Temperature and depth profiles of Chinook salmon and the energetic costs of their long-distance homing migrations

Matthew L. Keefer*, Tami S. Clabough, Michael A. Jepson, Tracy Bowerman, Christopher C. Caudill

Department of Fish and Wildlife Sciences, College of Natural Resources, University of Idaho, 875 Perimeter Drive MS 1136, Moscow, ID 83844-1136, USA

ABSTRACT

River warming poses an existential threat to many Pacific salmon (*Oncorhynchus* spp) populations. However, temperature-mediated risks to salmon are often complex and addressing them requires species- and population-specific data collected over large spatial and temporal scales. In this study, we combined radiotelemetry with archival depth and temperature sensors to collect continuous thermal exposure histories of 21 adult spring- and summer-run Chinook salmon (*O. tshawytscha*) as they migrated hundreds of kilometers upstream in the Columbia River basin. Salmon thermal histories in impounded reaches of the Columbia and Snake rivers were characterized by low daily temperature variation but frequent and extensive vertical movements. Dives were associated with slightly cooler salmon body temperatures (~ 0.01 to 0.02 °C/m), but there was no evidence for use of cool-water thermal refuges deep in reservoirs or at tributary confluences along the migration route. In tributaries, salmon were constrained to relatively shallow water, and they experienced ~ 2–5 °C diel temperature fluctuations. Differences in migration timing and among route-specific thermal regimes resulted in substantial among-individual variation in migration temperature exposure. Bioenergetics models using the collected thermal histories and swim speeds ranging from 1.0 to 1.5 body-lengths/s predicted median energetic costs of ~ 24–40% (spring-run) and ~ 37–60% (summer-run) of initial reserves. Median declines in total mass were ~ 16–24% for spring-run salmon and ~ 19–29% for summer-run salmon. A simulated + 2 °C increase in water temperatures resulted in 4.0% (spring-run) and 6.3% (summer-run) more energy used per fish, on average. The biotelemetry data provided remarkable spatial and temporal resolution on thermal exposure. Nonetheless, substantial information gaps remain for the development of robust bioenergetics and climate effects models for adult Chinook salmon.

1. Introduction

Most anadromous salmonids have both energetically-demanding adult migrations (Brett, 1995; Rand et al., 2006) and narrow thermal preferences (Pörtner and Farrell, 2008; Eliason et al., 2011). This life history combination makes many populations vulnerable to climate warming (Crozier et al., 2008; Jonsson and Jonsson, 2009; Mantua et al., 2010), especially those that currently encounter warm water in migration corridors (Keefer et al., 2008; Hinch et al., 2012; Strange, 2012) or on spawning grounds (Gilhousen, 1990; Bowerman et al., 2018). Evidence linking warm-water exposure to reduced adult survival and lower lifetime fitness has been rapidly accumulating (Pankhurst and King, 2010; Eliason et al., 2013; Jeffries et al., 2014). However, quantifying thermal experiences of individuals over long and complex migrations and then directly linking those experiences to survival and

fitness outcomes remains technically challenging (Cooke et al., 2008; Keefer and Caudill, 2016).

Studies that pair telemetry with animal-borne bio-loggers have produced useful insights into the behavioral ecology of a broad suite of species in diverse natural habitats (Cooke et al., 2004; Hammerschlag et al., 2011; Wilmers et al., 2015). Anadromous salmonid applications have included studies of vertical movements and thermal habitat selection in oceans and estuaries (Walker et al., 2000; Hayes et al., 2011; Teo et al., 2013), behavioral thermoregulation in rivers and lakes (Donaldson et al., 2009; Keefer et al., 2009; Roscoe et al., 2010; Hasler et al., 2012), depth selection and burst swimming behaviors near dams (Johnson et al., 2010; Burnett et al., 2014), and acute and cumulative temperature exposure during freshwater homing migration (Strange, 2010; Caudill et al., 2013; Keefer et al., 2015). Biotelemetry studies often generate large, richly detailed datasets. However, the scientific

* Corresponding author.
  E-mail address: mkeefer@uidaho.edu (M.L. Keefer).

and heuristic value of many datasets is often unrealized due to data complexity or to the narrow scope of the original study objectives (Payne et al., 2014; Walker et al., 2015).

This paper revisits data collected in 2000 and 2002 when we tagged adult Chinook salmon (*Oncorhynchus tshawytscha*) with radio transmitters carrying pressure and temperature sensors. The original research objective was to monitor salmon migration depth in relation to supersaturated dissolved gas produced by Columbia and Snake River hydroelectric dams in the northwestern United States (Johnson et al., 2005, 2010). The radiotelemetry data provided fish location, pressure data were used to calculate fish depth, and temperature data were needed for dissolved gas exposure models, because gas solubility varies with temperature and depth (Johnson et al., 2007). While our previous focus was on salmon migration depth in dam tailraces and reservoirs, rising river temperatures and growing awareness of the concomitant survival and fitness consequences of exposure have elevated the value of examining the thermal histories. We have recently used the temperature dataset to assess salmon body temperatures inside adult fishways at Snake River dams (Caudill et al., 2013) and to evaluate relationships among thermal exposure, migration phenology, and behavioral thermoregulation in the portion of their migration corridor that is impounded by hydroelectric dams (Keefer et al., 2018).

Whereas Caudill et al. (2013) and Keefer et al. (2018) present body temperature data collected while salmon passed dams and reservoirs, here we focus on a small subset that had continuous temperature and migration depth data over their complete long-distance (> 500 river km) freshwater migrations to natal sites. The 21 individuals that met our criteria were from representative spring-run (April-May) and summer-run (June-July) Chinook salmon that passed at least seven main stem dams and reservoirs, traversed sections of large unimpounded rivers, and then entered natal tributaries and hatcheries throughout the upper Columbia River and Snake River basins. Several of the source populations are listed as threatened under the U.S. Endangered Species Act (National Marine Fisheries Service, 2011) and there is considerable concern about adverse climate warming effects on their conservation and management (Independent Scientific Advisory Board, 2007; Crozier et al., 2008, 2017). The main stems of the Columbia and Snake rivers have steadily warmed over the last several decades, and annual peak water temperatures are routinely ~ 21–24 °C and there is an extended warm-water season relative to historical conditions (Quinn et al., 1997; Crozier et al., 2008). The warm conditions are physiologically stressful for adult Chinook salmon (McCullough, 1999; Richter and Kolmes, 2005), and increase the energetic costs and mortality risks of adult salmon in the Columbia River basin, most recently evidenced by the mass adult mortality events for adult summer-run Chinook salmon and sockeye salmon (*O. nerka*) in 2015 (e.g., NOAA Fisheries, 2016).

