

Contribution to the Theme Section 'Tracking fitness in marine vertebrates'

Variable thermal experience and diel thermal patterns of homing sockeye salmon in coastal marine waters

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ABSTRACT: Temperature is recognized as a key factor influencing physiology, behaviour and survival of anadromous salmonids, yet little is known about their thermal experience, nor factors affecting it, during marine homeward migrations. In 2006 and 2010, approximately 1000 Fraser River sockeye salmon *Oncorhynchus nerka* were captured and tagged in coastal marine waters, ~215 km from the river mouth, during their spawning migration. Individual salmon were blood sampled, gastrically implanted with temperature loggers fixed to radio or acoustic tags, and released. We recovered 50 loggers from freshwater locales containing 14690 hourly temperature readings. Mixed-effects models were used to characterize marine thermal experience, and examine the association of thermal experience with initial physiological status as well as oceanographic and meteorological conditions. Sockeye salmon thermal experience was highly variable (8.4°C to 20.5°C), and we detected opposite diel patterns between study years that could be associated with moon phase, behavioural thermoregulation, olfactory/celestial navigation or predator avoidance. We were unable to find any relationships between thermal experience and environmental conditions or fish physiological state. Nonetheless, we found that the greatest variability in thermal experience was attributed to within-individual variation, suggesting that environmental and physiological variables need to be examined at different temporal and spatial scales, and/or additional environmental and physiological variables need to be assessed. Overall, the factors associated with the thermal experience of homing sockeye salmon in coastal marine environments are more complex than previously thought, and multiple year studies are needed before generalizing behavioural patterns observed from single year studies.

KEY WORDS: Temperature · Sockeye salmon · Migration · Behaviour · Physiology · Oceanography · Thermal logger · Telemetry

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INTRODUCTION

Reproductive migrations are challenging life history events often associated with the convergence of physiological and environmental transitions (Dingle

1996). This is certainly true for anadromous salmonids that encounter variable environmental conditions during their migration from ocean feeding grounds to freshwater spawning sites. Among environmental variables, temperature is thought to be the 'master'

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abiotic factor for fish (Fry 1968). Anadromous salmonids have a narrow range of temperatures that they routinely feed and rear in (Brett 1952, Elliott 1976, 1991, Larsson & Berglund 2005), and temperature is known to influence their distribution, migratory behaviour, physiology, growth, bioenergetics, and survival across all life stages (Friedland 1998, Richter & Kolmes 2005, Crozier et al. 2008, Jonsson & Jonsson 2009, Martins et al. 2012a). Changes to ocean temperatures are predicted under climate change scenarios (IPCC 2007), making it important to understand the present thermal experience of anadromous salmonids in the ocean in order to predict their response to future changes in ocean temperatures. However, little is known about the thermal experience of anadromous salmonids during their reproductive migration in marine waters, especially in relation to biotic and abiotic factors (Drenner et al. 2012).

In particular, the reproductive migration of anadromous salmonids through coastal marine waters is a critical phase due to salmonids encountering variable environmental conditions (e.g. salinities and temperatures) and high predator densities at the same time as altering their mechanisms for orientation and physiological state (Hinch et al. 2006, Thorstad et al. 2010). Fine-scale movement patterns of homing salmonids in coastal marine waters have been previously studied using ultrasonic tracking, acoustic telemetry and thermal data loggers (reviewed in Drenner et al. 2012). Behaviour can be highly variable among species, but homing salmonids typically migrate in the upper 50 m of the water column (Døving et al. 1985, Quinn et al. 1989, Ruggerone et al. 1990, Davidsen et al. 2013)—with the exception of chum salmon *Oncorhynchus keta* and Chinook salmon *Oncorhynchus tshawytscha*, which have been found to migrate at depths of >200 m (Candy & Quinn 1999, Tanaka et al. 2000). Homing salmonids also orient themselves with the thermocline (Westerberg 1982, Døving et al. 1985, Quinn et al. 1989), exhibit diel patterns (Madison et al. 1972, Quinn et al. 1989, Ruggerone et al. 1990, Candy & Quinn 1999, Walker et al. 2000), show a preference for a narrow range of temperature (Quinn et al. 1989, Walker et al. 2000) and undertake vertical migrations that expose fish to variable temperatures (e.g. 5 to >20°C; Døving et al. 1985, Quinn et al. 1989, Olson & Quinn 1993, Walker et al. 2000) and salinities (e.g. 7.8 to 33.6 ppt; Quinn et al. 1989, Olson & Quinn 1993). However, at present there are few direct measures of thermal experience for coastal migrating salmonids, and we know very little about the factors associated with thermal experience during this life stage.

It is speculated that vertical positioning in the water column (and thus environmental experience) during return migrations may be related to a number of factors including olfactory homing (Døving et al. 1985, Quinn et al. 1989, Ruggerone et al. 1990), behavioural thermoregulation (Tanaka et al. 2000), predator avoidance and fish physiological state (Olson & Quinn 1993, Hansen & Quinn 1998, Hinch et al. 2006). Olfactory homing is thought to be the major mechanism used by salmonids for navigation during this stage of migration (Hasler & Scholz 1983, Døving & Stabell 2003, Ueda 2011). Surface waters in coastal marine areas likely contain olfactory cues from natal streams that salmonids must 'sample' to aid in navigation (Døving & Stabell 2003). However, the choice of utilizing a particular depth or temperature could depend on trade-offs involved in minimizing energy use (Tanaka et al. 2000), maintaining physiologic homeostasis and reducing encounters with predators. For example, homing salmonids in coastal waters are undergoing physiological preparations for freshwater entry and reproduction which involves reconfiguring ion exchange systems and developing gonads, both of which are associated with elevated physiological stress (Høgåsen 1998, Hinch et al. 2006, Flores et al. 2012). Management of energy reserves is also crucial during this phase, especially for semelparous Pacific salmonids *Oncorhynchus* spp., which rely on finite energy reserves to fuel the remainder of migration (Crossin et al. 2009a). Exposure to above optimal temperatures, as can occur in surface waters, could cause increases in stress hormone concentrations (Jeffries et al. 2012), more rapid energy use (Brett 1971, Lee et al. 2003), alteration of reproductive maturation (Pankhurst & King 2010) and osmoregulatory failure (Jeffries et al. 2012). Further complicating such 'trade-offs', in laboratory experiments with salmonids held in full strength seawater, chum salmon and sockeye salmon *Oncorhynchus nerka* that are more 'freshwater-prepared' in terms of their osmoregulatory systems experienced higher levels of stress and lower survival (Hirano et al. 1990, Cooperman et al. 2010). Thus one might expect more freshwater-prepared migrants to spend more time in surface waters that are warmer and less saline. In general, we would expect that homing salmonids should take advantage of natal stream olfactory cues, which would potentially exist in warmer, less saline surface waters, under appropriate physiological conditions (i.e. when fish are less stressed or more freshwater-prepared) and/or when there are fewer visual oriented predators in the vicinity (i.e. during the night).

The concept of species-specific thermal optima is well established for freshwater-rearing and migrating salmonids (Brett 1952, Richter & Kolmes 2005, Jonsson & Jonsson 2009). Recently, investigators have discovered that thermal tolerance can vary substantially among populations within a single species (e.g. Fraser River sockeye salmon) and between sexes within a population, but this research only focused on freshwater environments (Farrell et al. 2008, Eliason et al. 2011, Martins et al. 2012b). There has been little research into whether population- or sex-specific differences in thermal optima exist in marine environments, although there is evidence of population-dependent responses to changing ocean conditions (e.g. salinity, wind-generated currents) in marine waters (Thomson & Hourston 2011).

To further our understanding of the factors associated with the thermal experience of homing anadromous salmonids in coastal marine waters, we analyzed data from recovered thermal data loggers that were attached to sockeye salmon during their coastal ocean return migration through the Strait of Georgia (SoG) to the Fraser River, British Columbia, Canada. The SoG is well studied in terms of its oceanography (Thomson 1981, 1994), and the linkage between salmon migratory behaviour and physiology has been well examined in this region (Hinch et al. 2006). However, there has been no research linking behaviour and physiology of homing salmonids in the marine environment to thermal experience. Our objectives were first to characterize the thermal experience of tagged sockeye salmon migrating through the SoG, and second to test whether thermal experi-

ence of sockeye salmon was associated with physiological state of fish, diel patterns, abiotic ocean conditions, meteorological conditions, migration timing, sex and population. This study represents the first attempt to directly link fish physiological state and environmental conditions to the thermal experience of homing anadromous salmonids in the marine environment using telemetry.

METHODS

Study site

The SoG is a deep inland basin located between mainland British Columbia and Vancouver Island (Fig. 1) that is approximately 200 km long, 40 km wide, and has an average and maximum water depth of 155 and 400 m, respectively. The southern part of the SoG is strongly influenced by freshwater discharge from the Fraser River. This warmer, less dense water entering the SoG creates a unique spatial habitat. Fraser River discharge dilutes seawater in the surface layer, causing a strongly stratified interface between the shallow (<10 m) brackish surface layer and the deeper (>10 m) more saline seawater (Thomson 1981). Tidal currents and wind-generated circulation also strongly influence the environment within the SoG (Thomson 1981). Currents in the northern SoG maintain a slow counter-clockwise rotation driven mainly by winds from the northwest. Currents in the southern part of the SoG are driven by a combination of winds and river discharge with currents circulating in a clockwise direction. These slower currents (~ 0.1 to 0.2 m s^{-1}) are also affected by the mixed, mainly semi-diurnal tidal currents, which are stronger in the south ($\sim 1 \text{ m s}^{-1}$), decreasing in strength northward. Rising tides result in flood currents entering the strait from the south and north (the tides meet in the northern sector of the SoG), while falling tides produce ebb currents that exit the SoG to the south and north.

