterior to the dorsal fin. The sockeye became active by the completion of surgery and injection. It had a numbered cinch tag inserted posterior to the dorsal fin, then were immediately returned over the side of the boat and observed until they swam away. All fish were on-board in holding tanks for less than 1 h though most (90%) were on-board for less than 10 min. All handling, biopsy, hormone implant and tagging protocols were approved by the University of British Columbia Animal Care Committee in accordance with the Canadian Council of Animal Care.

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Acoustic telemetry

Salmon carrying transmitters were detected on telemetry receiver lines in marine and freshwater environments (see KRC 2007 for details). The focus of this paper is primarily on the marine receiver lines (Figure 1). The Queen Charlotte Strait (QCS) receiver line was positioned across Queen Charlotte Strait just north of Port Hardy, BC. The Northern Strait of Georgia (NSOG) receiver line was positioned across northern Strait of Georgia between the towns of Comox and Powell River, BC. These lines were approximately 470 and 730 km from the tagging locale in Rennell Sound, respectively and were intended to detect transmitter carrying fish migrating along the eastern side of Vancouver Island. The Lippy Point (LP) line and the Juan de Fuca (JDF) line were approximately 470 and 835 km from the tagging locale, respectively and were positioned to detect transmitter carrying fish migrating along the west coast of Vancouver Island. The Southern Strait of Georgia (SSOG) line was positioned to encircle the arms of the Fraser River mouth and ensured detection of fish as they entered the Fraser River. Additional receivers were placed throughout the Fraser River and at key spawning areas (KRC 2007; Crossin et al. 2009a).

Laboratory assays

DNA analysis was used for population identification of biopsied sockeye with procedures used commonly on Fraser River sockeye (Beacham et al. 1995, 2004). Plasma concentrations of testosterone ([T]) and 17β-estradiol ([E_2]) were measured by radioimmunoassay and used to determine fish sex, as secondary sexual characteristic were not fully expressed at time of handling. Plasma concentration of ions ([Na^+], [Cl^-]), glucose ([glu]), lactate ([lactate]), and osmolality were quantified by procedures described in Farrell et al. (2001). A kinetic assay was used to assess gill tissue Na^+,K^+-ATPase activity (McCormick 1993). The gonads and carcass of the sacrificed proxy fish were thawed and weighed and the carcass was homogenized for proximate analysis in order to estimate GSE (see Crossin et al. 2004 for methods).

Statistical analyses

Homing sockeye salmon are known to exhibit a fair degree of life-history variation in terms of somatic energy concentrations and degrees of reproductive investment at the population level (Hendry and Berg 1999; Crossin et al. 2004). This variation is very evident in salmon as they leave the ocean and enter natal rivers. What is not known is whether this variation is detectable while still far at sea, near the onset of homeward migration while salmon are still foraging and are at an early stage of reproductive development. One of our goals in this paper is to examine possible life-history variation at the population level upon capture at sea, but small samples sizes for some populations precluded a proper population-level analysis. For example, some populations had as few as two fish while others had upwards of 100. Populations belonging to similar migration run-timing groups (and by association making up-river migrations of similar distance (FRAP 1995)) tend to show similar patterns of somatic energy and

reproductive investment. We thus decided to pool populations by run-timing group in order to increase samples sizes for a more robust analysis. We used Multivariate Analysis of Variance (MANOVA) to explore physiological differences among run-timing groups at time of capture. Variables included in the MANOVA models were: [glu], [lactate], osmolality, [cortisol] and gill Na^+,K^+-ATPase. Excluded from MANOVA models were variables known to vary fundamentally between the sexes (e.g. [T], [E_2], FL). We followed these MANOVAs with a series of one-way Analyses Of Covariance (ANCOVA), with group as the main effect and Julian date as a covariate, to identify the relative importance of individual variables underlying multivariate relationships and to account for any variation due to sampling date as fish were captured over a 6-day period. The sexes were analyzed separately. A posteriori tests were used to identify populations that differed when an ANCOVA model was significant. In this way, we examined the initial physiology of the three run-timing groups upon capture.

With respect to the telemetered fish, we examined physiological differences between fish that successfully reached the first acoustic receiver line at QCS and those that did not. A two-factor ANCOVA was used, in which fate (i.e. detected vs. non-detected) and run-timing group were primary and secondary factors respectively, and Julian date the covariate. We also compared travel times between the Rennell Sound and QCS among hormonally treated and control/sham groups. Finally, we conducted a series of Pearson's correlation analyses to assess relationships between travel times from the point of release to specific acoustic receiver locations and physiological variables.

All analyses were conduced using JMP 4.0. Because of multiple comparisons, we conducted Bonferroni corrections to minimize the potential for Type II errors. Due to the high conservatism of Bonferroni corrections, we indicate significance at $\alpha = 0.05$, 0.01 and at Bonferroni corrected levels allowing readers to define for themselves which levels are most biologically meaningful. Prior to analyses, all physiological data were $\log_{10}$ transformed to reduce heteroscedasticity.

