Using Stock-Specific Thermal Physiology to Simulate In-River Mortality of Fraser River Sockeye Salmon

by

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Abstract

Annual estimates of mortality en-route to spawning grounds for certain populations of Fraser River Sockeye salmon (*Oncorhynchus nerka*) can routinely exceed 50% posing challenges for harvest management and salmon conservation. High estimates of mortality are also correlated with high migration temperatures, suggesting temperature is one of the main factors. However, these estimates of apparent mortality are uncertain as they currently rely on discrepancies between up-river spawning ground estimates and lower river escapement estimates adjusting for estimates of in-river catch. Therefore, applying thermal physiology may serve as a tool to explain the potential contribution temperature-related mortality could have in calculating annual apparent mortality estimates for specific populations. I incorporated short- and long-term mortality functions based on population-specific aerobic scope temperature thresholds and an aggregate accumulation of degree-days threshold to a simulation model to estimate en-route mortality associated with temperature exposure for six Fraser River Sockeye salmon populations: Early Stuart, Gates Creek, Stellako, Chilko, and Weaver Creek. I compared simulated temperature based mortality rates to apparent mortality estimates (i.e., difference between estimates) and tested model sensitivity to uncertainty in short- and long-term LD50, arrival timing, and movement rate parameters. Results show that high temperature is likely a key driver of large en-route loss as both simulated mortality and apparent mortality estimates were higher in warmer years and lower in cooler years. I attribute the simulated mortality rates being generally lower than apparent mortality to the role that other sources of mortality can play (e.g., source error, high discharge). Simulated mortality rates were most sensitive to the short-term LD50 parameter, followed by the long-term LD50 and arrival timing parameters. However, simulated mortality rates were not sensitive to changes in movement rates. The model can explain temperature-related population-specific differences in apparent mortality between co-migrating populations (e.g., up to 80% absolute differences between Chilko and co-migrating populations) and provides evidence that these differences are driven by differences in aerobic scope. My results could inform managers of the relative importance of key parameters (short- and long-term mortality, and arrival timing) when estimating population-specific temperature-related mortality.

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List of Acronyms

DFO   Department of Fisheries and Oceans

DBE   Difference Between Estimates

DBEr   Difference Between Estimates Mortality Rate

RSA   Run Size Adjustments

FRSMM Fraser River Sockeye Management Model

BOTS   Bots are Objects for Tracking States

Glossary

Accumulated Degree Days
Cumulative temperature (°C) experienced by adult salmon during a set period of time (e.g., freshwater migration).

Aerobic Scope
The difference between routine and maximum oxygen consumption. Used to determine the total amount of energy available for activity for a given temperature.

En-Route Mortality
Mortality occurring while migrating from lower river (e.g., Mission) to their spawning grounds. Also termed "in-river loss".

Escapement
Fish that escape past a fishery.

Run Timing Group
Stocks of Fraser River Sockeye salmon that initiate upstream spawning migration at similar times. Run timing groups are: Early Stuart that migrate in June/July, Early Summer that migrate in July/August, Summer that migrate in August, and Later Summer that migrate in September/October.

1. Introduction

Water temperature affects many aspects of fish physiology (Fry 1971, Moore and Wohlschlag 1971), making this taxa particularly susceptible to climate warming (Ficke et al. 2007). High water temperature has been identified as a key factor contributing to increased mortality in several fish species leading to conservation concerns and economic losses to fisheries (La and Cooke 2011, Cooke et al. 2012). Estimating the background rate of natural mortality is already a difficult challenge for fisheries scientists (Hewitt and Hoenig 2005, Patterson et al. 2007b, La and Cooke 2011) and the compounding effect of climate change will only exacerbate this problem. Thermal physiology, which provides a mechanistic understanding of how mortality varies with water temperature, could be an important tool for assessing the future of climate-sensitive fisheries (Pörtner and Knust 2007, Hague et al. 2011).

Global increases in river temperatures as a result of recent climate warming (Petersen and Kitchell 2001, Webb and Nobilis 2007) may threaten salmon migration success (Goniea et al. 2006, Keefer et al. 2008). High river temperatures affect the physiology of migrating salmon which in turn affects short-term (0 to 96hrs; e.g., Farrell et al. 2008) and long term survival (> 96hrs; e.g., Wagner et al. 2005, Crossin et al. 2008). A key physiological process affecting short-term survival is aerobic collapse, which occurs when the total amount of aerobic energy available is insufficient to support activity demands. Aerobic scope, which estimates the total amount of energy available for activity, has a dome-shaped relationship to temperature that peaks at an optimum (T_{opt}) and is zero at very low and very high temperatures (T_{crit}) (*Figure 1*). Short-term exposure to high temperatures near T_{crit} causes aerobic collapse where anaerobic metabolism can completely replace aerobic metabolism leading to oxidative stress and possible immediate death (Pörtner and Knust 2007, Keefer et al. 2008, Steinhausen et al. 2008). Long-term survival can also be negatively affected by continued exposure to suboptimal temperatures above T_{opt} that elevate routine metabolic costs causing further depletion of limited energy reserves (Rand et al. 2006, Pörtner and Knust 2007).

In addition to temperature-metabolism relationships, long-term exposure to warm water increases the rate of parasite development and disease incidence in fish, which may cause pre-mature death of migrating anadromous salmon (Wagner et al. 2005, Bradford et al. 2010). Accumulated degree-days can be used to estimate prolonged exposure to warm water and therefore be applied as an indicator of long-term survival probability for adult salmon returning to freshwater (Hinch et al. 2012).

This study derives mortality rates as a function of long-term and short-term physiological responses to temperature and applies them in a simulation model of Fraser River Sockeye salmon (*Oncorhynchus nerka*) upstream migration to determine whether apparent mortality can be explained by thermal physiology for this economically important and culturally iconic species for use in management. The Fraser River Sockeye salmon fishery is well suited to test the application of a stock-specific thermal physiology models to management because of the following factors: high population diversity; extensive water temperature data; specific knowledge of Sockeye salmon physiology in relation to migration biology; and an immediate need for an alternative mortality estimation approach. The Fraser River is home to seven Pacific salmon species and is one of the largest producers of wild salmon in the world (Northcote and Larkin 1989), with Sockeye salmon being the most commercially valuable (Cooke et al. 2004). Managers of Sockeye salmon fisheries are rethinking how they manage the 19 major stocks because large in-river losses have been attributed to rising river temperatures (Hague and Patterson 2008). Average peak summer water temperatures in the Fraser River have increased by more than 1.5°C over the past 40 years (Patterson et al. 2007a). As a consequence of these elevated temperatures and changes to river entry timing, all Fraser River Sockeye salmon stocks now experience river temperatures that routinely exceed 19°C at some point during their upriver migration and some stocks experience 4°C warmer average water temperatures than historical levels (Patterson et al. 2007b). For instance, in 2004, extremely high river temperatures were a key factor explaining the estimated 57% overall en-route mortality rate of Fraser River Sockeye salmon (2004 Southern Salmon Fishery Post-Season Review Committee 2005, Mathes et al. 2010). However, there was considerable variability in mortality estimates (10% to 95%) among stocks, highlighting the need to match stock-specific physiology with thermal exposure to more accurately estimate migration mortality.

Fraser River Sockeye salmon consist of multiple stocks with different migration challenges and physiological adaptations to historic migration conditions (Farrell et al. 2008, Eliason et al. 2011). Migration challenges range considerably among stocks, and include: average river temperatures from 9°C to 22°C; arrival times to the Fraser River estuary from June to November; upriver migration distances from 50 km to 1,250 km; Fraser River discharge from 2,000 m^3 s^{-1} to 10,000 m^3 s^{-1}; and elevation gains from 10 m to 1,200 m. Stocks that migrate over greater distances and elevations tend to have larger heart muscle and broader aerobic scope, which provides an ability to withstand a wider range of temperatures (Eliason et al. 2011). In addition, temperature levels corresponding to aerobic scope parameters, T_{opt} and T_{crit}, are closely associated with historical average temperatures experienced by each stock (Lee et al. 2003, Eliason et al. 2011). Estimating the variation in migration survival associated with temperature for an individual fish will depend primarily on the upriver migration distance to spawning grounds (i.e., exposure time) and the timing of upstream migration, where the latter influences water temperatures that fish experience (Cooke et al. 2004, Eliason et al. 2011).

Matching thermal exposure to stock-specific thermal tolerances could be used to forecast stock-specific migration mortality over the migration season (e.g., Farrell et al. 2008, Hague et al. 2011). Stock-specific aerobic scope relationships with temperature have yet to be formally incorporated into management practices, but they have been used as a biological rationale for predictive methods of (a) estimating en-route mortality during the fishing season (Hague and Patterson 2008, Macdonald et al. 2010); (b) modelling future en-route losses under alternative climate scenarios (Hague et al. 2011); and (c) comparing mortality estimates derived from escapement discrepancies with tagging loss estimates for individual stocks (Farrell et al. 2008). For Fraser River Sockeye salmon, managers estimate migration mortality for each major stock at the end of each season. In general, managers estimate one in-river loss rate for each group of stocks that initiate spawning migration at similar times (i.e., a run timing group), even though physiology and thermal tolerances vary substantially among stocks. It is likely that one loss rate applied to an aggregate of stocks will result in biased estimates of total mortality for individual stocks. A finer scale mortality estimation approach integrating

what we know about stock-specific physiological processes into current methods may therefore improve mortality rate estimates.

Measured discrepancies between abundance estimates obtained at lower and upper river sites, after accounting for catch, are the most consistent indication of in-river losses for Fraser River Sockeye salmon (Cummings et al. 2011), but can be supplemented by additional tagging data (e.g., Keefer et al. 2008) and/or carcass observations (e.g., Patterson et al. 2007b). Specifically, managers use the difference between estimates (DBE) of escapement past Mission (lower river escapement estimate) and spawning grounds, after accounting for in-river catch estimates, as a proxy for en-route loss from environmental conditions (Macdonald et al. 2010). Since 1992, the DBE influences how many fish will be added back to catch and spawning escapement to generate total run size for a given year and stock, termed run size adjustment (RSA). However, there are many uncertainties associated with catch, Mission escapement, and spawning ground escapement estimates (Xie et al. 2002, Schubert & Houtman 2007, Patterson et al. 2007b) and little biological evidence exists as to whether DBEs are realistic given the temperatures experienced by fish (Macdonald et al. 2010). In particular, fish kill investigations rarely found any direct physical evidence to rationalize the large DBEs that were observed in eight out of fifteen years (Patterson et al. 2007b). Error in any or all contributions to DBEs can propagate through to total run size and stock productivity estimates, which can in turn lead to over- or under-estimation of fishery reference points. Temperature-mortality relationships based on physiological tolerance could provide a more scientifically defensible method of estimating in-river mortality that is independent of the DBE method.