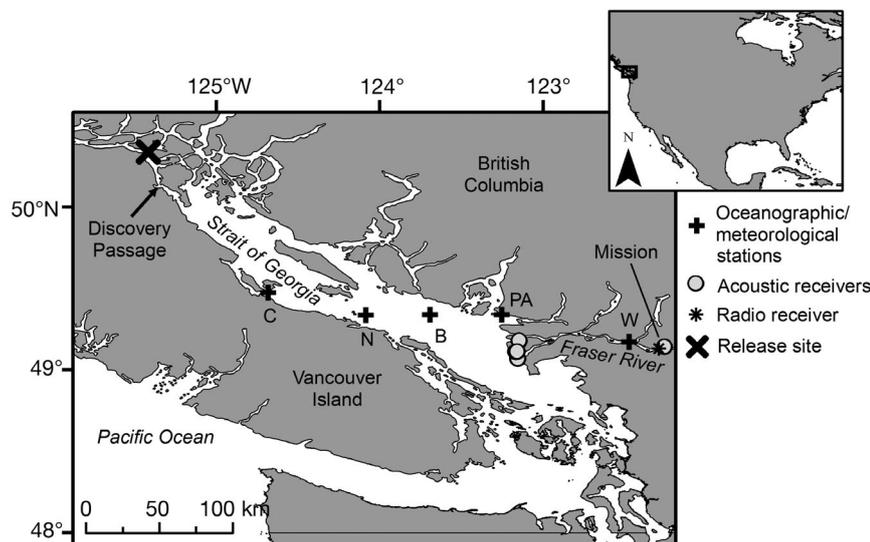


Fig. 1. Study area. 'C' = Chrome Island, 'N' = Nanoose Bay, 'B' = Buoy 46146, 'PA' = Point Atkinson, 'W' = Whonnock

Fish capture, biopsy and tagging

All tagging and sampling was conducted with the approval of the Animal Care Committee of the University

of British Columbia, in accordance with the Canadian Council on Animal Care. As part of a larger project monitoring sockeye salmon movements and survival, ~1000 adult sockeye salmon returning to the Fraser River were captured by commercial purse seine or commercial troll fishery in northern Discovery Passage ~215 km from the mouth of the Fraser River (Fig. 1) during August of 2006 and 2010. After capture, individual fish were brought on board the vessel and transferred to a holding tank that was flushed with free-flowing ambient saltwater. Pre-sampling holding durations for troll and purse seine caught fish were <15 min and <30 min, respectively. Non-lethal handling and sampling of unanaesthetized (Cooke et al. 2005) sockeye salmon followed 1 of 2 procedures. The full procedure started by moving an individual fish from the holding tank onto a foam-padded, v-shaped trough with a constant supply of cold saltwater. A 3 ml blood sample was taken from the caudal vein to assess blood plasma concentrations for stress parameters (glucose, cortisol, lactate), osmolality (an overall measure of physiological condition), sex hormones (testosterone, estradiol) and ion concentrations (i.e. Na^+ , K^+ , Cl^- , indicative of osmoregulatory state). The blood sample was stored on ice until the rest of the procedure was completed. Next, a small (<4 mm) gill tissue sample was taken from gill filament tips for a microarray analysis that was part of a separate research project, the details of which will be presented elsewhere. An adipose fin punch (0.5 g) was then taken for DNA population identification and stored in 95% ethanol prior to analysis. Fork length (FL) was measured to the nearest cm. Lastly, a transmitter ('tag') with an attached thermal logger was inserted gastrically using a plastic applicator, and fish were immediately released overboard. The reduced procedure, performed on approximately 50% of fish, was the same as described above, but without blood and gill tissue sampling. The full sampling procedure took less than 3 min (Cooke et al. 2005). After the fish was released, the blood samples were centrifuged, and the blood plasma transferred into liquid NO_2 .

The transmitters applied to fish were either Vemco acoustic tags (various models of V16 tags, Vemco; all 16 mm diameter and <70 mm length) or Lotek radio tags (model MCFT-3A-3V, Lotek Wireless; 16 mm diameter and 51 mm length). Thermal data loggers (iButton DS1921Z, Maxim Integrated Products; factory stated resolution = $\pm 0.1^\circ\text{C}$, accuracy = $\pm 1^\circ\text{C}$) were fixed to the transmitters with Plasti Dip® (PlastiDip International). In a separate study by our team that tested thermal data logger accuracy and

precision under laboratory conditions, mean iButton accuracy was reported as $0.4 \pm 0.3^\circ\text{C}$ and mean precision was reported as $0.2 \pm 0.0^\circ\text{C}$, which was more accurate than values reported by the manufacturer (Donaldson et al. 2009). Thermal data loggers were programmed to measure and store hourly temperature readings and associated date and time.

After release, individual fish movements were monitored using fixed telemetry arrays positioned along the sockeye salmon migration route at the lower Fraser River and Mission (Fig. 1). Acoustic tags could be detected at the lower Fraser River and at Mission, whereas radio tags could only be detected at Mission because radio signals are attenuated in saltwater. Tags were recovered by means of capture in commercial, aboriginal or sport fisheries, or by recovery on the spawning grounds by Fisheries and Oceans Canada (DFO) stock assessment crews. Rewards were provided to encourage return of thermal loggers.

Laboratory assays

Individual population origin was determined from DNA analysis of adipose fin clips (Beacham et al. 2004). Plasma osmolality, ions (Na^+ , K^+ , Cl^-), glucose and lactate were measured using the procedures outlined in Farrell et al. (2001). Plasma cortisol, testosterone and 17β -oestradiol were measured using commercial enzyme-linked immunosorbent assay (ELISA) kits (Neogen). Testosterone and 17β -oestradiol samples were extracted in ethyl ether in accordance with the manufacturer's protocols. Cortisol, testosterone and 17β -oestradiol samples were all run in duplicate at appropriate dilutions. Additional details on assays are provided in Farrell et al. (2001).

Tag recovery and oceanographic data collection

We used data from 50 recovered thermal data loggers representing the marine thermal experience of 50 individual sockeye salmon from 2006 ($n = 19$) and 2010 ($n = 31$). Out of the 50 recovered thermal data loggers, 2 were fixed to acoustic tags and 48 were fixed to radio tags. Radio tags are more likely to be noticed by persons handling fish than are acoustic tags due to the visible protrusion of the radio antenna from the mouth of the fish. In total, 35 (21 males, 14 females) of these fish were physiologically sampled. Data from the thermal loggers were downloaded and paired with telemetry data by matching the date and

time from the thermal loggers to date and time of radio or acoustic tags registering at detection sites (Fig. 1). This enabled us to extract fish thermal experience from the point of release in northern Discovery Passage to detection in the Fraser River either at the mouth of the Fraser River (for acoustic tags) or at Mission (for acoustic and radio tags) (Fig. 1). However, the Mission detection site is located approximately 75 km upriver from the SoG, and for this study we were only concerned with fish thermal experience within the SoG (i.e. prior to Fraser River entry). To determine point of river entry for radio tags, we used migration rate data from detection of acoustic tags on receivers at river entry and at Mission combined with visual inspection of individual fish temperature plots to look for evidence of river entry based on abrupt increases in temperature when fish entered the Fraser River. Based on this, we determined that there was a thermal signature associated with river entry and discarded temperature observations that followed past this point from the data set for all radio tags. The final data set included 14 690 hourly temperature readings. The study duration (date from when the first fish was released and the last fish entered the Fraser River) ranged from August 11 to September 6 in 2006 and August 11 to September 21 in 2010.

Oceanographic and meteorological data (i.e. water temperature, sea surface salinity, tide height, and various wind velocity and wind stress variables) from the SoG were compiled from Department of Fisheries and Oceans (DFO) coastal lighthouse monitoring sites (Chrome Island, Nanoose Bay, and Point Atkinson lightstations) and Environment Canada meteorological Buoy 46146 (Fig. 1). Oceanographic and meteorological variables were chosen based on biological knowledge of the factors influencing oceanography in the SoG. We compared oceanographic trends between monitoring sites to verify that the sites we selected were representative of conditions in the SoG. Vertical profile data taken from the Nanoose Bay monitoring site was used to characterize the vertical temperature and salinity structure of the water column. To match oceanographic and meteorological variables with individual fish temperature observations taken on an hourly scale, we also needed environmental data measured on an hourly scale. Therefore, we used data from 2 monitoring sites that measured variables on hourly basis to match with individual fish temperature observations based on matching date and time to the nearest hour. Tide height was measured at Point Atkinson, and all other oceanographic and meteorological variables were measured at Buoy 46146. Buoy 46146 recorded

near surface water temperatures at ~3 m depth, and wind variables were measured 10 m above the sea surface. Although of interest, sea surface salinity was not available as mean hourly data, and was therefore not paired with fish temperature observations. Fraser River hourly temperature data was gathered from DFO Environmental Watch Program monitoring buoys in the lower Fraser River (Whonnock; Fig. 1).

