

# Effects of river temperature and climate warming on stock-specific survival of adult migrating Fraser River sockeye salmon (*Oncorhynchus nerka*)

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## Abstract

Mean summer water temperatures in the Fraser River (British Columbia, Canada) have increased by  $\sim 1.5^\circ\text{C}$  since the 1950s. In recent years, record high river temperatures during spawning migrations of Fraser River sockeye salmon (*Oncorhynchus nerka*) have been associated with high mortality events, raising concerns about long-term viability of the numerous natal stocks faced with climate warming. In this study, the effect of freshwater thermal experience on spawning migration survival was estimated by fitting capture–recapture models to telemetry data collected for 1474 adults (captured in either the ocean or river between 2002 and 2007) from four Fraser River sockeye salmon stock-aggregates (Chilko, Quesnel, Stellako-Late Stuart and Adams). Survival of Adams sockeye salmon was the most impacted by warm temperatures encountered in the lower river, followed by that of Stellako-Late Stuart and Quesnel. In contrast, survival of Chilko fish was insensitive to the encountered river temperature. In all stocks, in-river survival of ocean-captured sockeye salmon was higher than that of river-captured fish and, generally, the difference was more pronounced under warm temperatures. The survival–temperature relationships for ocean-captured fish were used to predict historic (1961–1990) and future (2010–2099) survival under simulated lower river thermal experiences for the Quesnel, Stellako-Late Stuart and Adams stocks. A decrease of 9–16% in survival of all these stocks was predicted by the end of the century if the Fraser River continues to warm as expected. However, the decrease in future survival of Adams sockeye salmon would occur only if fish continue to enter the river abnormally early, towards warmer periods of the summer, as they have done since 1995. The survival estimates and predictions presented here are likely optimistic and emphasize the need to consider stock-specific responses to temperature and climate warming into fisheries management and conservation strategies.

**Keywords:** capture–mark–recapture, climate change, large-scale telemetry, ocean and river capture, Pacific salmon, stochastic simulations, upriver migration

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## Introduction

Recent changes in climate, in particular temperature, have affected ecological processes across a broad range of taxa (IPCC, 2007). Fish are particularly susceptible to climate warming because high temperatures alter the rates of their physiological processes, destabilize the

structure of their macromolecules and accelerate the development of pathogens (Fry, 1971; Marcogliese, 2001; Crockett & Londrville, 2006). Documented population-level responses of fish to warming climates in many regions around the globe include changes in abundance, shifts in the timing of life-history events and shifts in latitudinal and depth distributions (e.g. Sabatés *et al.*, 2006; Pörtner & Knust, 2007; Dulvy *et al.*, 2008; Taylor, 2008). Thus, understanding and predicting the effects of expected future warming trends on these

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organisms have become fundamental challenges for fish and fisheries scientists (Roessig *et al.*, 2004; Harley *et al.*, 2006).

Pacific salmon (*Oncorhynchus* spp.) serve as good biological indicators of the breadth of climate warming effects on fish because their anadromous life cycle exposes them to environmental challenges in both marine and freshwater environments (Fleming & Jensen, 2002). Several studies have suggested that the abundance of Pacific salmon may decline if water temperatures continue to change as predicted by climate models (Levy, 1992; Mote *et al.*, 2003; Bryant, 2009), and particularly as a result of warming river temperatures during spawning migrations (Morrison *et al.*, 2002; Rand *et al.*, 2006; Ferrari *et al.*, 2007; Hague *et al.*, in press). Indeed, warm temperatures during freshwater spawning migrations in recent years have been associated with high mortality rates in some stocks across the Northeast Pacific (Naughton *et al.*, 2005; Crossin *et al.*, 2008; Keefer *et al.*, 2008; Mathes *et al.*, 2010). However, recent physiological studies on adult migrants have suggested that populations (i.e. stocks) within the same species and river system can differ in their thermal tolerance, reflecting local adaptation to temperatures experienced during their historic migrations (Lee *et al.*, 2003; Farrell *et al.*, 2008). Thus, studies are needed that examine stock-specific responses to warming temperatures during spawning migrations.

The spawning migrations of Fraser River sockeye salmon (*Oncorhynchus nerka*) are one of the best studied of any Pacific salmon species (reviewed in Hinch *et al.*, 2006). The numerous sockeye salmon stocks that spawn in the Fraser River vary considerably in thermal exposure (on average 13.6–17.4 °C across stocks) during their spawning migration and now encounter warmer temperatures than in any time since records were kept. In fact, mean summer river temperature has increased by ~1.5 °C since the 1950s and 13 of the last 20 summers have been the warmest on record (Patterson *et al.*, 2007). These recent years of high summer river temperatures have already been associated with extremely high levels of migration mortality in some Fraser River sockeye salmon stocks (MacDonald *et al.*, 2000; Williams, 2005; Farrell *et al.*, 2008). Furthermore, since 1995, several sockeye salmon stocks that used to enter the Fraser River early in the fall have advanced their river migration by 3–6 weeks (Cooke *et al.*, 2004; Hinch, 2009), which has exposed them to peak summer temperatures that are on average ~3 °C higher than what they would normally encounter (Patterson *et al.*, 2007). The reasons for this abnormal behaviour are not fully understood (see Crossin *et al.*, 2007, 2009; Cooke *et al.*, 2008), but the result is that early migrants suffer extremely high river mortality (60–95%, Cooke *et al.*, 2004; Hinch, 2009). In

view of these recent events, an assessment by a panel of experts determined that Fraser River sockeye salmon's adult migrating life stage is the most vulnerable to expected changes in climate (McDaniels T, Wilmot S, Healey M, Hinch S, unpublished results).

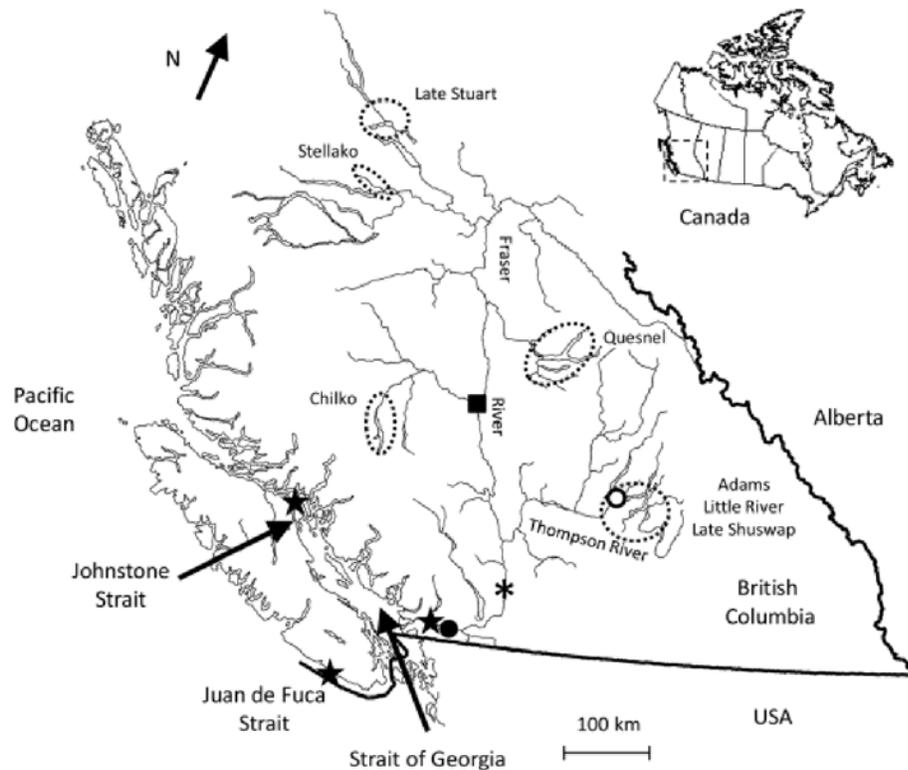
In this paper, our objectives were to determine how the freshwater thermal experience during the spawning migration influences stock-specific survival of Fraser River sockeye salmon and assess how stocks will fare with future warming of the river. We used biotelemetry data collected between 2002 and 2007 for 1474 fish from four stock-aggregates of Fraser River sockeye salmon. Survival rate estimates were obtained using a capture–recapture modelling approach that has been extensively used in studies of birds and mammals but rarely with fish (Burnham, 1993; Pine *et al.*, 2003). We then used stochastic simulations to generate predictions of future survival under a climate change scenario for the Fraser River (Morrison *et al.*, 2002). Given that Fraser River sockeye salmon stocks vary in a number of characteristics that affect their chances of surviving under high temperatures [e.g. energy density (Crossin *et al.*, 2004), optimum temperature for aerobic scope (Lee *et al.*, 2003) and river entry timing and behaviour (Cooke *et al.*, 2004)], we anticipated substantial variation in survival among stocks in response to temperature and climate warming.

## Materials and methods

### Study system

The Fraser River watershed covers nearly one-third of the province of British Columbia (Dorcey 1991; Fig. 1), and is the largest salmon producing system in Canada. The Fraser River mainstem, the longest river (~1378 km) in the province, is free of dams and provides a migration route for >150 sockeye salmon stocks. For fisheries management purposes, these sockeye salmon stocks are aggregated into four groups based on run-timing (i.e. timing of river entry): Early Stuart, Early Summer, Summer and Late runs (Gable & Cox-Rogers, 1993).

In this study, we initially focused on four Summer-run stocks (Chilko, Quesnel, Stellako and Late Stuart) and three Late-run stocks (Adams, Little River and Late Shuswap). However, because the Stellako and Late Stuart stocks enter the Fraser River at approximately the same time, have similar upstream migration routes for most of their journey and experience similar environments in their respective natal watersheds, we grouped them together for the purpose of our analyses. For the same reasons, Adams, Little River and Late Shuswap sockeye salmon were also grouped. There is ample evidence that stocks with similar migration routes and river entry timing do not differ in cardiac morphology and thermal optimum for swimming performance (Lee *et al.*, 2003; E. Eliason, University of British Columbia, unpublished re-



**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), the Mission detection station (filled circle), the last detection station located on the migration route of the Chilko, Quesnel, Stellako-Late Stuart (filled square) and Adams (open circle) stocks, and Hells Gate (asterisk), where river temperature measurements for the lower river were taken. Dotted ellipses indicate approximate spawning regions for the study stocks.

sults); therefore pooling the stocks mentioned above was reasonable as they would be physiologically quite similar. The groupings resulted in four stock-aggregates: Chilko, Quesnel, Stellako-Late Stuart and Adams, and had the added benefit of increasing the sample sizes available for some aggregates.