We used the biotelemetry data to address three objectives. First, we summarized the variation in salmon body temperatures and migration depths as fish passed through impounded reaches of the migration corridor and through tributaries where thermal regimes were far less affected by dams. Second, we assessed whether salmon encountered relatively cool- or cold-water sites deep in reservoirs, which could hypothetically be used as thermal refuges. Several reservoirs have sections that are 30–50 m deep, where researchers and fisheries managers have speculated that cool-water refuges associated with groundwater or perhaps higher-density cold water from tributaries may be available to migrants, but there has been limited deep-water temperature monitoring to date. Our previous behavioral thermoregulation research has highlighted adult use of cool water in tributary confluence areas (Goniea et al., 2006; Keefer et al., 2018), but we did not directly consider salmon depth as a covariate in those studies. Third, we used the collected temperature histories in a bioenergetics model to simulate the relative metabolic costs of homing migration (e.g., Rand et al., 2006; Plumb, 2018). We compared simulated costs for spring- versus summer-

run fish using a range of plausible swim speeds, and then modeled the effects of a + 2 °C river-warming scenario.

2. Methods

2.1. River temperatures

To provide a historical context on Columbia and Snake River temperatures we assembled mean daily water temperature data collected by the U.S. Army Corps of Engineers (archived at: www.cbr.washington.edu/dart/) at Bonneville Dam (lower Columbia River, river km [rkm] ~ 235), Priest Rapids Dam (upper Columbia River, rkm ~ 639), and Ice Harbor Dam (lower Snake River, rkm ~ 538). The data were collected at water quality monitoring sites in the dam forebays. To show approximate conditions encountered by spring- and summer-run Chinook salmon, we present seasonal (April-May, June-July) mean temperatures at the three sites.

2.2. Salmon collection and tagging

Adult spring- and summer-run Chinook salmon were collected and tagged at Bonneville Dam (Fig. 1) in April–July of 2000 (*n* = 213) and 2002 (*n* = 183). Fish trapping, anesthesia, handling, tagging, transport, and downstream release protocols were described previously by Keefer et al. (2004, 2005) and Johnson et al. (2005). Briefly, upstream-migrating salmon were diverted from the Washington-shore adult fishway into the Bonneville adult fish facility. Salmon selected for tagging were further diverted into an anesthetic tank, measured (fork length, cm), and then intragastrically tagged with a uniquely-coded 3-V radio data storage transmitter (RDST; Model LTD_100, Lotek Wireless, Inc., Newmarket, Ontario). The transmitters (9-cm × 2-cm, 34 g in air) broadcast a unique radio frequency every 5 s that could be detected by antennas and receivers along migration routes. The RDSTs also logged fish body temperature every one min and pressure (i.e., fish depth) every 5 s. The RDST settings allowed archival storage of approximately 40 d of depth and temperature data and produced data files of ~ 600,000 records per fish. The manufacturer-reported accuracy for the pressure sensor was 4.8 kPa (~ 0.5 m). Temperature sensor resolution was reported to be 0.02 °C with accuracy of ± 0.15 °C at ambient temperatures of 0–20 °C and ± 0.10 °C at 20–35 °C.

Data stored on the transmitters were not available unless tags were recovered, so salmon with relatively high recapture probability were preferentially tagged. Samples were therefore predominated by Chinook salmon with known origin whose migrations passed adult trapping facilities, especially the Lower Granite Dam trap in the lower Snake River (rkm ~ 695, Fig. 1). Adult salmon origin at the time of tagging was assessed by the presence of hatchery fin clips and/or a passive integrated transponder (PIT) tag that was implanted during the juvenile life stage (see Keefer et al., 2018). Our sampling broadly reflected seasonal run timing, but the prerogative to recover RDST data outweighed our effort to tag random subsamples of the runs at large. We note that the requirement for archival tag recovery presents the potential for underestimation of thermal exposure at the population scale if salmon with higher exposures had higher mortality or lower recapture probability.

2.3. Salmon monitoring

RDST-tagged salmon were monitored in Columbia and Snake River dam tailraces, inside dam fishways, in reservoirs, and in tributaries to assess a diverse mix of study objectives (Johnson et al., 2005; Keefer et al., 2005; Caudill et al., 2013). Multiple radio receivers and antennas were deployed at each of the four lower Columbia River and four lower Snake River dams (Fig. 1). Additional radio antennas were used along some reservoirs, near confluences of most major Columbia and Snake
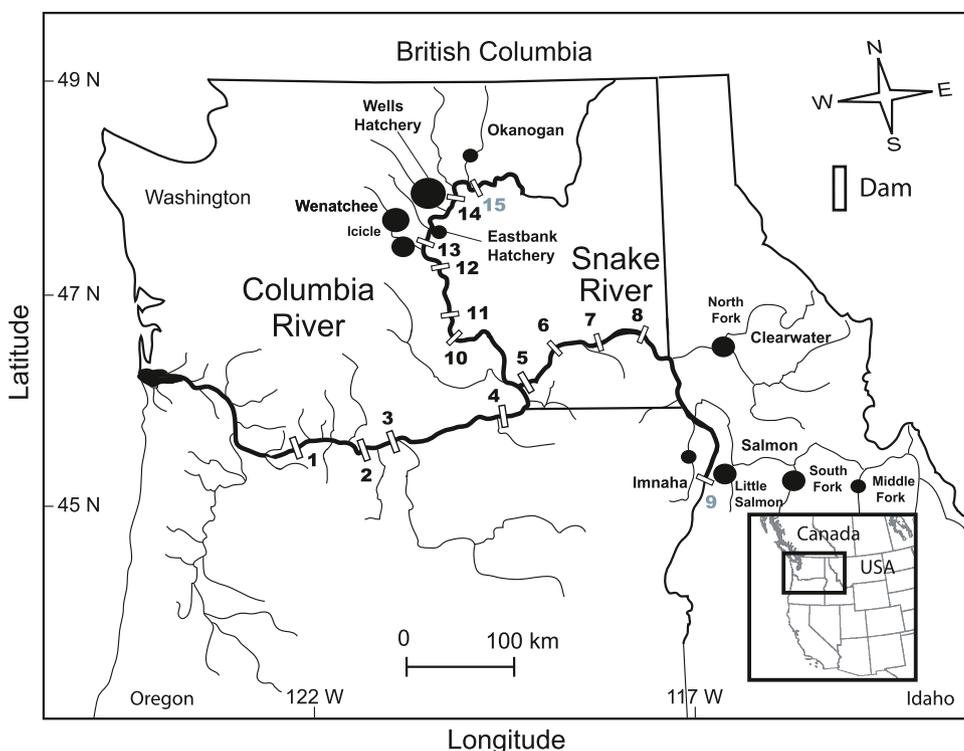
Fig. 1. Map of the Columbia River study area. Solid circles show approximate locations where 21 RDST-tagged spring– and summer–run Chinook salmon were recaptured and are scaled to the number of fish per site (range = 1–6 salmon/site). Black bold numbers indicate main stem Columbia and Snake River dams, including (1) Bonneville, (2) The Dalles, (3) John Day, (4) McNary, (5) Ice Harbor, (6) Lower Monumental, (7) Little Goose, (8) Lower Granite, (10) Priest Rapids, (11) Wanapum, (12) Rock Island, (13) Rocky Reach, and (14) Wells. Gray bold numbers indicate main stem dams with no adult salmon passage, including (9) Hells Canyon and (15) Chief Joseph dams. Inset map shows the study area in the northwestern United States.