Data analysis

Data exploration followed protocols presented in Zuur et al. (2010) and was applied separately for oceanographic variables and physiological variables. Examination of multi-panel scatterplots indicated possible co-linearity between environmental variables (e.g. between sea surface temperature and Fraser River temperature) and between physiological variables (e.g. between lactate and cortisol). Therefore, we used Pearson correlation coefficient >0.8 and variance inflation factor (VIF) >3 to identify and remove collinear variables (Zuur et al. 2010). Variables that we selected to include in our analysis are presented below (variables chosen to be removed are indicated in parentheses and were closely related to one or more other variable included in the analysis): sea temperature at 3 m depth (Fraser River temperature), along-shore wind stress (along-shore wind velocity, wind stress magnitude), cross-shore wind stress (cross-shore wind velocity, wind stress magnitude), lactate (glucose, cortisol, osmolality), testosterone (estradiol), and Na^+ and Cl^- ions (osmolality, K^+ ion).

We used a mixed-effects model analysis because the data consisted of multiple temperature measurements of the same fish. Initial analysis fitting mixed-effects models to the raw time-series data for individual fish revealed substantial residual variability. Therefore, to increase the signal to noise ratio we aggregated fish body temperature and environmental data by computing the median values for each hour of the day (i.e. 24 median values for each individual; Murtaugh 2007). Two models were fit separately for oceanographic/meteorological and physiological variables. The first model (referred to as 'ocean' model) was fit using oceanographic/meteorological variables, and the second model (referred to as 'physio' model) incorporated significant variables from the 'ocean' model with physiological variables. The reasoning behind a separate analysis of oceanographic/meteorological compared to physiological variables, rather than incorporating all variables in

the same model, was because not all fish for which we had temperature data were physiologically sampled. Therefore, sample sizes for the physiological dataset were lower than for the oceanographic/meteorological dataset ($n = 1200$ for 'ocean' model, and $n = 816$ for 'physio' model).

Predictor variables included as fixed effects in the 'ocean' model were sea temperature at 3m depth (ST3m), along-shore wind stress (AlShWS), cross-shore wind stress (CrShWS), tide height (tide), and study year. To test for the effects of sampling blood and gill tissue on subsequent thermal experience, we also included a variable indicating whether the fish was sampled or not sampled (referred to as 'sampled'). For each fixed variable in the 'ocean' model (except study year, tide and sampled), we included 2 variables representing a within-subject effect (centered predictor variables within an individual) and a between-subject effect (mean of the predictor variable for an individual). Including both a within- and a between-individual component for predictor variables accounts for not all fish experiencing the same conditions while migrating due to differences in migration timing between individuals (see van de Pol & Wright [2009] and Dingemanse & Dochtermann [2013] for details on the importance of incorporating within- and between-individual predictors when predictor values for within-individual vary between individuals). To test for diel patterns in fish thermal experience, we included periodic terms [$\sin(2\pi \times \text{hour}/24)$, $\cos(2\pi \times \text{hour}/24)$] into the 'ocean' model as fixed effects. Within-subject centering was not applied to periodic terms as all individuals in the data set 'experienced' each of the 24 h. Visual inspection of hourly fish temperature plots indicated possible differences in diel patterns of fish thermal experience between study years. Therefore we included interaction terms for study year with the periodic terms.

Predictor variables included as fixed effects in the 'physio' model were the significant variables from the 'ocean' model together with a centered variable for lactate (indicates stress), testosterone (indicates reproductive maturity), Na^+ (indicates freshwater preparedness), Cl^- (indicates freshwater preparedness) and sex. Using interaction plots we identified possible interactions between sex and testosterone. Therefore we included interactions for sex with testosterone in the 'physio' model.

We determined appropriate random effects to include in our models by comparing models that included all fixed effect terms with all possible combinations of random effect groups (all models included

the individual level) using Akaike information criterion (AIC) (Burnham & Anderson 2002). AIC selection revealed that the most parsimonious model included random effects for (from lowest to highest level): individual fish, stock complex (population or groups of populations of sockeye salmon), and run-timing group (aggregates of stocks complexes). Run-timing groups are management-derived distinctions based on the biology of the populations (i.e. dates they migrate into the Fraser River; Beacham et al. 2004). In our data set, there were 3 run-timing groups (from earliest migration date to latest): early-summer ($n = 8$), summer-run ($n = 9$), and late-run ($n = 33$). Late-run fish historically exhibited a 'milling' period prior to river entry, but since 1995, portions of late-run fish began entering the river 3 to 6 weeks earlier than historic norms. Late-run fish that enter the river early are called 'early' migrating late-run fish. This behavioral phenomenon has been the focus of numerous studies because 'early' migrants experience high levels of mortality in freshwater (Cooke et al. 2004, Hinch et al. 2012). Based on this interesting biological phenomenon, we subdivided the late-run group into 2 groups: 'early' late-runs ($n = 15$), and 'normal' late-runs ($n = 18$). 'Early' migrating late-run fish were those that migrated earlier into the Fraser River than historic norms, and 'normal' migrating late-run fish were those that migrated at historic norms.

Median fish temperature values were transformed to their reciprocal to reduce heterocedasticity identified with plots of residuals by fitted values. In addition, variance structures for the variables 'study year' and 'sampled' were subsequently included to reduce heterocedasticity associated with these predictors (Pinheiro & Bates 2002). Autocorrelation plots for the residuals indicated temporal correlation for fish temperature observations. To account for temporal correlation, we fit both the 'ocean' and 'physio' models with an auto-regressive correlation structure of order 1 (AR1). Backwards model selection was done using marginal F -tests to select a reduced model containing only significant terms. Variables were removed when $p > 0.01$, a conservative threshold that was chosen to account for multiple testing (Zuur et al. 2009). We computed marginal (based on significant fixed effects) and conditional (based on fixed and random effects) R^2 values as described in Nakagawa & Schielzeth (2013). All data exploration and statistical analysis were performed in R v. 2.15.2 (R Core Development Team 2012), using packages 'nlme' (Pinheiro et al. 2012) and 'AICcmodavg' (Mazerolle 2012).

RESULTS

Characterization of fish thermal experience and ocean conditions

Visual inspection of individual fish hourly temperature plots showed common patterns related to initial thermal experience after release and subsequent diel

thermal patterns. The marine thermal experience for 8 individual sockeye salmon (Fig. 2) from the release location in Discovery Passage to Fraser River entry reveals the range of thermal habitats experienced. Individual fish were selected from our larger dataset from both years of study based on patterns that are described hereafter being visually apparent. Hourly individual fish temperature plots for all 50 individual

