High river temperature reduces survival of sockeye salmon (*Oncorhynchus nerka*) approaching spawning grounds and exacerbates female mortality

Eduardo G. Martins, Scott G. Hinch, David A. Patterson, Merran J. Hague, Steven J. Cooke, Kristina M. Miller, David Robichaud, Karl K. English, and Anthony P. Farrell

Abstract: Recent studies have shown that warm temperatures reduce survival of adult migrating sockeye salmon (*Oncorhynchus nerka*), but knowledge gaps exist on where high-temperature-related mortality occurs along the migration and whether females and males are differentially impacted by river temperature. In this study, we monitored 437 radio-tagged Fraser River sockeye salmon and used capture–mark–recapture modelling approaches to investigate whether river thermal conditions differentially influence (*i*) spatial patterns of survival along a 413-km stretch of migration and (*ii*) survival of the sexes. Regardless of water temperature, survival decreased in the river section containing the most hydraulically difficult passages of the migration. However, when water temperature was warm (19 °C), survival decreased even further in the final 186 km of the migration prior to reaching the spawning grounds, particularly in females. Female and male survival differed but only when they experienced warm river temperatures. Under such conditions, the overall freshwater migration survival of males was 1.6 times higher (0.79 ± 0.09 standard error, SE) than that of females (0.50 ± 0.11 SE). As maturing female sockeye salmon maintain higher levels of plasma cortisol compared with males, we suspect that females could be immunocompromised and thus less resistant to pathogens whose rates of development are accelerated by warm temperatures.

Résumé : Des études récentes ont montré que les températures chaudes réduisent la survie des saumons rouges (*Oncorhynchus nerka*) en migration; il existe, cependant, des lacunes dans nos connaissances : on ignore où la mortalité reliée aux températures élevées se produit durant la migration et si les femelles et les mâles sont affectés différemment par la température de la rivière. Notre étude a suivi 437 saumons rouges porteurs d'étiquettes radio du fleuve Fraser et a utilisé une modélisation de type capture–marquage–recapture pour examiner si les conditions thermiques de la rivière affectent différemment (*i*) les patrons spatiaux de survie le long du parcours de migration de 413 km et (*ii*) la survie de chacun des sexes. Indépendamment de la température de l'eau, la survie diminue dans la section du fleuve qui contient les zones de passage de la migration les plus difficiles du point de vue hydraulique. Cependant, lorsque la température de l'eau est élevée (19 °C), la survie diminue encore plus dans les derniers 186 km de la migration, avant d'atteindre les zones de fraie, particulièrement chez les femelles. La survie des femelles et celle des mâles sont différentes, mais seulement lorsque la température de la rivière est élevée. Dans ces conditions, la survie globale des mâles durant leur migration en eau douce est 1,6 fois plus grande (0,79 ± 0,09 erreur standard, SE) que celle des femelles (0,50 ± 0,11 SE). Puisque les saumons rouges femelles durant la

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E.G. Martins. Centre for Applied Conservation Research, Department of Forest Sciences, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada; Fish Ecology and Conservation Physiology Laboratory, Institute of Environmental Science and Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada.
S.G. Hinch. Centre for Applied Conservation Research, Department of Forest Sciences, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada; Institute for Resources, Environment and Sustainability, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.
D.A. Patterson and M.J. Hague.* Fisheries and Oceans Canada, Cooperative Resource Management Institute, School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.
S.J. Cooke. Fish Ecology and Conservation Physiology Laboratory, Institute of Environmental Science and Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada.
K.M. Miller. Fisheries and Oceans Canada, Pacific Biological Station, 3190 Hammond Bay Road, Nanaimo, BC V9T 6N7, Canada.
D. Robichaud and K.K. English. LGL Limited, 9768 Second Street, Sidney, BC V8L 3Y8, Canada.
A.P. Farrell. Department of Zoology and Faculty of Land and Food Systems, The University of British Columbia, Vancouver, BC V6T 1Z4, Canada.

Corresponding author: Eduardo G. Martins (e-mail: egmartins@gmail.com).

*Present address: Pacific Salmon Commission, Vancouver, BC V6E 1B5, Canada.

maturation maintiennent des concentrations plus élevées de cortisol plasmatique que les mâles, nous soupçonnons que les femelles peuvent être immunovulnérables et ainsi moins résistantes aux pathogènes dont les taux de développement sont accélérés par la température chaude.

[Traduit par la Rédaction]

Introduction

Temperature is the most important abiotic factor influencing the physiology of fishes and the pathogenicity of their disease organisms (Fry 1971; Marcogliese 2001). It is thus not surprising that fish are particularly vulnerable to mortality during periods of high water temperatures (Davis 2002). Indeed, several studies conducted on various stocks (i.e., populations or groups of different populations) of sockeye salmon (*Oncorhynchus nerka*) in the northeastern Pacific have shown that warm river temperature (i.e., >18 °C) is associated with high mortality during spawning migrations (e.g., Naughton et al. 2005; Keefer et al. 2008; Martins et al. 2011). Several mechanisms, which may act solely or synergistically, have been proposed as the cause for mortality under warm river temperatures: (*i*) a reduction or collapse of aerobic scope (i.e., the difference between resting and maximal oxygen consumption rates; Farrell et al. 2008), which restricts tolerance to extreme temperatures by limiting a fish's ability to allocate energy to essential tissues (Pörtner 2001); (*ii*) accelerated depletion of finite endogenous energy reserves (Rand et al. 2006), which is associated with an exponential increase in resting metabolism with increasing temperatures (Fry 1971); and (*iii*) accelerated proliferation of pathogens (Crossin et al. 2008; Bradford et al. 2010*b*), which beyond their pathogenicity also impair swimming performance of adult sockeye salmon (Tierney and Farrell 2004).

The numerous sockeye salmon stocks that spawn in the Fraser River (British Columbia, Canada) now encounter warmer water temperatures than any time in the historical record — mean summer water temperature has increased by ~1.8 °C since the 1950s and 13 of the last 20 summers have seen the warmest river temperatures on record (Patterson et al. 2007). Although these recent years of high summer river temperatures have already been associated with high levels of spawning migration mortality in some Fraser River sockeye salmon stocks (Macdonald et al. 2010; Mathes et al. 2010; Martins et al. 2011), no studies to date have investigated whether spatial patterns of migration mortality are influenced by the river thermal condition. In fact, even basic information on whether adult Fraser River sockeye salmon survival varies along migratory routes is limited to a few studies. For example, Hell's Gate Canyon (Fig. 1) in the Fraser River is a notoriously demanding hydraulic challenge for adult migrating sockeye salmon and a locale where substantial mortality can occur for some stocks (Hinch and Rand 1998; Hinch and Bratty 2000). Furthermore, mortality levels of 10% and 15% have been detected in the lower (i.e., 126 km before Hell's Gate) and upper Fraser River (i.e., 366–418 km after Hell's Gate), respectively, among individuals of three stocks that had been radio-tagged in the ocean (Cooke et al. 2006). Understanding how temperature could influence these spatial patterns of survival of adult migrating sockeye salmon is important as it may shed light on whether high temperature causes mortality mainly owing to acute (e.g., a collapse of aerobic scope, in which case mortality should be exacerbated in energetically demanding sections of the migration) or chronic effects (e.g., energy depletion or proliferation of pathogens, in which case survival should be reduced towards the end of the migration).