Results

Fish capture

In total, we biopsied, tagged and released 196 sockeye salmon: 59% were from Late Summer-run populations bound for the Fraser River ($N = 116$: 78 males, 36 females, 2 unknown), 21% were from Fraser River Summer-run populations ($N = 41$: 28 males, 13 females) and 16% were from Fraser River Early Summer-run populations ($N = 31$: 18 males, 12 females, 1 unknown). Only 4% ($N = 8$) were from populations bound for other watersheds (i.e. central British Columbia coast or Puget Sound in Washington State) or were unidentifiable. Six populations comprised 93.5% of all the Fraser River samples with Adams sockeye dominating the total (59%). We limited statistical analyses to the run-timing groups which contained the largest six populations: Scotch (Early Summer-run), Birkenhead (Summer-run), Chilko (Summer-run), Horsefly (Summer-run), Stellako (Summer-run) and Adams (Late-run). DNA analyses on our sacrificed proxy fish revealed that four fish were Early Summer-run (males), eight were Summer-run (3 males, 5 females) and 22 were Late-run (10 males, 12 females).

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Baseline physiology

We found no significant differences among the three run-timing groups in plasma [Na^+], [Cl^-], [glu], [lactate], [cortisol], and gill Na^+,K^+-ATPase activity (MANOVA, Wilks' λ $F = 1.701, p = 0.054, N = 164$). When the sexes were analyzed separately, the strongest physiological difference among run-timing groups was in male [T] ($p = 0.003, N = 113$; Table 1) with Early Summer-run fish having nearly twice the circulating levels as the other groups. Plasma [Cl^-] also differed among timing groups ($p = 0.03, N = 174$; Table 1) with Early Summer-run fish having lower concentrations than Late Summer-run fish. Only gill Na^+,K^+-ATPase activity and [T] showed significant, negative associations with Julian date (ANCOVA, all $p < 0.001$; Table 1).

GSE levels estimated from co-migrating sockeye which were sacrificed did not differ by sex ($p = 0.464$). Using data pooled between sexes, run-timing groups differed ($p = 0.006$) with Early Summer-run sockeye having less somatic energy than either Summer-run or Late Summer-run sockeye; the latter two groups did not differ (Table 1). Testes masses differed among timing groups ($p = 0.010$) with those from Early Summer-run males being 62% heavier than those from Summer-run fish and 95% heavier than those from Late Summer-run fish (Table 1). Ovary masses did not significantly differ among timing groups ($p = 0.064$), though the trend was only marginally non-significant and similar to that observed in male gonads. Early Summer-run females had ovaries that were 51 and 30% heavier than Summer-run and Late Summer-run females, respectively (Table 1).

Hormone treatments, travel times and fate

In total, 60% of all the transmitter carrying sockeye received hormone implants (GnRH or GnRH+T), whereas 40% received either shams or were controls. At the time of implantation, we did not know the population or run-timing group of any individuals. After DNA analyses were complete, we determined that 31 Early Summer-runs were treated (8 GnRH, 9 GnRH+T, 7 sham, 7 control), 41 Summer-runs were treated (11 GnRH, 14 GnRH+T, 6 sham, 11 control) and 116 Late Summer-runs were treated (42 GnRH, 30 GnRH+T, 11 sham, 33 control).

In total, 7% of tagged Fraser River sockeye ($N = 13$; 7 hormone treated – 3 GnRH, 4 GnRH+T; 6 non-treated – 4 sham, 2 control) reached the northern end of Vancouver Island (Figure 1). Eleven sockeye were detected on the QCS receiver line, one was detected on the LP line and one (GnRH-treated) by-passed detection on the LP line but was detected further south on the JDF line. All detected fish were males. Detections occurred from August 9–17. Of the 12 fish detected on the QCS and LP lines, 31% ($N = 4$: 2 hormone treated – 1 GnRH, 1 GnRH+T; 2 non-treated – both sham) were detected on the SSOG line and entered the Fraser River. Because of the small sample size of fish which were detected on acoustic lines, we pooled run-timing groups for subsequent analyses and focused attention on salmon that were 'detected' on the first acoustic lines (QCS or LP lines) and compared them to salmon that were 'not detected' on these lines. Also because of small sample sizes, we pooled both treatment groups (GnRH and GnRH+T) into a single 'hormone-treated' group and the sham and control groups into a single 'non-treated' group.

We found no difference in body length-corrected travel times to the first acoustic lines between hormone treated and non-treated fish (ANCOVA, $p = 0.138$). We pooled treated and non-treated fish in order to assess an overall mean ocean

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Table 1. Least squares means (±SEM, N = sample sizes) of energy, size and physiological variables, by run-timing group, of homing Fraser River sockeye salmon (*O. nerka*) captured in Rennell Sound, Queen Charlotte Islands in 2006.

Variables	Run timing group	Least squares mean ± SEM	N	Run timing group p	Julian date p
Gross somatic energy † (MJ kg^{-1})	Early Summer	9.2 ± 0.25[a]	6	0.006**	n/a
	Summer	10.2 ± 0.27[b]	8		
	Late	10.1 ± 0.12[b]	22		
Gonad mass[a] (g)	Early Summer ♀	100.2 ± 14.6	2	0.064	n/a
	Summer ♀	66.4 ± 9.4	5		
	Late ♀	77.2 ± 6.0	12		
	Early Summer ♂	76.1 ± 9.8[a]	4	0.010**	n/a
	Summer ♂	47.0 ± 8.0[b]	3		
	Late ♂	39.0 ± 5.4[b]	10		
Nose to fork length (cm)	Early Summer ♀	57.10 ± 0.67	10	0.866	0.985
	Summer ♀	57.00 ± 0.60	13		
	Late ♀	57.34 ± 0.35	35		
	Early Summer ♂	59.58 ± 0.72	13	0.586	0.551
	Summer ♂	58.99 ± 0.50	27		
	Late ♂	58.78 ± 0.31	73		
Plasma [glu] (mmol L^{-1})	Early Summer	7.21 ± 0.26	24	0.060	0.324
	Summer	7.82 ± 0.19	40		
	Late	7.34 ± 0.11	110		
Plasma [lactate] (mmol L^{-1})	Early Summer	10.97 ± 1.01	24	0.699	0.312
	Summer	11.13 ± 0.73	40		
	Late	11.17 ± 0.44	110		
Plasma [Na^+] (mmol L^{-1})	Early Summer	179.31 ± 2.33	24	0.421	0.780
	Summer	180.88 ± 1.70	40		
	Late	182.35 ± 1.02	110		