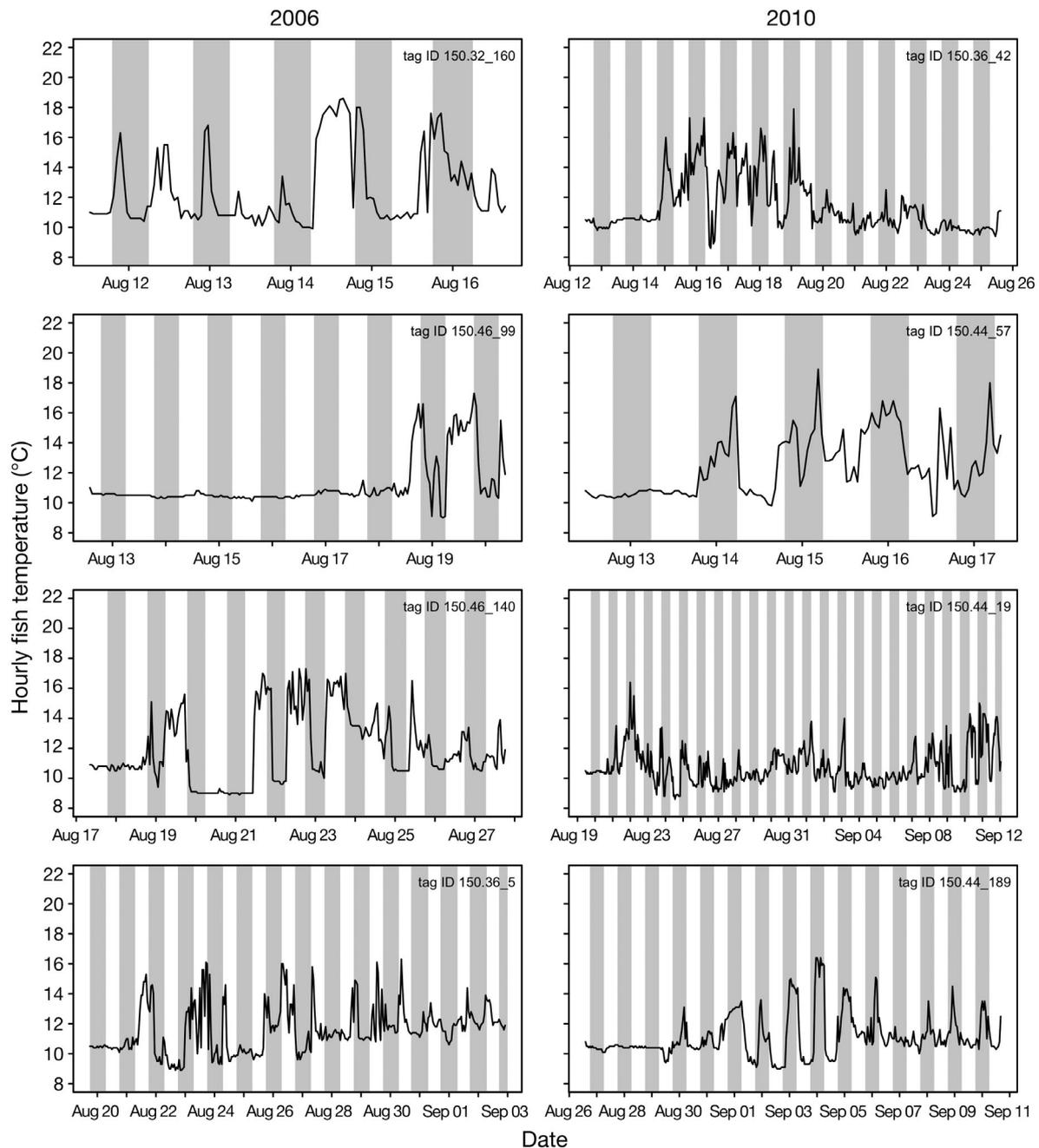


Fig. 2. Hourly thermal ($^{\circ}\text{C}$) experience recorded from 8 sockeye salmon from time of release in Discovery Passage to entry into Fraser River. Fish in the left column are from 2006, those in the right column are from 2010. Grey shaded regions indicate nighttime. Individual fish were selected due to thermal profiles being representative of patterns described in text

fish reveal patterns similar to those shown here (see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m496p109_supp.pdf).

We identified 2 'stages' of fish thermal experience from individual fish hourly temperature plots. The first stage was immediately following release, in which fish experienced a period of relatively consistent temperature of approx. 10 to 12°C. The duration of time a fish spent in the 'consistent' thermal experience stage varied between individuals. This is exemplified in hourly temperature plots for the fish represented by tag IDs 150.32_160 and 150.46_99, where the former remained in the 'consistent' stage after release for <1 d whereas the latter remained in the 'consistent' stage after release for approx. 6 d (Fig. 2). We performed a changepoint analysis in R v. 2.15.2 (R Core Development Team 2012), using the package 'changepoint' (Killick & Eckley 2013), to determine the point when the mean temperature began to vary for individual fish after release. Based on the changepoint analysis, the mean (\pm SD), minimum and maximum number of days spent in 'consistent' thermal experience stage after release was 2.0 ± 1.4 d, 0.3 d, and 6.0 d, respectively. The coefficient of variation, mean (\pm SD), minimum and maximum hourly thermal experience during 'consistent' stage was 0.04, $10.6 \pm 0.4^\circ\text{C}$, 9.0°C , and 13.4°C , respectively. All hourly temperature readings from the 'consistent' temperature stage were excluded from our subsequent data analysis that focused on the remaining period of fish thermal experience due to the possibility of the 'consistent' temperature stage being associated with a capture or tagging effect or the environment at the site of release (see 'Discussion'). This reduced our overall sample size from 14 690 to 12 232 hourly temperature observations.

Following the stage of 'consistent' thermal experience, hourly thermal experience of individual fish became more variable and this trend continued throughout the remainder of the marine migration to freshwater entry. Within the 'variable' thermal experience stage, there was extensive variability in hourly thermal experience both within-individuals and between-individuals. For example, within the 2010 study year, the fish represented by tag ID 150.36_42 experienced a wide range of temperatures (i.e. 8.6 to 17.9°C) with frequent temperature variations, whereas the fish represented by tag ID 150.44_189 experienced a slightly narrower range of temperatures (i.e. 9.0 to 16.4°C) and less frequent temperature variations (Fig. 2). The coefficient of variation, mean (\pm SD), minimum and maximum hourly thermal experience during the 'variable' stage

was 0.16, $11.4 \pm 1.8^\circ\text{C}$, 8.5°C , and 20.5°C , respectively. The 2 stages of thermal experience (i.e. 'consistent' and 'variable') are interpreted separately in the 'Discussion'.

Diel patterns were also observed in individual hourly fish temperature plots, and there appeared to be opposite diel patterns between study years. In 2006, fish generally exhibited a diel pattern of experiencing warmer temperatures during the day and cooler temperatures during the night, as can be observed in individual hourly temperature plots for the fish represented by Tag IDs 150.46_99, 150.46_140, and 150.36_5 (Fig. 2). In contrast, fish tagged in 2010 generally exhibited a diel pattern of experiencing warmer temperatures during the night and cooler temperatures during the day, as can be observed in individual hourly temperature plots presented for all the fish in that year (Fig. 2). Diel patterns in thermal experience also varied between-individuals within a study year and within-individuals. For example, the fish represented by tag ID 150.32_160 from 2006 showed signs of both diel patterns described above. In contrast, the fish represented by tag ID 150.36_40 from the same study year showed a more consistent diel pattern of experiencing warmer temperatures during the day and cooler temperatures at night (Fig. 2).

During the 'variable' stage of thermal experience, we observed some variability in thermal experience among stock complexes (Fig. 3). However, variability observed among stock complexes was largely attributed to differences among run-timing groups (Fig. 3). Among run-timing groups, summer-run fish experienced the warmest temperatures and 'normal' late run fish experienced the lowest temperatures (Fig. 3). In addition, fish from the 'early' late-run group experienced warmer temperatures than fish from the 'normal' late-run group (Fig. 3) even though they are made up of the same stock complex and migrate through the SoG at similar times.

Descriptive statistics for oceanographic/meteorological variables used in our model measured over the study duration (Table 1) revealed that mean values for these conditions were similar between the 2 years of study. However, in 2010, surface waters reached higher maximum temperatures and both components of wind stress were higher for both minimum and maximum values. Mean temperature below the thermocline (>20 m) in 2006 and 2010 was $9.4 \pm 0.3^\circ\text{C}$ and $9.3 \pm 0.3^\circ\text{C}$, respectively. Vertical profiles of salinity and temperature structure of the water column in 2006 and 2010 show that surface waters reached warmer temperatures and lower

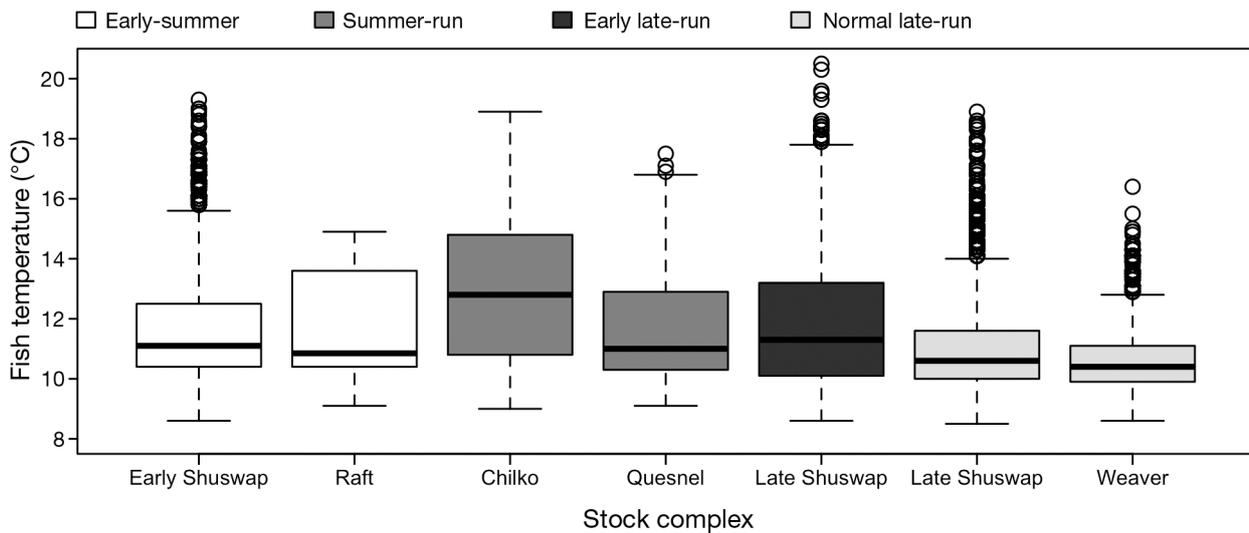


Fig. 3. Boxplots of the thermal experience for various stock complexes represented in the data set. Only temperature data from the 'variable' stage of thermal experience are shown (see 'Results: Characterization of fish thermal experience and ocean conditions'). The run-timing group that a stock complex belongs to is indicated above the figure. Run-timing groups are ordered by date they entered into the Fraser River, from left (earlier) to right (later). Within a run-timing group, stock complexes are not ordered in any particular manner. Solid bold horizontal lines represent median temperature, box limits represent the interquartile range (IQR), and whiskers represent $1.5 \times$ the IQR. Open circles represent outliers

salinities in 2010 (Fig. 4). Temperature and salinity below the thermocline were similar between the 2 years (Fig. 4).