River tributaries, and at Priest Rapids and Wanapum dams on the upper Columbia River. Detections at PIT-tag antennas supplemented salmon movement histories, including at two upper Columbia River dams with limited (Rock Island Dam) or no (Wells Dam) radio antennas. Typical radio detection histories included blocks of records as fish passed through tailraces and dam fishways, interspersed with hours to days of non-detections as they moved through reservoirs and unimpounded river reaches where antennas were widely spaced (i.e., > 10 rkm separated most non-dam monitoring sites).

2.4. RDST data collection and processing

The raw radiotelemetry data were regularly downloaded from receivers and assembled into annual databases. Trained biologists used a set of rule-based decisions to filter (i.e., 'code') the telemetry datasets to identify when fish passed individual antenna sites; each coded migration history was then reviewed by experienced personnel. Temperature and depth data from recovered RDSTs were downloaded and processed using the manufacturer-recommended methods. Quality control screens included tests for values outside expected ranges and cross-checks with the radiotelemetry data for appropriate date-time stamps. To facilitate data analysis and presentation, we reduced the RDST temperature and depth data to 30-min time steps (i.e., to 48 records per fish per day). The temperature, depth, and coded radiotelemetry and PIT-tag data were then temporally integrated. Based on the radiotelemetry histories, each RDST depth and temperature record was assigned to a main stem reach, tributary reach, or hatchery site. Main stem reaches included: (1) 297 rkm of the lower Columbia River from the release sites ~ 10 rkm downstream from Bonneville Dam to the Columbia River–Snake River confluence (four dams and reservoirs); (2) 241 rkm of the lower Snake River from the Columbia River confluence to the upstream end of Lower Granite reservoir (four dams and reservoirs); and (3) ~ 233–337 rkm of the upper Columbia River from the Snake River confluence to sites ranging from the Wenatchee River mouth to the Okanogan River mouth (3–4 dams and reservoirs, plus the ~ 80-rkm unimpounded Hanford Reach downstream from Priest Rapids Dam; Fig. 1). We combined multiple dam-to-dam reaches to simplify analyses and because adjacent

reservoir temperatures are highly correlated in each year (Crozier et al., 2017; Keefer et al., 2018).

2.5. Data analyses

Study animals selected for this summary were 21 RDST-tagged salmon that: (1) were not harvested in the main stem Columbia and Snake rivers; (2) entered their presumed natal tributary or hatchery within the 40-d transmitter archiving window; and (3) were recaptured upstream from Lower Granite Dam on the Snake River or Rock Island Dam on the upper Columbia River. These criteria assured that each salmon migrated > 500 rkm upstream in total and passed at least seven main stem dams and reservoirs.

To address the first objective, salmon depth and temperature exposure were summarized by calculating mean, standard deviation (SD), and range (5th–95th percentiles) metrics for each fish in each reach. To measure cumulative temperature exposure, we summed degree days (DD, the average daily temperature exposure above 0 °C) for each salmon using their 30-min archival temperature records in each reach and in total and dividing by 48. DD estimates were limited to the 40-d data storage limit, and all temperature histories ended after migration but well before spawning commenced in early September for spring-run salmon (Murdoch et al., 2009; Bowerman et al., 2017) and mid-October for summer-run salmon (e.g., Myers et al., 1998). We used linear regression to evaluate the relationship between migration timing (i.e., tag date) and DD accumulation over the period of data collection.

For the second objective, we used generalized linear mixed models (GLMM) to test if Chinook salmon were cooler while deep in reservoirs. The models tested for association between the paired 30-min salmon depth and body temperature data while treating individual salmon as random effects (i.e., a random-intercept model; PROC GLIMMIX; SAS Institute, 2000). Separate GLMMs were run for the lower Columbia, upper Columbia, and lower Snake reaches because different salmon were present in each reach.

Lastly, we used a derivation of the Wisconsin bioenergetics model to compare the relative metabolic costs of migration for individual fish based on: 1) observed temperature histories, and 2) on a river warming
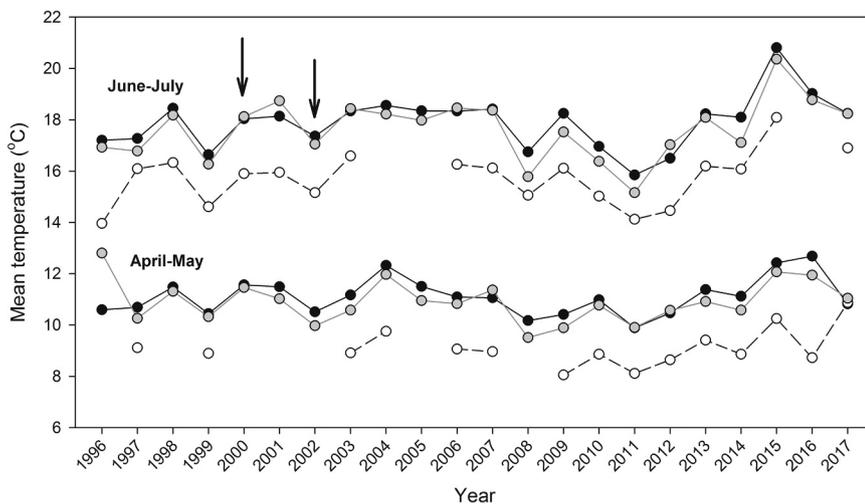
Fig. 2. Mean daily Columbia and Snake River water temperatures in April-May and June-July recorded at the Bonneville Dam (•), Priest Rapids Dam (○) and Ice Harbor Dam (◉) water quality monitoring sites from 1996 to 2017. Arrows highlight 2000 and 2002 data. Means are not shown for Priest Rapids Dam in years when ≥ 20% of the daily values were missing in either 2-month period. Data collected by U.S. Army Corps of Engineers and archived at: www.cbr.washington.edu/dart/.