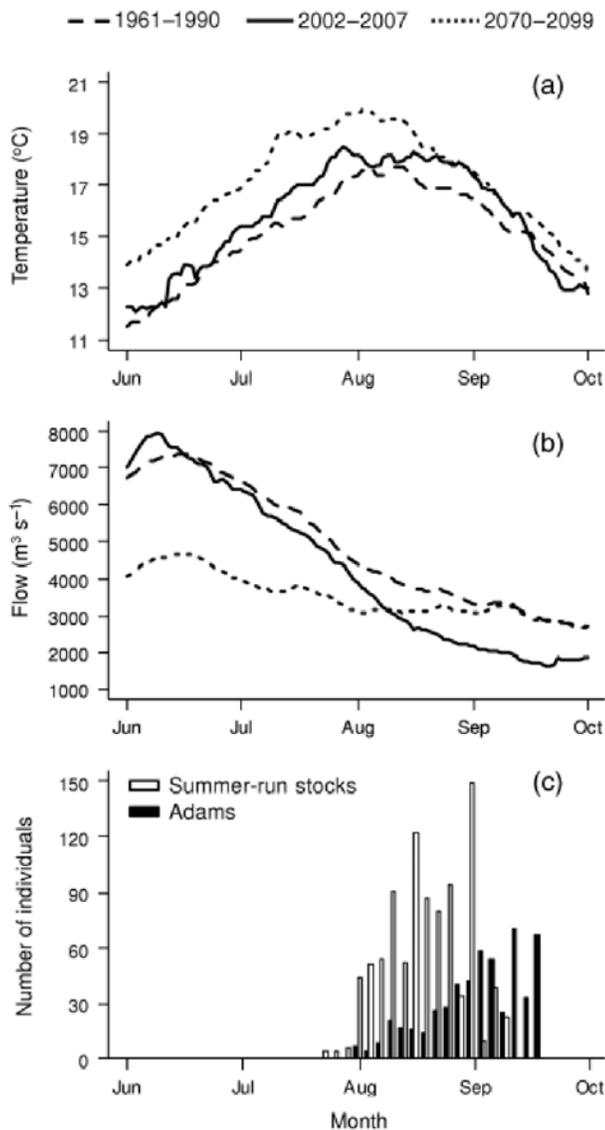
Temperatures encountered in the lower Fraser River by our study stocks can vary substantially, depending on river entry timing. For example, in our study years, most individuals of the Summer-run stocks and a significant proportion of individuals of the Adams stock entered the Fraser River in August, when temperatures in the lower river were at the peak (i.e.  $>17^{\circ}\text{C}$ ; Fig. 2a and c). In contrast, individuals entering the Fraser River in September experienced temperatures as low as  $14^{\circ}\text{C}$  (Fig. 2a and c). Flows, on the other hand, were relatively constant and low during the time window when our study stocks migrated along the lower Fraser River (Fig. 2b and c). Future temperature and flow conditions in the lower Fraser River during the migration season are expected to change with climate warming when compared with the historic period of 1961–1990 (Morrison *et al.*, 2002). For our study stocks in particular (i.e. from mid-July to mid-September), temperatures are expected to be on average  $\sim 2^{\circ}\text{C}$  warmer in the future

under a moderate climate change scenario, while flows are expected to be on average  $\sim 1000\text{ m}^3\text{ s}^{-1}$  lower (Fig. 2).

#### *Capturing and radio-tagging sockeye salmon*

Migrating adult sockeye salmon were captured-tagged-released at three locales: Juan de Fuca and Johnstone Straits in 2002, 2003 and 2006, and  $\sim 70\text{ km}$  upstream of the Fraser River mouth in 2005, 2006 and 2007 (Fig. 1). Marine capture occurred during August on board either test or commercial purse seine fishing vessels (English *et al.*, 2004, 2005; Robichaud & English, 2007). River capture occurred from early August to early September in 2005, early July to early September in 2006 and late June to mid-September in 2007. Salmon were captured in 2005 and 2006 by tangle nets (with a small mesh size to prevent fish from being gilled) and fishwheels in 2007 (Robichaud & English, 2006, 2007; Robichaud *et al.*, 2008).

Only sockeye salmon that were in good external physical condition (i.e. no significant scale loss or seal-induced injuries) and that quickly recovered equilibrium after being transferred to holding totes were selected for radio-tagging. Individuals



**Fig. 2** Average daily (a) temperature and (b) flow experienced by sockeye salmon in the lower Fraser River during the spawning migration season of our study years (i.e. 2002–2007, except 2004). Also shown are the modelled historic (1961–1990) and future (2070–2099) (a) temperature and (b) flow expected for the lower Fraser River [data provided by John Morrison, Fisheries and Oceans Canada; see details of modelling approach in Morrison *et al.* (2002)]. Panel (c) shows the number of individuals of the Summer-run stocks (i.e. Chilko, Quesnel and Stellako-Late Stuart pooled) and Adams stock that were detected at Mission within a 3-day period during the migration season of our study years.

were placed in a V-shaped tagging trough where a tube positioned close to the fish's head provided a constant supply of ambient water. All sockeye salmon were measured (nose-fork length) and had a clip of the adipose fin tissue taken. DNA was extracted from the sampled adipose fin tissue and stock identity was determined using microsatellite and major

histocompatibility complex markers (as per Beacham *et al.*, 2004, 2006). 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 (T. Beacham, Fisheries and Oceans Canada, personal communication; see also Beacham *et al.*, 2004). Although a subset of the sockeye salmon underwent physiological sampling to address other research questions between 2003 and 2007 (i.e. 3 mL blood sample, <4 mm piece of gill filament tips, 5 × 5 mm lateral body muscle piece), physiological sampling did not appear to affect the survival of radio-tagged fish (English *et al.*, 2004; Robichaud & English, 2006, 2007; Robichaud *et al.*, 2008; see also Cooke *et al.*, 2005).

A radio transmitter (16 × 46 mm with a 460 mm antenna, weighing 6.2 g in water; model MFCT-3A, Lotek Wireless Inc., Newmarket, Ontario, Canada) was orally inserted into the stomach of each fish using a smooth plastic applicator. Previous studies on sockeye salmon have not found any evidence that gastric radio-tagging causes mortality, based on experiments where fish are held in pens for 24 h, and reported that fish appeared healthy and vigorous after the holding period (Cooke *et al.*, 2005; English *et al.*, 2005). Moreover, fish did not regurgitate tags during the holding period (Cooke *et al.*, 2005; English *et al.*, 2005), likely because sockeye salmon stop feeding while still in the ocean (and before tagging in our study) and their stomach shrinks, which helps to hold the tag in place (Ramstad & Woody, 2003). Sockeye salmon were held in the water-filled tagging trough for <3 min. Anaesthesia was not used because released fish could be consumed if caught by fishers or other animals. In addition, anaesthesia substantially increases holding and handling time of fish and is rarely used for gastric tagging procedures (Bridger & Booth, 2003). All sampling protocols were approved by the University of British Columbia Animal Care Committee in accordance with the Canadian Council of Animal Care.

#### *Radio-tracking sockeye salmon*

Radio-tagged sockeye salmon were monitored using 16–24 detection stations deployed in strategic locations along the Fraser River. Each detection station consisted of one receiver (models SRX400, SRX400A or SRX600, Lotek Wireless Inc.) with two or three antennas (three- or four-element Yagi, Max Inc., Hannover Park, IL, 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 some years at some spawning regions using a three-element Maxrad antenna (AF Antronics Inc., Urbana, IL, USA). Details on the specific location of the detection stations along with the telemetry data management and analyses procedures are provided in English *et al.* (2004, 2005), Robichaud & English (2006, 2007) and Robichaud *et al.* (2008).

The first detection station encountered by all released salmon was the Mission station (Fig. 1). Any individual not passing this detection station was not included in our analyses. For the Adams stock, survival was estimated from the Mission detection station to a detection station located close to their spawning region, at the bottom end of the Little River

(~413 km from Mission; Fig. 1). Because of logistic issues and a limited budget it was not possible to place detection stations close to the spawning grounds of the Chilko, Quesnel and Stellako-Late Stuart stocks in most of the study years. For the few years when detection stations were placed near their spawning grounds, the number of tagged fish in each stock was insufficient to properly analyse the data. In addition, these terminal detection stations were deployed later in the migration season, raising the possibility that some of our tagged fish would have moved into the spawning grounds before the detection stations were operational. Because of these issues, survival of the Chilko, Quesnel and Stellako-Late Stuart fish was estimated from Mission to the Fraser-Chilcotin confluence (~400 km from Mission; Fig. 1). This stretch of river provides no thermal refugia (i.e. lakes and cold tributaries) for Summer-run stocks (Donaldson *et al.*, 2009), so that any acute effects of temperature on survival are more likely to occur in this portion of their migration. In addition, estimating survival to the Fraser-Chilcotin confluence allowed us to make direct comparisons among the Summer-run stocks. It also allowed us to control for the effect of distance when comparing survival of the Summer-run stocks to that of the Adams stock as the distance travelled by these stocks between detection stations was similar.

Each sockeye salmon was assigned to one of the following three categories: *detected survivor* if detected at the last detection station (a small number of fish undetected at the last detection station but later detected further upstream by other stations or using mobile tracking were also assigned to the *detected survivor* category), *undetected* if not detected at the last detection station (i.e. en route loss, unreported fisheries capture or undetected survivors) and *fishery recovery* if caught and reported by fisheries. The fishery that operates upstream of Mission is carried out by recreational and subsistence (i.e. First Nations) groups using a variety of different gear types. Recovery of radio-tagged sockeye salmon caught in these fisheries was facilitated by a public awareness campaign advertising a small reward to encourage the return of transmitters.

We used river temperature measured on the date of a fish's detection at the Mission station as a predictor of its survival in our models. During preliminary analyses, we found that the temperature measured on the date of detection at the Mission station was highly correlated to the average temperature that a surviving fish encountered in the lower and middle reaches of the river ( $0.75 < \text{Pearson's } r < 0.90$ ,  $P < 0.01$  for all stocks) – hence it could be used as an index for thermal conditions experienced by our study fish. We note however that river temperature values used here were measured at Hells Gate, Qualark, located 135 km upstream of Mission (Fig. 1). We decided to use temperature data from the Hells 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 coming from Hells Gate have been extensively used by researchers to model future Fraser River temperatures and by management agencies to monitor thermal conditions for migrating salmon (Morrison *et al.*, 2002; Hague & Patterson, 2007; Hague *et al.*, 2008, in press). The usefulness of temperatures measured at

Hells Gate as a surrogate for thermal conditions experienced by salmon in the Fraser River mainstem has been validated by several independent studies. Daily river temperatures measured in Hells Gate have been shown to be very similar to those recorded at several other locations in the lower river (Patterson *et al.*, 2007) and to even correlate with temperatures measured at locations further upstream (Hague *et al.*, 2008). Furthermore, using radio-tags equipped with thermal loggers, a recent study has revealed that temperatures experienced by adult migrating sockeye salmon over a stretch of 240 km of the lower and middle Fraser River were not only highly correlated to river temperatures measured daily at Hells Gate, but also were on average only  $< 0.4$  °C cooler than river temperatures (Donaldson *et al.*, 2009).