The objective of this study is to determine whether apparent mortality can be explained by thermal physiology. I used a simulation model as a mechanistic approach for estimating in-river mortality from thermal exposure. Run reconstruction models have been used to quantitatively assess in-season salmon fisheries for over 60 years (Starr and Hilborn 1988). Run reconstructions simulate fish migration through space and time to generate forecasts of stock-specific catch, exploitation rates, and arrival and spawning ground abundances (Starr and Hilborn 1988, English et al. 2007). Using a run reconstruction model enables me to incorporate cumulative exposure to temperature in addition to movement rates and migration timing to generate direct en-route mortality

rate estimates. Mortality functions are based on short-term (aerobic scope) and long-term (degree-days) temperature thresholds for six Sockeye salmon stocks. I conducted a sensitivity test to determine how parameter uncertainty associated with mortality functions, arrival timing, and movement rates influences mortality rate estimates. I compared simulated mortality rates to DBEs to assess whether thermal physiology is consistent with the current method for estimating apparent mortality.

2. Methods

2.1 Overview

I used a spatially explicit individual-based model to simulate in-river mortality of migrating adult Sockeye salmon as a function of cumulative exposure to typical Fraser River temperatures occurring during the migration season. The Fraser River Salmon Management Model (FRSMM) is calibrated for six co-migrating Sockeye salmon stocks based on arrival timing and abundance at Mission, B.C. and migration rates estimated from tagging studies. Temperature-related mortality is based on a weighted combination of simulated short- and long-term exposure of fish to historical temperatures in the Fraser River. The following sections describe the input data, simulation model structure, and sensitivity analyses I used to determine whether apparent mortality can be explained by thermal physiology.

2.2 Data

I chose six major Sockeye salmon stocks: Early Stuart, Gates Creek, Quesnel, Chilko, Stellako, and Weaver Creek (*Figure 2*), based on the reliability and availability of migration data as well as representation of at least one stock from each of the major run-timing groups: Early Stuart (June/July), Early Summer (July/August), Summer (mid to late August), and Late Summer (August/September). Arrival timing to Mission, total run size, spawning ground escapement, and DBEs for each stock were provided by the Pacific Salmon Commission. Mean daily temperature from thirteen stations along the Fraser River were obtained from Fisheries and Oceans Canada (Patterson et al. 2007a, Hague & Patterson 2008). Migration rates for each run-timing group were estimated from radio telemetry studies in 2002 and 2006 (English et al. 2005, 2007).

Arrival timing was determined from the median date at which 50% of the migrating stock passed the hydroaccoustic counting facility at Mission, BC (Hague and Patterson 2008). Due to the complexity of modeling actual arrival timing distributions, which contain spikes in abundance, distributions were smoothed using a normal distribution. I used the central 90% range of arrival timing at Mission to fit the normal curve and excluded the outer 10% to avoid uncertain stock compositions resulting from overlap between run-timing groups. However, I used the total number of fish that passed Mission for a given stock and year to compute the arrival timing distribution.

The model simulates a mortality rate, whereas the DBE is an absolute mortality estimate. For comparison purposes, I converted DBEs to a mortality rate by dividing the DBE by the total run size estimated to have passed Mission, hereafter referred to as DBEr.

$$d_r = d / N \qquad \text{Eq. (1)}$$

where d_r is the DBEr, d is the DBE, and N is the total run size at Mission.

2.3 Model

The FRSMM framework simulates co-migrating populations in the presence of varying environmental conditions that could affect movement rates and survival. Effects on the movement and survival of the populations as they migrate can be both acute and cumulative as explained below. The simulation model represents migrating salmon both as aggregated groups, or "boxcars", and as individual fish. The boxcar component represents the majority of migrating salmon from each stock as aggregate abundances $N_{i,t,r}$ grouped by stock (i), time step (t) and reach (r). This component tracks aggregate stock movement along a one-dimensional spatial grid comprised of a sequence of 10 km reaches. A 12-hour time step was chosen because Sockeye salmon typically migrate 25 km to 30 km per day in the Fraser River (English et al. 2005). Stock-specific arrival timing distributions at Mission, movement, and in-river mortality are used to simulate changes in aggregate abundances as salmon migrate upriver from Mission to spawning grounds. Empirical temperature data derived from temperature monitoring stations are used to simulate realistic river conditions experienced by migrating salmon. Migration is

initiated at Mission because I focus only on in-river mortality even though some natural mortality may occur during inshore migration through marine areas.

The individual-based component of the model uses a random subsample of individual fish from each stock to track cumulative impacts of environmental stressors on survival rates. These individuals are referred to using the recursive acronym BOTS (i.e., **B**OTS are **O**bjects for **T**racking **S**tates). Individual BOTS move according to the same rules (described below) as the boxcar component of the stock to which they belong. The number of BOTS present in each stock is actively managed throughout a simulation to ensure that (i) BOTS are present in the same locations and time steps as the aggregate boxcar component, thus accurately reflecting conditions experienced by the total stock, and (ii) the number of BOTS is sufficient to provide statistically reliable values for survival and migration rates at each location and time step. BOTS and aggregate boxcar stocks therefore experience similar mortality risks, but when BOTS die, new BOTS are spawned from the survivors as needed to meet the above conditions (i–ii). Thus, cumulative environmental experiences of the stock are maintained in the BOTS and vice versa.

2.4 Movement

The movement sub-model of FRSMM simulates fish movement through a sequence of stock-specific reaches R, ranging from Mission, B.C. to the spawning grounds. For clarity reasons, the movement model is described using a single stock migrating over time steps $t = 1,2,...T$ and reaches $r = 1,2,...R$. The stochastic movement model in FRSMM involves a set of transition probabilities θ_i $(i = 1,2,...9)$ representing the proportion of fish present in location i at time $t\text{-}1$ that move to 9 possible new locations in one time step. There are no restrictions on θ_i except the usual probability constraints, namely that all $0 \le \theta_i \le 1$ and $\sum_{i=1}^{i=R} \theta_i = 1$. The latter constraint forces all fish to remain somewhere within the pre-defined set of reaches.

Transition probabilities are computed using an ordered multinomial logit model defined by an average response variable $y = X\beta$, where the covariates X could include factors such as discharge and temperature that may affect movement rates, and a spread parameter σ_J, which determines the range of reaches over which fish will spread around the expected reach. In the simulations presented here, I assume a constant movement that is independent of environmental conditions as well as a spread that is constant among stocks. Simulating movement involves two steps: (1) generate the transition probabilities based on the average movement rate and spread, and (2) randomly distribute the total number of fish present in reach r at time t to a new set of reaches at time $t+1$. The procedure is slightly different for individual BOTS as explained below.

Define parameters $0 = c_1 < c_2 < ...c_9$ representing the upper cutpoints on the number of reaches a fish could move in one time step. For Sockeye salmon migrating up the Fraser River at an average speed of 12.5 km/12-hr, it is assumed that fish cannot move more than 80 km (i.e., 8 reaches), which means that $c_9 = R = 8$. For this application I assume that the cutpoints are equally spaced, although they do not need to be in all cases (i.e., physical bottlenecks in the migration path). Given these conditions, a cumulative probability distribution is computed for each cutpoint c_i via

$$
\Theta_i = \begin{cases} 0 & i = 0 \\ 1 - \text{logit}^{-1}\left((y - c_i)/\sigma_J\right) & 1 < i < R \\ 1 & i = R \end{cases}
$$

Then, the probability of moving from reach r to reach $r + c_i$ is computed for each i by taking differences between the cumulative probabilities, i.e.,

$$
\theta_i = \begin{cases} \Theta_i & i = 1 \\ \Theta_i - \Theta_{i-1} & i > 1 \end{cases}
$$

Finally, the total number of fish $N_{t,r}$ present in reach r at time t is re-distributed among potential new reaches r to $r+c_9$ via random draw from a multinomial distribution, i.e.,

$$N_{t+1,r:r+c_9} \sim \text{Multinomial}\left(N_{t,r}, \theta_{r:r+c_9}\right)$$

where the notation $r:r+c_9$ indicates a vector of reaches from r to $r+c_9$. BOTS move according to the same rules except that the multinomial draw uses a sample size of 1.

2.5 Mortality

Temperature-related mortality risks are captured by BOTS because these simulated individuals keep track of the environmental conditions experienced during migration through all reaches between Mission, B.C. and the spawning grounds. The in-river mortality component of the simulation model attempts to represent short-term mortality risk caused by both aerobic collapse and long-term mortality risk from cumulative exposure to high temperature. The probability of death at each timestep is calculated independently for each exposure type and for each BOT as a function of accumulated temperatures over the most recent 96-hour interval (short-term) as well as the entire duration (long-term) in fresh water. A cumulative normal distribution function is used to represent a sigmoidal dose-response relationship between the probability of death and each temperature variable. For short-term temperature mortality risk, this model has the form

$$\Phi\left(T_{S,t,b,i} \mid \mu_{S,i}, \sigma_{S,i}\right) = \int_{x=-\infty}^{x=T_{S,t,b,i}} \exp\left[-\left(x - \mu_{S,i}\right)^2 \Big/ 2\sigma_{S,i}^2\right] \qquad \text{Eq. (2)}$$

where $T_{S,t,b,i}$ is short-term (S) average temperature at time t computed over the eight most recent 12-hour time steps for BOT b, i is the stock to which BOT belongs, and $\mu_{S,i}, \sigma_{S,i}$ are the mean and standard deviation, respectively, of the cumulative normal distribution for stock i. Parameter $\mu_{S,i}$ represents the temperature at which there is a

50% probability of death and $\sigma_{S,i}$ determines the steepness of the function around this point. The model for long-term temperature-related mortality is identical to Eq. (2) except substituting long-term accumulated temperature $T_{S,t,b,i}$ over the entire freshwater residency and long-term temperature parameters $\mu_{L,i}, \sigma_{L,i}$. For the remainder of this paper, I refer to parameters $\mu_{S,i}, \mu_{L,i}$ as the short-term and long-term LD50 values, respectively.

Short-term LD50's are based on stock-specific maximum aerobic scope temperature threshold values (*Figure 1*) (Lee et al. 2003, Eliason et al. 2011). Although it is uncertain what aerobic scope level is needed to complete migration, temperatures reducing aerobic scope to 80% of its maximum can impact survival (Farrell et al. 2008, E. Eliason, personal communication, January 18, 2013,). Therefore, I set the base case short-term LD50 to reflect stock-specific temperature thresholds associated with 80% of maximum aerobic scope. I tested the uncertainty in the value by changing the short-term LD50 to reflect temperature thresholds associated with 50% to 90% of maximum aerobic scope in 10% intervals. Standard deviations used in sensitivity analyses were approximated using the 95% confidence intervals of the stock-specific aerobic scope curves (Eliason et al. 2011).

Limited information on the mechanisms by which long-term temperature exposure impact migration success focus on the negative impacts of an extended freshwater residency and high water temperature (Hinch et al. 2012). Accumulated degree-days greater than 500 to 600 can result in severe development of the disease *P. minibicornis*, which could impact migration success (Wagner et al. 2005). Therefore, I assigned the base case long-term LD50 to 600 degree-days across all stocks with standard deviation parameters equal to 50 degree-days (Wagner et al. 2005). I tested the sensitivity of simulated mortality rates to the uncertainty in the degree-day threshold by changing the long-term LD50 to 500 and 700 degree-days.