In recent years, sexual differences in heart morphology and physiology (Clark et al. 2009; Sandblom et al. 2009) and plasma concentrations of stress hormones (Sandblom et al. 2009; Hruska et al. 2010; Roscoe et al. 2011) have been uncovered in maturing Fraser River sockeye salmon, raising the possibility that intersexual variation in mortality occurs during the spawning migration. In fact, several studies where Fraser River sockeye salmon from different stocks were either monitored in the laboratory (Patterson et al. 2004; Nadeau et al. 2010), held in the laboratory and then released to the wild (Crossin et al. 2008), or tracked in the wild (Roscoe et al. 2011) have revealed lower survival for maturing females compared with males (males survive 1.5- to 6-fold better). In the only study where the effects of temperature were investigated, fish were held in tanks at one of two temperatures (10 or 18 °C) for 24 days before being acoustically tagged and released into the river. Analyses of the telemetry data revealed that sexual differences in survival occurred only among fish that had been held at the higher temperature (Crossin et al. 2008). Nevertheless, to our knowledge no study has examined sexual differences in survival of sockeye salmon (or any other Pacific salmon species) en route to spawning grounds in relation to their in-river thermal experience (see Supplementary data[1]), and indeed, in general there appears to be little appreciation for intersexual variation in fisheries research or management (Hanson et al. 2008).

In this study, we coupled biotelemetry and capture–mark–recapture modelling approaches to estimate the effect of river temperature on river section- and sex-specific survival of 437 adult migrating Fraser River sockeye salmon. We focused on the Late Shuswap stock (Fig. 1), which includes the Adams River, Little River, and Late Shuswap populations. The Late Shuswap stock is part of a large multistock complex denoted by fisheries managers as Late-runs because they historically (i.e., 1977–1994) entered the Fraser River in the late summer to early fall. Conservation concerns for the Late-run complex have heightened since 1995, when large segments, including the Late Shuswap stock, advanced their river entry date by 3–6 weeks (Cooke et al. 2004; Hinch 2009). As a result, much of the stock now start their migration at much warmer summer river temperatures, which are ~3–5 °C warmer than what they would encounter under historical timing behaviours (Patterson et al. 2007).

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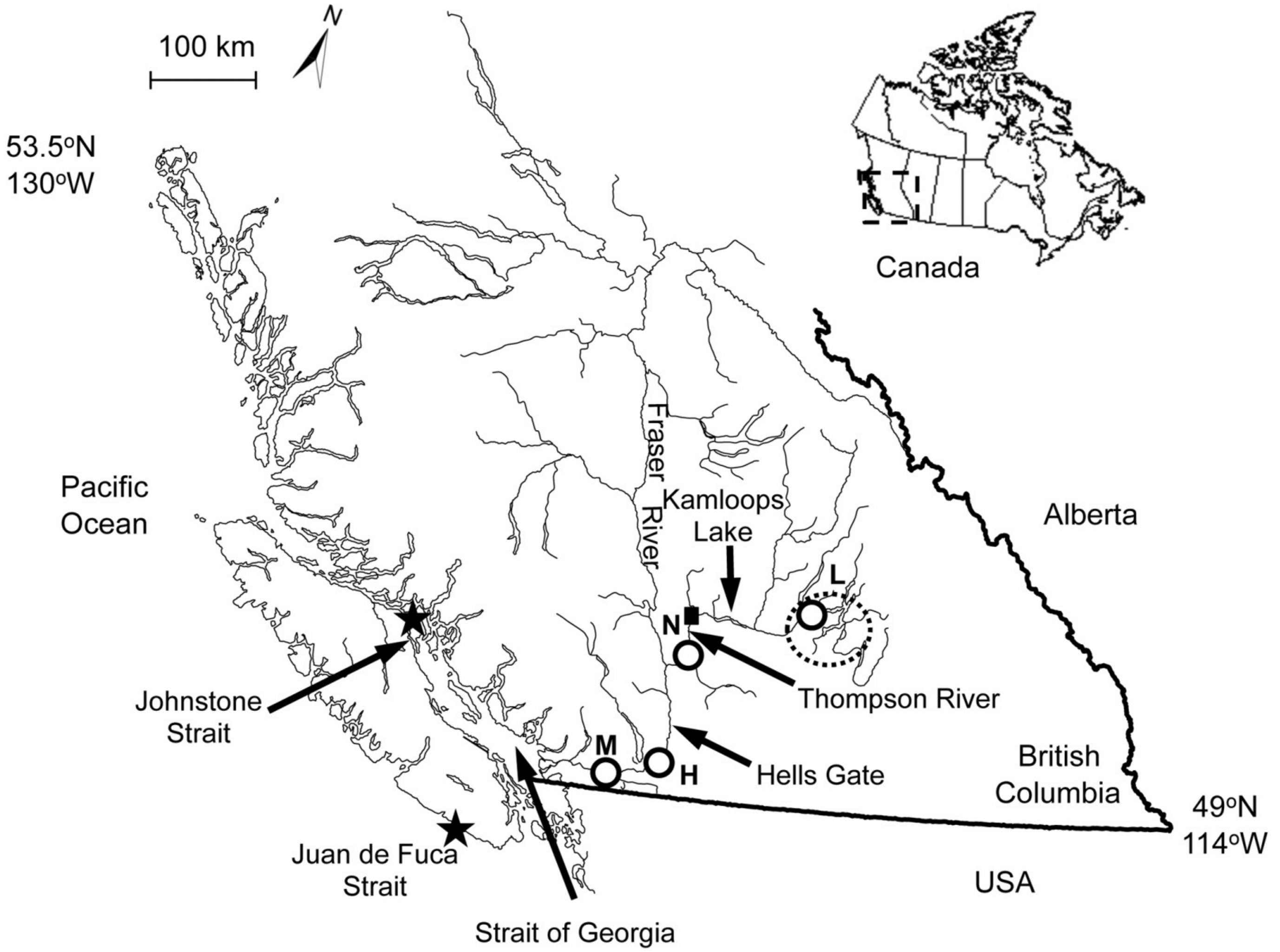
[1] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/f2011-154.