Although flows can also affect the survival of adult migrating Fraser River sockeye salmon (MacDonald, 2000; Rand *et al.*, 2006), it is more likely to impact the survival of stocks that migrate late in the spring (i.e. Early Stuart-run stocks) and early in the summer (i.e. Early Summer-run stocks), when flows are the highest because of the spring freshet (Fig. 2b). Our study stocks migrate upriver when flows are the lowest during the migration season and under levels that are unlikely to provide any migratory challenge and to greatly affect their survival (i.e.  $< 4500 \text{ m}^3 \text{ s}^{-1}$ ; Fig. 2b; see also Rand *et al.*, 2006). In addition to flow being unlikely to impact survival of our study stocks, we found in our preliminary analyses that it is positively correlated to temperature during the time that our study stocks are migrating upriver (Pearson's  $r = 0.67$ ,  $P < 0.01$ ; see also Fig. 2b). Furthermore, because of the expected advance of the spring freshet with climate warming, flow in the Fraser River is predicted to be on average  $1000 \text{ m}^3 \text{ s}^{-1}$  lower in the future than it has historically been during the time our study stocks migrate upriver (Fig. 2b; see also Morrison *et al.*, 2002). Therefore, only temperature was used as a predictor of survival in our models.

#### Statistical modelling of detection histories

The three categories of sockeye salmon fate were converted to detection histories in the format required by Burnham's model for joint analyses of live recaptures and dead recoveries data (Burnham, 1993). In this study, Burnham's model parameters for survival ( $S$ ), recovery ( $r$ ), fidelity ( $F$ ) and recapture ( $p$ ; here referred to as detection) rates were interpreted as follows.  $S$  is the probability that a sockeye salmon detected at the Mission detection station survives to the last detection station (i.e. Fraser-Chilcotin confluence for the Summer-run stocks and bottom end of Little River for the Adams stock);  $r$  is the proportion of reported fishing mortality that occurred in the fishery operating between the Mission detection station and the last detection station;  $F$  is the probability that a surviving sockeye salmon is at risk of detection by not straying and by swimming through the coverage area of the last detection station;  $p$  is the probability that a surviving sockeye salmon is detected, given that it is at risk of detection by the last detection station. Only survival, recovery and detection rates were modelled here. Fidelity rate was fixed at 1.0 because straying among our study stocks is rare and the detection

range of each station was assessed and adjusted to ensure that radio-tagged sockeye salmon would swim through the area covered by the last detection station (see English *et al.*, 2004, 2005; Robichaud & English, 2006, 2007; Robichaud *et al.*, 2008).

For each individual stock, we fit a number of alternative models to evaluate which set of variables better accounts for variation in survival, recovery and detection rates. Detection rates were constrained to be (with notation in parentheses) either constant (.) or to vary by year (year). Survival and recovery rates were constrained to be either constant (i.e. no effects; [.] ) or to vary by temperature (temp); year (year); temperature and year (temp + year); interaction between temperature and year (temp × year). Preliminary examination of the dataset for 2006, when salmon were captured-tagged-released (hereafter captured) in the ocean and the river, showed that in-river survival of ocean-captured sockeye salmon was higher than that of river-captured fish (see also Robichaud & English, 2007). Therefore, models where survival rates were constrained to vary by the capture environment (capenv) rather than year (i.e. [capenv], [temp + capenv] and [temp × capenv]) were also fit to assess if the capture environment better accounts for annual variation in survival. Similarly, models where recovery rates were constrained to vary by the capture environment rather than year were also assessed.

A total of 128 models generated from all possible combinations of model structures for survival, recovery and detection rates were fit to the data of each stock. Model selection was carried out using the Akaike Information Criterion adjusted for overdispersion (as described below) and small sample sizes (QAIC<sub>c</sub>; Burnham & Anderson, 2002). According to this criterion, the model with the lowest QAIC<sub>c</sub> value is the most parsimonious one describing the data and other models differing from this one in <2, 4–7 and >10 units ( $\Delta_i$ ) are regarded as having substantial, considerably less and essentially no support from the data, respectively (Burnham & Anderson, 2002; see also Richards, 2005).

Currently, there is no available method to assess the goodness-of-fit of capture–recapture models to the data when they include individual covariates (e.g. river temperature experienced by individual fish) (White & Burnham, 1999). Thus, the models were simply checked for estimability problems and an estimate of the overdispersion parameter ( $\hat{c}$ ) of the most parameterized model remaining after model checking was computed by dividing its deviance by its degrees of freedom. This estimate of  $\hat{c}$  was then used to accommodate lack of fit due to overdispersion on model selection and to inflate the variance–covariance matrix of model parameter estimates. Overdispersion parameter estimates obtained the way described above are usually biased high for capture–recapture models but were within an acceptable range for the models used here (i.e.  $1 < \hat{c} < 2$  for all stocks).

The QAIC<sub>c</sub> weight ( $w_i$ ) of the models was also computed and can be interpreted as the probability of a given model in the set being the most parsimonious one to describe the data (Burnham & Anderson, 2002). To account for model selection uncertainty, model-averaged survival and recovery rate estimates and their associated standard errors were computed using the  $w_i$  of the models included in a 95% confidence set for the best model (Burnham & Anderson, 2002). Although we

present only models whose  $\Delta_i < 2$  (i.e. with substantial support from the data), a full list of models included in the 95% confidence set of models for each stock is available online as Supporting Information.

Estimates of model-averaged survival and recovery rates are presented for the range of river temperatures experienced by sockeye salmon of each stock. Model-averaged estimates were computed for both ocean and river-captured fish. However, for the stocks whose 95% confidence set of models also included models with the year effect, model-averaged estimates were computed based on ocean-captured fish and the year with highest survival (best scenario); and on river-captured fish and the year with lowest survival (worst scenario). These scenarios are referred to as ocean-captured and river-captured, respectively. The models were constructed using package RMARK (Laake & Rextad, 2008) in R-2.8.1 (R Development Core Team, 2008) and fit in program MARK (White & Burnham, 1999).

### *Simulating historic and future thermal experience*

To predict the total survival of each of our Fraser River sockeye salmon stocks as a function of temperature, we first simulated their average thermal experience at Mission in a historic and future period. Thermal experience was simulated at the scale of run-timing groups (i.e. Summer and Late-runs) rather than stocks because of data gaps for many years at the stock level. Briefly, for each simulation the shape of the daily run size frequency distribution was specified by performing a parametric (normal) bootstrap of parameters from a mixed-normal model fit to historic run distributions (see Hague & Patterson, 2007 for model structure), while maintaining the parameter covariation structure. Simultaneously, the river entry date (the first date the run was observed at Mission in each year) and the run length (the number of consecutive days over which a run was observed at Mission) were also bootstrapped from normal distributions fit to historic data. The temperature and proportion of the hypothetical run passing Mission on a single day was recorded and used to compute the weighted average temperature experienced by the run in each simulation. This process allowed us to incorporate the uncertainty in temperatures experienced by each run-timing group as a function of interannual variability in the timing and shape of the daily run size frequency distributions.

The distribution of run shape, river entry dates and run length was generated from historic daily run size frequency data collected by a hydro-acoustic facility near Mission and provided by the Pacific Salmon Commission (Vancouver, BC), which in the case of the Summer-run was available from 1977 to 2008. The Adams stock is one of several groups of Late-run sockeye salmon that normally hold for 3–6 weeks in the Fraser River estuary and lower Strait of Georgia (Fig. 1) before entering the river. However, since 1995, large segments of these stocks have forgone this holding behaviour (Cooke *et al.*, 2004). In our analyses of Adams sockeye salmon, we extracted historic data to consider both river entry-timing scenarios. The first scenario, termed *normal-timed*, assumed that Late-run sockeye salmon will resume their historic river

entry timing. This future timing scenario, as well as the historic scenario, was generated using daily run size frequency data from 1977 to 1994, the time period when Late-run sockeye salmon typically exhibited their holding behaviour. The second scenario, termed *early-timed*, assumed that large segments of Late-run sockeye salmon will continue to enter the Fraser River early (i.e. similar to current behaviour), forgoing holding in the Strait of Georgia. The *early-timed* scenario was generated using daily run size frequency data from 1995 to 2008, a period when many Late-run sockeye salmon advanced their river entry.

Historic temperature values used in the simulations of thermal experience were taken from daily modelled mean temperature data in the lower Fraser River from 1961 to 1990 (from Morrison *et al.*, 2002). This time period has been suggested by IPCC as the baseline against which the impacts of future climate change should be assessed (IPCC-TGICA, 2007). Future temperature values under the IPCC IS92a climate change scenario (Leggett *et al.*, 1992) were obtained from daily modelled mean temperature data for the Fraser River from 2010 to 2099 (from Morrison *et al.*, 2002). For each run-timing group, a total of 1000 simulations of weighted average thermal experience at Mission were run for each year of the historic period (1961–1990) and the future period (2010–2099), which was split into three 30-year periods (2010–2039, 2040–2069, 2070–2099) as in Morrison *et al.* (2002).

#### *Simulating historic and future survival*

Predictions of historic and future survival as a function of thermal experience (constructed as described in the previous section) were simulated using the parameter values of the models describing survival of Quesnel, Stellako-Late Stuart and Adams sockeye salmon (simulations were not run for the Chilko stock because its survival was virtually unaffected by temperature; see 'Results and Discussion'). In each simulation, parameters for every model within the 95% confidence set of models of each stock were sampled from a multivariate normal distribution with parameters given by the model parameter estimates and associated variances–covariances (Gelman & Hill, 2006). The sampled parameters of each model were used to compute survival rates for each simulated temperature value of the historic and future periods and survival was then averaged by model  $w_i$ . The process was repeated 1000 times to account for parameter uncertainty in the simulations of survival. Random samples with probabilities given by the simulated model-averaged survival rates were then taken from a binomial distribution and the proportion of successes for each temperature value was computed and used as a prediction of survival (Gelman & Hill, 2006).