I assumed that the two individual sources of temperature-related mortality affect total mortality rates $m_{b,i,t}$ of each BOT in the following additive way,

$$m_{b,i,t} = w\Phi\left(T_{S,t,b,i} \mid \mu_{S,i}, \sigma_{S,i}\right) + \left(1 - w\right)\Phi\left(T_{L,t,b,i} \mid \mu_{L,i}, \sigma_{L,i}\right)$$ Eq. (3)

where the weight w = 0.50. These BOT-specific mortality rates are used in Bernoulli draws to determine whether each BOT present in reach r (reach is implicit in the above formulas) lives or dies at time t. BOTS that die are removed from the model along with their accumulated temperature histories. The mean mortality rate $\overline{m}_{i,t,r}$ and variance $\tau^2_{i,t,r}$ computed over all BOTS for stock i at time t in reach r are then used to determine the overall mortality of the aggregate boxcar stock at each time step and reach. Method-of-moment estimators are used to calculate Beta distribution function shape and scale parameters for each stock, time step, and reach, i.e.,

$$\hat{\alpha}_{i,t,r} = \overline{m}_{i,t,r}\left[\frac{\overline{m}_{i,t,r}\left(1 - \overline{m}_{i,t,r}\right)}{\tau^2_{i,t,r}} - 1\right]$$ Eq. (4)

$$\hat{\beta}_{i,t,r} = \left(1 - \overline{m}_{i,t,r}\right)\left[\frac{\overline{m}_{i,t,r}\left(1 - \overline{m}_{i,t,r}\right)}{\tau^2_{i,t,r}} - 1\right]$$ Eq. (5)

Finally, the total number of fish dying from temperature-related mortality is randomly drawn from a Beta-Binomial distribution, i.e.,

$$D_{i,t,r} \sim Beta\text{-}Bin\left(N_{i,t,r}, \hat{\alpha}_{i,t,r}, \hat{\beta}_{i,t,r}\right)$$ Eq. (6)

2.6 Sensitivity Analysis

I performed sensitivity analyses to evaluate how uncertainties in model parameter values associated with Mission arrival timing, movement rates, and LD50 values can each affect simulated mortality rates.

Sockeye salmon arrival timing to Mission can greatly impact the types of environmental conditions that fish encounter, and thus migration survival (Cooke et al. 2004, Hague and Patterson 2008, Donaldson et al. 2010). Uncertainties in arrival timing exist because a mixture of stocks arrive together at Mission counting facilities, and errors

ranging from 0 to 4 days can occur in assigning acoustic signals to specific Sockeye salmon stocks (M. Lapointe, personal communication, March, 11, 2013). The baseline simulation model uses stock-specific mean arrival timing determined from the date at which 50% of the run passes Mission counting facility, while sensitivity tests assess mortality rate estimates as a result of +/- 2 days and +/- 4 days around this date.

Movement rates may affect mortality estimates because slower movement could decrease survival as a result of increased temperature exposure (Keefer et al. 2008). Error in residence time estimates may exist in the model because movement rates are only based on two years of tagging data and are generated for run-timing groups, not by stock (English et al. 2005, 2007). I used run-timing group movement rate estimates as the base case for the movement rate parameter for each stock and sensitivity analyses to test how +/- 25% and +/-50% changes in these rates might affect mortality. For example, if a run-timing group had a movement rate of 25 km/day moving from Mission to Hope and I increased it by 25%, then the new movement rate would be 31.25 km/day from Mission to Hope. Each subsequent movement rate would change throughout the migration by that same percentage.

Aerobic scope is used to set the short-term LD50 temperature threshold, which directly affects mortality estimates by defining how sensitive fish are to a given temperature range. Uncertainties in aerobic scope estimates arise from (1) biological aerobic scope measurements that only include fish that have survived experiments, and (2) fish may be less sensitive to temperature exposure than what tagging and lab studies indicate because of added handling and confinement stress (Martins et al. 2012, Robinson et al. 2013). Furthermore, the maximum aerobic scope needed to complete migration probably varies among individuals (Farrell et al. 2008, Hague et al. 2011). In a sensitivity analysis, I tested temperatures associated with 50% to 90% of maximum aerobic scope in 10% intervals relative to the base case, which was 80% of maximum aerobic scope. Setting the short-term LD50 parameter to reflect temperatures associated with 90% of maximum aerobic scope may address issue (1) having only data from fish that survived. What is believed to be 90% of maximum aerobic scope may be lower due to fish that did not survive experiments and were not accounted for when calculating scope curves. Alternatively, setting the short-term LD50 to reflect less than 80% of maximum aerobic scope may address issue (2) the possibility that wild fish are less

sensitive because of experimental stress. This is because temperatures reflecting less than 80% of maximum aerobic scope suggest less sensitivity to temperature.

The degree-day threshold sets the long-term LD50, which directly affects mortality by defining how sensitive fish are to prolonged temperature exposure. At 500 to 600 degree-days, parasite infection ranges from moderately severe to extremely severe. The impact on fish could range from enfeebled swimming performance to significant impairment and deterioration (Wagner et al. 2005). The simulation model uses 600 degree-days as a general threshold for all stocks. I test how sensitive modeled mortality rates are to a +/- 100 degree-days change in the long-term LD50 parameter to deal with the uncertainty of whether 500 or 600 degree-days significantly affect migration success.

Conclusions from my sensitivity test focus on parameters that resulted in greater than 10% differences in simulated mortality rates relative to the base case, i.e.,

$$a = b - s$$
Eq. (7)

Where a is the absolute simulated mortality rate difference, b is the simulated base case mortality rate, and s is the sensitivity test simulated mortality rate.

3. Results

Simulated annual en-route mortality rates under the base case model were lower, on average, than the DBEr for most stocks and years. The only exceptions were Stellako and Quesnel stocks for 2004 when the model estimated an additional 49% and 21% mortality rate than the DBEr for Stellako and Quesnel, respectively (*Figure 3*). Although on different scales, the simulated mortality rates and DBEr estimates followed a similar pattern across years and stocks. For example, both DBEr and simulated mortality rates indicated substantially higher en-route mortality during 2003 and 2004, which were warmer years than average (*Figure 4*) and lower mortality during 2002, which was a cool year. For warm years, both the simulated mortality rates and DBEr estimates were as high as 86% and 66%, respectively, and in cool years were nearly zero. Chilko at the base scenario did not track the DBEr because all of the simulated temperature-related mortality rates were equal to zero for all years.

Stock-specific absolute differences in simulated mortality rates were as high as 80% in the Summer run-timing group. For example, both Stellako and Quesnel stocks experienced 84% and 86% simulated mortality rates, respectively, for 2004 when Fraser River temperatures reached a maximum of 21.5°C, and were above 20°C for 10 consecutive days during their migration in August. Chilko Sockeye salmon also migrate in August, but their simulated mortality rate was zero.

Simulated mortality rates were non-linearly related to the short-term LD50 parameter for all stocks. Increasing the short-term LD50 from the temperature at 80% of maximum aerobic scope (base case) to 70% (i.e., increasing the temperature threshold) decreased the simulated mortality rate from 18% to zero for Stellako and 11% to zero for Quesnel for 2003 (*Figure 3*). Alternatively, decreasing the short-term LD50 from the temperature at 80% of maximum aerobic scope to 90% (i.e., decreasing the temperature threshold) increased the simulated mortality rate from 18% to 89% for Stellako and from 11% to 80% for Quesnel Sockeye salmon for 2003. For 2004 migration conditions,

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increasing the short-term LD50 from the temperature at 80% to 70% of maximum aerobic scope decreased the simulated en-route mortality rate from 84% to 54% for Stellako and from 86% to 43% for Quesnel Sockeye salmon. Decreasing the short-term LD50 from the temperature at 80% to 90% of maximum aerobic scope increased mortality from 84% to 92% for Stellako and 86% to 93% for Quesnel Sockeye salmon for 2004.

Simulated en-route mortality rates were less sensitive to the long-term LD50 than short-term LD50 parameter. Decreasing the long-term LD50 from 600 degree-days (base case) to 500 degree-days increased the simulated mortality rate for Early Stuart from 15% to 90% for 2006, which was the warmest year experienced by Early run-timing groups, and from zero to 12% for Chilko Sockeye salmon for 2006 (*Figure 5*). Increasing the long-term LD50 parameter from 600 degree-days to 700 degree-days decreased the simulated mortality rate from 15% to 3% for Early Stuart for 2006, but did not change mortality for Chilko because it was already zero for all years under the base case long-term LD50 parameter. Decreasing the long-term LD50 from 600 degree-days to 500 degree-days for 2002, which was the coolest year, increased mortality from 1% to 38% for Early Stuart, but only from zero to 5% for Chilko Sockeye salmon. Increasing the long-term LD50 to 700 degree-days did not affect mortality for either stock because it was already zero under the base case long-term LD50 parameter. Early Stuart Sockeye salmon accumulated high degree-days even in cool years making them most sensitive to changes in the long-term LD50 parameter.

Simulated mortality rates for Weaver Creek Sockeye salmon were sensitive to changes in arrival timing over more years than any other stock. Based on environmental conditions for 2002 and 2004, a 4-day earlier or 4-day later shift in arrival timing compared to the base case caused 9% to 12% absolute increases and 11% to 13% absolute decreases in mortality, respectively. Mortality only increased with later arrival timing for 2003 conditions when the simulated mortality rate increased from 37% to 51% with arrival timing two days later (*Figure 6*). For 2003, the base case arrival timing (August 28th) was the earliest of all years for Weaver Creek Sockeye salmon, and corresponded to the seasonal increase in river temperatures rather than the seasonal decrease that normally occurs at this time (*Figure 4*). Early arrivals therefore

experienced higher temperatures and higher simulated mortality rates whereas later arrivals experienced cooler temperatures and lower mortality, on average.

Simulated mortality rates differed only slightly from the base case with changes in movement rates (*Table 1*). The absolute difference in simulated mortality rates was less than approximately 3% when decreasing or increasing the movement rate by 25% and 50%.

4. Discussion

My results suggest that thermal physiology may explain some portion of apparent upriver migration mortality of Fraser River Sockeye salmon. Simulated mortality rates based on thermal physiology were consistent with empirical studies showing a negative impact of high temperatures (Cooke et al. 2004, Crossin et al. 2008, Farrell et al. 2008) as well as stock-specific differences in migration survival (Hague et al. 2011, Eliason et al. 2011). The overall mortality ascribed to thermal physiology was on average less than DBE values currently used to estimate in-river loss, suggesting that factors other than temperature also drive loss estimates. I show that short- and long-term temperature-related mortality combined with arrival timing variation could be important determinants of stock-specific simulated mortality rates. In contrast, variations in migration rates were not influential, and therefore knowing the relative importance of different parameters can guide the utility of future research and provide advice to management on the likely impact of key factors on estimating temperature-related mortality.