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Plasma [Cl^-] ($mmol\,L^{-1}$)	Early Summer	151.77 ± 1.53^{a}	24	0.030*	0.316
	Summer	$153.37 \pm 1.11^{a,b}$	40		
	Late	155.60 ± 0.67^{b}	110		
Plasma osmolality ($mOsm\,kg^{-1}$)	Early Summer	380.96 ± 4.33	24	0.407	0.200
	Summer	382.15 ± 3.16	40		
	Late	386.04 ± 1.90	110		
Gill Na^+,K^+-ATPase ($\mu mol\,ADP\,mg^{-1}\,protein\,h^{-1}$)	Early Summer	3.19 ± 0.43	24	0.279	**<0.001 (–)**
	Summer	3.32 ± 0.33	40		
	Late	3.79 ± 0.19	110		
Plasma [cortisol] ($pg\,mL^{-1}$)	Early Summer	369.67 ± 15.37	24	0.966	0.201
	Summer	373.88 ± 11.54	40		
	Late	370.68 ± 6.94	110		
Plasma [T] ($pg\,mL^{-1}$)	Early Summer ♀	121.00 ± 28.25	10	0.483	**<0.001 (–)**
	Summer ♀	86.78 ± 13.26	13		
	Late ♀	78.51 ± 23.67	35		
	Early Summer ♂	89.01 ± 13.12^{a}	13	**0.003**	**<0.001 (–)**
	Summer ♂	46.33 ± 9.09^{b}	27		
	Late ♂	38.69 ± 5.61^{b}	73		
Plasma [E_2] ($pg\,mL^{-1}$)	Early Summer ♀	4.96 ± 1.52	10	0.215	0.112
	Summer ♀	4.45 ± 1.38	13		
	Late ♀	3.59 ± 0.80	35		

Note: Data were pooled between sexes except where indicated. Estradiol levels were negligible for male fish and were not reported. *p* values from ANCOVAs, where Julian date was a covariate, are presented. The direction of the relationship between Julian date and a given variable, when significant, is indicated by (+) or (–). All variables were $\log_{10}$ transformed prior to analysis. Values marked with a single asterisk indicates significance at $\alpha = 0.05$, and a double asterisk indicates significance at $\alpha = 0.01$. Bold faced values indicate significance at Bonferroni corrected α-values: 0.005 for females, 0.006 for males.

[a]Due to technical difficulties, we could not measure somatic energy or gonad mass in the biopsied fish. Energy and gonad data were collected from sockeye captured on a single date in the middle of our sampling period. The sexes did not differ, so data were pooled.

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

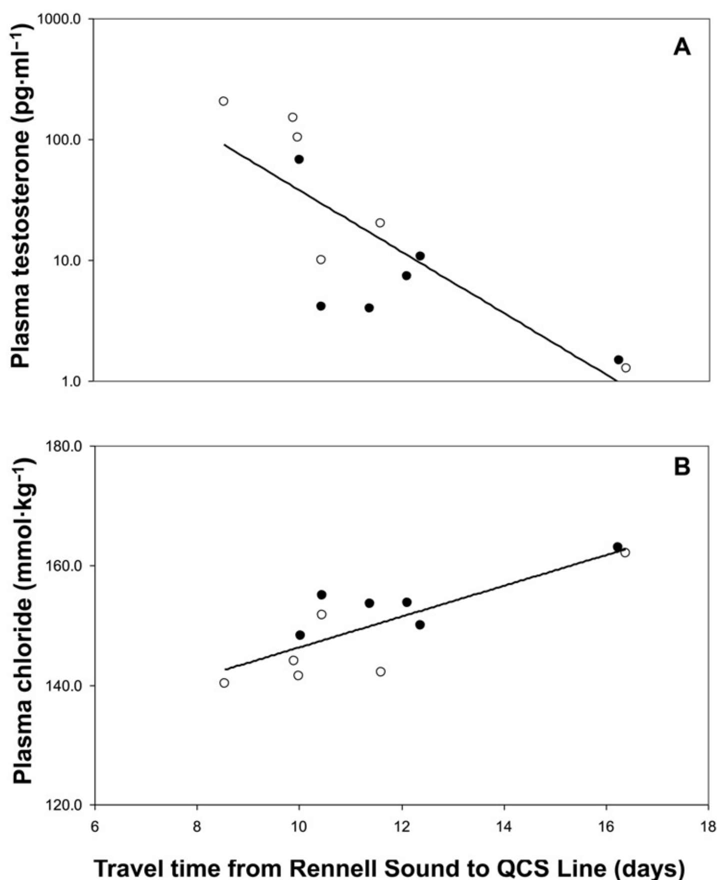


Figure 2. Relationships of plasma testosterone (panel A) and chloride (panel B) with travel times of sockeye salmon after being biopsied, tagged, and hormonally implanted in Rennell Sound, Queen Charlotte Islands. Hormonally treated fish are represented by open circles, and controls are filled circles. The acoustic receiver line at Queen Charlotte Strait (QCS line) was ~470 km from the release locale in Rennell Sound. Due to small samples size, run-timing groups and hormonal treatments were pooled for the analysis. Separate ANCOVAs revealed no significant differences between travel times to QCS by run-timing or hormonal treatment (see Results section).