The median of the distribution of survival rate predictions was used as the expected historic and future survival rates and the 2.5th and 97.5th quantiles as the limits of the 95% prediction interval. Predictions presented here were based on ocean-captured sockeye salmon, as we assumed their survival rate estimates were less influenced by potential effects of capture stress, which is likely higher in the relatively warmer lower Fraser River (see 'Results and Discussion'). Because we simu-

lated total survival, to facilitate interpretation of results we also made the assumption that mortality due to fishing at any given temperature will be the same between the historic and future periods. All simulations were written in R code and run in R-2.8.1 (R Development Core Team, 2008).

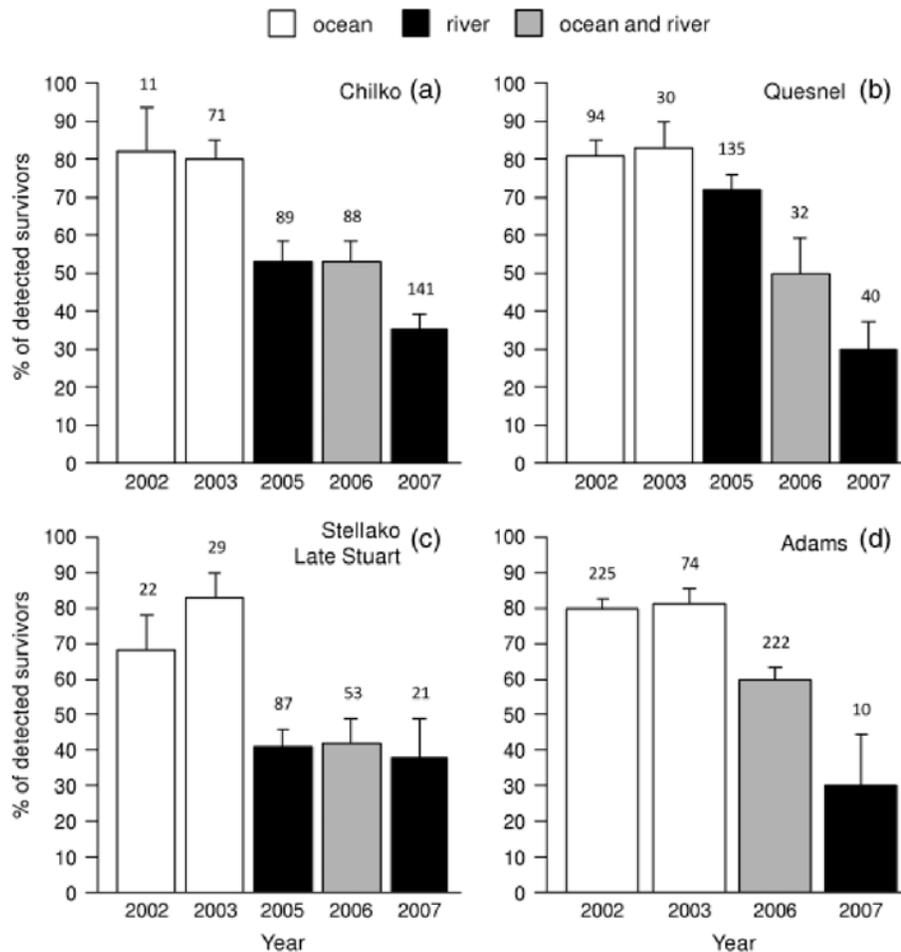
#### **Results**

A total of 3262 sockeye salmon were captured-tagged-released between 2002 and 2007. In this study, 1474 sockeye salmon (400 Chilko, 331 Quesnel, 212 Stellako-Late Stuart and 531 Adams) were known to have passed the Mission detection station and were included in the data set and analyses. Of these totals, 53% Chilko, 68% Quesnel, 50% Stellako-Late Stuart and 71% Adams sockeye salmon were classified as detected survivors, although the exact percentages varied substantially across years (Fig. 3). All stocks had ~70–80% detected survivors in 2002 and 2003 and this percentage dropped in subsequent years, reaching values as low as 30% in 2007 (Fig. 3). As expected given preliminary analyses, the highest percentages of detected survivors were observed in years when capture of salmon was done exclusively in the ocean (Fig. 3).

#### *Survival and recovery rate estimates*

There was substantial support for an effect of temperature on survival rates of sockeye salmon in all stocks (Table 1). However, models with no temperature effects on survival rates were also strongly supported for the Chilko stock (Table 1). For all stocks, variation in survival across years was associated with the capture environment, although models with the year effect on survival rates were also strongly supported for Quesnel sockeye salmon (Table 1). Models with the effect of temperature on recovery rates had substantial support from the data in all stocks, with the exception of Stellako-Late Stuart (Table 1). Models including either the effect of the capture environment (Stellako-Late Stuart and Adams) or no effects on recovery rates (all stocks) were also strongly supported by the data (Table 1).

In all stocks, model-averaged survival rates decreased with increasing temperatures and were higher and less impacted by temperature for ocean-captured sockeye salmon than for river-captured fish (Fig. 4). The Chilko stock had the smallest decrease in survival with increasing temperatures (from 16 to 19 °C: 6% and 23% decrease in survival for ocean and river-captured fish, respectively), followed by Quesnel (10% and 67%), Stellako-Late Stuart (21% and 55%) and Adams (23% and 83%). Model-averaged recovery rates increased with increasing temperatures and were similar for



**Fig. 3** Percentage of sockeye salmon classified as detected survivors between 2002 and 2007 for each one of the (a–d) study stocks. Different shades of grey denote the environment(s) where sockeye salmon were captured-tagged-released in a given year. Error bars denote +1 SE. Sample sizes (i.e. number of sockeye salmon known to have passed the Mission detection station) in each year are indicated on top of error bars.

ocean and river-captured sockeye salmon in all stocks (Fig. 5), with the exception of Stellako-Late Stuart (Fig. 5c). In this stock, model-averaged recovery rates were virtually the same at all temperatures and were higher for ocean-captured sockeye salmon than for river-captured fish – but note the large uncertainty associated with the model-averaged estimate of recovery rates for ocean-captured fish (Fig. 5c).

#### *Predictions of historic and future survival*

The simulations revealed that the expected thermal experience of the Summer-run sockeye salmon may steadily increase from the historic period (1961–1990) into the future (2010–2099), for a total increase of  $\sim 2^\circ\text{C}$  by the end of the century (Fig. 6a). Consequently, the expected survival of Quesnel and Stellako-Late Stuart

sockeye salmon was predicted to decrease into the future by a total of 9% and 16% in 2070–2099, respectively (Fig. 6c). The expected thermal experience and survival of Late-run Adams sockeye salmon were highly sensitive to the entry-timing behaviour assumed in the simulations. If Late-run Adams sockeye salmon resume their historical river entry timing, then the expected temperature experienced by the fish may increase only  $\sim 1^\circ\text{C}$  from 1961–1990 to 2079–2099 (Fig. 6b), and their expected survival may not decrease substantially into the future (Fig. 6d). However, if large segments of the run maintain their current behaviour of early river entry, then their expected thermal experience may increase by a total of  $\sim 5^\circ\text{C}$  from 1961–1990 to 2079–2099 (Fig. 6b), and survival may steadily decrease into the future by a total of  $\sim 16\%$  at the end of the century (Fig. 6d).

**Table 1** Model selection statistics summary for models describing survival, recovery and detection rates of the sockeye salmon stocks examined

Model	QAIC <sub>c</sub>	$\Delta_i$	$w_i$	K
<i>Chilko</i>				
$S_{(\text{capenv})} r_{(\text{temp})} p_{(\cdot)}$	400.74	0.00	0.18	5
$S_{(\text{capenv})} r_{(\cdot)} p_{(\cdot)}$	401.29	0.55	0.14	4
$S_{(\text{temp} + \text{capenv})} r_{(\text{temp})} p_{(\cdot)}$	401.53	0.79	0.12	6
$S_{(\text{temp} + \text{capenv})} r_{(\cdot)} p_{(\cdot)}$	402.07	1.33	0.09	5
<i>Quesnel</i>				
$S_{(\text{temp} + \text{year})} r_{(\cdot)} p_{(\cdot)}$	336.49	0.00	0.27	8
$S_{(\text{temp} + \text{capenv})} r_{(\cdot)} p_{(\text{year})}$	337.84	1.35	0.14	9
$S_{(\text{temp} + \text{year})} r_{(\text{temp})} p_{(\cdot)}$	338.40	1.91	0.10	9
<i>Stellako-Late Stuart</i>				
$S_{(\text{temp} + \text{capenv})} r_{(\cdot)} p_{(\cdot)}$	210.96	0.00	0.23	5
$S_{(\text{temp} + \text{capenv})} r_{(\text{capenv})} p_{(\cdot)}$	211.97	1.01	0.14	6
$S_{(\text{temp} \times \text{capenv})} r_{(\text{capenv})} p_{(\cdot)}$	212.80	1.84	0.09	7
$S_{(\text{temp} \times \text{capenv})} r_{(\cdot)} p_{(\cdot)}$	212.96	2.00	0.08	6
<i>Adams</i>				
$S_{(\text{temp} + \text{capenv})} r_{(\cdot)} p_{(\cdot)}$	487.87	0.00	0.15	5
$S_{(\text{temp} + \text{capenv})} r_{(\text{temp})} p_{(\cdot)}$	487.94	0.07	0.15	6
$S_{(\text{temp} \times \text{capenv})} r_{(\text{temp})} p_{(\cdot)}$	488.99	1.12	0.09	7
$S_{(\text{temp} + \text{capenv})} r_{(\text{temp} + \text{capenv})} p_{(\cdot)}$	489.50	1.63	0.07	7
$S_{(\text{temp} \times \text{capenv})} r_{(\cdot)} p_{(\cdot)}$	489.62	1.75	0.06	6
$S_{(\text{temp} + \text{capenv})} r_{(\cdot)} p_{(\text{year})}$	489.78	1.91	0.06	8
$S_{(\text{temp} + \text{capenv})} r_{(\text{capenv})} p_{(\cdot)}$	489.86	1.99	0.06	6

Models are ranked by increasing order of the QAIC<sub>c</sub> value and only models with  $\Delta_i < 2$  (i.e. substantial support from the data) for each stock are shown. See text for description of QAIC<sub>c</sub>,  $\Delta_i$ ,  $w_i$  and model predictors. K is the number of parameters in the model.