Fig. 1. Map of central and southern British Columbia, with inset of Canada, showing the Fraser River watershed, the approximate locations of the capture–tagging–release sites (filled stars) and the detection stations (open circles: M, Mission; H, Hope; N, Nicola River; L, Little River). Detection data at the Nicola River station was augmented by another station located ~30 km upstream (filled square) in 2003. The location where river temperature was measured is indicated (i.e., Hell's Gate). The dotted ellipse indicates the spawning region for the Late Shuswap stock group.



Although this unusual early-entry behaviour has had the unfortunate consequence of high river mortality (Cooke et al. 2004; Hinch 2009), it has also provided a unique opportunity to test the hypotheses that the river thermal experience influences the spatial pattern of mortality during the spawning migration and sexual differences in migration survival. We predicted that (*i*) survival would decrease in river sections containing areas of difficult passage, (*ii*) survival would be lower for females compared with males, and (*iii*) warm temperatures would exacerbate the spatial and sex effects.

Materials and methods

Capturing and radio-tagging sockeye salmon

The capture and radio-tagging of sockeye salmon in our study has been detailed by Martins et al. (2011). Briefly, adult migrating sockeye salmon were captured, tagged, and released in 2002, 2003, and 2006 at two marine locations, Juan de Fuca and Johnstone Straits, on the west coast of Canada (Fig. 1). Captured individuals were placed in a V-shaped tagging trough where the gills were continuously irrigated with ambient seawater. A radio transmitter (MFCT-3A, 46 mm × 16 mm with a 460 mm × 2 mm antenna, weighing 6.2 g in water, Lotek Wireless, Inc., Newmarket, Ontario, Canada) was orally inserted into the stomach of each fish using a smooth plastic applicator. A 3 mL blood sample was taken from a subset of sockeye salmon to determine sex by measuring plasma concentrations of sex hormones (Fostier et al. 1983; McMaster et al. 1992). As Fraser River sockeye salmon catches consist of individuals from multiple stocks, DNA stock identification analysis was performed on adipose fin clips to ensure all individuals included in our analyses were from the Late Shuswap stock. DNA analysis for stock identification is a standard technique used in fisheries management and research of Fraser River sockeye salmon and overall has 96% accuracy (Beacham et al. 2004). Validation studies have confirmed no regurgitation of radio-tags and no short-term mortality associated with tagging and biopsy procedures of unanaesthetized sockeye salmon (English et al.

2004; Cooke et al. 2005). All protocols were approved by the University of British Columbia Animal Care Committee in accordance with the Canadian Council of Animal Care.

Radio-tracking and data management

Radio-tagged sockeye salmon were tracked during their river migration with fixed receiver stations deployed in strategic locations along the Fraser and Thompson Rivers. Each station consisted of one radio receiver (SRX400, SRX400A, or SRX600, Lotek Wireless, Inc., Newmarket, Ontario, Canada) with two or three antennas (3- or 4-element Yagi, Max, Inc., Hannover Park, Illinois, USA, or Grant Systems Engineering, Inc., King City, Ontario, Canada) placed >10 m above water level. Mobile tracking by foot, boat, and helicopter was also performed in the Late Shuswap spawning region (Fig. 1) using a three-element Maxrad antenna (AF Antronics, Inc., Urbana, Illinois, USA).

Detection data from four receiver stations were used to generate survival estimates for three distinct river sections along the Fraser and Thompson Rivers (Fig. 1): (*i*) the Mission – Hope section (83 km), which is characterized by low elevation gain (0.4 $m \cdot km^{-1}$), no thermal refugia (Donaldson et al. 2009), and high fishing pressure compared with other sections; (*ii*) the Hope – Nicola River section (144 km), which is characterized by high elevation gain (1.3 $m \cdot km^{-1}$), limited thermal refugia (Donaldson et al. 2009), canyon topography with associated constricted passages, complex flows, and high water velocities (e.g., Hell's Gate and Thompson Canyon), and low to moderate fishing pressure; and (*iii*) the Nicola River – Little River section (186 km), which is characterized by intermediate elevation gain (0.7 $m \cdot km^{-1}$), availability of lakes for thermal refugia, and minimal fishing pressure. Temporary gaps in detection owing to operational issues in one of the receiver stations (Nicola River in 2003) were augmented by detection data gathered from a nearby upstream station (Fig. 1). Only those fish passing the detection station at Mission (Fig. 1), located ~290 km from the marine capture–release sites (equivalent to a 13-day migration; Crossin et al. 2007), were included in our analyses. Reported fishery catches of radio-tagged fish upstream of Mission (N = 7 or 1.6% of the fish passing Mission) were removed from the dataset.