Model results for fish thermal experience

Variables included in the models and the model selection procedures are presented in Table 2. The final 'ocean' model included a significant effect for the interaction of study year with the periodic terms that represent diel patterns [$\sin(2\pi \times \text{hour}/24)$:study year; $df = 1146$, $p < 0.0004$; and $\cos(2\pi \times \text{hour}/24)$:study year; $df = 1146$, $p < 0.0001$]. Predictions of median hourly fish thermal experience over a day for each of the study years indicate opposite diel patterns in fish thermal experience between the study years (Fig. 5). In 2006, fish experienced peak temperatures around midday (12:00 h to 14:00 h), and the

lowest temperatures during the night (24:00 h to 02:00 h), whereas in 2010, fish experienced peak temperatures during the night (24:00 h to 02:00 h), and the lowest temperatures around midday (12:00 h to 14:00 h; Fig. 5). In addition, fish in 2006 experienced higher and more variable median hourly temperatures than fish from 2010 (Fig. 5).

After incorporating the above significant variables from the 'ocean' model into the 'physio' model, the physiologic variables were not significant ($p > 0.01$) and were therefore removed prior to removal of any oceanographic variables during backward selection (Table 2). For this reason we fell back to using the 'ocean' model as it took advantage of the full data set rather than a subset of data for physiologically sampled fish. The significant fixed effects alone (marginal R^2) in our final model explained only $\sim 11\%$ of the variability in the data. The fixed effects and random effects (conditional R^2) explained $\sim 50.3\%$.

Table 1. Descriptive statistics (mean \pm SD [min., max.]) for oceanographic and meteorological variables used in our model (except tide) over the study duration: August 11 to September 6 in 2006 and August 11 to September 21 in 2010. Hourly measurements were taken at Buoy 46146 in the Strait of Georgia. Temperature was measured at 3 m depth. Along-shore wind stress is positive when directed to 290° true compass bearing, and cross-shore wind stress is positive when directed toward 20° true compass bearing

	Sea surface temperature ($^\circ\text{C}$)	Along-shore wind stress (N m^{-2})	Cross-shore wind stress (N m^{-2})
2006	16.0 ± 2.3 [11.3, 21.3]	-0.03 ± 0.04 [-0.20, +0.09]	0.00 ± 0.01 [-0.03, +0.04]
2010	16.4 ± 2.4 [11.4, 23.6]	0.00 ± 0.07 [-0.31, +0.37]	0.00 ± 0.02 [-0.11, +0.13]

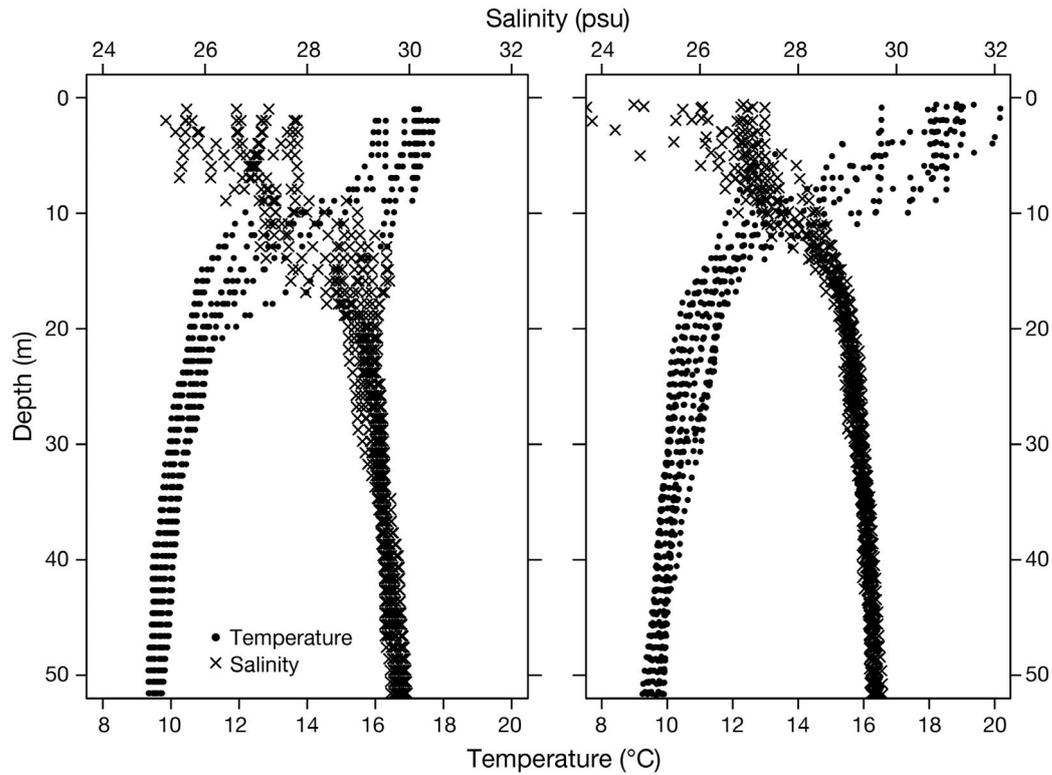


Fig. 4. Vertical profile of the Strait of Georgia taken at Nanoose Bay in (A) 2006 and (B) 2010. All measurements taken over the month of August are shown

Among random effects in our model, the amount of variability associated with individual, stock complex, and run-timing effects was ~30.7, <0.0001, and ~8.5%, respectively. The remaining variability (~49.7%) was due to within-individual variation.

Model predictions for the expected median thermal experience for each run-timing group (i.e. early-summer, summer-run, 'early' late-run, and 'normal' late-run), were 11.9, 12.4, 11.9, and 11.2°C, respectively. Model predictions show that summer-run fish

Table 2. Fixed effects and model selection procedure for the 'ocean' and 'physio' models. For variables in the 'ocean' model, 'wi-' and 'bi-' before variables represent a within-individual and a between-individual effect respectively (see 'Methods: Data analysis'). Variables are reported in the order they were removed from the model during backwards selection. p-values are reported for each variable after removal of previous non-significant variables. In the 'step removed' column, a '-' indicates the variable was retained in the final model

'Ocean' model			'Physio' model		
Step removed	Variable	p	Step removed	Variable	p
1	wi-ST3m	0.95	1	Cl	0.44
2	bi-CrShWS	0.87	2	Sodium	0.53
3	Sampled	0.74	3	Sex:Testosterone	0.09
4	bi-AlShWS	0.51	4	Testosterone	0.52
5	wi-CrShWS	0.50	5	Sex	0.42
6	wi-AlShWS	0.13	6	Lactate	0.03
7	Tide	0.05	-	Study year	0.07
8	bi-ST3m	0.02	-	$\sin(2\pi \times \text{hour}/24)$	0.11
-	Study year	0.15	-	$\cos(2\pi \times \text{hour}/24)$	<0.0001
-	$\sin(2\pi \times \text{hour}/24)$	0.09	-	$\sin(2\pi \times \text{hour}/24):$ study year	0.0008
-	$\cos(2\pi \times \text{hour}/24)$	<0.0001	-	$\cos(2\pi \times \text{hour}/24):$ study year	<0.0001
-	$\sin(2\pi \times \text{hour}/24):$ study year	0.0004			
-	$\cos(2\pi \times \text{hour}/24):$ study year	<0.0001			

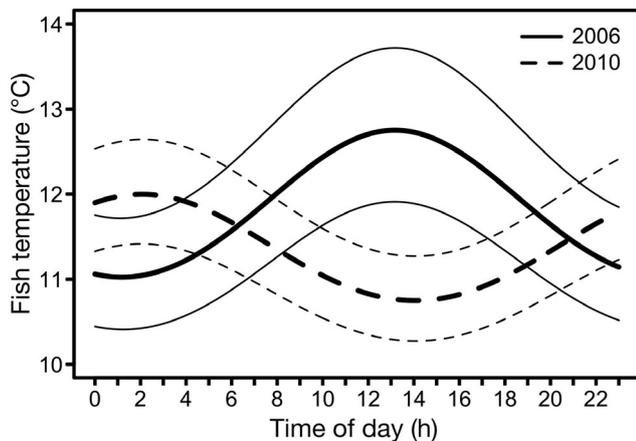


Fig. 5. Model predictions for median hourly fish thermal experience over a 24 h period for the 2 study years (2006 and 2010). Thin solid and dashed lines above and below bolded solid and dashed lines, respectively, indicate 95% confidence intervals

experience the highest temperatures among run-timing groups (on average between 0.5 and 1.5°C warmer), and 'early' late-run fish experience temperatures that are on average 0.7°C warmer than 'normal' late-run fish.

DISCUSSION

The present study used small thermal data loggers to track individual homing sockeye salmon thermal experience in a coastal marine environment as they migrated to freshwater, and related fish thermal experience to environmental conditions and physiological state of individual fish. By tracking individual fish thermal experience, we were able to observe 2 'stages' of fish thermal experience; the first stage being characterized by a period of 'consistent' thermal experience followed by a 'variable' stage with opposite diel patterns between the study years. Based on our models, the 'variable' stage of thermal experience was not associated with environmental conditions or fish physiological state, and the greatest variability in thermal experience in the data was attributed to within-individual variation.