travel time and migration speed to the first lines (mean travel time $= 11.9$ days ± 0.7 SEM; mean migration speed $= 41.0\,\mathrm{km\,day^{-1}} \pm 0.8$ SEM). The only significant correlations found between travel times of salmon which reached the first acoustic lines and physiological measures at release were with plasma [T] (Pearson's $r = -0.813, p = 0.0013$, $N = 12$) and [Cl^-] (Pearson's $r = 0.817$, $p = 0.0012$, $N = 12$) (Figure 2).

Physiology of 'detected' versus 'not detected' sockeye and effects of handling procedures

There were no physiological differences detected between detected ($N = 13$) and non-detected ($N = 108$) male sockeye (two-factor ANCOVA, all $p > 0.05$), though Julian

date showed strong negative relationships with gill ATPase and plasma testosterone (both $p < 0.001$; Table 2). Analysis was restricted to males as only males were detected in this study.

Because capture and handling can be a potentially stressful experience to fish, we explored the possibility that the large number of 'not detected' fish was caused by our procedures by examining the data distribution for cortisol and lactate concentrations using box and whisker plots for fish that were and were not detected (Figure 3). Generally, 'not detected' fish were more variable in their stress responses having both the highest and lowest cortisol and lactate concentrations. The 25 to 75th percentile range for 'not detected' and 'detected' groups showed considerable overlap for both variables though the range was about 20–30% higher in 'not detected' versus 'detected' groups.

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Discussion

Baseline physiological patterns among run-timing groups

Trade-offs between somatic energy storage and reproductive investment are well documented in Pacific salmon at the beginning of upriver migrations to spawning areas, and these have presumably evolved to balance the varying costs and benefits imposed by migrations (Kinnison et al. 2001, 2003; Hendry et al. 2004). In general, capital breeding salmon show trade-offs that favour somatic energy storage and lead to reductions in gamete production when upriver migrations are long and arduous (Hendry et al. 2004), and these trade-offs have a genetic basis (Kinnison et al. 2001). Generally, and by necessity, sockeye salmon populations travelling the furthest upriver tend to enter the river before those making shorter migrations (Hendry and Berg 1999; Crossin et al. 2004). In this study, we found significant energetic and reproductive differences among population-groups of sockeye salmon from a common watershed at an early stage of homeward migration in the Northeast Pacific Ocean. Furthermore, these differences were detectable at a time when salmon were still actively foraging and presumably free from energetic constraint. Variation in an adaptive life-history trait, specifically freshwater migration timing, was the best explanation for the energetic and reproductive differences we observed.

As predicted, sockeye from populations entering the Fraser River earliest each summer, the Early Summer-run sockeye, were the most reproductively mature as indicated by their circulating [T] and testes (significant, $p = 0.010$) and ovary (marginally non-significant, $p = 0.064$) masses. However, we had predicted that the Early Summer-run fish would have the highest GSE concentrations in preparation for their long and energetically demanding up-river migrations (e.g. Hendry and Berg 1999; Kinnison et al. 2001, 2003; Crossin et al. 2004), but this was not the case. Rather the Early Summer-run fish had lower GSE concentrations than Summer- and Late Summer-run sockeye. If we assume that all fish were feeding maximally, this probably means that the Early Summer-run fish were allocating more somatic energy to gamete production at the time of capture and at that stage of migration than Summer- and Late Summer-run fish. Indeed, the relatively low [T] and the higher GSE concentrations in the Summer- and Late Summer-runs support this suggestion, though the lower somatic energy levels and greater degree of reproductive investment by Early Summer-runs may appear to be in direct conflict with documented patterns

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Table 2. Least squares means (±SEM, N = sample sizes) of size and physiological variables, by fate groups, of homing Fraser River sockeye salmon (*O. nerka*) captured in Rennell Sound, Queen Charlotte Islands in 2006.

Variables	Fate	Least squares mean ± SEM	N	Fate p	Run-timing group	Julian date p
Nose to fork length (cm)	Detected	60.14 ± 0.81	13	0.199	0.951	0.109
	Not detected	58.77 ± 0.25	108			
Plasma [glu] (mmol L^{-1})	Detected	7.64 ± 0.39	13	0.855	0.391	0.121
	Not detected	7.43 ± 0.10	108			
Plasma [lactate] (mmol L^{-1})	Detected	9.56 ± 1.50	13	0.220	0.512	0.135
	Not detected	11.24 ± 0.36	108			
Plasma [Na^+] (mmol L^{-1})	Detected	176.31 ± 3.47	13	0.204	0.747	0.262
	Not detected	182.08 ± 0.84	108			
Plasma [Cl^-] (mmol L^{-1})	Detected	150.99 ± 2.33	13	0.098	0.429	0.064
	Not detected	154.79 ± 0.56	108			
Plasma osmolality (mOsm kg^{-1})	Detected	377.95 ± 6.50	13	0.236	0.554	0.778
	Not detected	384.94 ± 1.57	108			
Gill Na^+,K^+-ATPase (μmol ADP mg^{-1} protein h^{-1})	Detected	4.15 ± 0.71	13	0.083	0.602	**<0.001 (⁻)**
	Not detected	3.68 ± 0.17	108			
Plasma [cortisol] (pg ml^{-1})	Detected	310.28 ± 26.32	13	0.222	0.810	0.381
	Not detected	358.14 ± 17.91	108			
Plasma [T] (pg ml^{-1})	Detected	37.53 ± 15.29	13	0.964	0.026*	**<0.001 (⁻)**
	Not detected	47.33 ± 4.81	108			