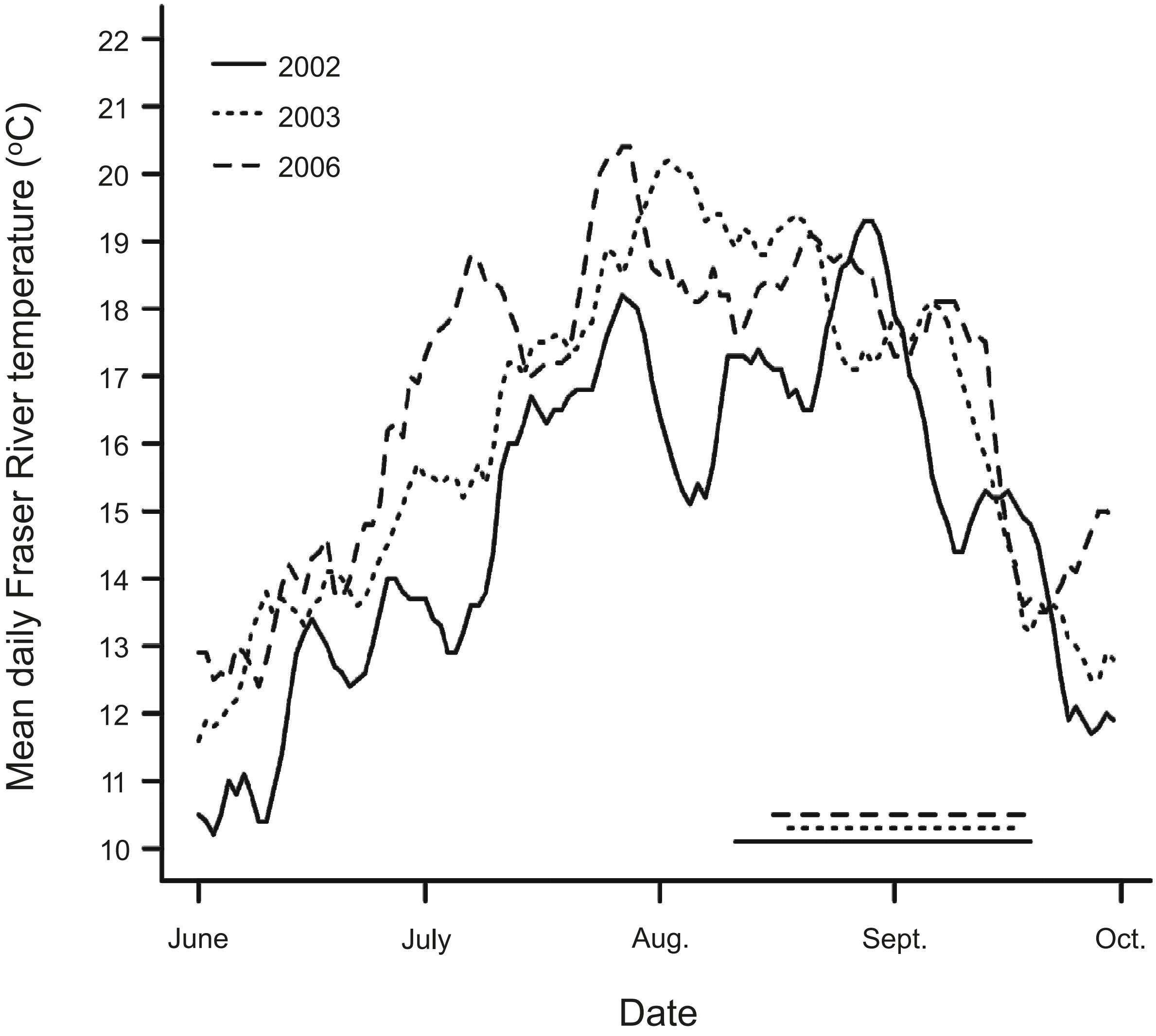
For each fish we recorded the daily mean Fraser River temperature (measured at Hell's Gate, Qualark, located ~50 km upstream of Hope; Fig. 1) on the date of its passage at the Mission station. We used temperature data from the Hell's Gate thermal logger because it provides the most complete and accurate river temperature recordings for the Fraser River mainstem (Patterson et al. 2007). In addition, temperature data from Hell's Gate have been extensively used by management agencies to monitor thermal conditions for migrating salmon (Hague and Patterson 2007; Hague et al. 2008). Daily river temperatures measured in Hell's Gate have been shown to be very similar to those recorded at several other locations in the lower Fraser River (Patterson et al. 2007), and to correlate with temperatures measured at locations further upstream (Hague et al. 2008). Furthermore, using radio-tags equipped with thermal loggers, a recent study revealed that the internal body temperatures of adult migrating Fraser River sockeye salmon were on average within 0.4 °C of the river temperatures measured daily at Hell's Gate (Donaldson et al. 2009). Our preliminary analyses revealed that temperature encountered by radio-tagged sockeye salmon in the lower Fraser River was highly negatively correlated to their date of passage at the Mission station (Pearson's $r = -0.78$, $t = -25.79$, df = 436, $P < 0.001$; Fig. 2). Furthermore, temperature encountered on the date of passage at the Mission station was highly positively correlated to the mean temperature that a surviving fish would have experienced during the migration (Pearson's $r = 0.80$, $t = 28.06$, df = 436, $P < 0.001$; Supplementary data, Fig. S1[1]) — hence it could be used as an index for thermal conditions experienced by our study fish.

Mark–recapture modelling

Condensed forms of the detection history data are presented in the Supplementary data (Tables S1 and S2[1]), which summarize the data in terms of the number of fish detected at station i (R_i) and the number of fish detected at station i that were first redetected at a subsequent station j (m_{ij}) (i.e., m-arrays; Lebreton et al. 1992). The detection history data were analysed using Cormack–Jolly–Seber (CJS) type models, which allow for separate estimation of survival (ϕ) and detection (p) probabilities and their associated variances and covariances (Lebreton et al. 1992). In most applications of CJS-type models, ϕ is an estimate of "apparent survival" as it equals the product between "true survival" (S) and the probability of individuals remaining in the sampling area (i.e., fidelity probability, F; Williams et al. 2001). As straying was rarely observed (one fish in 438 identified as belonging to the Late Shuswap stock) and detection ranges ensured that radio-tagged fish would swim through the area covered by the receiver stations, we assumed that $F \cong 1.0$ and that our estimates of ϕ represent S. It was previously shown that detection probabilities were high and consistent among the receiver stations used here ($p \cong 0.98$) and that there was little variation in detection efficiency across years (English et al. 2004, 2005; Robichaud and English 2007). Consequently, in all model structures for the two sets of candidate models presented below, detection probability was modelled as invariant across stations and years; hereafter models are only referenced by the structure for survival probability. The CJS-type models presented below were constructed and fit in program MARK (White and Burnham 1999). Program MARK estimates survival and detection probabilities, as well as their variances, through maximum-likelihood methods assuming a multinomial distribution of detection histories (White and Burnham 1999; see also Lebreton et al. 1992). Furthermore, survival and detection probabilities can be modelled as a linear function of explanatory variables through a logit link function (Cooch 2001).

The first set of candidate models was used to assess whether survival varied across river sections and years. Temperature (temp) was included in the base model of the first candidate model set (i.e., model S_{temp}) given its established importance for determining the spawning migration survival of Late Shuswap sockeye salmon (Martins et al. 2011). Additional models in the set included the effect of river section (section), year (year), and all possible combinations of variables and second-order interactions among them. A total of 13 models were included in this first set and the general model was represented by $S_{\text{temp} \times \text{section} + \text{temp} \times \text{year} + \text{section} \times \text{year}}$ (note:

Fig. 2. Mean daily water temperature in the Fraser River during the sockeye salmon migration seasons of 2002, 2003, and 2006. Mean daily values were computed from temperature data measured in Hell's Gate, Qualark, ~50 km upstream of the town of Hope. Horizontal lines denote the range of dates that the radio-tagged Late Shuswap sockeye salmon passed at the Mission station.



the model includes both the main effects and interactions, but to simplify notation only the interactions are shown).

To assess whether survival varied by sex, a second set of candidate models was fit to data from a subset of the radio-tagged fish in 2003 and 2006 for which sex information was available (hormone analyses to determine sex were not conducted in 2002). Because the all-fish analysis (described above) revealed no interannual variation in survival and that changes in survival across river sections depended on temperature encountered by the fish in the lower river (see Results), the base model for the analysis of survival by sex included an interaction between temperature and section (i.e., model $S_{\text{temp} \times \text{section}}$). Additional models in the set included the effect of sex and all possible combinations of variables and second-order interactions among them. A total of five models were included in this second set and the general model was represented by $S_{\text{temp} \times \text{section} + \text{temp} \times \text{sex} + \text{section} \times \text{sex}}$.