scenario where mean body temperatures for each fish were increased by 2 °C each day. The Wisconsin model was originally described by Hewett and Johnson (1987) and more recently by Deslauriers et al. (2017). In our application, we calculated metabolic rate (MR g of O_2 per day) as:

$$MR = \alpha W^\beta e^{\gamma T} e^{\varphi U}$$

where W = salmon mass (g), T = salmon body temperature (°C), and U = swimming speed (cm/s). We used the values in Rand et al. (2006) for the parameter estimates α (intercept for oxygen consumption, 0.0023 g O_2/g/d), β (slope of the allometric mass function for standard metabolism, −0.109), γ (the rate at which the function increases with temperature, 0.0609), and φ (coefficient for swim speed dependence on metabolism, 0.012 s/cm). Daily energy density (ED) estimates were calculated using the mass-dependent equations in Stewart and Ibarra (1991):

$$ED = 0.986W + 5,763 \text{ when } W < 4,000\, g$$

$$ED = 0.527W + 7,598 \text{ when } W > 4,000\, g$$

with an oxycalorific coefficient of 13,560 J/g (Rand et al., 2006). In the model, metabolic losses were iteratively converted to lost mass on a daily time step. Initial total energy density (J/g) for each tagged salmon was calculated from the proximate analysis relationships in Bowerman et al. (2017):

$$ED = 0.004W + 8,944$$

We estimated Chinook salmon mass on their tag date with a fork length (FL) × mass quadratic regression relationship from adult Chinook salmon we weighed and measured at Bonneville Dam in 2004–2013 (mass = $0.0034FL^2 − 0.2681FL + 6.7347$; r^2 = 0.94, n = 3038). We also had to estimate swim speed data for the RDST-tagged fish. Swim speeds are difficult to derive from ground speeds (i.e. rate of travel calculated between detections) in the heterogeneous habitats encountered over a long migration, especially given the energy-conserving behavioral strategies employed by upstream-migrating salmon (Hinch and Rand, 2000; Standen et al., 2004). Rather than estimating day- and site-specific values for each fish, we therefore ran the bioenergetics models using swim speeds ranging from 1.0 to 1.5 body lengths (BL)/s. The range was based on an electromyogram telemetry study of adult spring Chinook salmon at Bonneville Dam where swim speeds averaged 1.40 BL/s in the tailrace, 1.13 BL/s inside fishways, and 1.06 BL/s in the dam forebay (Brown et al., 2006). Simulated swim speeds of 1.0–1.5 BL/s were also used for salmon movement in tributaries, based on the assumption that the range of speeds reported by Brown et al. (2006) in heterogeneous environments reflected energetically efficient behaviors. A conservative speed of 0.5 BL/s was used for salmon inside hatchery traps.

The Wisconsin model had some important limitations when applied to homing migrations of adult salmon. For example, the model did not account for fish replacing lost mass with water (e.g., Bowerman et al., 2017; Plumb, 2018), resulting in potential underestimation of the metabolic costs of movement. The model also did not address the reallocation of somatic energy towards gonad development during migration, which Bowerman et al. (2017) estimated at 2% for male and 14% for female Chinook salmon from the South Fork Salmon River, Idaho. The energetic costs of maturation-driven morphological changes also were not captured (e.g., increased snout length; Bowerman et al., 2017). Given these limitations, as well as the necessary assumptions about swim speed, and the unknown frequency of anaerobic versus aerobic activity (Brown et al., 2006), we present only the model-generated estimates of lost mass and lost total energy. Results are therefore best viewed as an index of the relative costs of migration among the study fish.

3. Results

3.1. Columbia and Snake River temperatures

Over the 22-year time series, mean spring (April-May) and summer (June-July) water temperatures at Bonneville and Ice Harbor dams differed by < 1.0 °C in almost all years (Fig. 2). Temperatures at Priest Rapids Dam were typically 2.0–2.5 °C cooler than at Bonneville and Ice Harbor dams in both seasons, though the Priest Rapids dataset had significant gaps in some years. Mean spring temperatures at Bonneville Dam in the RDST study years were 11.6 °C (2000) and 10.5 °C (2002), or about half a degree warmer (2000) and cooler (2002) than the 1996–2017 spring mean (11.1 °C). Mean summer temperatures at Bonneville Dam were 18.0 °C (2000) and 17.4 °C (2002), or 0.1 °C warmer (2000) and 0.5 °C cooler (2002) than the 1996–2017 mean (17.9 °C). The warmest year in the time series was 2015, when mean temperatures at Bonneville Dam were 12.4 °C (spring) and 20.8 °C (summer), approximately 0.9–1.9 °C warmer (spring) and 2.8–3.5 °C warmer (summer) than in 2000 and 2002. Conditions in 2015 were therefore analogous to or warmer than the + 2 °C scenario used in the bioenergetics simulation.

3.2. Recovered RDST sample summary

The 21 Chinook salmon that met our inclusion criteria included 16 in 2000 (7.5% of 213 tagged) and 5 in 2002 (2.7% of 183 tagged). The 21 salmon were released throughout the spring and summer runs; 19 had hatchery fin clips, two had no clips, seven were presumed female, and 14 were presumed male based on morphological traits (Table 1).

Table 1
Dates that 21 adult Chinook salmon were collected and RDST-tagged at Bonneville Dam, their origin (H = known hatchery, W = presumed wild), estimated sex based on morphology, fork length (FL, cm), and final recovery locations in tributaries and at hatchery traps and weirs. rkm = river kilometer from Columbia River mouth. NFH = National Fish Hatchery.