The 'consistent' stage of fish thermal experience directly following release ranged in duration between individuals in our data set and could be attributed to a number of potential factors. The first possible explanation is that there is an effect of capture and tagging on subsequent fish behaviour after release that influences their thermal experience either directly (by fish seeking out cooler

waters to facilitate physiological recovery from a stressor) or indirectly (by fish exhibiting an escape response after release by diving down to cooler waters). In other studies using similar methods of tracking anadromous salmonid behaviour in the ocean, authors have noted a 'tagging' effect on fish behaviour immediately following release (Quinn et al. 1989, Candy & Quinn 1999 Walker et al. 2000). Quinn et al. (1989), for example, noted that homing sockeye salmon that were manually tracked in a location near our release site initially dived to deep waters after release before ascending to surface waters, and in some cases this feature was distinguishable from subsequent behaviour.

Another possibility is that the thermal environment is homogeneous throughout the vertical water column in the location our fish were released, thus providing no scope for variation in thermal experience. Based on vertical profile data taken in Discovery Passage during tagging in 2010, temperature was homogeneous (approx. 10.8°C) throughout the upper 50 m of the water column (S. M. Drenner unpubl. data). Furthermore, a study examining depth use of homing sockeye salmon that were tagged and released in the same location as our study found that sockeye salmon swam at an average depth of 26.2 m in an area directly downstream of the migration pathway of the release site; however, the same fish were observed swimming at more shallow depths (e.g. ~9.0 m) when they were in the SoG, which could expose them to higher temperatures (Wilson et al. 2014, this volume). We conclude that the observed 'consistent' thermal experience immediately following release in our study could be associated with one or more factors, such that the vertical environment is homogeneous at the release site and capture and/or handling may influence the duration of time a fish remains in this environment before migrating into the thermally stratified waters of the SoG. For these reasons, and because we were trying to relate thermal experience to surface conditions in the SoG, we did not include temperature recordings from this stage in our subsequent analysis. Combining depth sensors with thermal loggers in future studies would help resolve behavioural issues we observed in the 'consistent' stage of thermal experience.

After the stage of 'consistent' thermal experience, sockeye salmon exhibited considerable variability in thermal experience that persisted to freshwater entry. Variability in thermal experience is likely related to vertical movements in and out of the warmer surface layer — as observed for sockeye salmon that were tagged with depth-sensing tags (Quinn et al.

1989). Interestingly, sockeye salmon did experience temperatures that were well above what is considered metabolically optimal in fresh water (i.e. $>18^{\circ}\text{C}$; Eliason et al. 2011) and as high as temperatures sockeye salmon experienced after entering the Fraser River. However, out of a total of 12232 hourly temperature readings in the 'variable' thermal experience stage, only 69 ($\sim 0.6\%$) of those readings were greater than or equal to 18°C , providing evidence that sockeye salmon generally avoid warmer surface water. Overall, during the 'variable' stage of thermal experience sockeye salmon showed a strong preference for cooler waters (mean temperature of 11.4°C) at or near the thermocline. Our finding of mean thermal experience of 11.4°C is below what is considered the thermal optimum for maintaining aerobic scope in freshwater environments by summer migrating sockeye salmon (Eliason et al. 2011). Moreover, metabolic costs are higher in salt water than in fresh water for sockeye salmon (Wagner et al. 2006), therefore the choice of occupying deeper and cooler water in the SoG could be a result of individuals attempting to minimize total metabolic costs in the marine environment at the expense of maximizing aerobic scope. Development of more robust models that predict metabolic rate from temperature for adult salmonids in saltwater would help resolve this trade-off.

During the 'variable' stage of thermal experience, we observed diel patterns in individual fish temperature plots that were opposite between study years. This observation was supported by our models, which found a significant effect for the variables representing an interaction of diel patterns with study year. Diel patterns have been noted for anadromous salmonids migrating in the open ocean (Ogura & Ishida 1992, 1995, Walker et al. 2000, Friedland et al. 2001, Ishida et al. 2001, Azumaya & Ishida 2005, Hedger et al. 2009, Walker & Myers 2009, Reddin et al. 2011) and for coastally migrating Pacific salmonids (Quinn et al. 1989, Walker et al. 2000). Among previous studies, the most common diel pattern was characterized by fish migrating in warmer, surface waters at night and cooler, deeper waters during the day. This pattern was consistent with diel patterns we observed in 2010. However, in 2006, diel patterns were opposite and were similar to those described in Teo et al. (2013) for post-spawning steelhead kelts in the ocean. Teo et al. (2013) noted that diving behaviour of steelhead kelts in the ocean appeared to be associated with the moon phase. During our study, the moon phase in 2006 at the first date of tagging (August 11) was waning and changed to a waxing moon phase towards the end of the study. In contrast,

the moon phase at the start of the study in 2010 (August 11) was a waxing moon and changed to a waning moon phase towards the end of the study. Therefore, the opposite diel patterns between our 2 study years could be associated with differences in moon phase. Other studies have suggested that diel patterns for anadromous salmonids in the ocean could be associated with other factors including season, location, foraging, behavioural thermoregulation, predation and olfactory homing (Quinn et al. 1989, Ogura & Ishida 1995, Tanaka et al. 2000, Walker et al. 2000, Hinke et al. 2005, Walker & Myers 2009). During the period of migration examined in our study, sockeye salmon have ceased feeding (Hinch et al. 2006), ruling out foraging as a hypothesis for diel patterns. Oceanographic data we collected indicated that in 2010, surface waters reached higher temperatures and lower salinities than in 2006. Therefore in 2010, sockeye salmon could have been more likely to avoid these conditions (which would occur during midday) to optimize energy use (i.e. behavioural thermoregulation) or osmoregulatory function. Diel patterns could also be a result of reducing encounters with pinned predators such as harbour seals *Phoca vitulina*. Harbour seal population numbers have increased to potentially carrying capacity levels in the SoG since a ban on harvesting was implemented in 1970's (Olesiuk et al. 1990), and are known to utilize homing Pacific salmonids as a food source in estuaries (Wright et al. 2007). Interestingly, Wright et al. (2007) speculated that harbor seal predation rates on salmonids were higher during the night, and could be in response to the behaviour of their prey (i.e. salmonids migrating in shallower waters at night), exemplifying the complexity of predator-prey behaviours. We conclude that diel patterns observed in our study could be related to a number of factors (i.e. moon phase, reducing encounters with predators, olfactory/celestial navigation, and behavioural thermoregulation) that our study was not designed to test for. Overall, our results suggest that diel patterns of homing sockeye salmon in coastal marine environments is far more complex than previously thought, and multiple year studies are needed before generalizing behavioural patterns observed from single year studies.

The significant fixed variables together (e.g. variables representing an interaction between diel patterns and study year) in our final model explained a relatively low amount of the variability in thermal experience. In addition, none of the physiological variables included in our model were significant predictors of fish thermal experience, which was surpris-

ing given that previous studies with Fraser River sockeye salmon sampled at the same capture site as ours found strong relationships between physiological state and subsequent migration rate and survival into freshwater environments (Cooke et al. 2006, 2008, Crossin et al. 2007, 2009a, 2009b). In this present study we could not clearly identify environmental and physiological correlates with thermal experience; in addition, variability in thermal experience was not well explained by the interaction of diel patterns and study year. These results suggests that thermal habitat choice is a much more complex process than is involved in governing coastal migration rates, and it likely involves multiple factors that we have alluded to above (e.g. minimizing metabolic costs, obtaining homing cues, avoiding predators).

The greatest variability in thermal experience was attributed to within-individual variation, and the second greatest variability was among individuals of a given stock complex. The SoG is a spatially and temporally complex environment and individual fish may experience fine-scale differences in the environment based on timing, location and chance that we are not able to account for. For example, although fish may share similar phenotypes, one fish may encounter more predators or experience different ocean conditions at a local scale. Furthermore, fine-scale differences in environmental experience at the scale of within-individuals could interact with the physiological state of the fish to produce variability in behaviour. To aid in our ability to explain differences in thermal experience within individuals, several areas could be further explored. For example, models that predict more fine-scale environmental conditions fish experience (based on individual migration rates) could be combined with tags that measure multiple environmental variables. In addition, gene expression could give a more detailed assessment of physiological state.

We observed variability in thermal experience among stock complexes that we attributed to variability among run-timing groups. Our model supported our observations from the data and indicated differences in thermal experience among run-timing groups as well as a relatively low variability explained by differences among run-timing group stock complexes. As previously described, run-timing groups are aggregates of stock complexes based on the time they enter the Fraser River. Because of this, stock complexes within a run-timing group would be expected to encounter similar conditions because they migrate at similar times, and different run-timing groups would be expected to experience differ-

ent conditions. Indeed, our model indicated that run-timing groups that migrate through the SoG at later dates generally experienced lower temperatures, which is consistent with surface water temperatures decreasing over the study duration. Interestingly, our model indicated differences within the late-run run-timing group: 'early' late-run fish experienced warmer temperatures than 'normal' late-run fish. 'Early' and 'normal' late-run fish migrate at similar times through the SoG (the only difference is the date of river entry) and would be expected to experience similar environmental conditions. A possible explanation of the temperature differences between the 2 late-run groups could be that there are differences in behavior; for example, 'early' late-run fish may be more likely to exhibit vertical migrations than 'normal' late-run fish. More frequent vertical migrations could be a reflection of a higher frequency of encountering predators or sampling natal olfactory cues in surface waters, which could increase the likelihood of 'early' late-run fish deciding to leave the marine system and enter the river.