Statistical analyses

Analysis of variance (ANOVA) was used to compare mean dates of detection and temperature at passage by the Mission station by sex and (or) year. Data normality and homogeneity of variances were assessed graphically and data transformation (i.e., $\log_{10}$ or square-root) was conducted if the data did not meet these assumptions. However, in all cases where assumptions were violated, a nonparametric test had to be used (i.e., Kruskal–Wallis and Friedman tests). The ratio between the number of females and males passing the Mission station in 2003 and 2006 were compared to a 1:1 ratio using a χ^2 test. These analyses were done in R-2.13.1 (R Development Core Team 2011).

Currently, there is no method to assess the goodness-of-fit (GOF) of mark–recapture models including individual covariates (e.g., temperatures experienced by individual fish) to the data. Therefore, GOF was assessed for the most general model excluding temperature effects (White and Burnham 1999), using the parametric bootstrap procedure (1000 replicates) implemented in program MARK. The most general models without temperature effects for the two analyses presented here (models $S_{\text{section} \times \text{year}}$ and $S_{\text{section} \times \text{sex}}$ for the all-fish and sexed-fish analysis, respectively) fit the data satisfactorily (both $P > 0.10$). Evidence of overdispersion (i.e., when the variability in the data is larger than the expected from the model) was found for model $S_{\text{section} \times \text{year}}$ ($\hat{c}$ = 1.69) but not for model $S_{\text{section} \times \text{sex}}$. The estimate of $\hat{c}$ for model $S_{\text{section} \times \text{year}}$ was used to account for overdispersion in model selection (see below) and to correct (i.e., inflate) variances of the survival estimates in the all-fish analysis.

Model selection was conducted using the Akaike information criterion (AIC; Burnham and Anderson 2002). In the all-fish analysis, model selection was done using the AIC adjusted for overdispersion and small sample sizes (QAIC_c), whereas in the sexed-fish analysis it was done using the AIC adjusted for small sample sizes only (AIC_c). For both analyses, the model with the lowest AIC value was identified as the most parsimonious one describing the data. Differences in AIC values (Δ_m) between model m and the most parsimonious model were used to calculate the AIC weights (w_m) of models in each candidate set. The ratio of w_m between any two models was used as a measure of the relative degree to which one model was better supported by the data than another. To account for model selection uncertainty on parameter estimates, model-averaged estimates of survival and associated standard errors were calculated based on the 95% confidence set for the best model (Burnham and Anderson 2002).

Visual inspection of detection histories revealed that all sexed individuals survived the Mission – Hope section (Table S2[1]). Therefore, survival for that section was fixed at 1.0 in the analysis of survival by sex. To control for distance effects on survival and make it possible to directly compare survival among river sections, estimates of survival standardized by the same distance (i.e., 83 km, which is equivalent to a 3-day migration for Late Shuswap fish; Crossin et al. 2007) were obtained by setting the relative section-specific lengths in program MARK. Overall survival during the whole river migration was computed by rescaling survival back to the full length of a river section and then multiplying out the estimates across all sections. Only model-averaged survival estimates for 14 and 19 °C are presented. The former represents temperatures near the median of the historical lower river temperature distribution experienced by the Late Shuswap stock, whereas the latter represents temperature extremes that these fish have encountered since they advanced their river-entry timing (Patterson et al. 2007; Eliason et al. 2011). However, model-averaged survival estimates for the full range of temperatures (13.3–19.4 °C) encountered by the study fish can be found in the Supplementary data (Figs. S2 and S3[1]).

Survival differences among river sections within a year or sex, and among years or between sexes within a river section, were tested using general χ^2 statistics implemented in program CONTRAST (Hines and Sauer 1989). Owing to the conservative nature of critical values corrected for multiple comparisons, particularly under a large number of possible pairwise comparisons, we assessed statistical significance under the classical $\alpha = 0.05$ level. However, we also indicate whether differences were significant after correcting critical values using the false discovery rate (FDR) method (Narum 2006) so that readers can decide for themselves which levels they would use to assess the statistical and biological significance of the differences in survival probabilities presented here. The threshold FDR-corrected values used were $\alpha = 0.012$ and $\alpha = 0.017$ for the all-fish (42 pairwise comparisons) and sexed-fish analysis (10 pairwise comparisons), respectively. Significant differences at the FDR-corrected values are indicated with the symbol ‡ by the P values presented throughout the Results and by the letters in Fig. 3.

Results

Data summary

A total of 437 Late Shuswap sockeye salmon radio-tagged in 2002, 2003, and 2006 passed the Mission station and were included in our analysis. Median dates of passage at the Mission station differed significantly among years (Kruskal–Wallis $H = 49.67$, df = 2, $P < 0.001$) but always occurred in early to mid September, with radio-tagged fish passing the Mission station about 10 days later in 2002 than in 2003 and 2006 (Table 1). The median temperature encountered by the radio-tagged sockeye salmon in the lower Fraser River also differed significantly among years (Kruskal–Wallis $H = 163.11$, df = 2, $P < 0.001$), being about 3 °C and 1 °C warmer in 2006 than in 2002 and 2003, respectively (Table 1).

A total of 184 Late Shuswap sockeye salmon radio-tagged in 2003 and 2006 were sexed. Sex ratios did not differ significantly from 1:1 in either 2003 ($\chi^2 = 3.13$, df = 1, $P = 0.08$) or 2006 ($\chi^2 = 0.11$, df = 1, $P = 0.73$) (Table 1). Mean dates of passage at the Mission station did not differ significantly between years (ANOVA $F = 0.53$, df = 1, $P = 0.47$) or sexes (ANOVA $F = 0.21$, df = 1, $P = 0.65$) and as with the all-fish data it occurred in early September (Table 1). The median temperature encountered by the sexed sockeye salmon in the lower Fraser River was about 1 °C warmer in 2006 than in 2003 (Friedman $F = 29.75$, df = 1, $P < 0.001$) but did not differ significantly between females and males (Friedman $F = 0.08$, df = 1, $P = 0.77$) (Table 1).