ID	Tag date	Origin	Sex	FL	Final collection location	rkm	Elevation (m)
1	4 Apr 2002	H	F	73.0	Rapid River Fish Hatchery[a]	981	~ 673
2	11 Apr 2002	H	F	70.5	Clearwater River	775	~ 325
3	13 Apr 2000	H	F	73.0	Rapid River Fish Hatchery[a]	981	~ 673
4	16 Apr 2000	H	M	75.0	North Fork Clearwater River	813	~ 304
5	16 Apr 2000	H	M	80.0	Icicle Creek, Leavenworth NFH	797	~ 1560
6	21 Apr 2000	H	M	79.0	Icicle Creek	796	~ 1560
7	30 Apr 2000	H	M	77.5	Icicle Creek, Leavenworth NFH	797	~ 1560
8	19 May 2002	W	M	77.5	Middle Fork Salmon River	1201	~ 1250
9	22 May 2002	W	F	74.5	South Fork Salmon River weir	1156	~ 1550
10	26 May 2000	H	M	80.5	Imnaha River weir	910	~ 1146
11	30 May 2000	H	F	77.5	South Fork Salmon River weir	1156	~ 1550
12	4 Jun 2000	H	M	99.0	Wenatchee River	774	~ 300
13	9 Jun 2000	H	M	74.0	Wells Hatchery	830	~ 215
14	16 Jun 2000	H	M	71.0	Wells Hatchery	830	~ 215
15	18 Jun 2000	H	M	82.5	Wells Hatchery	830	~ 215
16	22 Jun 2000	H	M	87.0	Wells Hatchery	830	~ 215
17	26 Jun 2000	H	M	92.0	Wenatchee River, Dryden trap; transfer to Eastbank Hatchery	782	~ 290
18	29 Jun 2000	H	M	72.0	Wells Hatchery	830	~ 215
19	7 Jul 2000	H	M	83.0	Wells Hatchery	830	~ 215
20	11 Jul 2002	H	F	94.0	Okanogan River	985	~ 250
21	19 Jul 2000	H	F	93.0	Eastbank Hatchery	762	~ 180

[a] On tributary to Little Salmon River.

Mean fork length was 80.3 cm (SD = 8.3 cm) and mean predicted mass was 7.34 kg (SD = 2.51 kg). Eight salmon were recovered upstream from Lower Granite Dam, including five in the Salmon River basin, two in the Clearwater River basin, and one in the Imnaha River (Fig. 1, Table 1). Thirteen were recovered upstream from Rock Island Dam: six at Wells Hatchery, five in the Wenatchee River basin, and one each at Eastbank Fish Hatchery and in the Okanogan River. We recovered 38,051 archival depth and temperature records (after reducing to 30-min intervals), equivalent to 793 d. Individual salmon histories averaged 1812 records (*range* = 1221–1920) and 38 d (*range* = 25–40 d).

3.3. Variation in body temperatures, migration depths, and DD accumulations

Salmon migration histories in the three impounded reaches were characterized by low within-individual variation in temperature exposure, despite frequent and extensive vertical movements (Figs. 3 and 4). Mean body temperatures in the three reaches ranged from 9.3° to 15.8 °C for spring-run fish and from 15.9° to 20.6 °C for summer-run fish. The range of temperatures experienced by individual fish (5th to 95th percentiles) were consistently low, averaging 1.6 °C in the lower Columbia (*n* = 21), 1.5 °C in the upper Columbia (*n* = 13), and 2.5 °C in the lower Snake (*n* = 8) reaches. Individual temperature SDs averaged 0.5 °C (lower Columbia), 0.5 °C (upper Columbia), and 0.7 °C (lower Snake). Mean individual salmon migration depths were 5.3 m (lower Columbia), 4.5 m (upper Columbia), and 5.3 m (lower Snake). The variability in depths (5th to 95th percentiles) was high, averaging 12.0 m, 11.3 m, and 13.8 m, respectively (Fig. 4). In total, 0.2% of 23,371 main stem depth records were negative (*mean* = −0.16 m), indicating fish were likely within ~ 0.5 m of the surface based on manufacturer-reported pressure sensor accuracy.

Most salmon had cooler and more variable body temperatures and occupied much shallower water in tributaries relative to main stem reaches; those that entered hatcheries experienced very stable temperatures (Figs. 3 and 4). Diel body temperature fluctuations of 2–3 °C were common in tributary reaches and were as high as 5 °C in the Imnaha River. The range of body temperatures (5th to 95th percentiles) experienced by individual salmon in tributaries averaged 2.9 °C and SDs averaged 0.9 °C. Mean body temperatures in tributaries and hatcheries were also substantially different: six salmon had means < 10 °C (in the

Clearwater River, Rapid River, and Icicle Creek-Leavenworth National Fish Hatchery); eleven had means between 11 °C and 14 °C (Wells Hatchery, Eastbank Fish Hatchery, and the Middle Fork Salmon, Rapid, Imnaha, and Wenatchee rivers); and four had means > 14 °C (South Fork Salmon, Wenatchee, and Okanogan rivers). On average, individual salmon depth in tributaries and hatcheries was 1.4 m, and depth ranges (5th to 95th percentiles) averaged 2.5 m. In total, 4.2% of 14,680 tributary and hatchery depth records were negative (*mean* = −0.16 m) indicating near-surface locations.

On average, Chinook salmon accumulated 341 DD (*range* = 194–619 DD) in the main stem Columbia and Snake River reaches. Accumulations over the total time that RDSTs collected data (40-d max) averaged 515 DD (*range* = 301–765 DD), including all records in main stem reaches, tributaries, and hatcheries. Migration date was positively correlated with DDs in the main stem reaches (linear regression: r^2 = 0.52, $P < 0.001$, *slope* = 2.84, $n = 21$) and over the full RDST histories (r^2 = 0.78, $P < 0.001$, *slope* = 3.52).

3.4. Thermal refuges and behavioral thermoregulation in reservoirs

In all three impounded reaches, salmon body temperatures decreased slightly with depth, but there was no evidence for use of cold-water thermal refuges deep in reservoirs (Fig. 5). In the lower Columbia, the GLMM indicated that body temperatures decreased by ~0.005 °C per m (F = 4.77, df = 12,347, P = 0.029, n = 21). The decrease was 0.012 °C per m in the upper Columbia reach (F = 53.29, df = 8498, $P < 0.001$, n = 13) and 0.016 °C per m in the lower Snake reach (df = 2491, F = 24.58, $P < 0.001$, n = 8). In visual review of each relationship, short-duration warm temperature exposure inside adult fishways and in dam forebays (see warm spikes near dams in Fig. 3) appeared to influence GLMM results more than exposure to cold deep water.