Note: Fish fate was based on being 'detected' or 'not detected' on acoustic receivers at northwestern Vancouver Island. GSE was not assessed in these fish. Only male fish were detected and as such the analysis was restricted to males. Estradiol concentrations are negligible in males and are not reported. P values from two-way ANCOVAs, where fate and run-timing groups were main and secondary factors respectively, and Julian date as a covariate, are presented. The direction of the relationship between Julian date and a given variable, when significant, is indicated by (+) or (–). All variables were $\log_{10}$ transformed prior to analysis. Values marked with an asterisk (*) indicates significance at $\alpha = 0.05$ and bold faced values indicate significance at Bonferroni corrected $\alpha = 0.006$.

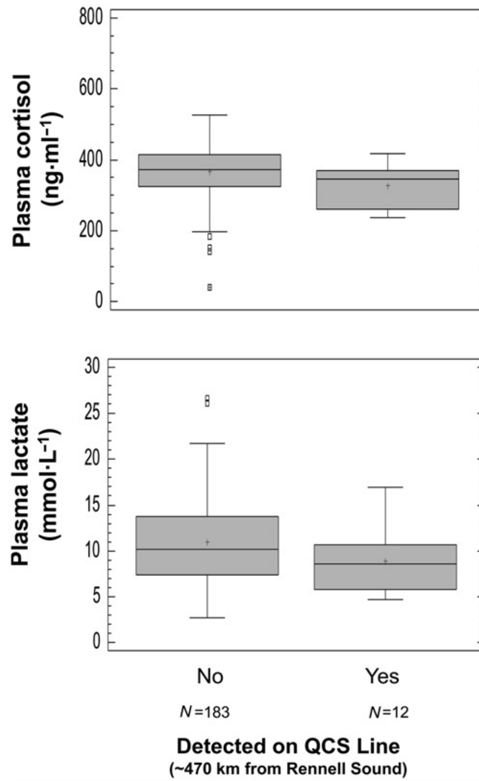


Figure 3. Box and whisker plots showing the mean (small star), median (horizontal line in grey box), the 25 and 75th percentiles (upper and lower lines of grey box), the 5 and 95th percentiles (upper and lower error bars) and extreme data points outside of those ranges, of plasma cortisol and lactate concentrations in sockeye salmon captured in Rennell Sound implanted with acoustic transmitters and detected on acoustic receiver lines long distances from their release locales. 'No' indicates that fish were not detected on that acoustic line and 'Yes' indicates that fish were detected.

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

of reproductive trade-offs that occur when salmon arrive at the river-mouth. For example, upon arrival, Early Summer-run fish (which make comparatively longer upriver migrations that Late Summer-run fish) will ultimately have higher somatic energy concentrations and smaller gonads than Late Summer-run fish due to the energetic demands of longer versus shorter upriver migrations. However, when one considers the chronology of spawning dates among the three groups of fish, it is perhaps expected that the Early Summer-run fish would mature at a faster rate whilst still far at sea and not yet reliant on fixed somatic energy reserves as the Early Summers will ultimately migrate upriver and spawn before the other groups. Thus, the variation we see approximately 850 km from the river mouth is still best explained by life-history variation in river entry timing and ultimately the relative difficulty of river migrations to be made. Despite having larger gonads whilst far at sea, gonads size in the Early Summer-run fish will eventually be overtaken by the Late Summer-run fish which enter the river weeks later than the Early Summer-runs and by association have more time for gamete production (Crossin et al. 2004).

One caveat to our analysis is that the energetic and gonad mass estimates were made on a group of fish separate from the core of our non-lethally biopsied fish. But this was unavoidable for estimation of gonad mass as this required fish dissection. Despite this, we have no reason to expect a bias in our results. The group of energy and gonad proxy fish were captured at the same time and place as the fish from the core of our study, and representatives from all three run-timing groups were present.

Regarding our third prediction, we found some evidence that earlier runs were more osmoregulatorily prepared for entry into freshwater as plasma [Cl^-] were lowest in Early Summer-run fish. However, plasma [Na^+] did not differ among run-timing groups, nor did plasma osmolality or gill Na^+,K^+-ATPase activities, suggesting that the osmoregulatory re-structuring associated with freshwater entry is perhaps not yet fully expressed at this very early stage of migration. Gill ATPase levels in all three run-timing groups were $> 3\,\mu mol\,ADP\,mg^{-1}\,protein\,h^{-1}$, which suggests that all were capable of maintaining effective homeostasis (Hinch et al. 2006). Furthermore, we did not find any differences in plasma metabolites and stress measures (i.e. [glu], [lactate] and [cortisol]) among groups, and mean levels for each were similar to those measured in coastally migrating sockeye in other studies (Cooke et al. 2006a, b; Hinch et al. 2006; Crossin et al. 2007; Crossin et al. 2009a).