Survival by river section

The most parsimonious model fit to the data in the all-fish analysis included an interaction between temperature and river section (Table 2). The models in which survival was invariant across river sections had no support from the data (Table 2). At 14 °C, survival was typically lowest in the middle section of the river (i.e., Hope – Nicola River) but only significantly so in 2002 (Fig. 3*a*). At 19 °C, survival declined as the migration progressed upstream, and survival was significantly lower in the Hope – Nicola River and Nicola River – Little River sections than the Mission – Hope section in all years (Fig. 3*b*). Although the 95% confidence set for the best model included models with year effects, no significant differences were detected among years in any section at either 14 or 19 °C (all $\chi^2 < 0.28$, df = 1, $P > 0.60$). Likewise, the overall freshwater migration survival did not differ significantly among years at either 14 °C (2002: $S = 0.91 \pm 0.05$ standard error, SE; 2003: $S = 0.92 \pm 0.05$ SE; 2006: $S = 0.93 \pm 0.05$ SE) or 19 °C (2002: $S = 0.65 \pm 0.13$ SE; 2003: $S = 0.69 \pm 0.10$ SE; 2006: $S = 0.72 \pm 0.08$ SE) (all $\chi^2 < 0.26$, df = 1, $P > 0.61$). These findings indicate that once the sockeye salmon thermal experience was accounted for in the models there was little variation in migration survival remaining to be explained by the year effect in our study.

Table 1. Dates of detection and temperature experienced at the Mission station by radio-tagged Late Shuswap sockeye salmon in 2002, 2003, and 2006.

Year/Sex	Detection date	Temperature (°C)	Sample size
All fish			
2002	13 Sept. (2 Sept. – 17 Sept.)	15.3 (15.1–17.0)	221
2003	2 Sept. (29 Aug. – 12 Sept.)	17.3 (16.1–17.7)	73
2006	4 Sept. (27 Aug. – 7 Sept.)	18.1 (17.6–18.6)	143
Sexed fish			
2003			
Females	4 Sept. (±8.4 days)	17.2 (15.8–17.7)	29
Males	1 Sept. (±10.2 days)	17.3 (16.1–18.0)	17
2006			
Females	1 Sept. (±8.3 days)	18.1 (17.6–18.8)	71
Males	3 Sept. (±6.8 days)	18.1 (17.8–18.5)	67

Note: Values shown are median (25%–75% percentiles) and mean (±1 standard deviation, SD) for non-normally and normally distributed data, respectively.

Table 2. Model selection statistics summary for models describing survival probability of Late Shuswap sockeye salmon during their spawning migration in the Fraser River in 2002, 2003, and 2006.

Model	QAIC_c	Δ_m	w_m	np_m
$S_{\text{temp} \times \text{section}}$	**355.60**	**0.00**	**0.34**	**7**
$S_{\text{temp} \times \text{section} + \text{year}}$	**356.45**	**0.85**	**0.22**	**9**
$S_{\text{temp} + \text{section}}$	**356.58**	**0.99**	**0.21**	**5**
$S_{\text{temp} + \text{section} + \text{year}}$	**357.21**	**1.61**	**0.15**	**7**
$S_{\text{temp} \times \text{section} + \text{temp} \times \text{year}}$	**360.27**	**4.67**	**0.03**	**11**
$S_{\text{temp} \times \text{year} + \text{section}}$	361.01	5.42	0.02	9
$S_{\text{temp} + \text{section} \times \text{year}}$	361.91	6.31	0.01	11
$S_{\text{temp} \times \text{section} + \text{section} \times \text{year}}$	362.91	7.31	0.01	13
$S_{\text{temp} \times \text{year} + \text{section} \times \text{year}}$	365.69	10.10	0.00	13
$S_{\text{temp} \times \text{section} + \text{temp} \times \text{year} + \text{section} \times \text{year}}$	366.82	11.22	0.00	15
S_{temp}	368.86	13.27	0.00	3
$S_{\text{temp} + \text{year}}$	369.61	14.02	0.00	5
$S_{\text{temp} \times \text{year}}$	373.41	17.82	0.00	7

Note: Models are ranked by increasing order of their QAIC_c value, and models included in the 95% confidence set for the best model are shown in bold. See text for description of QAIC_c, Δ_m, w_m, and variables (i.e., temp, section, and year). np_m is the number of estimable parameters in model m and includes one parameter for the detection probability, p.

Table 3. Model selection statistics summary for models describing survival probability of female and male Late Shuswap sockeye salmon during their spawning migration in the Fraser River in 2003 and 2006.

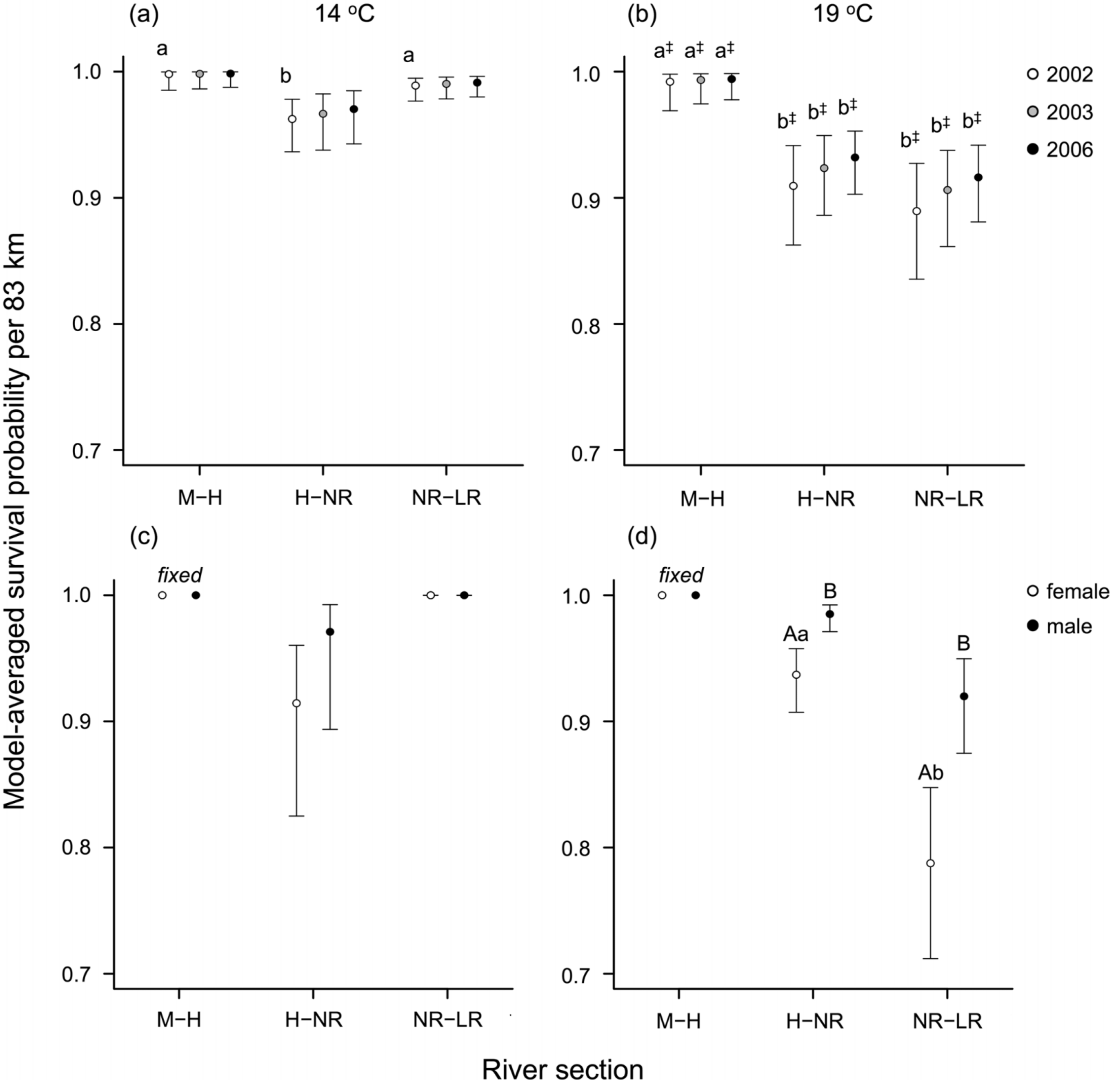
Model	AIC_c	Δ_m	w_m	np_m
$S_{\text{temp} \times \text{section} + \text{sex}}$	**231.61**	**0.00**	**0.45**	**6**
$S_{\text{temp} \times \text{section} + \text{section} \times \text{sex}}$	**232.78**	**1.17**	**0.25**	**7**
$S_{\text{temp} \times \text{section} + \text{temp} \times \text{sex}}$	**233.64**	**2.03**	**0.16**	**7**
$S_{\text{temp} \times \text{section} + \text{temp} \times \text{sex} + \text{section} \times \text{sex}}$	**234.30**	**2.69**	**0.12**	**8**
$S_{\text{temp} \times \text{section}}$	238.49	6.88	0.01	5