3.5. Bioenergetics simulations

Median estimates of energetic costs by spring Chinook salmon using their mean daily body temperatures during migration through main stem habitats and into spawning tributaries were 24.4% (1 BL/s), 30.7% (1.25 BL/s), and 39.6% (1.5 BL/s) (Fig. 6). The corresponding changes in lost mass were 15.6% (1 BL/s), 19.4% (1.25 BL/s), and
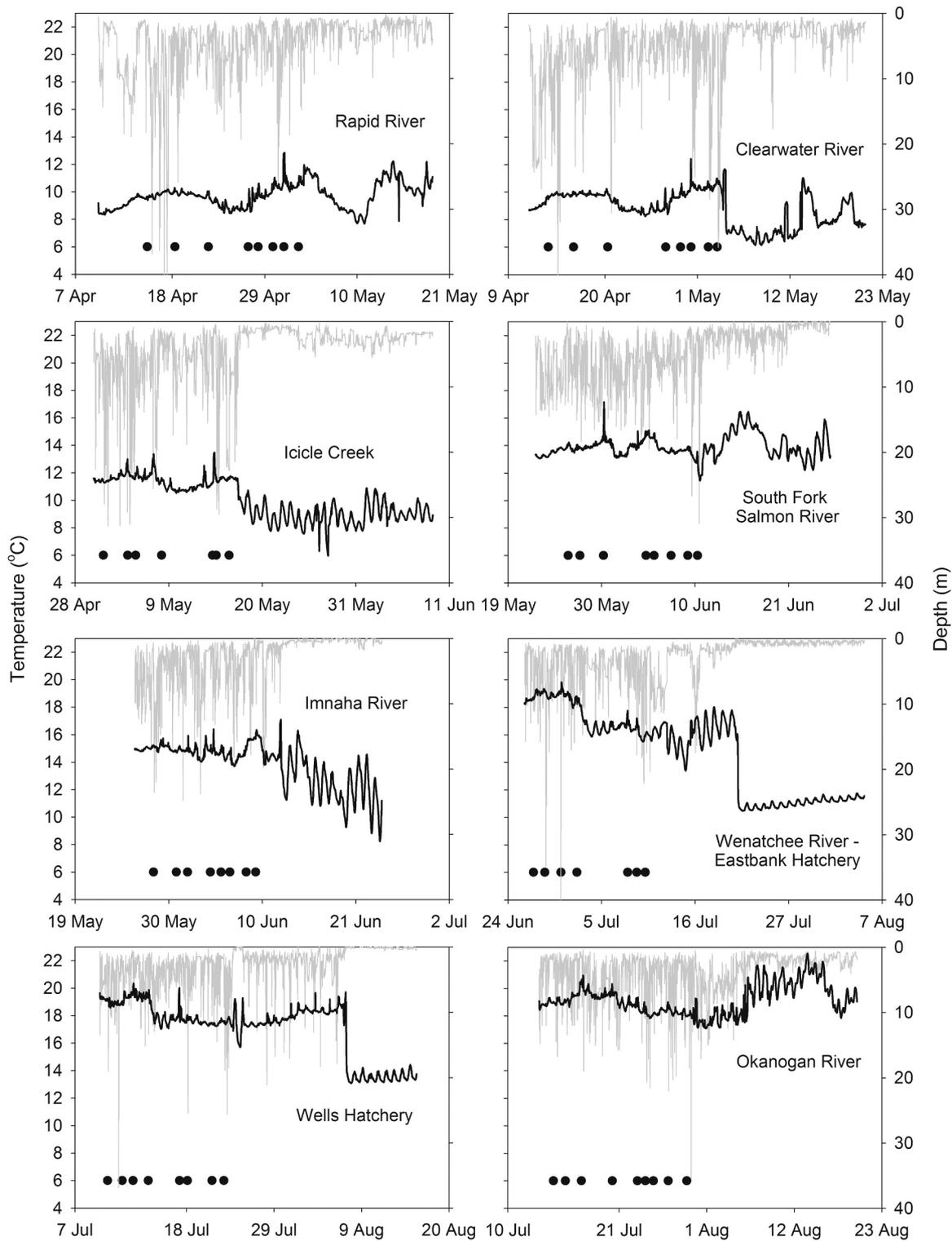
Fig. 3. Depth (m, gray lines) and body temperature (°C, black lines) histories from eight representative RDST-tagged Chinook salmon as they migrated through the Columbia and Snake rivers and into natal tributaries and hatcheries. Black circles show dates when fish passed main stem Columbia or Snake River dams. Text refers to recapture location (see Table 1).

24.2% (1.5 BL/s). The lowest spring-run estimates were for an Icicle River salmon with a 29-d temperature history; the highest estimates were for a fish with a 40-d history that returned to the Middle Fork Salmon River (mass) and one with a 35-d history that returned to the South Fork Salmon River (total energy). The warmer temperatures experienced by summer-run fish resulted in higher energy use, with median estimates of 37.1% (1 BL/s), 46.9% (1.25 BL/s), and 59.7% (1.5

BL/s). Estimates of lost mass were 19.0%, 23.5%, and 29.1%, respectively. The lowest estimates were for fish collected at the Eastbank (mass) and Wells (total energy) hatcheries and the highest estimates were for the Okanogan River fish; all three had 40-d temperature histories.

Simulating a + 2 °C warming in all reaches resulted in additional total energy losses that averaged 4.0% (*range* = 2.5–5.8%) for spring-
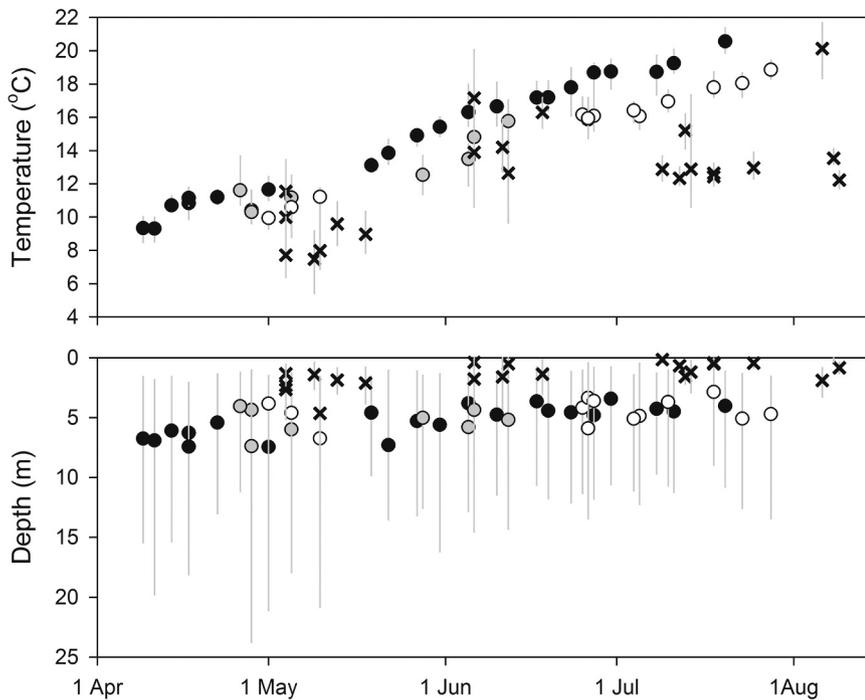
Fig. 4. Reach-specific mean body temperature and migration depth of 21 Chinook salmon in relation to the date each fish entered the lower Columbia River reach (•), lower Snake River reach (●), upper Columbia River reach (○), and spawning tributaries or hatcheries (×). Confidence intervals show the 5th and 95th percentile for each fish.