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Ocean survival, migration travel times and effects of exogenous GnRH and testosterone

We explored the hypothesis that GnRH and testosterone are important factors controlling the rate of salmon migrations to a natal river. Extending from a wide body of literature on birds, fish and other animals showing fundamental correlations between reproductive hormones and rates of migrations (see Dingle 1996), and from our own previous work with salmon (Cooke et al. 2006a, 2008; Crossin et al. 2007, 2009a), we predicted that sockeye induced to a more reproductively advanced state via exogenous hormones would travel faster through the marine environment than control individuals. Other physiological systems, like the ionoregulatory system, have also been implicated in migration timing (e.g. Crossin et al. 2009a). An experimental test of the effects of hormones would thus be key to identifying the specific proximate mechanisms underlying variation in migratory rates and timing. Despite the small number of fish that were ultimately detected at acoustic receiver stations, the data suggest that hormonal treatment did not accelerate rates of migration between the release locale at Rennell Sound and Vancouver Island, a result which contradicts our hypothesis but which may be due to a Type II error. In fact, the non-hormonal treated control fish had somewhat faster migration rates (i.e. short travel times), though they were not statistically different than the treated fish. Due to small samples sizes however, it was impossible to assess whether population of origin played a role in these results, but it is worth noting the detected fish included control and treated fish from all three run-timing groups.

Irrespective of hormonal treatment, travel times were strongly correlated with initial, pre-treatment testosterone and plasma chloride concentrations; salmon with relatively high testosterone and low chloride levels traveled the fastest. Travel time was not correlated with any of the other metabolite or stress response variable. Initial testosterone was the strongest variable correlated with travel time, which is

what we had predicted. It is thus ironic that treatment with GnRHa and testosterone had no discernable effect. As sockeye depart the open ocean and enter near-coastal, estuarine and then freshwater environments during homeward migration, plasma chloride levels decline in relation to decreasing salinity (Hinch et al. 2006). It is thus possible that the chloride-travel time relationship we observed is a reflection of how ionoregulatory variation within individuals fish affects their preparedness and hence motivation, for migration towards natal rivers. The observed range in initial chloride levels was very similar to that observed from Fraser sockeye captured in the same locale in 2003, the only other year for which data are available (Hinch et al. 2006).

The exceedingly low detection rate and high mortality of biopsied and acoustic tagged sockeye in this study were unexpected. There was no obvious relationship between treatment type and migration success: 13 fish reached northern Vancouver Island (6 non-hormone enhanced, 7 hormone enhanced) and 4 of these fish actually entered the Fraser River (2 non-hormone enhanced, 2 hormone enhanced). We did not expect to see an effect of hormone enhancement on migration survival of sockeye because of the results of a preliminary study we conducted in which we examined the physiological effect of exogenous injections of GnRH and testosterone on reproductive and osmoregulatory physiology of maturing saltwater residing pink salmon (*O. gorbuscha*; Crossin et al. 2009b). In that study, 250 salmon were divided into four treatment groups (GnRH, GnRH+T, T and control/sham) and survival during the nearly 5-month long experiment was $>90\%$ in all treatments groups (Crossin et al. 2009b). Thus, we must look beyond the experimental treatments to the pre-release physiological information and handling procedures, to the environmental conditions during migration and to fisheries exploitation in order to shed light on our results. There were no significant physiological differences between those fish that were detected ($N = 13$) and those that were never detected ($N = 174$) during the study, though the direction of the relationships and the skewed samples sizes between groups suggest that statistical significance may be masked by the large standard errors in fish that were detected. Measures of stress ([lactate], [cortisol]), ionoregulation ([Na^+], [Cl^-], osmolality) and reproductive maturity ([T]) all were trending higher in fish that were undetected, and gill Na^+,K^+-ATPase activities were trending lower. Taken together, this suggests that fish that were undetected (and presumed to have died) were more physiologically stressed, less reproductively advanced, and less ionoregulatorily suited for saltwater migration. We have previously found that ocean migrating sockeye that died before entering freshwater were also relatively stressed and had highly variable measures of osmoregulation (Cooke et al. 2006a, b).

Fisheries were occurring at places and times that overlapped with the position of the tagged sockeye and 4% of our fish were reported as being captured. Fisheries were particularly active at the top end of Vancouver Island where our first acoustic receiver line was positioned (Figure 1). Of the 11 sockeye detected on QCS line, 9 were detected between August 9 and 13, with the other two sockeye detected on August 17. During the 5-day period between the 9 and 13th, over 884,000 sockeye were commercially harvested (unpublished data from Jim Cave, Pacific Salmon Commission, Vancouver, BC). This does not include estimates of Native harvest, which was also occurring. It is thus conceivable that the total harvest of sockeye was in excess of 1 million fish. Native fisheries were also occurring in Rennell Sound at the same time that we were capturing and releasing the fish in this study, and harvest

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

claimed approximately 6000 sockeye. Considering that we released only 196 tagged sockeye over a very narrow window of sampling dates, and given their tendency toward schooling, it is very likely that a large percentage of the undetected fish were lost to harvest. Only a small fraction of our tags were actually returned from fisheries, though the percentages were similar to acoustic tags return percentages from other studies (Crossin et al. 2009a). Predation by marine mammals may also have been a contributing factor but we have no data to assess this possibility.