CONCLUSIONS

Changes in global temperatures could alter the physical structure of coastal marine environments (IPCC 2007) and have profound effects on their biota (Pörtner & Farrell 2008). Average annual sea surface temperatures in the SoG have already increased by 1°C over the past century (Chittenden et al. 2009), and are predicted to continue to rise based on changes in precipitation patterns and timing of freshet input from the Fraser River (Johannessen & Macdonald 2009). For sockeye salmon that are already near the southern limit of their distribution (Welch et al. 1998), the ability to adapt to meet changing conditions is paramount. In order to understand how sockeye salmon will adapt to future conditions, we need to understand current behaviours and the factors associated with these behaviours. Our research showed that sockeye salmon homing in the SoG experience diel patterns in thermal experience as well as variable temperatures. The variability in thermal experience was largely attributed to within-individual variation that was not explained by either physiological state of fish or environmental conditions. These results suggest that individual attributes and fine-scale environmental conditions may be vital to homing sockeye salmon. More detailed assessment of fish physiological state (through gene expression work) combined with tags that measure

multiple environmental conditions would aid our understanding of behaviour during this life-stage. Overall, the factors governing sockeye salmon thermal experience during homing migration in coastal marine waters is complex and may vary between years. However, variability in thermal experience suggests that homing sockeye salmon may be able to adapt to changing environmental conditions in coastal marine waters.

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LITERATURE CITED

- Azumaya T, Ishida Y (2005) Mechanism of body cavity temperature regulation of chum salmon (*Oncorhynchus keta*) during homing migration in the North Pacific Ocean. *Fish Oceanogr* 14:81–96
- Beacham TD, Lapointe M, Candy JR, McIntosh B and others (2004) Stock identification of Fraser River sockeye salmon using microsatellites and major histocompatibility complex variation. *Trans Am Fish Soc* 133:1117–1137
- Brett JR (1952) Temperature tolerance in young Pacific salmon, genus *Oncorhynchus*. *J Fish Res Board Can* 9: 265–323
- Brett JR (1971) Energetic responses of salmon to temperature: a study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am Zool* 11:99–113
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretical approach. Springer-Verlag, New York, NY
- Candy JR, Quinn TP (1999) Behavior of adult Chinook salmon (*Oncorhynchus tshawytscha*) in British Columbia coastal waters determined from ultrasonic telemetry. *Can J Zool* 77:1161–1169
- Chittenden CM, Beamish RJ, McKinley RS (2009) A critical review of Pacific salmon marine research relating to climate. *ICES J Mar Sci* 66:2195–2204
- Cooke SJ, Hinch SG, Farrell AP, Lapointe MF and others (2004) Abnormal migration timing and high en route mortality of sockeye salmon in the Fraser River, British Columbia. *Fisheries* 29:22–33
- Cooke SJ, Crossin GT, Patterson DA, English KK and others (2005) Coupling non-invasive physiological assessments with telemetry to understand inter-individual variation in behaviour and survivorship of sockeye salmon: development and validation of a technique. *J Fish Biol* 67: 1342–1358
- Cooke SJ, Hinch SG, Crossin GT, Patterson DA and others (2006) Physiology of individual late-run Fraser River sockeye salmon (*Oncorhynchus nerka*) sampled in the ocean correlates with fate during spawning migration. *Can J Fish Aquat Sci* 63:1469–1480
- Cooke SJ, Hinch SG, Crossin GT, Patterson DA and others (2008) Physiological correlates of coastal arrival and river entry timing in late summer Fraser River sockeye salmon (*Oncorhynchus nerka*). *Behav Ecol* 19:747–758
- Cooperman MS, Hinch SG, Crossin GT, Cooke SJ and others (2010) Effects of experimental manipulation of salinity and maturation status on the physiological condition and mortality of homing adult sockeye salmon held in a laboratory. *Physiol Biochem Zool* 83:459–472
- Crossin GT, Hinch SG, Cooke SJ, Welch DW and others (2007) Behaviour and physiology of sockeye salmon homing through coastal waters to a natal river. *Mar Biol* 152:905–918
- Crossin GT, Hinch SG, Cooke SJ, Cooperman MS and others (2009a) Mechanisms influencing the timing and success of reproductive migration in a capital breeding semelparous fish species, the sockeye salmon. *Physiol Biochem Zool* 82:635–652
- Crossin GT, Hinch SG, Welch DW, Cooke SJ and others (2009b) Physiological profiles of sockeye salmon in the Northeastern Pacific Ocean and the effects of exogenous GnRH and testosterone on the rates of homeward migration. *Mar Freshwat Behav Physiol* 42:89–108
- Crozier LG, Hendry AP, Lawson PW, Quinn TP and others (2008) Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. *Evol Appl* 1:252–270
- Davidsen JG, Rikardsen AH, Thorstad EB, Halttunen E and others (2013) Homing behaviour of Atlantic salmon (*Salmo salar*) during final phase of marine migration and river entry. *Can J Fish Aquat Sci*, doi:10.1139/cjfas-2012-0352
- Dingemans NJ, Dochtermann NA (2013) Quantifying individual variation in behaviour: mixed-effect modelling approaches. *J Anim Ecol* 82:39–54
- Dingle H (1996) Migration: the biology of life on the move. Oxford University Press, Oxford
- Donaldson MR, Cooke SJ, Patterson DA, Hinch SG and others (2009) Limited behavioural thermoregulation by adult up-river migrating sockeye salmon (*Oncorhynchus nerka*) in the lower Fraser River mainstem, British Columbia. *Can J Zool* 87:480–490
- Døving KB, Stabell OB (2003) Trails in open water: sensory cues in salmon migration. In: Collin SP, Marshall NJ (eds) Sensory processing in aquatic environments. Springer-Verlag, New York, p 39–52
- Døving KB, Westerberg H, Johnsen PB (1985) Role of olfaction in the behavioral and neuronal responses of Atlantic salmon, *Salmo salar*, to hydrographic stratification. *Can J Fish Aquat Sci* 42:1658–1667
- Drenner SM, Clark TD, Whitney CK, Martins EG, Cooke SJ, Hinch SG (2012) A synthesis of tagging studies examining the behaviour and survival of anadromous salmonids in marine environments. *PLoS ONE* 7:e31311
- Eliason EJ, Clark TD, Hague MJ, Hanson LM and others (2011) Differences in thermal tolerance among sockeye salmon populations. *Science* 332:109–112
- Elliott JM (1976) The energetics of feeding, metabolism and growth of brown trout (*Salmo trutta* L.) in relation to body weight, water temperature and ration size. *J Anim Ecol* 45:923–948
- Elliott JM (1991) Tolerance and resistance to thermal stress