run fish and 6.3% (*range* = 3.8–12.3%) for summer-run fish. Two salmon had predicted energetic losses > 90% of initial total energy when swim speeds were 1.5 BL/s, one each from the Okanogan and Wenatchee rivers. Additional lost mass averaged 2.3% (*range* = 1.4–3.5%) for spring Chinook salmon and 2.8% (*range* = 2.0–4.5%) for summer Chinook salmon (Fig. 6).

4. Discussion

The combination of radiotelemetry and bio-loggers in this study produced continuous, spatially-referenced body temperatures and migration depths at an unprecedented spatial scale (~ 525–970 rkm) for homing Chinook salmon. The three principal study findings were that: (1) individual salmon body temperatures varied only slightly during passage through the Columbia and Snake River migration corridors but fluctuated much more widely in natal tributaries and hatcheries where thermal regimes also diverged widely; (2) there was very little evidence that Chinook salmon encountered cool- or cold-water refuges deep in reservoirs, that their frequent diving was associated with behavioral thermoregulation, or that they use refuges at tributary confluences; and (3) individuals typically lost ~ 24–60% of their modeled energetic

reserves and ~ 15–29% of their modeled mass during migration and initial prespawn holding period, with considerably higher costs for summer- than spring-run populations.

4.1. Variation in body temperatures, migration depths, and DD accumulations

Diel variation in body temperature increased during migration. Most individual salmon temperature ranges were ≤ 2 °C in the lower and upper Columbia River reaches, despite fish traversing > 200 rkm over 1–3 weeks in each reach. The stable body temperatures reflect the thermal inertia and large volume of the Columbia River, which has mean annual discharge of ~ 5400 m³/s at The Dalles Dam (Naik and Jay, 2011). Thermal homogeneity is reinforced by run-of-river operations at the ten downstream Columbia River dams, which promote vertically well-mixed reservoirs (Yearsley, 2009). There has been very little deep-reservoir temperature monitoring that could be used to identify the presence or distribution of cool-water refuges potentially used by migrants. However, a small number of surface-to-substrate thermistor strings were deployed in the forebays of lower Columbia River dams in spring and summer of 2018. Preliminary data indicate
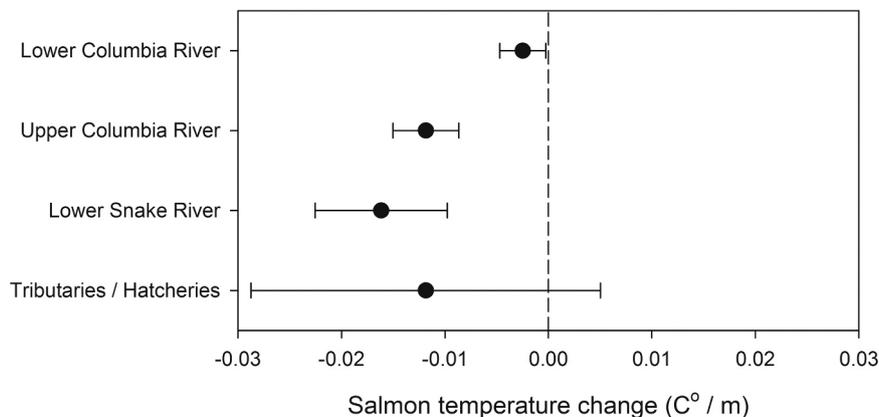

Fig. 5. Change in Chinook salmon body temperature in relation to fish depth in the study reaches, as predicted by general linear mixed models (GLMM) that used the 30-min temperature and depth data and treated individual salmon as random effects. Whiskers show the 95% confidence intervals.
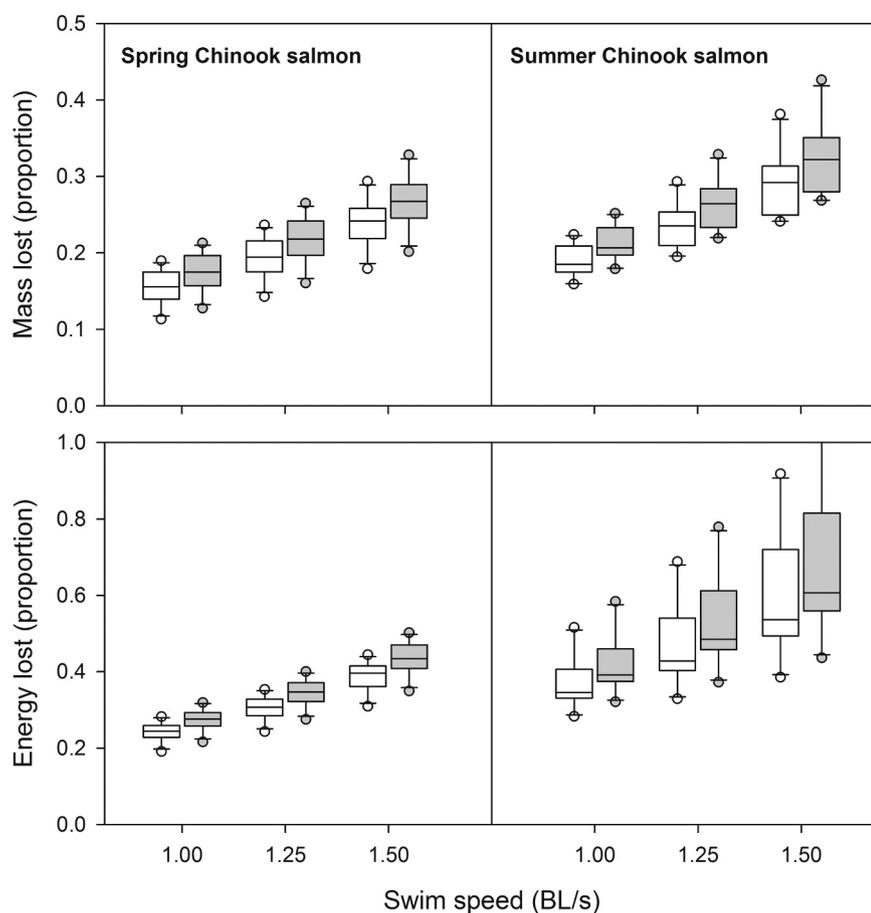
Fig. 6. Declines in total mass (top) and energetic reserves (bottom) of tagged spring and summer Chinook salmon during their migration from near Bonneville Dam to natal tributaries, estimated using a bioenergetics model with salmon swim speeds varying from 1.0 to 1.5 BL/s. Box plots (5th, 10th, 25th, 50th, 75th, 90th, and 95th percentiles,) represent estimates from the observed RDST temperature data (white boxes) and from a simulated + 2 °C warming scenario (gray boxes).