In conclusion, it seems likely that the low detection of sockeye in this study was due largely to the effects of fisheries harvest, but certainly variation in individual physiological state, environmental stressors, predation and handling have cumulative effects which in this study were unquantifiable. Whatever its causes, we were not able to effectively evaluate the effects of GnRH and testosterone on homing behaviour. The role of these hormones on rates of migratory travel and migrating timing, in general, remains an interesting subject to test.

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Acknowledgements

Field sampling required considerable institutional support and many helpful hands. We thank James Walkus, and the skipper and crew of the *Lahaina Joye*: Ron Johnston, Tony Elliot, Glenn Elliot and Tony Roma. Many thanks to Aswea Porter for her superb management of the telemetry dataset, to Adrian Ladouceur for his techno-carpentry skills and to Norma Ginther for her general organization skills. Also, thanks to the Pacific Salmon Commission, particularly Mike Lapointe, Steve Latham, and Jim Cave, the Environmental Watch program at Fisheries and Oceans Canada and the Census of Marine Life for organization assistance. This work was funded by a grant from the Southern Endowment fund of the Pacific Salmon Commission, and by a National Sciences and Engineering Research Council of Canada (NSERC) Strategic Grant to SGH and APF and others. GTC was supported by an NSERC Canada Graduate Scholarship (CGS-D3).

References

Beacham TD, Lapointe M, Candy JR, McIntosh B, MacConnachie C, Tabata A, Kaukinen K, Deng L, Miller KM, Withler R. 2004. Stock identification of Fraser River sockeye salmon using microsatellites and major histocompatibility complex variation. Trans Am Fish Soc. 133:1117–1137.

Beacham TD, Withler RE, Wood CC. 1995. Stock identification of sockeye salmon by means of minisatellite DNA variation. North Am J Fish Mang. 15:249–265.

Brett R. 1995. Energetics. In: Groot C, Margolis L, editors. Pacific salmon life histories. Vancouver: University of British Columbia Press. p. 1–68.

Burgner RL. 1991. Life history of sockeye salmon. In: Groot C, Margolis L, editors. Pacific salmon life histories. Vancouver: University of British Columbia Press. p. 3–117.

Cooke SJ, Crossin GT, Patterson DA, English KK, Hinch SG, Young JL, Alexander R, Healey MC, Van Der Kraak G, Farrell AP. 2005. Coupling non-invasive physiological assessments with telemetry to understand inter-individual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. J Fish Biol. 67:1–17.

Cooke SJ, Hinch SG, Crossin GT, English KK, Lister A, Patterson DA, Healey MC, Farrell AP, Van Der Kraak G, Shrimpton JM. 2008. Physiological correlates of migration behaviour in Late Summer Fraser River sockeye salmon. Behav Ecol. 19:747–758.

Cooke SJ, Hinch SG, Crossin GT, Patterson DA, English KK, Healey MC, Shrimpton JM, Van Der Kraak G, Farrell AP. 2006a. Mechanistic basis of individual mortality in Pacific salmon during spawning migrations. Ecology. 87:1575–1586.

Cooke SJ, Hinch SG, Crossin GT, Patterson DA, English KK, Shrimpton JM, Van Der Kraak G, Farrell AP. 2006b. Physiology of individual Late-run Fraser River sockeye salmon (*Oncorhynchus nerka*) sampled in the ocean correlates with fate during spawning migration. Can J Fish Aquat Sci. 63:1469–1480.

Crossin GT, Hinch SG. 2005. A non-lethal method for assessing the somatic energy content of freely migrating adult Pacific salmon. Trans Am Fish Soc. 134:184–191.

Crossin GT, Hinch SG, Cooke SJ, Cooperman MS, Patterson DA, Welch DW, Hanson KC, Olsson I, English KK, Farrell AP. 2009a. Mechanisms influencing the timing and success of reproductive migration in a capital breeding, semelparous fish species: the sockeye salmon. Physiol Biochem Zool. In press.

Crossin GT, Hinch SG, Cooke SJ, Patterson DA, Lotto AG, Van Der Kraak G, Zohar Y, Klenke U, Farrell AP. 2009b. Testing the synergistic effects of GnRH and testosterone on the reproductive physiology of pre-adult pink salmon. J. Fish Biol. In press.

Crossin GT, Hinch SG, Cooke SJ, Welch DW, Batten SD, Patterson DA, Van Der Kraak G, Shrimpton JM, Farrell AP. 2007. Behaviour and physiology of sockeye salmon homing through coastal waters to a natal river. Mar Biol. 152:905–918.

Crossin GT, Hinch SG, Farrell AP, Higgs DG, Lotto AG, Oakes JD, Healey MC. 2004. Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. J Fish Biol. 65:788–810.

Dingle H. 1996. Migration: the biology of life on the move. Cambridge: Oxford University Press.

Døving KB, Westerberg H, Johnsen PB. 1985. Role of olfaction in the behavioral and neuronal responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. Can J Fish Aquat Sci. 42:1658–1667.

Farrell AP, Gallaugher PE, Fraser J, Pike D, Bowering P, Hadwin AKM, Parkhouse W, Routledge R. 2001. Successful recovery of the physiological status of coho salmon on-board a commercial gillnet vessel by means of a newly designed revival box. Can J Fish Aquat Sci. 58:1932–1946.

Fraser River Action Plan. 1995. Fraser River sockeye salmon. Report prepared by Fraser River action plan, Fishery Management Group, Canadian Department of Fisheries and Oceans, July 1995. 55 pp.