Similar patterns between simulated en-route mortality rates and DBEr values suggest that temperature is one of the key factors contributing to en-route mortality; however, some portion of apparent mortality could arise from alternative causes. For instance, discharge related mortality is not accounted for in the model, but could account for observed losses of Early Stuart migrants because they arrive during the spring freshet. High discharge forces migrating salmon to use more energy than normal, which reduces energy reserves and can cause higher mortality (Macdonald et al. 2000, Rand et al. 2006). Indirect fishing related mortality is also not represented in the model. Salmon that have encountered fishing gear, or are caught and released, experience physical abrasion and stress from entanglement in nets, human handling, and air exposure (Gale et al. 2013). Furthermore, the combined effect of indirect fishing related mortality and temperature could account for large portions of apparent losses during warm temperature years (Wilkie et al. 1996, Davis 2002, Martins et al. 2011).

Temperature-related mortality alone cannot explain all en-route mortality; therefore, the values represented here are likely the minimum associated with direct thermal exposure.

Variation in stock-specific mortality among Fraser River Sockeye salmon populations could result from differences in thermal exposure (Macdonald 2000), variations in swimming behaviour (Macdonald et al. 2010), and more recently temperature dependent differences in aerobic scope capacity (Martins et al. 2011). Altering migration timing, and therefore thermal exposure, did result in variations in survival within stocks. However, in my simulations, co-migrating stocks exposed to similar environmental conditions still had distinct differences in mortality, suggesting thermal exposure risk alone is not sufficient to explain the documented mortality discrepancies for co-migrating stocks (see Macdonald et al. 2010). Similarly, altering swimming behaviour by adjusting migration rates did not change simulated mortality rates. However, my results are consistent with stock-specific differences in aerobic scope, using the short-term mortality function (i.e., higher short-term LD50 parameter), being sufficient to simulate the levels of mortality differences observed in empirical studies. For example, Martins et al. (2011) reported that Chilko mortality rates are 32% and 42% lower than Stellako and Quesnel, respectively, using empirical tagging data. Herein, Chilko Sockeye salmon experienced much lower simulated temperature-related mortality to Stellako and Quesnel Sockeye salmon despite all three stocks migrating at the same time and experiencing similar temperature exposure. My work provides a link between stock-specific thermal physiology (Eliason et al. 2011) and realistic thermal exposure profiles to generate plausible patterns in mortality among co-migrating stocks.

The non-linear response of simulated mortality rates to changes in the short-term LD50 results from the steepness of the short-term mortality function and temperature exposure. With a steep slope, each shift in the short-term LD50 results in a large change in the probability of mortality. The slope of the sigmoidal mortality function around the short-term LD50 is set by the confidence intervals around the aerobic scope curve. Confidence intervals decrease, on average, with increasing percent of maximum aerobic scope, indicating that more individual variability in aerobic scope occurs at high temperatures (i.e., low percent of maximum aerobic scope); however, this also steepens the slope around the short-term LD50 parameter with increasing percent of maximum aerobic scope. As the short-term LD50 parameter is shifted to reflect +10% change of

maximum aerobic scope (i.e., decreasing temperature thresholds), the steeper slope causes larger changes in mortality, whereas a -10% change (i.e., increasing temperature thresholds) reduces the mortality function steepness, causing weaker sensitivity to temperature. However, for 2004, temperatures were consistently high; therefore, decreasing temperature sensitivity caused a small increase in mortality because cooler temperatures occurred less frequently. Alternatively, for 2003, decreasing temperature sensitivity caused large increases in mortality because, in addition to a steeper mortality slope, lower temperatures were experienced more frequently.

Simulated mortality rates were generally insensitive to the long-term LD50 mortality parameter, which may be attributed to underestimating long-term temperature exposure by assuming continual migration. Simulated mortality rates for Early Stuart were sensitive to changes in the long-term LD50, whereas mortality rates for Weaver Creek Sockeye salmon were insensitive. However, Early Stuart and Weaver Creek Sockeye salmon exhibit similar severity of disease infection as a result of freshwater residency time despite large differences in migration distance (~1200 km versus ~120 km) (Jones et al. 2003). Weaver Creek Sockeye salmon exhibit migration delays where they remain in one location for an extended period of time rather than continuously moving as predicted by the simulation model. Some fish exhibit such holding behaviour in the Fraser River instead of Harrison Lake, which prolongs their freshwater residency time in warm water and can increase their accumulation of degree-days. For example, tagged Weaver Creek Sockeye salmon holding in the warmer Fraser River, instead of the cooler Harrison Lake, accumulated over 800 degree-days and never made it to spawning grounds (Mathes et al. 2010). Ignoring holding behaviour in the simulation model can underestimate the long-term thermal exposure for short distant migrants like Weaver Creek Sockeye salmon because what takes three days to migrate in the simulation model takes about a month in reality. For instance, tagging data suggest around 70% mortality in warm years (Farrell et al. 2008, Mathes et al. 2010), which is consistent with the DBEr, and is probably a result of high temperature over a long duration of freshwater residency time (Farrell et al. 2008, Mathes et al. 2010).

Weaver Creek Sockeye salmon are most sensitive to arrival timing because they arrive in early fall while river temperatures are declining. I found that early arrivals experience higher mortality because they enter the river when temperatures are high,

and later arrivals experience lower mortality because they enter the river after temperatures have cooled, on average. For example, for 2004 all tagged early arriving Weaver Creek Sockeye salmon experienced temperatures near their critical threshold (>19.5°C) and none survived to reach spawning grounds (Farrell et al. 2008). Also, Weaver stocks have been entering the river two to six weeks earlier than historical timing, which can cause substantially higher mortality rates (Cooke et al. 2004, Lapointe et al. 2004, English et al. 2005). The abnormal arrival timing and associated exposure to higher temperatures than experienced historically, combined with a lower aerobic scope threshold, makes Weaver Creek Sockeye salmon vulnerable to temperature-related mortality.

Simulated mortality rates were not sensitive to Sockeye salmon movement rates, which may be because the model assumes that total mortality risk is an additive and equally weighted combination of short- and long-term temperature exposure. An equally weighted, additive mortality function was chosen arbitrarily because no data exist to support more complex models. Such as assumption may limit the models' ability to simulate long-term mortality because, when short-term mortality is absent, the highest long-term mortality rate is 50%. Slower movement rates prolong simulated migration times, thereby increasing the accumulated degree-days and risk of death by long-term temperature-related mortality. However, while the probability of long-term mortality increases with migration time, the probability of short-term mortality decreases, at least near the end of the migration, because temperatures are generally cooler near the spawning grounds. Future research involving FRSMM should investigate a competing risks of death model that could consider short-term and long-term mortality as mutually exclusive events. This type of mortality function affects the baseline mortality in a multiplicative way, which has been shown to produce higher estimates of mortality than the additive approach (Rosalba et al. 2007). However, using a competing risks of death function is not appropriate when independence between cause of death cannot be safely assumed and incidence of multiple causes of mortality is high (Rosalba et al. 2007). Although not mutually exclusive, the incidence of both types mortality causing death is rare given that short-term temperature exposure affects fish early in migration and long-term nearer to spawning grounds.

5. Conclusion

Fraser River Sockeye salmon managers are faced with the task of determining an adjustment to total run-size based on estimates of in-river mortality for 19 major stocks as part of post-season management analyses. My analysis could augment current tools, such as DBE estimates and expert opinion, used to weight the evidence before deciding on RSA values for the six stocks I examined. Two advantages of using thermal physiology relationships to provide an estimate of in-river mortality are (1) that en-route mortality estimates are independent of DBEs and the associated problems with source data errors (Macdonald et al. 2010) and (2) they account for stock-specific differences in temperature-related mortality risk.

The FRSMM modeling approach allowed me to examine the relative importance of key parameters (short- and long-term mortality, migration rate, arrival timing) when estimating stock-specific temperature-related mortality, as well as to identify the importance of future research in this area. I show that short-term mortality is probably most important to simulated en-route mortality rates, followed by the long-term mortality, and arrival timing. Simulated mortality rates were sensitive to changes in the short-term mortality function for all stocks, suggesting research effort should primarily be focused on establishing stock-specific critical temperature thresholds at 96 hours. The mortality rates were less sensitive to long-term mortality, but more effort should be placed on establishing stock-specific degree-day accumulation thresholds given that I used a general Fraser Sockeye salmon data set to for this parameter. As such, the simulated mortality rate should be considered a minimum estimate for Weaver Creek because of the holding behaviour that is not reflected in the model. Efforts to improve arrival timing information would be beneficial given how sensitive mortality rates were to changes in migration timing of all stocks. The sensitivity to arrival date is really a surrogate for exposure to different temperatures with changes in entry date. This suggests that post-season determinations of RSA that focus on temperature exposure will need to be

cognizant that subtle changes in thermal profiles matched to migration profiles can result in large differences in mortality.

Understanding how elevated water temperatures will impact Sockeye salmon migration survival becomes increasingly important for conservation and management as future scenarios of climate change show continued alterations to river temperatures. Hydrological models for the Fraser River predict 2°C to 4°C average warming of peak summer water temperatures over the next few decades (Morrison et al. 2002, Ferrari 2008) and a tripling of the number of days water temperatures will exceed 19 °C by the end of the 21st century (Hague et al. 2011). As river temperatures increase, so does the need to adopt a method for estimating the impact on migration success that is based on thermal physiology. Currently, indicators of en-route mortality are empirical measurements containing uncertainty and bias. I show that stock-specific thermal physiology could be used to provide an additional indicator of Fraser River Sockeye salmon en-route mortality that may explain portions of loss that occur from high river temperatures.

Table 1 Range of simulated en-route mortality rate estimates for all stocks for years 2002 to 2006. Changes >10% are indicated by bold font.