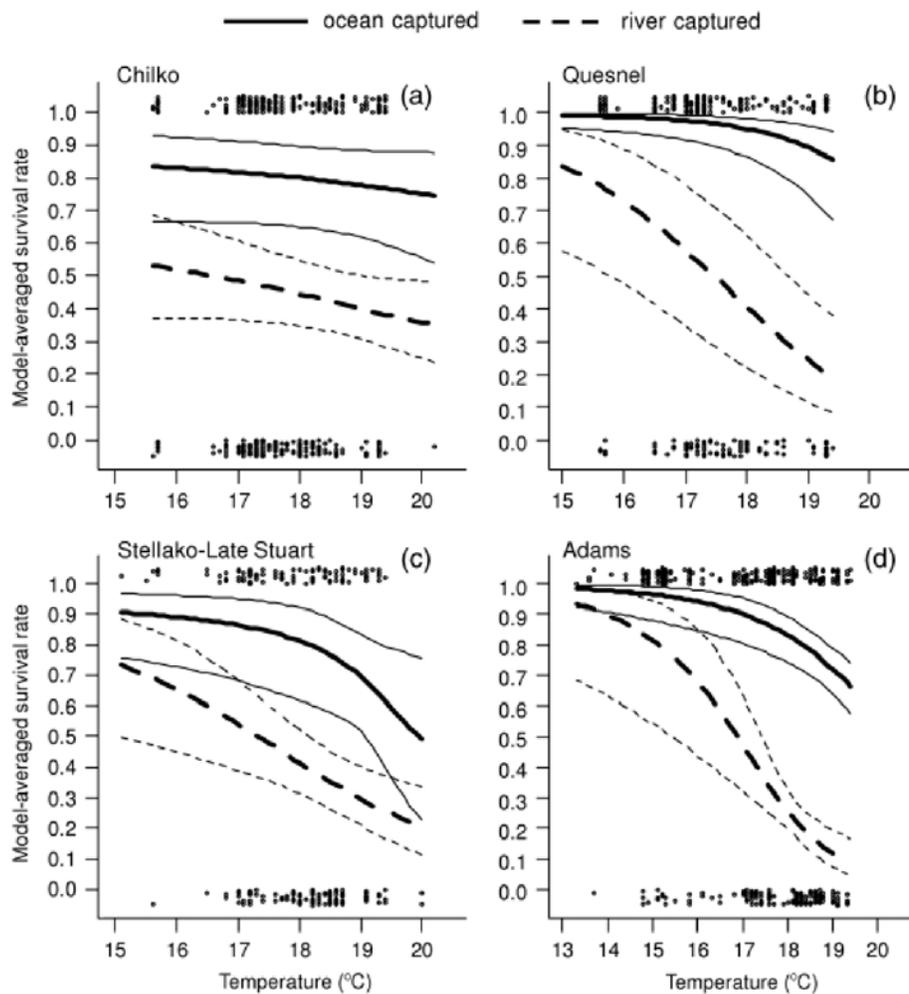
## Discussion

### *Association of temperature with survival and recovery rates*

Overall, river temperatures had a negative effect on survival rates of all stocks examined here, but a positive effect on their recovery rates (with the exception of Stellako-Late Stuart). This positive recovery–temperature relationship for some stocks suggests that sockeye salmon experiencing high temperatures are more susceptible to fisheries capture. Alternatively, this pattern could also be explained by either more frequent fisheries openings or higher fishing effort during warmer periods of the summer. Whichever is the case, the recovery–temperature relationship raises the question of whether the observed decrease in survival with increasing temperatures was caused only by an increase in fisheries-related mortalities at high temperatures. To investigate this possibility for the Chilko, Quesnel and Adams stocks, we first assumed a tag reporting rate of 0.60 (based on some limited data presented in English *et al.*, 2004, 2005; Robichaud & English, 2006, 2007;

Robichaud *et al.*, 2008) and used that to extract the proportion of total mortality that is related to fishing from our recovery rate estimates. We then used the complement of this proportion to calculate the amount of natural mortality from total mortality (Williams *et al.*, 2001). By computing natural mortality at 17 and 19 °C, the temperature range where we observed reported fisheries capture, we found that it did not increase with temperature for Chilko sockeye salmon, but it increased by more than 2.5-fold at 19 °C for Quesnel and Adams fish. These findings suggest that the decrease in survival with increasing temperatures for Chilko fish was indeed caused only by an increase in fishing mortality at high temperatures. On the other hand, the findings suggest that the negative survival–temperature relationship for Quesnel and Adams fish was partially caused by a substantial increase in natural mortality at warmer temperatures. In what follows, we discuss the relative contribution of several potential mechanisms that could be associated with temperature-related mortality in our study stocks – energy depletion, development and virulence of pathogens and reduced aerobic scope (i.e. difference between basal and maximal metabolic rates; Fry, 1971).

Warm river temperatures increase energy consumption by fish and migration failure can occur if sockeye salmon energy reserves fall below a critical threshold (Rand & Hinch, 1998; Rand *et al.*, 2006). Exposure to high water temperatures also increases the rate of development of pathogens in sockeye salmon, causing physiological stress, decreased swimming performance and disease (Gilhousen, 1990; Fagerlund *et al.*, 1995; Wagner *et al.*, 2005). As these two mechanisms act in a cumulative fashion, they are more likely to affect survival in the final stages of the migration. Therefore, temperature-driven energy depletion and pathogen development might not have contributed to our survival estimates for Quesnel and Stellako-Late Stuart sockeye salmon because the last detection station used to classify these fish as survivors was located several hundred kilometres from their spawning grounds. Also, long distance migrants such as Quesnel and Stellako-Late Stuart sockeye salmon have high energy reserves and are energetically efficient swimmers (Crossin *et al.*, 2004), which makes them less likely to run out of energy until the very end of their migration. Mortalities associated with the cumulative effects of temperature were more likely to have occurred in Adams sockeye salmon, whose last detection station was just a short migration from the spawning grounds. In addition, Adams sockeye salmon have the lowest densities of somatic energy and are likely the least energetically efficient swimmers of our study stocks (Crossin *et al.*, 2004).



**Fig. 4** Model-averaged survival rate estimates for the (a–d) sockeye salmon stocks examined. Thick and thin lines denote model-averaged estimates and  $\pm 1$  SE, respectively. Note that data points on the bottom of panels may include a fraction undetected survivors that were classified as en route losses.

Increased mortality at high water temperatures for the Quesnel, Stellako-Late Stuart and Adams stocks could also have been caused by elevated temperature reducing aerobic scope – a mechanism that has been identified as responsible for high en route mortality of Fraser River sockeye salmon in recent, warm years (Farrell *et al.*, 2008). Reductions in aerobic scope that occur above the thermal optimum for swimming performance ( $T_{opt}$ , the temperature where aerobic scope is at the maximum) limit the fish's ability to allocate energy to essential tissues, which restricts whole-animal tolerance to extreme temperatures (Pörtner, 2002; Farrell *et al.*, 2008; Pörtner & Farrell, 2008; Farrell, 2009). Under such circumstances, oxidative stress is enhanced and any further increase in temperature causes insufficient scope to sustain aerobic swimming, leading to anaerobic activity, exhaustion and death by lactic acidosis or

cardiac collapse (Pörtner, 2001, 2002; Farrell, 2002, 2009; Farrell *et al.*, 2008). Although  $T_{opt}$  has not been measured for the Quesnel, Stellako-Late Stuart and Adams stocks, we think that temperatures above  $T_{opt}$  were likely experienced by some individual sockeye salmon of these stocks during our study. Recent studies on other Fraser River sockeye salmon stocks (e.g. Weaver Creek and Seton) have shown that their  $T_{opt}$  was closely related to the historic average temperature experienced during the spawning migration (Lee *et al.*, 2003; Farrell *et al.*, 2008). Assuming that  $T_{opt}$  of the stocks examined here is also related to their historic average thermal experience ( $\sim 17^\circ\text{C}$  for the Quesnel and Stellako-Late Stuart stocks and  $\sim 14^\circ\text{C}$  for the Adams stock), it is clear that many individuals from these stocks may have experienced temperatures above  $T_{opt}$  (see data points in Fig. 4) and that mortalities due to

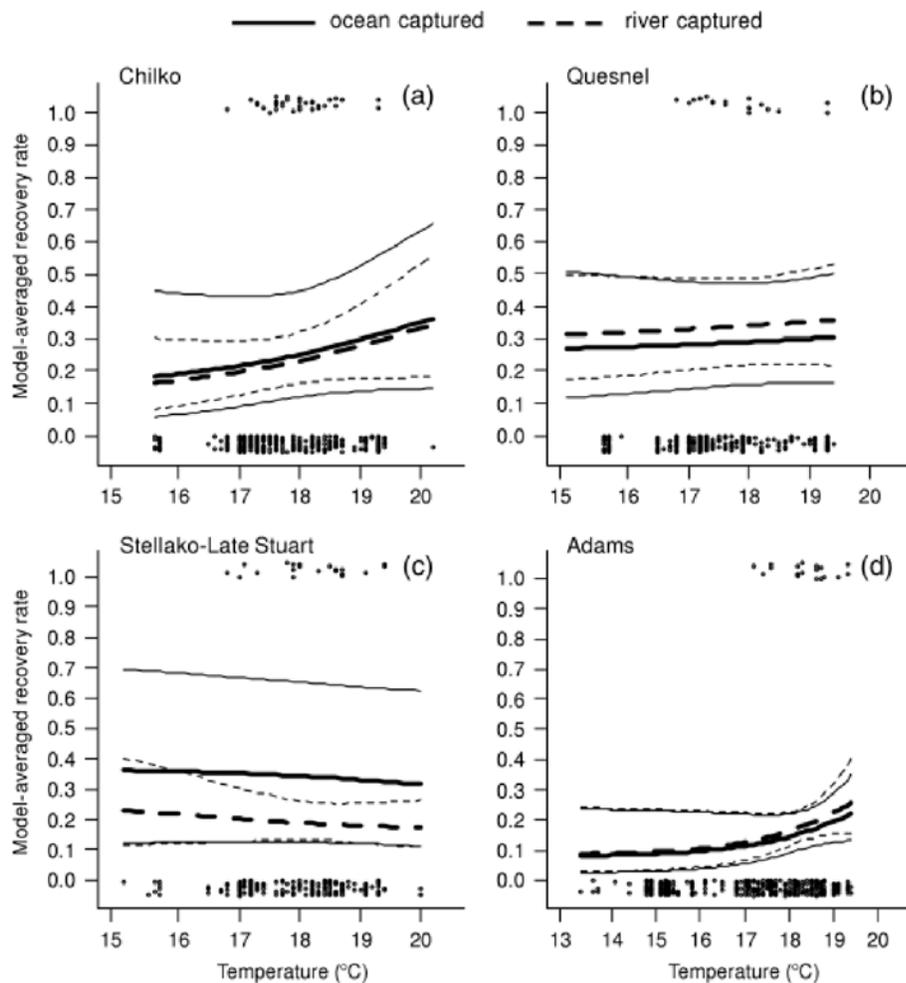


Fig. 5 Model-averaged recovery rate estimates for the (a–d) sockeye salmon stocks examined. Thick and thin lines denote model-averaged estimates and  $\pm 1$  SE, respectively. Note that data points on the bottom of panels may include a fraction of unreported fisheries recoveries that were classified as en route losses.