French R, Bilton H, Osako M, Hartt A. 1976. Distribution and origin of sockeye in offshore waters of the North Pacific Ocean. Int N Pac Fish Comm Bull. 34:1–113.

Healey MC. 2000. Pacific salmon migrations in a dynamic ocean. In: Harrison PJ, Parsons TR, editors. Fisheries oceanography: an integrative approach to fisheries ecology and management. Oxford: Blackwell Science. p. 29–54.

Hendry AP, Berg OK. 1999. Secondary sexual characters, energy use, senescence, and the cost of reproduction in sockeye salmon. Can J Zool. 77:1663–1675.

Hendry AP, Bohlin T, Jonsson B, Berg OK. 2004. To sea or not to sea? Anadromy vs. non-anadromy in salmonids. In: Hendry AP, Stearns SC, editors. Evolution illuminated: Salmon and their relatives. New York: Oxford University Press. p. 92–126.

Hinch SG, Cooke SJ, Healey MC, Farrell AP. 2006. Behavioural physiology of fish migrations: salmon as a model approach. In: Sloman K, Balshine S, Wilson R, editors. Fish physiology Vol. 24: behaviour and physiology of fish. San Diego: Elsevier Press. p. 239–295.

Hinch SG, Cooperman MS, Crossin GT, Olsson I. 2007. Investigations to determine the cause of early migration behaviour and magnitude of in-river survival and losses above Mission for adult Late-run Fraser River sockeye. Preliminary Report to the Pacific Salmon Commission Southern Boundary Restoration and Enhancement Fund on research conducted in 2006, p 113.

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010

Houston AH. 1990. Blood and circulation. In: Schreck CB, Moyle PB, editors. Methods for fish biology. Bethesda: American Fisheries Society. p. 273–334.

Kinnison MT, Unwin MJ, Hendry AP, Quinn TP. 2001. Migratory costs and the evolution of egg size and number in introduced and indigenous salmon populations. Evolution. 55:1656–1667.

Kinnison MT, Unwin MJ, Quinn TP. 2003. Migratory costs and contemporary evolution of reproductive allocation in male chinook salmon. J Evol Biol. 16:1257–1269.

Kintama Research Corporation. 2007. Interim Report: Investigations to determine the cause of early migration behaviour for adult Late-run Fraser River sockeye. Kintama research component report to the Pacific Salmon Commission Contract No. SF-2006-I-32. April 17, 2007.

Kitahashi T, Alok D, Ando H, Kaeriyama M, Zohar Y, Ueda H, Urano A. 1998. GnRH analog stimulates gonadotropin I gene expression in maturing sockeye salmon. Zool Sci. 15:761–765.

McCormick SD. 1993. Methods for nonlethal gill biopsy and measurement of Na^{+},K^{+}-ATPase activity. Can J Fish Aquat Sci. 50:656–658.

Mylonas CC, Tabata Y, Langer R, Zohar Y. 1995. Preparation and evaluation of polyanhydride microspheres containing gonadotropin-releasing hormone (GnRH), for inducing ovulation and spermiation in fish. J Controlled Release. 35:23–34.

Mylonas CC, Zohar Y. 2001. Use of GnRHa-delivery systems for the control of reproduction in fish. Rev Fish Biol Fisheries. 10:463–491.

Onuma TA, Sato S, Katsumata H, Makino K, Hu W, Jodo A, Davis ND, Dickey JT, Ban M, Ando H, et al. 2009. Activity of the pituitary-gonadal axis is increased prior to the onset of spawning migration of chum salmon. J. Exp. Biol. 212:56–70.

Plate EM, Wood CC, Hawryshyn CW. 1999. GnRH affects activity and jumping frequency in adult sockeye salmon, *Oncorhynchus nerka*. Fish Physiol Biochem. 28:245–248.

Quinn TP, Terahart BA, Groot C. 1989. Migratory orientation and vertical movements of homing adult sockeye salmon, *Oncorhynchus nerka*, in coastal waters. Anim Behav. 37:587–599.

Sato A, Ueda H, Fukaya M, Kaeriyama M, Zohar Y, Urano A, Yamauchi K. 1997. Sexual differences in homing profiles and shortening of homing duration by gonadotropin-releasing hormone analog implantation in lacustrine sockeye salmon (*Oncorhynchus nerka*) in Lake Shikotsu. Zool Sci. 14:1009–1014.

Tanaka H, Takagi Y, Naito Y. 2000. Behavioural thermoregulation of chum salmon during homing migration in coastal waters. J Exp Biol. 203:1825–1833.

Thomson KA, Ingraham WJ, Healey MC, Leblond PH, Groot C, Healey CG. 1992. The influence of ocean currents on latitude of landfall and migration speed of sockeye salmon returning to the Fraser River. Fish Oceanogr. 1:163–179.

Ueda H, Yamauchi K. 1995. Biochemistry of fish migration. In: Hochachka PW, Mommsen TP, editors. Environmental and ecological biochemistry. Amsterdam: Elsevier. p. 265–297.

Young JL, Hinch SG, Cooke SJ, Crossin GT, Patterson DA, Farrell AP, Van Der Kraak G, Lotto AG, Lister A, Healey MC, et al. 2006. Physiological and energetic correlates of *en route* mortality for abnormally early migrating adult sockeye salmon (*Oncorhynchus nerka*) in the Thompson River, British Columbia. Can J Fish Aquat Sci. 63:1067–1077.

Downloaded By: [Canadian Research Knowledge Network] At: 19:38 18 February 2010