Note: Models are ranked by increasing order of their AIC_c value, and models included in the 95% confidence set for the best model are shown in bold. See text for description of AIC_c, Δ_m, w_m, and variables (i.e., temp, section, and sex). np_m is the number of estimable parameters in model m and includes one parameter for the detection probability, p.

Survival by sex

The most parsimonious model fit to the data in the sexed-fish analysis included sex effects in addition to the interaction between temperature and river section (Table 3). This model was 45 times better supported by the data than the equivalent model without sex effects (model $S_{\text{temp} \times \text{section}}$), which was not even included in the 95% confidence set for the best model (Table 3). The pattern of variation in survival of females and males across river sections mirrored that revealed by the all-fish analysis, but it showed a more pronounced pattern of decrease in survival as the migration progressed upstream under warm conditions (compare Fig. 3*a* with 3*c*,

Fig. 3. Model-averaged survival probability estimates (per 83 km) by river section and year (*a*, *b*) and by river section and sex (*c*, *d*) for sockeye salmon experiencing 14 and 19 °C in the lower Fraser River. See Tables 2 and 3 for a list of the models used in the computation of model-averaged estimates. River sections are denoted by M–H (Mission – Hope), H–NR (Hope – Nicola River), and NR–LR (Nicola River – Little River). Lower case letters denote significant differences among river sections within a given year or sex, whereas upper case letters denote significant differences between sexes within a given river section. The symbol ‡ by the letters denote differences that were significant at the FDR-corrected significance level. Error bars are ±1 standard error, SE.



and 3*b* with 3*d*). However, the only significant difference detected was for females at 19 °C, which had lower survival in the Nicola River – Little River section than in the Hope – Nicola River section (Fig. 3*d*). Survival of females and males experiencing 14 °C did not differ significantly in any of the river sections (Fig. 3*c*) or for the overall freshwater migration (females: $S = 0.86 \pm 0.11$ SE; males: $S = 0.95 \pm 0.07$ SE; $\chi^2 = 2.07$, df = 1, $P = 0.15$). In contrast, at 19 °C, survival of females was significantly lower than that of males in both the Hope – Nicola River and Nicola River – Little River sections (Fig. 3*d*). The overall freshwater migration survival at 19 °C was also significantly lower for females ($S = 0.50 \pm 0.11$ SE) than for males ($S = 0.79 \pm 0.09$ SE) ($\chi^2 = 6.38$, df = 1, $P = 0.012^{\ddagger}$).

Discussion

Our findings revealed that survival of adult migrating Late Shuswap sockeye salmon varied across river sections, but the spatial pattern of variability depended on the temperature experienced by fish in the lower Fraser River. For example, survival of fish experiencing 14 °C was consistently high across sections but typically lowest in the middle river section (i.e., Hope – Nicola River section). In contrast, survival of fish experiencing 19 °C was lower overall and decreased monotonically throughout the migration, particularly in females. The decreased survival in the Hope – Nicola River section at both temperatures is consistent with previous work that identified moderate to high levels of mortality in adult migrating sockeye salmon in this hydraulically challenging migratory corridor (e.g., Hinch and Bratty 2000; Cooke et al. 2006). Likewise, the reduced survival in the middle and final river sections of fish experiencing 19 °C is consistent with extensive experimental and field research on the mechanisms by which high temperature affects survival of adult migrating sockeye salmon (e.g., Crossin et al. 2008; Farrell et al. 2008; Bradford et al. 2010*b*). High water temperature reduces aerobic scope and thus limits a fish's ability to swim aerobically through fast water, such as that encountered in the Hope – Nicola River section. This reduction in aerobic scope forces a greater dependence on anaerobic activity, which leads to exhaustion, prolonged recovery times, and potentially mortality (Farrell et al. 2008). Such an acute temperature effect may have been responsible for the further decrease in survival observed at 19 °C in the hydraulically challenging Hope – Nicola River section.