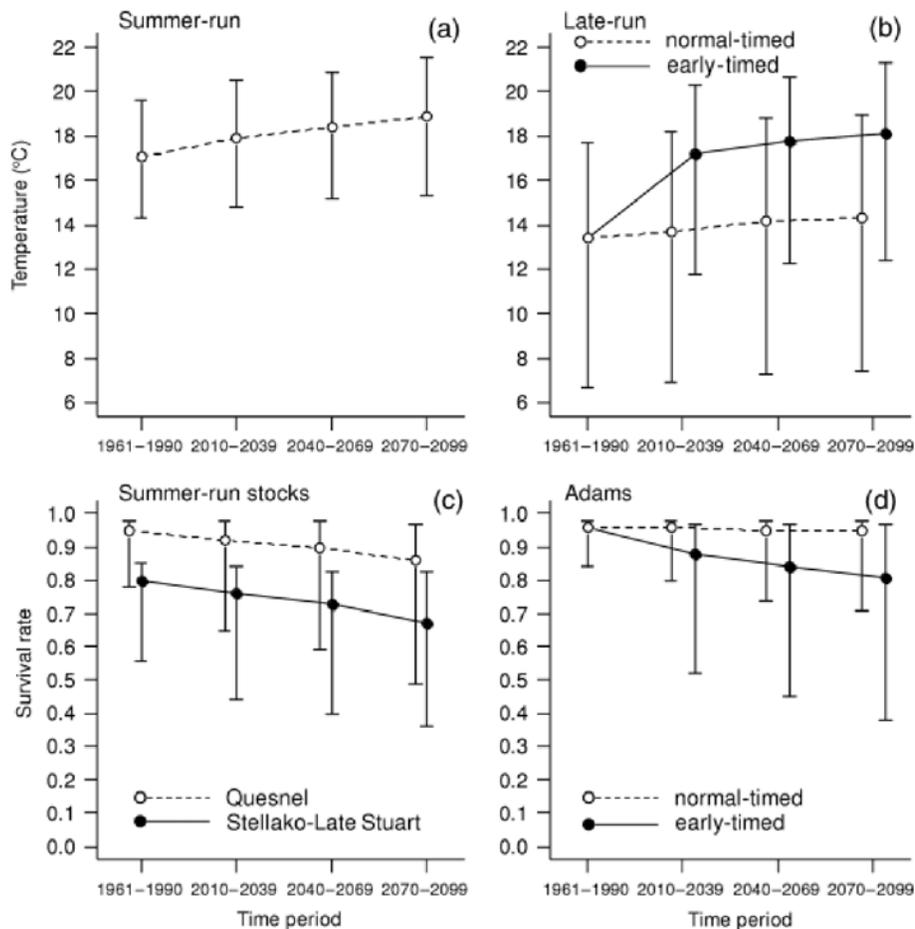
insufficient aerobic scope to sustain migration may have occurred.

Why was the survival of Chilko sockeye salmon insensitive to temperature? As with the Quesnel and Stellako-Late Stuart stocks, any mortality due to energy depletion or development of pathogens induced by temperature would be unlikely to occur before the end of their migration. Nonetheless, we believe the Chilko stock to be behaviourally, morphologically and physiologically unique compared with other Fraser River sockeye salmon stocks. Underwater videography in the wild revealed that Chilko fish are the most energetically efficient swimmers of several Fraser River sockeye salmon stocks (Hinch & Rand, 2000), possessing one of the most fusiform body shapes and investing the least energy into gamete production – thus they are well designed for energy conservation during

migration (Crossin *et al.*, 2004). Furthermore, recent swimming respirometry experiments revealed no thermal dependence of swimming performance and aerobic scope between 12 and 22 °C for Chilko sockeye salmon (E. Eliason, University of British Columbia, unpublished results), implying a broad  $T_{opt}$  that encompasses any temperatures we observed in our study. Therefore, though a reduction in aerobic scope under the high temperatures observed in our study may have contributed to the mortality of Quesnel, Stellako-Late Stuart and Adams sockeye salmon, we would not expect this for a perhaps more eurythermal Chilko fish.

#### *Effect of capture environment on survival*

Ocean-captured sockeye salmon consistently had higher survival rates than river-captured fish across all



**Fig. 6** Simulation results for the thermal experience of (a) Summer and (b) Late-runs and (c, d) for the historic (1961–1990) and future survival (2010–2099) of the sockeye salmon stocks examined. Results for (b) Late-run and (d) Adams stock are presented for normal and early-timed fish. Circles denote the median of the distribution of simulated (a, b) temperatures and (c, d) survival rates. Error bars denote the 95% prediction interval.

stocks and all temperatures experienced on the date of detection at the Mission station. There are two possible explanations for the higher survival of ocean-captured fish, which are not mutually exclusive. The first is related to a general stressor caused by handling and tagging. Previous studies suggest that <10% of mortality following release could be related to handling or tagging and that this mortality would occur within the first 1 or 2 days following release (English *et al.*, 2005; Hinch *et al.*, 2008). Thus, any handling-related deaths in ocean-captured fish would have occurred before reaching the Mission detection station, which is ~290 km, or at least a 6-day migration, from the ocean capture sites. Therefore, our survival rate estimates for ocean-captured fish would reflect only natural and in-river fisheries related mortality. Conversely, survival estimates for river-captured fish were more likely to include mortality related to acute handling and tagging effects because the

river capture site was only 10 km, or less than 1-day migration, from the Mission detection station.

Second, stress-related mortality associated with capture is exacerbated by warm temperature (Wilkie *et al.*, 1996; Kieffer, 2000; Davis, 2002), and this likely occurs because warm temperature enhances baseline stress levels. Indeed, during capture, the river (15–20 °C) was warmer than the ocean (10–13 °C) and the concentration of plasma lactate and glucose, both indicators of physiological stress (Barton, 2002; Iwama *et al.*, 2006), were higher in sockeye salmon captured in the river than in those captured in the ocean in the 2006 spawning migration season (Crossin *et al.*, 2009; Donaldson *et al.*, 2010). Further evidence that warm temperatures in the river enhanced stress-related mortality associated with capture is provided by removing the 10% baseline handling mortality mentioned above from the survival estimates of river-tagged fish at the lowest and warmest

temperatures. By doing so, differences in survival between ocean- and river-tagged Quesnel, Stellako-Late Stuart and Adams fish virtually disappear at the lowest temperatures, but still range between 0.2 and 0.6 across stocks at the warmest temperatures (see Fig. 4b–d).

Baseline stress levels may be further exacerbated in freshwater by the fact that fish are undergoing a major osmoregulatory change while in the lower Fraser River (Shrimpton *et al.*, 2005; Hinch *et al.*, 2006), and presumably by higher relative densities and exposure to pollutants and new pathogens. In addition, salmon were captured in the river using tangle nets and fishwheels, which are presumably more stressful capture methods than purse seine (used to capture fish in the ocean) because fish may get tangled in the net or be confined for long periods at high densities in fishwheels before being handled and released. Thus, poorer survival of river-captured sockeye salmon could be at least partially attributable to stress during capture and handling that is enhanced by a suite of stressors in the freshwater environment and the capture methods.

#### *Model predictions of future survival*

Our simulations showed that future survival of adult migrating Quesnel, Stellako-Late Stuart and Adams sockeye salmon is expected to decrease when compared to the historic period. Contrary to our expectations, the simulations revealed that the magnitude of the decrease in future survival will not vary substantially among these stocks (i.e. between 9% and 16%). However, the expected decrease of 16% in future survival of the Adams stock may be realized only if fish retain their current early river entry timing. This finding emphasizes the importance of river entry timing in mitigating the effects of temperature and future climate warming on survival of adult migrating Fraser River sockeye salmon.

There are two caveats to our modelling of survival rates that likely led to optimistic predictions of future survival. First, our survival estimates only capture a portion of the migration route for the Quesnel and Stellako-Late Stuart sockeye salmon because the last detection station for these fish was located several hundred kilometres from their spawning grounds. Thus, as discussed above, our survival estimates and predictions for Quesnel and Stellako-Late Stuart do not include mortality related to the cumulative effects of temperature (i.e. energy depletion and disease progression), which are more likely to occur towards the end of the migration. Additional temperature-related mortality can also be expected at the end of their migration because these stocks often experience even higher

temperatures upstream of the last detection station (MacDonald *et al.*, 2007).

The second caveat is that the survival models developed here were not parameterized with extreme high river temperatures (i.e.  $>21^{\circ}\text{C}$ ), which are expected to become more frequent in the Fraser River under future climate change. Thus, predictions of future survival rates at temperatures  $>21^{\circ}\text{C}$  required extrapolation beyond the data sets used in fitting our models and this practice likely resulted in optimistically high survival rates. Extreme high temperatures and record daily highs during large segments of the summer occurred in the Fraser River in 2004 but data from that year was not available because broad-scale telemetry was not conducted. In that year, extreme high river temperatures were undoubtedly a significant factor in the high migration mortality observed ( $\sim 57\%$  overall mortality; Williams, 2005), and early migrating Late-run stocks were particularly hard hit – a telemetry study that year on Late-run Weaver Creek sockeye salmon found  $\sim 70\%$  migration mortality (Farrell *et al.*, 2008; Mathes *et al.*, 2010).

These optimistic predictions of survival rates could be realized, however, if sockeye salmon adapt to climate warming (Carlson & Seamons, 2008; Crozier *et al.*, 2008a) and/or with a reduction of in-river harvesting. As we modelled total survival, fishing mortality due to current levels of in-river harvesting is implicit in our estimates and predictions of survival rates. Reducing in-river harvesting could improve future survival of some Fraser River sockeye salmon stocks during spawning migration, provided that mortality due to fishing is noncompensatory (i.e. fishing mortality is additive to natural mortality such that total mortality decreases approximately linearly with reductions in harvesting; Anderson & Burnham, 1976; Williams *et al.*, 2001). Therefore, future studies should investigate how different levels of harvest contribute to total mortality of Fraser River sockeye salmon.