Parameter	Range of Parameter	Stock	Range of Mortality Rates				
			2002	**2003**	**2004**	**2005**	**2006**
Short-term LD50	50 to 90% maximum aerobic scope including base case (80% max)	Early Stuart	0 – 0.01	0.06 – 0.12	**0.11 – 0.28**	0.03 – 0.04	**0.11 – 0.82**
		Gates Creek	0	**0 – 0.65**	**0 – 0.85**	0	0 – 0.01
		Stellako	**0.10**	**0 – 0.89**	**0.07 – 0.92**	**0 – 0.22**	**0 – 0.57**
		Quesnel	**0 – 0.34**	**0 – 0.80**	**0 – 0.93**	0 – 0.07	**0 – 0.82**
		Chilko	0	0	**0 – 0.71**	0	0
		Weaver	**0.06 – 0.29**	**0.06 – 0.49**	**0.14 – 0.36**	0 – 0.04	**.09 – 0.49**
Long-term LD50	500 and 700 degree-days and base case (600 degree-days)	Early Stuart	**0 – 0.38**	**0 – 0.73**	**0 – 0.49**	**0 – 0.70**	**.03 – 0.90**
		Gates Creek	0	0.12	0.21	0	0
		Stellako	0 – 0.01	0.18 – 0.20	0.84	0	0 – 0.10
		Quesnel	0	0.10 – 0.11	0.86	0	0
		Chilko	0 – 0.05	**0 – 0.13**	**0 – 0.14**	0 – 0.02	0 – 0.12
		Weaver	0.18 – 0.20	0.37 – 0.39	0.32 **–** 0.34	0	0.41 – 0.43
Arrival timing mean	2 days and 4 days +/- Mission arrival timing (base case) and base case	Early Stuart	0 – 0.06	0.08 – 0.12	0.10 **–** 0.14	0.03 – 0.05	**0.11 – 0.24**
		Gates Creek	0 – 0.07	0.08 – 0.12	**0.15 – 0.27**	0	0 – 0.01
		Stellako	0 – 0.06	**0.07 – 0.34**	0.83 **–** 0.84	0	0
		Quesnel	0 – 0.04	**0.05 – 0.20**	0.82 – 0.86	0	0
		Chilko	0	0 – 0.01	0 – 0.01	0	0
		Weaver	**0.07 – 0.32**	**0.33 – 0.51**	**0.22 – 0.42**	0 – 0.01	0.39 – 0.47
Movement rate	+/- 25,50% of base case and base case	Early Stuart	0.01	0.12	0.12 – 0.13	0.04	0.15
		Gates Creek	0	0.12	0.21	0	0
		Stellako	0	0.18	0.84	0	0
		Quesnel	0	0.11	0.86 – 0.87	0	0
		Chilko	0	0	0	0	0
		Weaver	0.20	0.37	0.31 – 0.33	0	0.43