In contrast to acute effects of warm temperature limiting aerobic scope, reduced survival near the end of the migration (i.e., Nicola River – Little River section) for fish experiencing 19 °C was likely caused by the effects of chronic exposure to warm temperatures. Chronic exposure to warm temperature is known to increase the rates of progression of pathogens in sockeye salmon, including the bacteria *Flexibacter columnaris*, the fungi *Saprolegnia* spp., and the myxosporean parasite *Parvicapsula minibicornis* (Gilhousen 1990; Tierney and Farrell 2004; Crossin et al. 2008). *Parvicapsula minibicornis*, for example, is highly prevalent in adult migrating Fraser River sockeye salmon and proliferates much faster under warm temperatures (Jones et al. 2003; Crossin et al. 2008). Advanced stages of infection are associated with severe damage to kidney and gills, with fish losing their ability to osmoregulate and (or) respire (Bradford et al. 2010*a*, 2010*b*). In controlled laboratory conditions, sockeye salmon experimentally infected with *P. minibicornis* started to perish at fast rates ~20 days after exposure (S. Larsson, Umeå University, Umeå, Sweden, unpublished data), an incubation period that corresponds to the approximate length of time our study fish took to approach their spawning area. Although the Nicola River – Little River section includes passage through Kamloops Lake, which offers thermal refugia at depth (Newell and Quinn 2005; Mathes et al. 2010; Roscoe et al. 2010), fish were likely already succumbing to intermediate or advanced stages of infection with *P. minibicornis* and could no longer benefit from cold water refugia in the final stage of migration.

To our knowledge, this is the first study to demonstrate a sex bias in the migration survival of an anadromous Pacific salmon species as a function of river temperatures encountered en route to the spawning grounds. Specifically, we found that female sockeye salmon had lower survival probabilities compared with males when the fish experienced warm temperatures in the lower Fraser River. This finding is consistent with previous work showing that lower female survival occurred only among sockeye salmon that had been held at warm temperatures in the laboratory (Crossin et al. 2008). Sexual differences in sockeye salmon survival at warm river conditions could potentially arise through sex-specific differences in aerobic scope and (or) resistance to pathogens. For example, although there is some evidence that male sockeye salmon maintain higher heart rates while roaming freely on the spawning ground (Clark et al. 2009), a recent study indicated that maturing females have higher heart rates when they are held in captivity (Sandblom et al. 2009). Combined with the female's smaller relative ventricular mass (Clark et al. 2009; Sandblom et al. 2009), these findings indicate that the available scope in cardiovascular oxygen transport is likely reduced in female sockeye salmon in stressful situations, which would make them more susceptible to mortality than the males owing to a temperature-mediated reduction in aerobic scope (Farrell et al. 2008; Sandblom et al. 2009). Moreover, maturing female sockeye salmon maintain significantly higher levels of plasma cortisol (Sandblom et al. 2009; Hruska et al. 2010; Roscoe et al. 2011), which has immunosuppressant effects on fish (Schreck et al. 2001). Therefore, female sockeye salmon could be more immuno-compromised than males during the migration and thus less resistant to infections such as those caused by *P. minibicornis*. Indeed, a general observation is that adult female salmonids are less resistant to pathogens compared with males and often suffer higher infection-related mortality (e.g., Currie and Woo 2008; Tveiten et al. 2010).

Differential mortality between sexes has been documented in other Pacific salmon species. Increases in male:female ratios from juvenile to adult returns have been observed in coho (*Oncorhynchus kisutch*) (Jensen and Hyde 1971; Holtby and Healey 1990; Spidle et al. 1998), Chinook (*Oncorhynchus tshawytshca*) (Olsen et al. 2006), and nonanadromous masu salmon (*Oncorhynchus masou*) (Tamate and Maekawa 2004), indicating female-biased mortality. This bias has been hypothesized to occur towards the end of the ocean residence (or the lake for the nonanadromous masu salmon stock), when females seem to forage more actively than males and presumably become more susceptible to predation or troll fisheries capture (Holtby and Healey 1990; Tamate and Maekawa 2004). Interestingly, the only similar type of study conducted with a Fraser River sockeye salmon stock (Cultus Lake) found opposite changes in sex ratio (1:1 in outmigrating smolts to female-skewed on the spawning grounds), which was attributed to male selectivity of the gill-net fishery and male-biased mortality in the ocean (Foerster 1954). Unlike the present study, none of the above studies have raised the possibility that sex differences in survival occurred during the freshwater stage of the spawning migration. More importantly, if the female-biased mortality under warm river temperatures reported here is a general phenomenon among Pacific salmon, then future climate warming will result in reduced proportions of females on the spawning grounds, which may bring about important consequences for these species.

Ecologically, increased levels of female mortality during the spawning migration could negatively impact the abundance and viability of Pacific salmon stocks because the number of spawning females limits stock abundance (Peterman et al. 2010). This is particularly concerning because even females reaching the spawning grounds after migrating under warm river conditions have a higher probability of dying before spawning (i.e., prespawn mortality; Gilhousen 1990; Keefer et al. 2010). Although it is possible that northern stocks (e.g., from Alaska) have been less impacted by recent warming than southern stocks (e.g., from Washington and British Columbia), which migrate under relatively warmer conditions that are conducive to the rapid development of pathogens (Crossin et al. 2008; Bradford et al. 2010*b*), future warming rates are expected to be higher in more northern latitudes (IPCC 2007). This prospect combined with observations that adult Pacific salmon seem to be locally adapted to the thermal regimes of their migratory rivers (Farrell et al. 2008; Eliason et al. 2011) suggest that adult migrants from northern stocks may be as impacted as those from southern stocks by future climate warming. However, persistent high levels of female mortality during spawning migration will likely increase selection pressure and potentially lead to a combination of behavioural or physiological adaptations. Examples include physiological adaptation to thermal tolerance through increases in aerobic scope capacity (Eliason et al. 2011) and behavioural adaption through changes in migration timing to avoid high temperatures (Reed et al. 2011). There is also the potential for evolutionary consequences for males. The reduced proportions of spawning females could create more intense competition between males for access to females, thus increasing the variance in reproductive success and stronger sexual selection among males (Kvarnemo and Ahnesjö 1996; Clutton-Brock 2007).

The potential ecological and evolutionary consequences of temperature-exacerbated mortality of females point to the need to explore management measures that are cognisant of intersexual (Hanson et al. 2008) and spatial variation in survival to enhance the probability that adequate numbers of females arrive on the spawning grounds. In regulated rivers there are some opportunities to control summer water temperatures through flow management strategies (e.g., Ruochuan et al. 1999; Macdonald et al. 2007) and temperature control devices (e.g., Shasta Dam in California; Nickel et al. 2004). In unregulated rivers where there are very limited options for mitigating against water temperature increases, a simple approach would be to protect lakes and cold water tributaries as these habitats have been shown to be used as refugia by Pacific salmon when temperatures are high (e.g., Newell and Quinn 2005; Goniea et al. 2006; Roscoe et al. 2010); a behaviour that can improve their survival during migration (Mathes et al. 2010). More complex approaches would involve a thorough evaluation of sex bias in catch by gear type, fishing location (both within and among river sections), and timing with subsequent development of new harvest strategies to reduce fisheries impacts on female migrants. We believe that timely incorporation of effective sex-specific strategies into the management of Pacific salmon will help to maintain a balance between harvest and conservation goals of these important species under a warming climate.

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