#### **Conclusions**

Our results revealed that the effect of temperature on survival of adult migrating Fraser River sockeye salmon varied among stocks. A surprising and encouraging finding was that survival of Chilko sockeye salmon was insensitive to temperature, although further research is still needed to investigate if temperature affects survival further upstream in their migration. Our simulation results, though likely optimistic, add to a growing body of evidence that survival of adult migrating Fraser River sockeye salmon will decrease as the climate warms (Rand *et al.*, 2006; Farrell *et al.*, 2008). However, an encouraging finding revealed by the

simulations was that survival of Adams sockeye salmon may decrease negligibly in the future if the fish revert to their historically normal river entry timing. Conversely, if this reversion does not occur, then the expected decrease in their future survival is alarming. Collectively, our findings emphasize the need to consider stock-specific responses to temperature and climate warming into fisheries management and conservation strategies for Fraser River sockeye salmon and, more generally, for Pacific salmon (see also Crozier *et al.*, 2008b). Also of note is that our results suggest that the environment where individuals are captured-tagged-released and the capture methods used are critical aspects of any study assessing the impacts of temperature and climate warming on survival of anadromous fish and hence should be carefully considered in the design of such studies.

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### References

Anderson DR, Burnham KP (1976) *Population ecology of the mallard. VI. The effect of exploitation on survival*. United States Department of the Interior: Fish and Wildlife Service, 128, 66 pp.

Barton BA (2002) Stress in fishes: a diversity of responses with particular reference to changes in circulating corticosteroids. *Integrative and Comparative Biology*, **42**, 517–525.

Beacham TD, Lapointe M, Candy JR *et al.* (2004) Stock identification of Fraser River sockeye salmon (*Oncorhynchus nerka*) using microsatellites and major histocompatibility complex variation. *Transactions of the American Fisheries Society*, **133**, 1106–1126.

Beacham TD, McIntosh B, MacConnachie C, Miller KM, Withler RE, Varnavskaya NV (2006) Pacific Rim population structure of sockeye salmon as determined from microsatellite analysis. *Transactions of the American Fisheries Society*, **135**, 174–187.

Bridger CJ, Booth RK (2003) The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. *Reviews in Fisheries Science*, **11**, 13–34.

Bryant MD (2009) Global climate change and potential effects on Pacific salmonids in freshwater ecosystems of southeast Alaska. *Climatic Change*, **95**, 169–193.

Burnham KP (1993) A theory for combined analysis of ring recovery and recapture data. In: *Marked Individuals in the Study of Bird Populations* (eds Lebreton JD, North PM), pp. 199–213. Birkhäuser Verlag, Basel.

Burnham KP, Anderson DR (2002) *Model Selection and Multi-Model Inference: A Practical Information-Theoretic Approach*. Springer-Verlag, New York, USA.

Carlson SM, Seamons TR (2008) A review of quantitative genetic components of fitness in salmonids: implications for adaptation to future change. *Evolutionary Applications*, **1**, 222–238.

Cooke SJ, Crossin GT, Patterson DA *et al.* (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. *Journal of Fish Biology*, **67**, 1342–1358.

Cooke SJ, Hinch SG, Crossin GT *et al.* (2008) Physiological correlates of coastal arrival and river entry timing in late summer Fraser River sockeye salmon (*Oncorhynchus nerka*). *Behavioral Ecology*, **19**, 747–758.

Cooke SJ, Hinch SG, Farrell AP *et al.* (2004) Abnormal migration timing and high en route mortality of sockeye salmon in the Fraser River, British Columbia. *Fisheries*, **29**, 22–33.

Crockett EL, Londraville RL (2006) Temperature. In: *The Physiology of Fishes* (eds Evans DH, Claiborne JB), pp. 319–342. CRC Press, Boca Raton, USA.

Crossin GT, Hinch SG, Cooke SJ *et al.* (2007) Behaviour and physiology of sockeye salmon homing through coastal waters to a natal river. *Marine Biology*, **152**, 905–918.

Crossin GT, Hinch SG, Cooke SJ *et al.* (2008) Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. *Canadian Journal of Zoology*, **86**, 127–140.

Crossin GT, Hinch SG, Cooke SJ *et al.* (2009) Mechanisms influencing the timing and success of reproductive migration in a capital breeding, semelparous fish species: the sockeye salmon. *Physiological and Biochemical Zoology*, **82**, 635–652.

Crossin GT, Hinch SG, Farrell AP, Higgs DA, Lotto AG, Oakes JD, Healey MC (2004) Energetics and morphology of sockeye salmon: effects of upriver migratory distance and elevation. *Journal of Fish Biology*, **65**, 788–810.

Crozier LG, Hendry AP, Lawson PW *et al.* (2008a) Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. *Evolutionary Applications*, **1**, 252–270.

Crozier LG, Zabel RW, Hamlet AF (2008b) Predicting differential impacts of climate change at the population level with life-cycle models of spring Chinook salmon. *Global Change Biology*, **14**, 236–249.

Davis MW (2002) Key principles for understanding fish bycatch discard mortality. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1834–1843.

Donaldson MR, Cooke SJ, Patterson DA *et al.* (2009) Limited behavioural thermoregulation by adult upriver-migrating sockeye salmon (*Oncorhynchus nerka*) in the Lower Fraser River, British Columbia. *Canadian Journal of Zoology*, **87**, 480–490.

Donaldson MR, Hinch SG, Patterson DA *et al.* (2010) Physiological condition differentially affects the behaviour and survival of two populations of sockeye salmon during their freshwater spawning migration. *Physiological and Biochemical Zoology*, **83**, 446–458.

Dorsey AHJ (1991) Water in the sustainable development of the Fraser River basin. In: *Water in Sustainable Development: Exploring our Common Future in the Fraser River Basin* (eds Dorsey AHJ, Griggs JR), pp. 3–18. Westwater Research Centre, University of British Columbia, Vancouver, Canada.

Dulvy NK, Rogers SI, Jennings S, Stelzenmüller V, Dye SR, Skjoldal HR (2008) Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology*, **45**, 1029–1039.

English KK, Koski WR, Sliwinski C, Blakley A, Cass A, Woodey JC (2005) Migration timing and river survival of Late-run Fraser River sockeye salmon estimated using radiotelemetry techniques. *Transactions of the American Fisheries Society*, **134**, 1342–1365.

English KK, Sliwinski C, Labelle M, Koski WR, Alexander R, Cass A, Woodey JC (2004) *Migration timing and in-river survival of Late-run Fraser River sockeye in 2003 using radio-telemetry techniques*. Report prepared by LGL Limited, Sydney, British Columbia, 103 pp.