Figure 1 Aerobic scope as a function of temperature (°C) for Weaver Creek and Chilko stocks. Showing temperatures associated with 50 to 90% of maximum aerobic scope as well as optimal (T_{opt}) and critical (T_{crit}) temperatures. Recreated from data was previously published in Lee et al. 2003 and Eliason et al. 2011.
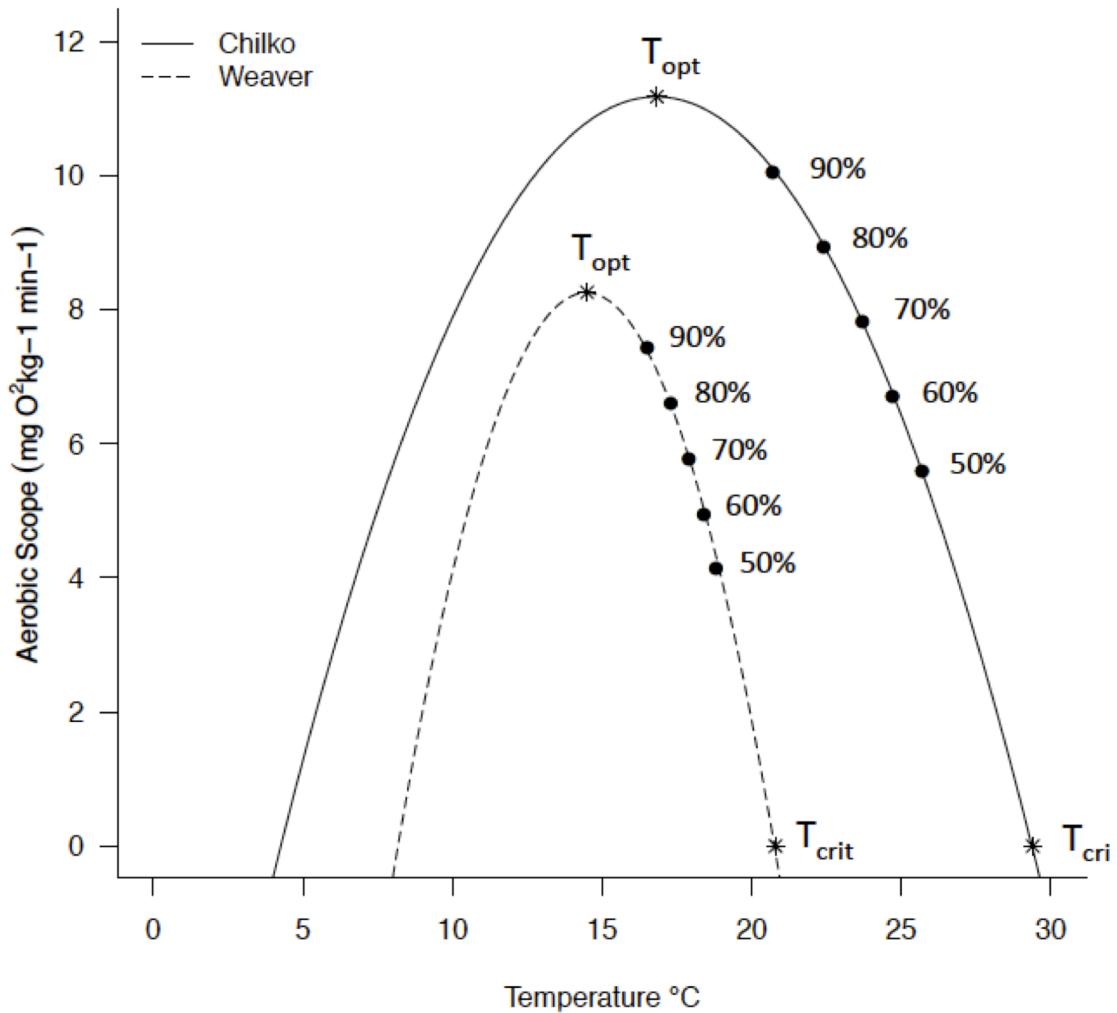
Figure 2 Fraser River map used in FRSMM simulation. Reach boundaries (●) are 10 km apart.
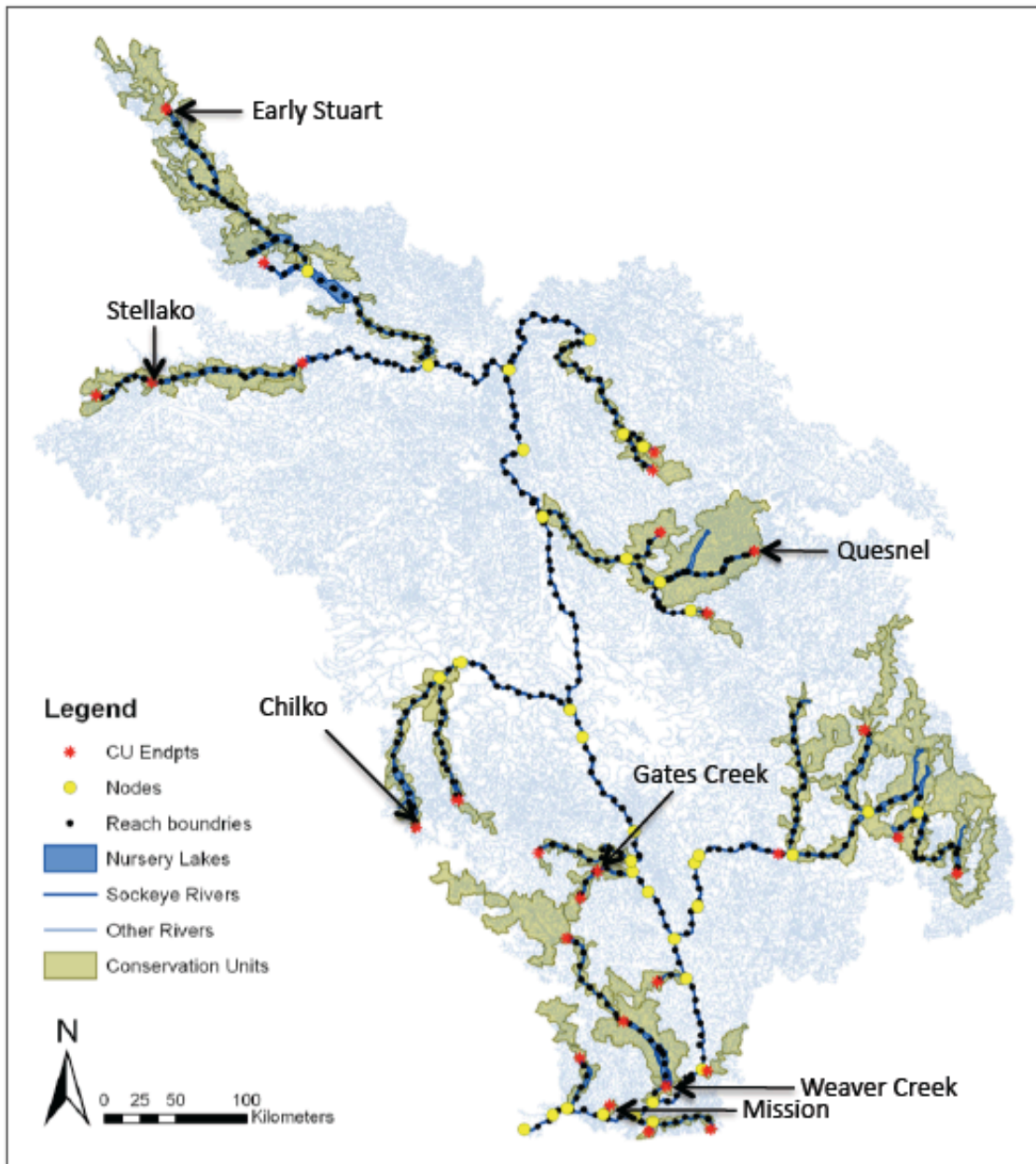
Figure 3 Short-term LD50 parameter sensitivity test, base case (●), and DBEr (○) mortality rate estimates for Quesnel and Stellako stocks for years 2002 to 2006. Base case short-term parameter mean was varied with temperatures associated with 50 (▽), 60 (▼), 70 (△), and 90% (▲) of maximum aerobic scope.
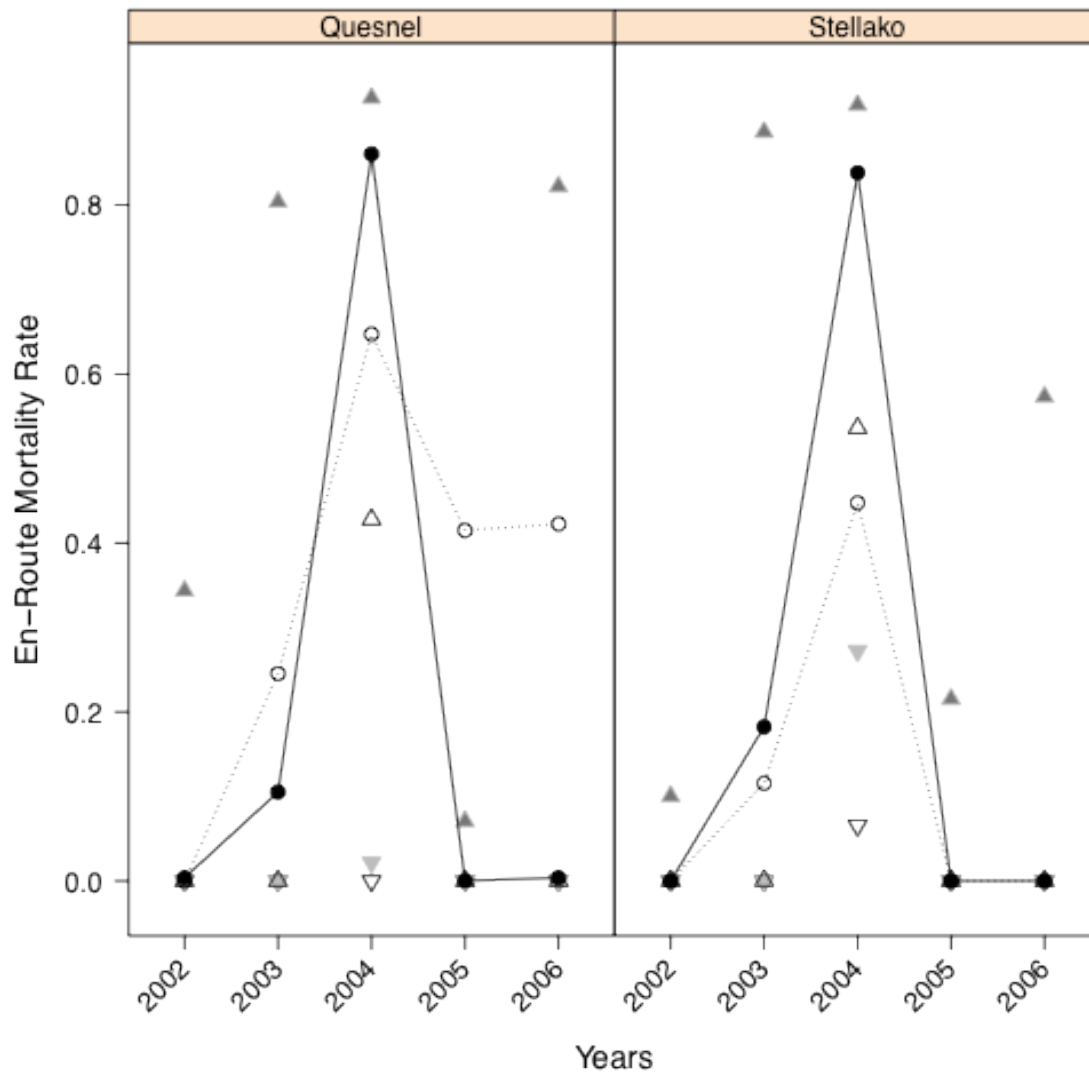
Figure 4   Fraser River water temperatures (°C) during the Sockeye salmon migration season from June 1st to September 30th (2002 to 2006) and 30 year mean with median date arrival timing for Early Stuart (ES), Gates Creek (GC), Stellako (S), Quesnel (Q), Chilko (C), and Weaver Creek (WC) stocks.
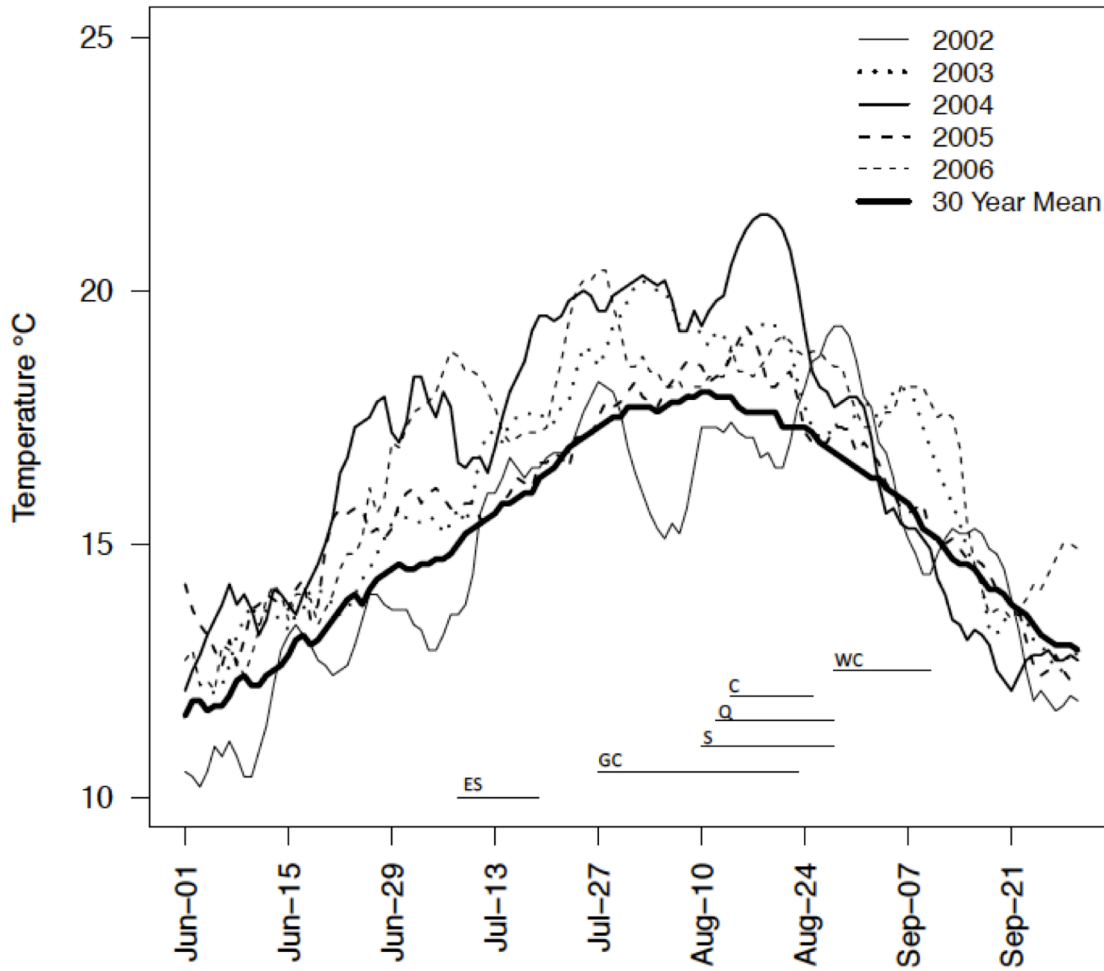
Figure 5   Long-term LD50 parameter sensitivity test, base case (●), and DBEr (○) mortality rate estimates for Early Stuart and Chilko stocks for years 2002 to 2006. Base case long-term parameter mean was varied by +100 (▲) and -100 (▼) degree-days.
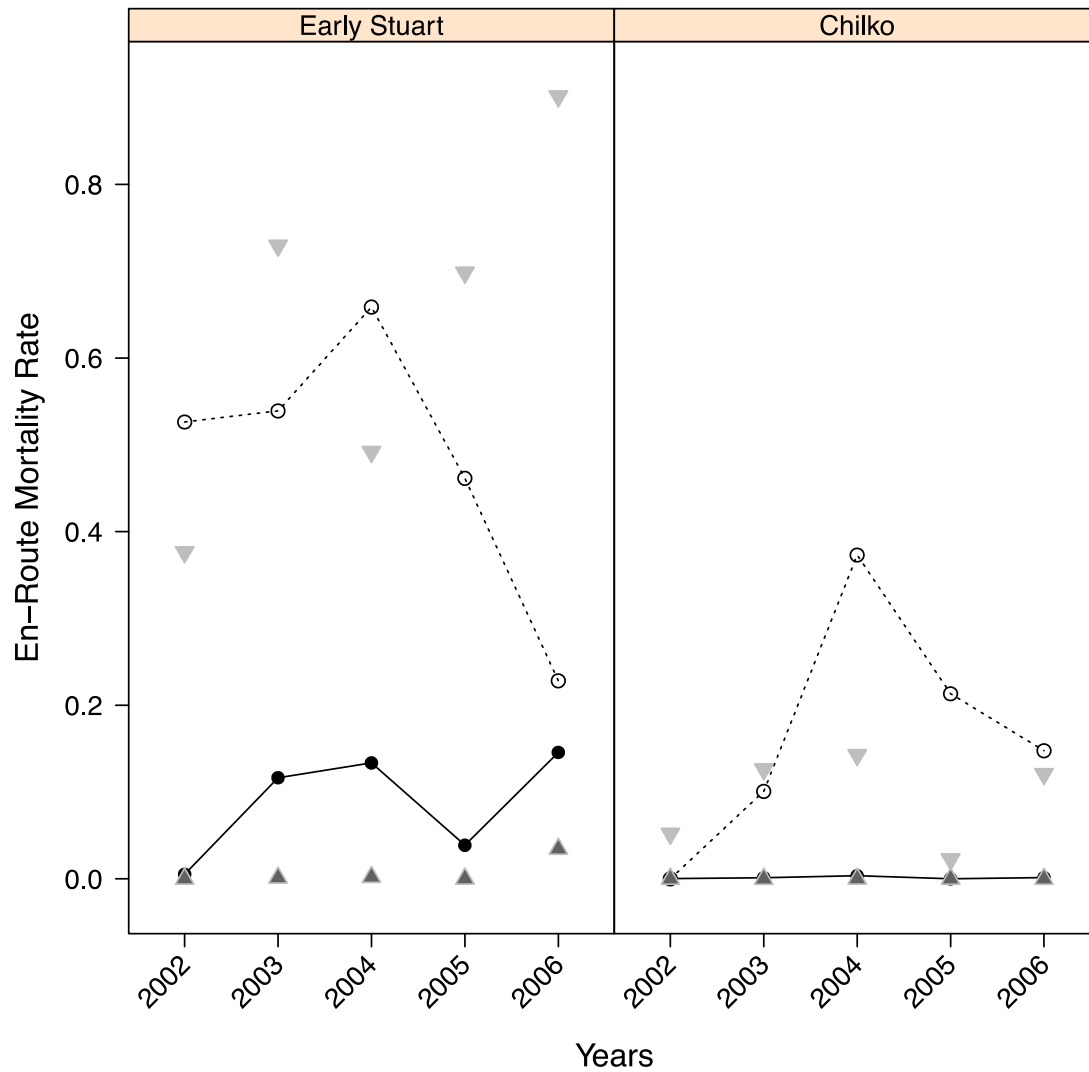
Figure 6   Arrival timing parameter sensitivity test, base case (●), and DBEr (○)
mortality rate estimates for Gates and Weaver Creek stocks for
years 2002 to 2006. Base case arrival timing parameter mean was
varied by +2 days (△) , -2 days (▽), +4 days (▲), and -4 days (▼).
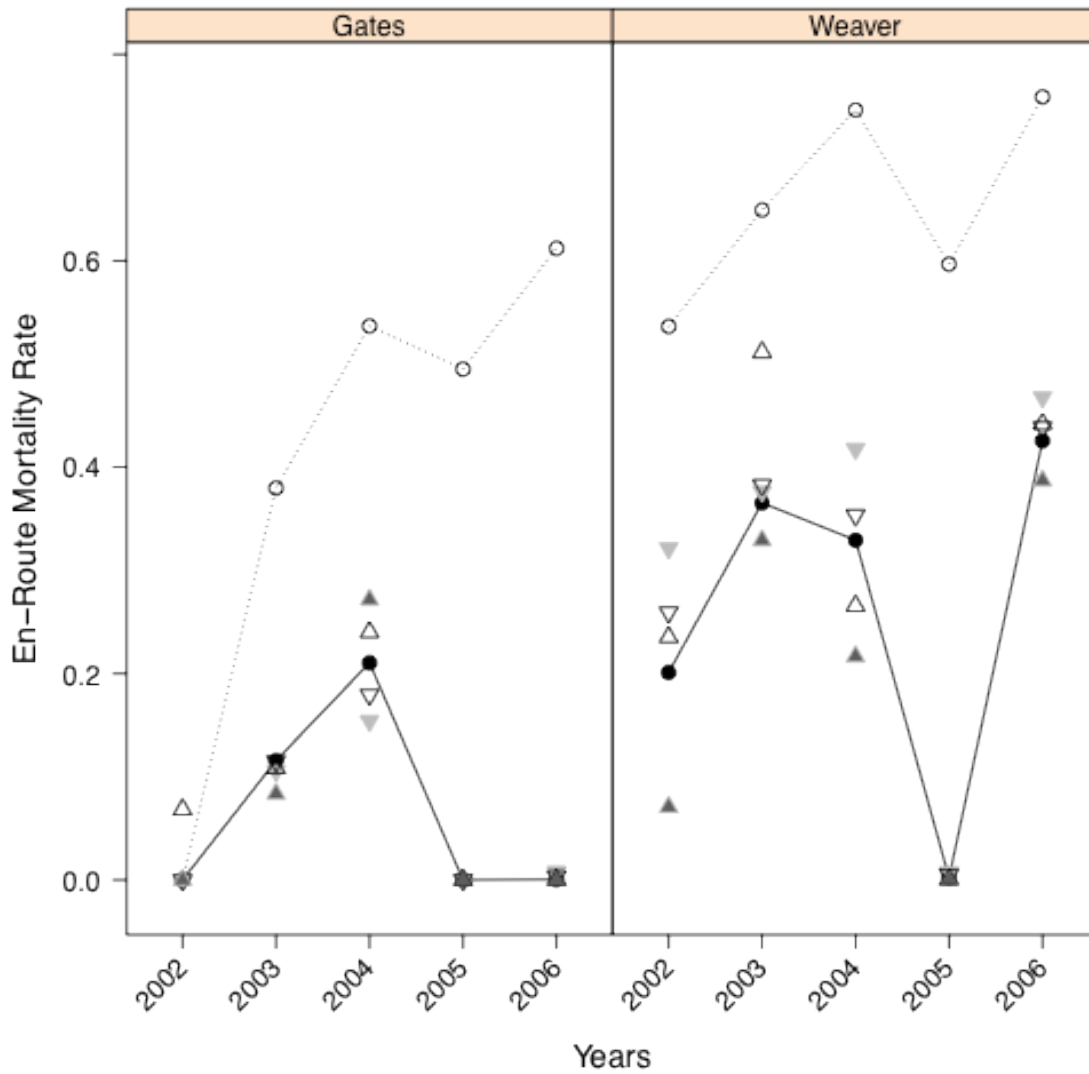
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Appendices