- in juvenile Atlantic salmon, *Salmo salar*. *Freshw Biol* 25: 61–70
- Farrell AP, Gallagher PE, Fraser J, Pike D and others (2001) Successful recovery of the physiological status of coho salmon on board a commercial gillnet vessel by means of a newly designed revival box. *Can J Fish Aquat Sci* 58: 1932–1946
- Farrell AP, Hinch SG, Cooke SJ, Patterson DA, Crossin GT, Lapointe M, Malthe MT (2008) Pacific salmon in hot water: applying metabolic scope models and biotelemetry to predict the success of spawning migrations. *Physiol Biochem Zool* 81:697–708
- Flores AM, Shrimpton JM, Patterson DA, Hills JA and others (2012) Physiological and molecular endocrine changes in maturing wild sockeye salmon, *Oncorhynchus nerka*, during ocean and river migration. *J Comp Physiol B* 182: 77–90
- Friedland KD (1998) Ocean climate influences on critical Atlantic salmon (*Salmo salar*) life history events. *Can J Fish Aquat Sci* 55:119–130
- Friedland KD, Walker RV, Davis ND, Myers KW, Boehlert GW, Urawa S, Ueno Y (2001) Open-ocean orientation and return migration routes of chum salmon based on temperature data from data storage tags. *Mar Ecol Prog Ser* 216:235–252
- Fry FEJ (1968) Responses of vertebrate poikilotherms to temperature. In: Rose AH (ed) *Thermobiology*. Academic Press, New York, NY, p 375–409
- Hansen LR, Quinn TR (1998) The marine phase of the Atlantic salmon (*Salmo salar*) life cycle, with comparisons to Pacific salmon. *Can J Fish Aquat Sci* 55:104–118
- Hasler AD, Scholz AT (1983) Olfactory imprinting and homing in salmon. Springer Verlag, New York, NY
- Hedger RD, Hatin D, Dodson JJ, Martin F, Fournier D, Caron F, Whoriskey FG (2009) Migration and swimming depth of Atlantic salmon kelts *Salmo salar* in coastal zone and marine habitats. *Mar Ecol Prog Ser* 392:179–192
- Hinch SG, Cooke SJ, Healey MC, Farrell AP (2006) Behavioral physiology of fish migrations: salmon as a model approach. In: Sloman KA, Wilson R, Balshine S (eds) *Fish physiology*, Vol 24. Elsevier, San Diego, CA, p 239–295
- Hinch SG, Cooke SJ, Farrell AP, Miller KM, Lapointe M, Patterson DA (2012) Dead fish swimming: a review of research on the early migration and high premature mortality in adult Fraser River sockeye salmon *Oncorhynchus nerka*. *J Fish Biol* 81:576–599
- Hinke JT, Foley DG, Wilson C, Watters GM (2005) Persistent habitat use by Chinook salmon *Oncorhynchus tshawytscha* in the coastal ocean. *Mar Ecol Prog Ser* 304:207–220
- Hirano T, Ogasawara T, Hasegawa S, Iwata M, Nagahama Y (1990) Changes in plasma hormone levels during loss of hypoosmoregulatory capacity in mature chum salmon (*Oncorhynchus keta*) kept in seawater. *Gen Comp Endocrinol* 78:254–262
- Høgåsen HR (1998) Physiological changes associated with the diadromous migration of salmonids. NRC Research Press, Ottawa
- IPCC (Intergovernmental Panel on Climate Change) (2007) *Climate change 2007: the physical science basis, fourth assessment report (AR4)*. Cambridge University Press, Cambridge
- Ishida Y, Yano A, Ban M, Ogura M (2001) Vertical movement of a chum salmon *Oncorhynchus keta* in the western North Pacific Ocean as determined by a depth-recording archival tag. *Fish Sci* 67:1030–1035
- Jeffries KM, Hinch SG, Sierociniski T, Clark TD and others (2012) Consequences of high temperature and premature mortality on the transcriptome and blood physiology of wild adult sockeye salmon (*Oncorhynchus nerka*). *Ecol Evol* 2:1747–1764
- Johannessen SC, Macdonald RW (2009) Effects of local and global change on an inland sea: the Strait of Georgia, British Columbia, Canada. *Clim Res* 40:1–21
- Jonsson B, Jonsson N (2009) A review of the likely effects of climate change on anadromous Atlantic salmon *Salmo salar* and brown trout *Salmo trutta*, with particular reference to water temperature and flow. *J Fish Biol* 75: 2381–2447
- Killick R, Eckley I (2013) changepoint: An R package for changepoint analysis. R package v. 1.0.5
- Larsson S, Berglund G (2005) The effect of temperature on the energetic growth efficiency of Arctic charr (*Salvelinus alpinus* (L.)) from four Swedish populations. *J Therm Biol* 30:29–36
- 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. *J Exp Biol* 206:3239–3251
- Madison DM, Horrall RM, Hasler AD, Stasko AB (1972) Migratory movements of adult sockeye salmon (*Oncorhynchus nerka*) in coastal British Columbia as revealed by ultrasonic tracking. *J Fish Res Board Can* 29: 1025–1033
- Martins EG, Hinch SG, Cooke SJ, Patterson DA (2012a) Climate effects on growth, phenology, and survival of sockeye salmon (*Oncorhynchus nerka*): a synthesis of the current state of knowledge and future research directions. *Rev Fish Biol Fish* 22:887–914
- Martins EG, Hinch SG, Patterson DA, Hague MJ and others (2012b) High river temperature reduces survival of sockeye salmon approaching spawning grounds and exacerbates female mortality. *Can J Fish Aquat Sci* 69:330–342
- Mazerolle MJ (2012) AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package v. 1.26
- Murtaugh PA (2007) Simplicity and complexity in ecological data analysis. *Ecology* 88:56–62
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142
- Ogura M, Ishida Y (1992) Swimming behavior of coho salmon, *Oncorhynchus kisutch*, in the open sea as determined by ultrasonic telemetry. *Can J Fish Aquat Sci* 49: 453–457
- Ogura M, Ishida Y (1995) Homing behavior and vertical movements of 4 species of Pacific salmon (*Oncorhynchus* spp.) in the Central Bering Sea. *Can J Fish Aquat Sci* 52: 532–540
- Olesiuk PF, Bigg MA, Ellis GM (1990) Recent trends in the abundance of harbour seals, *Phoca vitulina*, in British Columbia. *Can J Fish Aquat Sci* 47:992–1003
- Olson AF, Quinn TP (1993) Vertical and horizontal movements of adult Chinook salmon *Oncorhynchus tshawytscha* in the Columbia River estuary. *Fish Bull* 91: 171–178
- Pankhurst NW, King HR (2010) Temperature and salmonid reproduction: implications for aquaculture. *J Fish Biol* 76: 69–85
- Pinheiro J, Bates D (2002) *Mixed effects models in S and S-*

- Plus. Springer, New York, NY
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Team RDC (2012) nlme. Linear and nonlinear mixed effects models. R package v. 3.1-106
- Pörtner HO, Farrell AP (2008) Physiology and climate change. *Science* 322:690–692
- Quinn TP, terHart BA, Groot C (1989) Migratory orientation and vertical movements of homing adult sockeye salmon, *Oncorhynchus nerka*, in coastal waters. *Anim Behav* 37:587–599
- R Core Development Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available at: www.R-project.org
- Reddin DG, Downton P, Fleming IA, Hansen LP, Mahon A (2011) Behavioural ecology at sea of Atlantic salmon (*Salmo salar* L.) kelts from a Newfoundland (Canada) river. *Fish Oceanogr* 20:174–191
- Richter A, Kolmes SA (2005) Maximum temperature limits for Chinook, coho, and chum salmon and steelhead trout in the Pacific Northwest. *Rev Fish Sci* 13:23–49
- Ruggerone GT, Quinn TP, McGregor IA, Wilkinson TD (1990) Horizontal and vertical movements of adult steelhead trout, *Oncorhynchus mykiss*, in the Dean and Fisher Channels, British Columbia. *Can J Fish Aquat Sci* 47:1963–1969
- Tanaka H, Takagi Y, Naito Y (2000) Behavioural thermoregulation of chum salmon during homing migration in coastal waters. *J Exp Biol* 203:1825–1833
- Teo SLH, Sandstrom PT, Chapman ED, Null RE, Brown K, Klimley AP, Block BA (2013) Archival and acoustic tags reveal the post-spawning migrations, diving behavior, and thermal habitat of hatchery-origin Sacramento River steelhead kelts (*Oncorhynchus mykiss*). *Environ Biol Fishes* 96:175–187
- Thomson RE (1981) Oceanography of the British Columbia coast. *Can Spec Publ Fish Aquat Sci* No. 56, p. 251
- Thomson RE (1994) Physical oceanography of the Strait of Georgia-Puget Sound-Juan de Fuca Strait System. *Can Tech Rep Fish Aquat Sci* 1948:36–101
- Thomson RE, Hourston RAS (2011) A matter of timing: the role of ocean conditions in the initiation of spawning migration by late-run Fraser River sockeye salmon (*Oncorhynchus nerka*). *Fish Oceanogr* 20:47–65
- Thorstad EB, Whoriskye F, Rikardsen AH, Aarestrup K (2010) Aquatic nomads: the life and migrations of the Atlantic salmon. In: Aas Ø, Einum S, Klemetsen A, Skurdal J (eds) *Atlantic salmon ecology*. Wiley-Blackwell, Oxford, p 1–23
- Ueda H (2011) Physiological mechanism of homing migration in Pacific salmon from behavioural to molecular biological approaches. *Gen Comp Endocrinol* 170:222–232
- van de Pol M, Wright J (2009) A simplistic method for distinguishing within- versus between-subject effects using mixed models. *Anim Behav* 77:753–758
- Wagner GN, Kuchel LJ, Lotto A, Patterson DA, Shrimpton JM, Hinch SG, Farrell AP (2006) Routine and active metabolic rates of migrating adult wild sockeye salmon (*Oncorhynchus nerka* Walbaum) in seawater and freshwater. *Physiol Biochem Zool* 79:100–108
- Walker RV, Myers KW (2009) Behavior of Yukon River Chinook salmon in the Bering Sea as inferred from archival tag data. *North Pac Anadromous Fish Comm Bull* 5: 121–130
- Walker RV, Myers KW, Davis ND, Aydin KY and others (2000) Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags. *Fish Oceanogr* 9:171–186
- Welch DW, Ishida Y, Nagasawa K (1998) Thermal limits and ocean migrations of sockeye salmon (*Oncorhynchus nerka*): long-term consequences of global warming. *Can J Fish Aquat Sci* 55:937–948
- Westerberg H (1982) Ultrasonic tracking of Atlantic salmon (*Salmo salar* L.) – II. Swimming depth and temperature stratification. *Inst Freshw Res Drottningholm Rep* 60: 102–120
- Wilson SM, Hinch SG, Drenner SM, Martins EG, Furey NB, Patterson DA, Cooke SJ (2014) Coastal marine and in-river migration behaviour of adult sockeye salmon en route to spawning grounds. *Mar Ecol Prog Ser* 496:71–84
- Wright BE, Riemer SD, Brown RF, Ougzin AM, Bucklin KA (2007) Assessment of harbor seal predation on adult salmonids in a Pacific Northwest estuary. *Ecol Appl* 17: 338–351
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York, NY
- Zuur AF, Ieno EN, Elphick CS (2010) A protocol for data exploration to avoid common statistical problems. *Methods Ecol Evol* 1:3–14

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