- Fagerlund UHM, McBride JR, Williams IV (1995) Stress and tolerance. In: *Physiological Ecology of Pacific Salmon* (eds Groot C, Margolis L, Clarke WC), pp. 459–504. University of British Columbia Press, Vancouver, Canada.
- Farrell AP (2002) Cardiorespiratory performance in salmonids during exercise at high temperature: insights into cardiovascular design limitations in fish. *Comparative Biochemical Physiology*, **132**, 797–810.
- Farrell AP (2009) Environment, antecedents and climate change: lessons from the study of temperature physiology and river migration of salmonids. *Journal of Experimental Biology*, **212**, 3771–3780.
- Farrell AP, Hinch SG, Cooke SJ, Patterson DA, Crossin GT, Lapointe M, Mathes MT (2008) Pacific salmon in hot water: applying aerobic scope models and biotelemetry to predict success of spawning migrations. *Physiological and Biochemical Zoology*, **81**, 697–708.
- Ferrari MR, Miller JR, Russell GL (2007) Modeling changes in summer temperature of the Fraser River during the next century. *Journal of Hydrology*, **342**, 336–346.
- Fleming IA, Jensen AJ (2002) Fisheries: effect of climate change on the life cycles of salmon. In: *Encyclopedia of Global Environmental Change*, Vol. 3 (ed. Munn T), pp. 309–312. John Wiley & Sons, Chichester, UK.
- Fry FEJ (1971) The effect of environmental factors on the physiology of fish. In: *Fish Physiology*, Vol. 6 (eds Hoar WS, Randall DJ), pp. 1–98. Academic Press, New York, USA.
- Gable J, Cox-Rogers S (1993) *Stock identification of Fraser River sockeye salmon: methodology and management application*. Pacific Salmon Commission Technical Reports, 5, 36 pp.
- Gelman A, Hill J (2006) *Data Analysis Using Regression and Multilevel/Hierarchical Models*. Cambridge University Press, Cambridge, UK.
- Gilhausen P (1990) Prespawning mortalities of sockeye salmon in the Fraser River system and possible causal factors. *International Pacific Salmon Fisheries Commission Bulletin*, **26**, 1–58.
- Hague MJ, Ferrari MR, Miller JR, Patterson DA, Russell GL, Farrell AP, Hinch SG (in press) Modelling the future hydroclimatology of the lower Fraser River and its impacts on the spawning migration survival of sockeye salmon. *Global Change Biology*.
- Hague MJ, Patterson DA (2007) *Quantifying the sensitivity of Fraser River sockeye salmon (Oncorhynchus nerka) management adjustment models to uncertainties in run timing, run shape and run profile*. Canadian Technical Reports of Fisheries and Aquatic Sciences, 2776, 55 pp.
- Hague MJ, Patterson DA, MacDonald JS (2008) *Exploratory correlation analysis of multi-site summer temperature and flow data in the Fraser River basin*. Canadian Technical Report of Fisheries and Aquatic Sciences, 2797, 60 pp.
- Harley CDG, Hughes AR, Hultgren KM *et al.* (2006) The impacts of climate change in coastal marine systems. *Ecology Letters*, **9**, 228–241.
- Hinch SG (2009) Overview and synthesis: early migration and premature mortality in Fraser River Late-run sockeye salmon. In: *Conference on Early Migration and Premature Mortality in Fraser River Late-Run Sockeye Salmon: Proceedings* (eds Hinch SG, Gardner J), pp. 8–14. Pacific Fisheries Resource Conservation Council, Vancouver, Canada. Available at: [http://www.psc.org/info\\_laterunsockeye.htm](http://www.psc.org/info_laterunsockeye.htm)
- Hinch SG, Cooke SJ, Healey MC, Farrell AP (2006) Behavioural physiology of fish migrations: salmon as a model approach. In: *Fish Physiology*, Vol. 24 (eds Sloman K, Balshine S, Wilson V), pp. 239–295. Elsevier Academic Press, San Diego, USA.
- Hinch SG, Cooperman MS, Crossin GT, Olsson I (2008) *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*. Report to the Pacific Salmon Commission, Southern Boundary Restoration and Enhancement Fund, 123 pp.
- Hinch SG, Rand PS (2000) Optimal swim speeds and forward assisted propulsion: energy conserving behaviours of up-river migrating salmon. *Canadian Journal of Fisheries and Aquatic Sciences*, **57**, 2470–2478.
- IPCC (2007) *Climate Change 2007: Impacts, Adaptation and Vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Parry ML, Canziani OF, Palutikof JP, van der Linden PJ, Hanson CE), 976 pp. Cambridge University Press, Cambridge, UK.
- IPCC-TGICA (2007) *General guidelines on the use of scenario data for climate impact and adaptation assessment*. Version 2. Prepared by Carter TR on behalf of the Intergovernmental Panel on Climate Change, Task Group on Data and Scenario Support for Impact and Climate Assessment, 66 pp.
- Iwama GK, Afonso LOB, Vijayan MM (2006) Stress in fishes. In: *The Physiology of Fishes* (eds Evans DH, Claiborne JB), pp. 319–342. CRC Press, Boca Raton, USA.
- Keefer ML, Peery CA, Heinrich MJ (2008) Temperature-mediated en route migration mortality and travel rates of endangered Snake River sockeye salmon. *Ecology of Freshwater Fish*, **17**, 136–145.
- Kieffer JD (2000) Limits to exhaustive exercise in fish. *Comparative Biochemistry and Physiology*, **126A**, 161–179.
- Laake J, Rextad E (2008) RMark: R Code for MARK Analysis. R package version 1.8.9. Available at: <http://www.phidot.org/software/mark/rmark> (accessed March 2009).
- Lee CG, Farrell AP, Lotto A, MacNutt MJ, Hinch SG, Healey MC (2003) The effect of temperature on swimming performance and oxygen consumption in adult sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon stocks. *Journal of Experimental Biology*, **206**, 3239–3251.
- Leggett J, Pepper WJ, Swart RJ (1992) Emissions scenarios for IPCC: an update. In: *Climate Change 1992. The Supplementary Report to the IPCC Scientific Assessment* (eds Houghton JT, Callander BA, Varney SK), pp. 69–95. Cambridge University Press, Cambridge, UK.
- Levy DA (1992) *Potential impacts of global warming on salmon production in the Fraser River watershed*. Canadian Technical Reports of Fisheries and Aquatic Sciences, 1889, 96 pp.
- Macdonald JS (2000) *Mortality during the migration of Fraser River sockeye salmon (Oncorhynchus nerka): a study of the effect of ocean and river environmental conditions in 1997*. Canadian Technical Report on Fisheries and Aquatic Sciences, 2315, 120 pp.
- MacDonald JS, Foreman MGG, Farrell AP *et al.* (2000) *The influence of extreme water temperatures on migrating Fraser River sockeye salmon (Oncorhynchus nerka) during the 1998 spawning season*. Canadian Technical Report of Fisheries and Aquatic Sciences, 2326, 117 pp.
- Macdonald JS, Morrison J, Patterson DA, Heinonen J, Foreman M (2007) *Examination of factors influencing Nechako River discharge, temperature, and aquatic habitats*. Canadian Technical Reports of Fisheries and Aquatic Sciences, 2773, 32 pp.
- Marcogliese DJ (2001) Implications of climate change for parasitism of animals in the aquatic environment. *Canadian Journal of Zoology*, **79**, 1331–1352.
- Mathes MT, Hinch SG, Cooke SJ, Crossin GT, Patterson DA, Lotto AG, Farrell AP (2010) Effect of water temperature, timing, physiological condition and lake thermal refugia on migrating adult Weaver Creek sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries and Aquatic Sciences*, **67**, 70–84.
- Morrison J, Quick MC, Foreman MGG (2002) Climate change in the Fraser River watershed: flow and temperature projections. *Journal of Hydrology*, **263**, 230–244.
- Mote PW, Parson EA, Hamlet AF (2003) Preparing for climatic change: the water, salmon, and forests of the Pacific Northwest. *Climatic Change*, **61**, 45–88.
- Naughton GP, Caudill CC, Keefer ML, Bjornn TC, Stuehrenberg LC, Peery CA (2005) Late-season mortality during migration of radio-tagged adult sockeye salmon (*Oncorhynchus nerka*) in the Columbia River. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 30–47.
- Patterson DA, Macdonald JS, Skibo KM, Barnes D, Guthrie I, Hills J (2007) *Reconstructing the summer thermal history for the lower Fraser River, 1941 to 2006, and implications for adult sockeye salmon (Oncorhynchus nerka) spawning migration*. Canadian Technical Reports of Fisheries and Aquatic Sciences, 2724, 43 pp.
- Pine WE, Pollock KH, Hightower JE, Kwak TJ, Rice JA (2003) A review of tagging methods for estimating fish population size and components of mortality. *Fisheries*, **28**, 10–23.
- Pörtner HO (2001) Climate change and temperature-dependent biogeography: oxygen limitation of thermal tolerance in animals. *Naturwissenschaften*, **88**, 137–146.
- Pörtner HO (2002) Climate variations and physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comparative Biochemistry and Physiology Part A*, **132**, 739–761.
- Pörtner HO, Farrell AP (2008) Physiology and climate change. *Science*, **322**, 690–692.
- Pörtner HO, Knust R (2007) Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science*, **315**, 95–97.
- R Development Core Team (2008) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0. Available at <http://www.R-project.org>.
- Ramstad K, Woody CA (2003) Radio tag retention and tag-related mortality among adult sockeye salmon. *North American Journal of Fisheries Management*, **23**, 978–982.
- Rand PS, Hinch SG (1998) Swim speeds and energy use of upriver-migrating sockeye salmon (*Oncorhynchus nerka*): simulating metabolic power and assessing the risk of energy depletion. *Canadian Journal of Fisheries and Aquatic Sciences*, **55**, 1832–1841.
- Rand PS, Hinch SG, Morrison J *et al.* (2006) Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. *Transactions of the American Fisheries Society*, **135**, 655–667.

- Richards SA (2005) Testing ecological theory using the information-theoretic approach: examples and cautionary results. *Ecology*, **86**, 2805–2814.
- Robichaud D, English KK (2006) *Assessing in-river migration behaviour and survival of Summer-run sockeye salmon caught and released in the Lower Fraser River in 2005*. Report prepared by LGL Limited, Sydney, Canada, 66 pp.
- Robichaud D, English KK (2007) *River entry timing, survival and migration behaviour of Fraser River sockeye salmon in 2006*. Report prepared by LGL Limited, Sydney, Canada, 113 pp.
- Robichaud D, English KK, Smith JJ (2008) *Feasibility of fishwheel use for escapement estimation and results from salmon radio-tracking on the lower Fraser River in 2007*. Report prepared by LGL Limited, Sydney, Canada, 140 pp.
- Roessig JM, Woodley CM, Cech JJ, Hansen LJ (2004) Effects of global climate change on marine and estuarine fishes and fisheries. *Reviews in Fish Biology and Fisheries*, **14**, 251–275.
- Sabatés A, Martín P, Lloret J, Raya V (2006) Sea warming and fish distribution: the case of the small pelagic fish, *Sardinella aurita*, in the western Mediterranean. *Global Change Biology*, **12**, 2209–2219.
- Shrimpton JM, Patterson DA, Richards JC, Cooke SJ, Schulte PM, Hinch SG, Farrell AP (2005) Ionoregulatory changes in different populations of maturing sockeye salmon *Oncorhynchus nerka* during ocean and river migration. *Journal of Experimental Biology*, **208**, 4069–4078.
- Taylor SG (2008) Climate warming causes phenological shift in Pink Salmon, *Oncorhynchus gorbuscha*, behaviour at Auke Creek. *Global Change Biology*, **14**, 229–235.
- Wagner GN, Hinch SG, Kuchel LJ *et al.* (2005) Metabolic rates and swimming performance of adult Fraser River sockeye salmon (*Oncorhynchus nerka*) after a controlled infection with *Parvicapsula minibicornis*. *Canadian Journal of Fisheries and Aquatic Sciences*, **62**, 2124–2133.
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study*, **46S**, 120–138.
- Wilkie MP, Davidson K, Brobbel MA, Kieffer JD, Booth RK, Bielak AT, Tufts BL (1996) Physiology and survival of wild Atlantic salmon following angling in warm summer waters. *Transactions of the American Fisheries Society*, **125**, 572–580.
- Williams B (2005) *2004 Southern salmon fishery post-season review, Part 1*. Fraser River sockeye Report. Available at: <http://www.dfo-mpo.gc.ca/Library/314601.pdf> (accessed July 2009).
- Williams BK, Nichols JD, Conroy MJ (2001) *Analysis and Management of Animal Populations*. Academic Press, San Diego, USA.

## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Table S1.** 95% confidence set of models describing survival ( $S$ ), recovery ( $r$ ) and detection ( $p$ ) rates of Chilko sockeye salmon. Models are ranked by increasing order of the QAIC<sub>c</sub> value. See text for description of QAIC<sub>c</sub>,  $\Delta_i$ ,  $w_i$  and model predictors.  $K$  is the number of parameters in the model.

**Table S2.** 95% confidence set of models describing survival ( $S$ ), recovery ( $r$ ) and detection ( $p$ ) rates of Quesnel sockeye salmon. Models are ranked by increasing order of the QAIC<sub>c</sub> value. See text for description of QAIC<sub>c</sub>,  $\Delta_i$ ,  $w_i$  and model predictors.  $K$  is the number of parameters in the model.

**Table S3.** 95% confidence set of models describing survival ( $S$ ), recovery ( $r$ ) and detection ( $p$ ) rates of Stellako-Late Stuart sockeye salmon. Models are ranked by increasing order of the QAIC<sub>c</sub> value. See text for description of QAIC<sub>c</sub>,  $\Delta_i$ ,  $w_i$  and model predictors.  $K$  is the number of parameters in the model.

**Table S4.** 95% confidence set of models describing survival ( $S$ ), recovery ( $r$ ) and detection ( $p$ ) rates of Adams sockeye salmon. Models are ranked by increasing order of the QAIC<sub>c</sub> value. See text for description of QAIC<sub>c</sub>,  $\Delta_i$ ,  $w_i$  and model predictors.  $K$  is the number of parameters in the model.

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