Appendix A.

Sensitivity analysis

Table A.1 T_{opt}, T_{crit}, and temperatures (°C) and standard deviations associated with 50 to 90% of maximum aerobic scope for each stock.

Stock	50%	60%	70%	80%	90%	T_{opt}	T_{crit}
Weaver	18.9 (0.52)	18.4 (0.40)	17.9 (0.26)	17.3 (0.12)	16.5 (0.03)	14.5	20.8
Gates	23.3 (0.88)	22.6 (1.12)	21.7 (1.04)	20.8 (0.49)	19.5 (0.08)	16.4	26.1
Chilko	25.7 (1.29)	24.7 (0.90)	23.7 (0.50)	22.4 (0.25)	20.7 (0.05)	16.8	29.4
Stellako	21.8 (0.28)	21.3 (0.19)	20.7 (0.19)	20 (0.28)	19 (0.40)	16.8	24.0
Quesnel	22.7 (0.32)	21.9 (0.25)	21 (0.26)	19.9 (0.34)	18.5 (0.17)	< 18.5	25.9
Early Stuart	23.3 (0.75)	22.7 (0.40)	21.9 (0.15)	21.1 (0.02)	19.9 (0.05)	17.2	25.8

Table A.2 Median date arrival timing at Mission (base case parameter) for all stocks for years 2002 to 2006.

Stock	2002	2003	2004	2005	2006
Early Stuart	8-Jul	13-Jul	10-Jul	19-Jul	15-Jul
Gates	27-Jul	2-Aug	28-Jul	23-Aug	17-Aug
Stellako	10-Aug	10-Aug	11-Aug	23-Aug	19-Aug
Chilko	17-Aug	14-Aug	15-Aug	25-Aug	19-Aug
Quesnel	17-Aug	16-Aug	12-Aug	28-Aug	20-Aug
Weaver	4-Sep	28-Aug	31-Aug	10-Sep	30-Aug

Table A.3 Simulated en-route mortality rates from all sensitivity tests for all stocks for years 2002 to 2006.

Test	Stock	2002	2003	2004	2005	2006
Base case						
	Chilko	0	0	0	0	0
	Early Stuart	0.01	0.12	0.13	0.04	0.15
	Gates	0	0.12	0.21	0	0
	Quesnel	0	0.11	0.86	0	0
	Stellako	0	0.18	0.84	0	0

Test	Stock	2002	2003	2004	2005	2006
	Weaver	0.20	0.37	0.33	0	0.43
Short-term LD50 at 50% Aerobic Scope						
	Chilko	0	0	0	0	0
	Early Stuart	0	0.11	0.12	0.03	0.12
	Gates	0	0	0	0	0
	Quesnel	0	0	0	0	0
	Stellako	0	0	0.07	0	0
	Weaver	0.06	0.06	0.14	0	0.09
Short-term LD50 at 60% Aerobic Scope						
	Chilko	0	0	0	0	0
	Early Stuart	0	0.11	0.11	0.04	0.11
	Gates	0	0.03	0.05	0	0
	Quesnel	0	0	0.02	0	0
	Stellako	0	0	0.27	0	0
	Weaver	0.12	0.12	0.18	0	0.16
Short-term LD50 at 70% Aerobic Scope						
	Chilko	0	0	0	0	0
	Early Stuart	0	0.06	0.13	0.04	0.11
	Gates	0	0.08	0.24	0	0.01
	Quesnel	0	0	0.43	0	0
	Stellako	0	0	0.54	0	0
	Weaver	0.17	0.15	0.24	0	0.28
Short-term LD50 at 90% Aerobic Scope						
	Chilko	0	0	0.71	0	0
	Early Stuart	0.01	0.10	0.28	0.04	0.82
	Gates	0	0.65	0.85	0	0.01
	Quesnel	0.34	0.8	0.93	0.07	0.82
	Stellako	0.10	0.89	0.92	0.22	0.57
	Weaver	0.29	0.49	0.36	0.04	0.49
Long-term LD50 at 500 degree-days						
	Chilko	0.05	0.13	0.14	0.02	0.12
	Early Stuart	0.38	0.73	0.49	0.70	0.90
	Gates	0	0.12	0.21	0	0
	Quesnel	0	0.10	0.86	0	0
	Stellako	0.01	0.2	0.84	0	0.01
	Weaver	0.18	0.38	0.32	0	0.41
Long-term LD50 at 700 degree-days						
	Chilko	0	0	0	0	0

Test	Stock	2002	2003	2004	2005	2006
	Early Stuart	0	0	0	0	0.03
	Gates	0	0.12	0.21	0	0
	Quesnel	0	0.11	0.86	0	0
	Stellako	0	0.19	0.84	0	0
	Weaver	0.20	0.39	0.34	0	0.42
Median arrival timing minus two days						
	Chilko	0	0	0	0	0
	Early Stuart	0	0.09	0.11	0.04	0.19
	Gates	0	0.12	0.18	0	0
	Quesnel	0	0.15	0.86	0	0
	Stellako	0	0.26	0.83	0	0
	Weaver	0.26	0.38	0.35	0	0.44
Median arrival timing minus four days						
	Chilko	0	0.01	0.01	0	0
	Early Stuart	0	0.08	0.10	0.03	0.24
	Gates	0	0.11	0.15	0	0.01
	Quesnel	0	0.2	0.85	0	0
	Stellako	0	0.34	0.83	0	0
	Weaver	0.32	0.38	0.42	0.01	0.47
Median arrival timing plus two days						
	Chilko	0	0	0	0	0
	Early Stuart	0.06	0.12	0.13	0.05	0.12
	Gates	0.07	0.11	0.24	0	0
	Quesnel	0.04	0.17	0.85	0	0
	Stellako	0.06	0.25	0.84	0	0
	Weaver	0.24	0.51	0.27	0	0.44
Median arrival timing plus four days						
	Chilko	0	0	0	0	0
	Early Stuart	0.01	0.13	0.14	0.05	0.11
	Gates	0	0.08	0.27	0	0
	Quesnel	0.01	0.05	0.82	0	0
	Stellako	0	0.07	0.83	0	0
	Weaver	0.07	0.33	0.22	0	0.39
Movement rate minus 25% of base case						
	Chilko	0	0	0	0	0
	Early Stuart	0.01	0.12	0.12	0.04	0.15
	Gates	0	0.12	0.21	0	0
	Quesnel	0	0.11	0.87	0	0

Test	Stock	2002	2003	2004	2005	2006
	Stellako	0	0.18	0.84	0	0
	Weaver	0.20	0.37	0.31	0	0.43
Movement rate minus 50% of base case						
	Chilko	0	0	0	0	0
	Early Stuart	0.01	0.12	0.12	0.04	0.15
	Gates	0	0.12	0.21	0	0
	Quesnel	0	0.11	0.87	0	0
	Stellako	0	0.18	0.84	0	0
	Weaver	0.20	0.37	0.31	0	0.43
Movement rate plus 25% of base case						
	Chilko	0	0	0	0	0
	Early Stuart	0.01	0.12	0.12	0.04	0.15
	Gates	0	0.12	0.21	0	0
	Quesnel	0	0.11	0.87	0	0
	Stellako	0	0.18	0.84	0	0
	Weaver	0.20	0.37	0.31	0	0.43
Movement rate plus 50% of base case						
	Chilko	0	0	0	0	0
	Early Stuart	0.01	0.12	0.12	0.04	0.15
	Gates	0	0.12	0.21	0	0
	Quesnel	0	0.11	0.87	0	0
	Stellako	0	0.18	0.84	0	0
	Weaver	0.20	0.37	0.31	0	0.43

Appendix B.

Sensitivity Analysis Comparison for all stocks

Figure B.1   Short-term LD50 parameter sensitivity test, base case (●), and DBEr (○) en-route mortality rate estimates for all stocks for years 2002 to 2006. Base case short-term mean was varied with temperatures associated with 50 (▽), 60 (▼), 70 (△), and 90% (▲) of maximum aerobic scope.
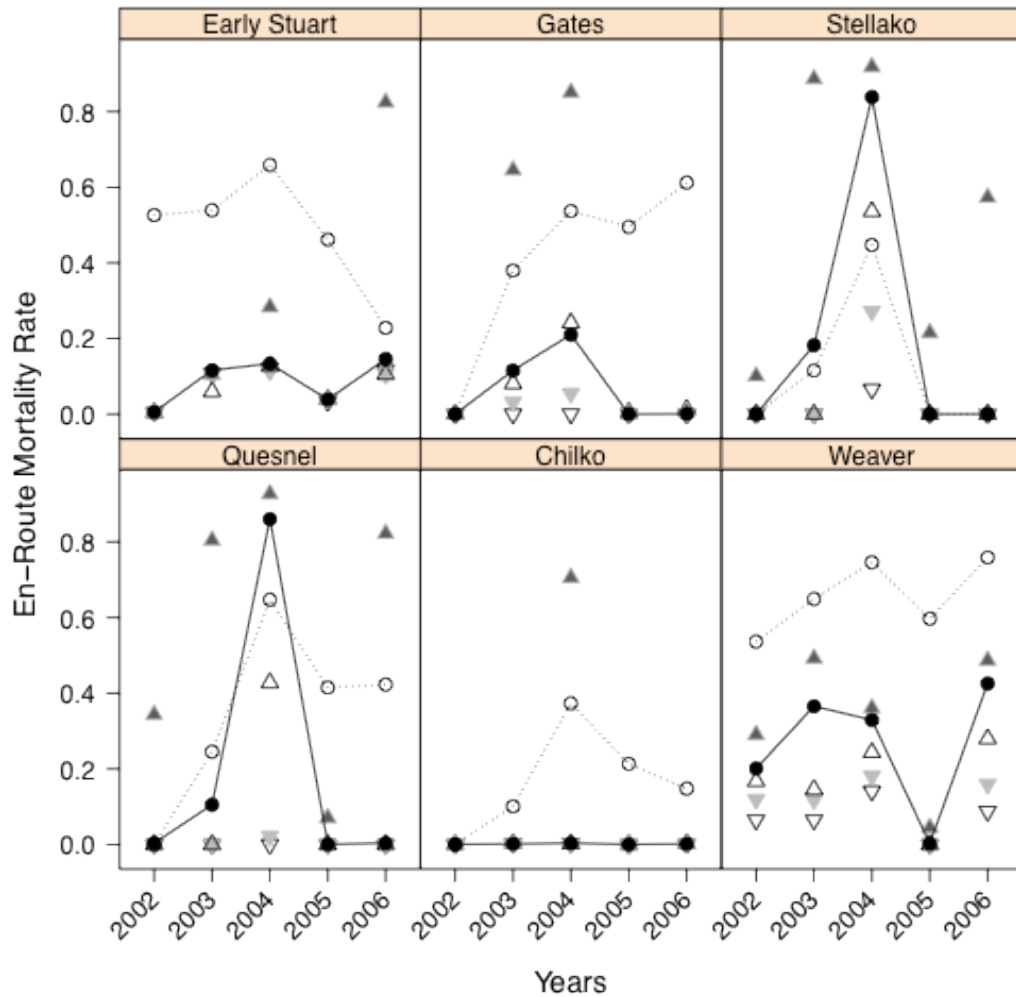
Figure B.2 Long-term LD50 parameter sensitivity test, base case (●), and DBEr (○) mortality rate estimates for all stocks for years 2002 to 2006. Base case long-term mean was increased by 100 (▲) and decreased by 100 (▼) degree-days.
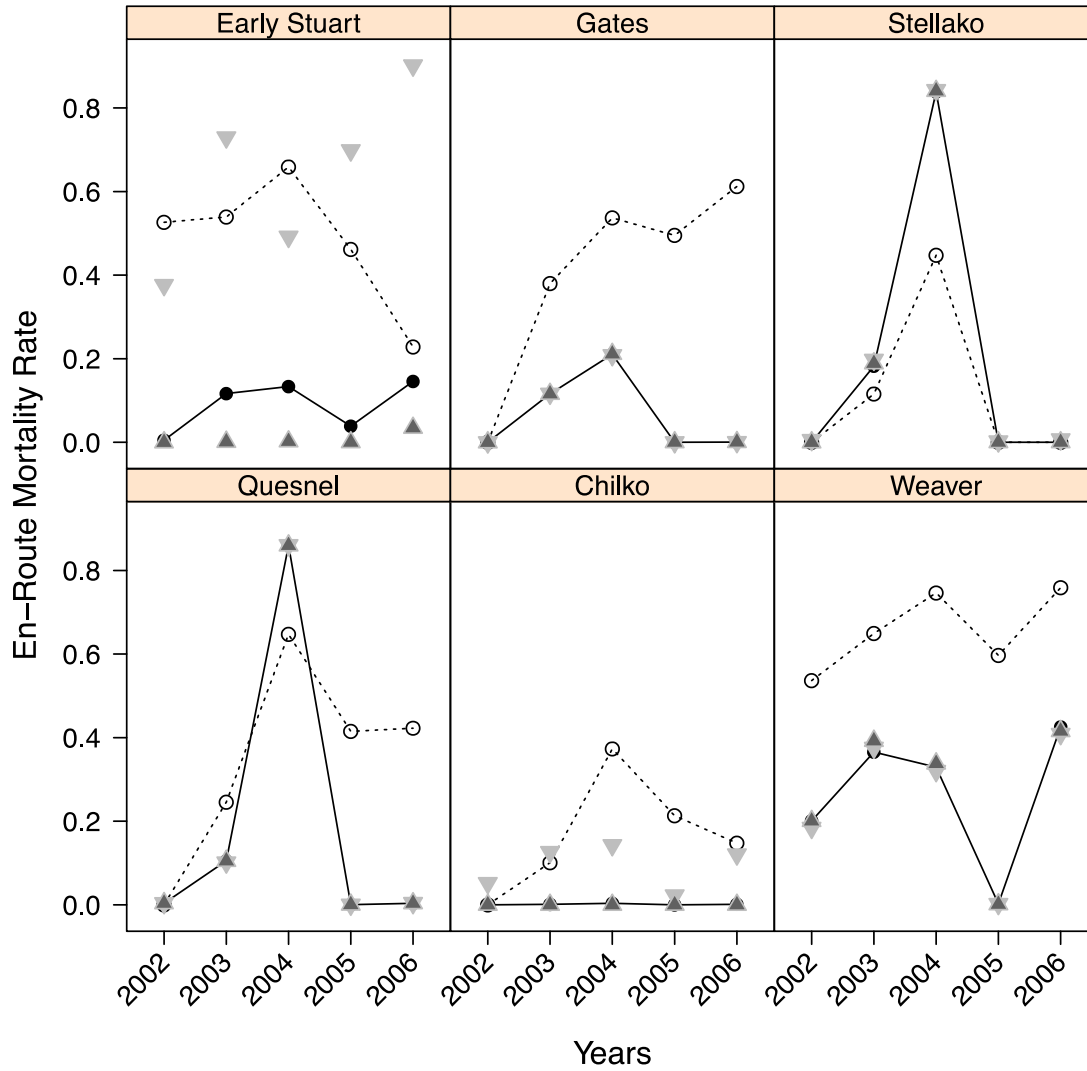
Figure B.3 Arrival timing sensitivity test, base case (●), and DBEr (○) mortality rate estimates. Base case arrival timing parameter mean was varied by +2 days (△) , -2 days (▽), +4 days (▲), and -4 days (▼) for all stocks for years 2002 to 2006.
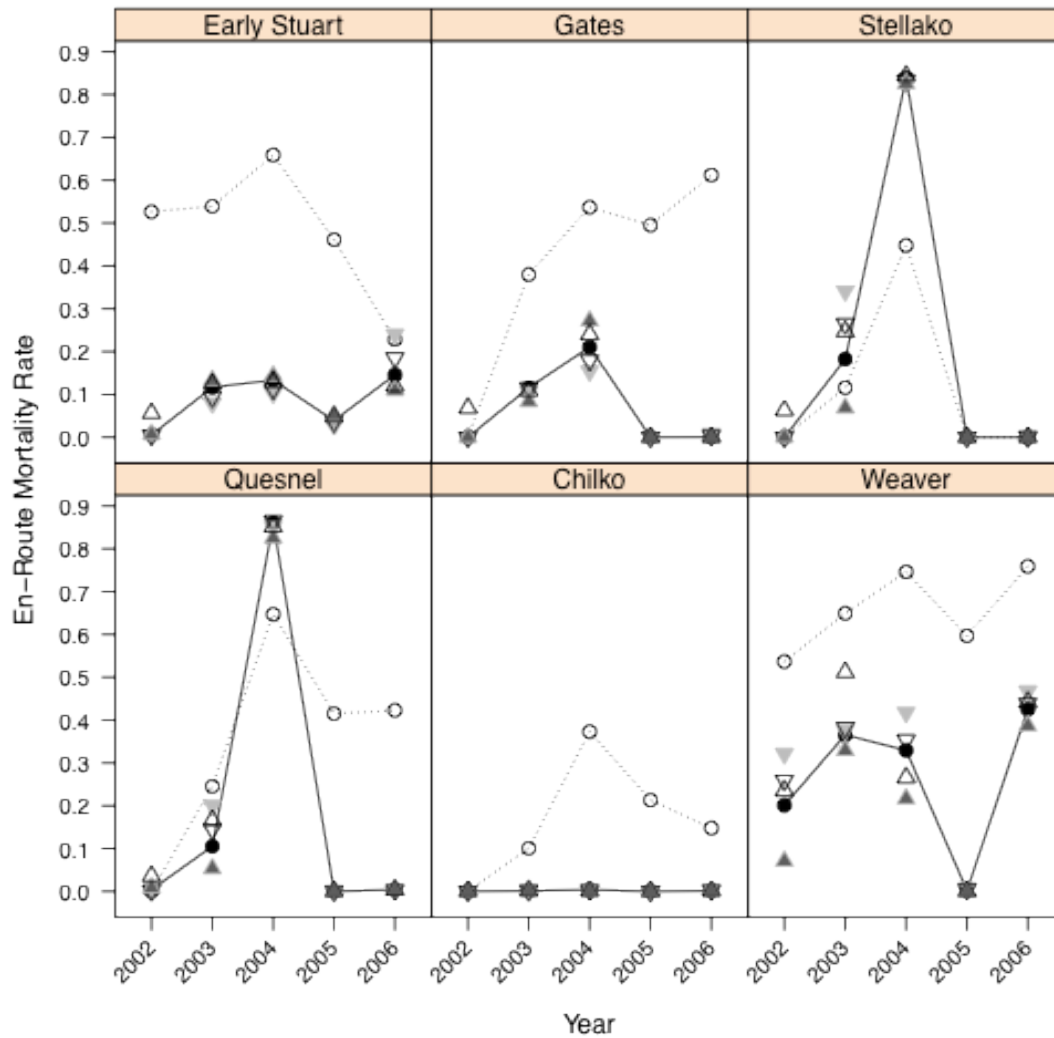
Figure B.4 Movement rate sensitivity test, base case (●), and DBEr (○) mortality rate estimates. Base case movement rate parameter was increased by 25% (△) and 50% (▲), and decreased by 25% (▽) and 50% (▼) for all stocks for years 2002 to 2006.