that there was almost no thermal stratification above Bonneville and The Dalles dams, but a vertical gradient of ∼ 2–3 °C occurred in the John Day Dam south forebay (Tina Lundell, U.S. Army Corps of Engineers, *personal communication*). Expanding the spatial footprint of this monitoring effort may identify additional cool-water sites.

In the lower Snake River reach, temperature heterogeneity was somewhat higher than in the Columbia River. The difference was due in part to summertime cold-water releases from Dworshak Dam on the North Fork Clearwater River (Fig. 1) and resultant downstream thermal layering in the lower Snake River (see Caudill et al., 2013 and references therein). Stratification in Lower Granite and Little Goose reservoirs, in particular, likely contributed to the somewhat higher variance in salmon body temperatures in the lower Snake River versus in the Columbia River reaches.

An explanation for the frequent diving and range of depths used by Chinook salmon in reservoirs remains unresolved. Our original hypothesis was that diving was related to fish sampling the water column for preferred thermal conditions, but our results did not provide compelling support for or against temperature-based motivation. Alternative explanations for the repeated diving may be related to navigation or orientation, including salmon searching for homing-related olfactory signals (e.g., Døving and Stabell, 2003; Keefer and Caudill, 2014) or route-selection processes that conserve energy (e.g., Standen et al., 2004), responses to proximate stimuli, or may simply reflect a behavior from the marine environment with little effect on fitness during upstream migration.

Most salmon were cooler in tributaries than in downstream reaches, reflecting the strong negative correlation between elevation and summer water temperature in the Pacific Northwest (Isaak et al., 2015; Steel et al., 2016). Exceptions included salmon that entered the Okanogan River (Washington) and Salmon River (Idaho), where summer water temperatures often exceed 21 °C in lower reaches, creating

stressful conditions and occasional migration barriers for anadromous adults (Hyatt et al., 2003; Keefer et al., 2008). Across the tributaries used by salmon, diel body temperature fluctuations of 2–3 °C were typical, and some individuals varied by 4–5 °C per day. Diel variation, combined with intra-tributary longitudinal variation (e.g., Fullerton et al., 2015), resulted in body temperature ranges that exceeded 6 °C for some salmon during the short time they were monitored in tributaries. Large diel and inter-day fluctuations are common in salmon-bearing rivers during spring and summer (Isaak et al., 2018) and likely become problematic only when they include temperatures warm enough to negatively affect physiological or reproductive processes (Steel et al., 2012; Dowd et al., 2015; Eliason and Farrell, 2016).

As expected, migration timing was a good predictor of cumulative thermal exposure. Release date accounted for about half (main stem reaches) and three quarters (complete histories) of the variance in DD accumulation. The migration timing effect was intuitive because main stem and tributary temperatures steadily increase from March to early August and remain near annual maxima into September. The unexplained variance in DD regressions can likely be attributed to the variable thermal regimes individuals encountered as they progressed upstream along divergent migration routes and intra-individual variation in upstream movement rate. DDs are arguably a coarse measure of thermal exposure as they do not directly address many important biological processes. However, they do provide a quantitative index that can be readily compared across species and populations. In other adult salmon studies, especially of sockeye salmon, researchers have identified potentially critical cumulative thresholds of ∼ 400–600 total DD, above which pathogen infection rates, disease progression, and mortality rates rapidly increase and physiological performance is reduced (Wagner et al., 2005; Crossin et al., 2008; Mathes et al., 2010). Much less has been reported about DD thresholds for mortality or fitness effects in adult Chinook salmon, but our estimates contribute to a

growing baseline of DD accumulations during adult life stages (e.g., Strange, 2012; Keefer et al., 2015, 2018; Naughton et al., 2018). Looking forward, we recommend that researchers consider metrics of thermal experience that are more directly linked to biological mechanisms such as thermal stress (e.g., DD > 20 °C, Keefer et al., 2018) that could be similarly standardized for among-population comparisons.

4.2. Thermal refuges and behavioral thermoregulation in reservoirs

The pressure sensor data showed that all Chinook salmon moved frequently between near-surface water and water > 10 m deep in reservoirs, and almost all occasionally dove to 20 m or more. Body temperatures changed very little during these movements. The GLMMs indicated cooling of just 0.01–0.02 °C per meter of depth (i.e., ~ 0.5–1.0 °C cooler over 50 m). A plausible interpretation is that reservoirs were vertically well-mixed, as described by Yearsley (2009), and deep water sites with markedly cooler water simply were not present. It is also possible that cool-water sites were available, but the 21 tagged salmon did not encounter or linger in those locations. That said, the much larger samples of RDST-tagged Snake River spring- and summer-run salmon described in Keefer et al. (2018) had very similar profiles to those reported here, with very little evidence of short-duration exposure to relatively cool water in reservoirs.

The 21 study fish also did not appear to use cool-water refuge sites at Columbia and Snake River tributary confluences, a thermoregulatory behavior that is common among fall-run Chinook salmon (Goniea et al., 2006; Keefer and Caudill, 2016) and summer-run steelhead (*O. mykiss*, Keefer et al., 2009, 2018; Hess et al., 2016). River temperatures during the spring Chinook salmon run may have been consistently cool enough that no thermoregulatory behaviors were necessary. The apparent lack of refuge use by summer-run fish was more surprising because some individuals had mean body temperatures of 19–22 °C on several consecutive dates, a temperature range that elicits thermal refuge use in their fall-run conspecifics (Goniea et al., 2006; Keefer et al., 2018). We have hypothesized that summer-run populations have adapted to move rapidly upstream, regardless of migration corridor temperatures, to ensure timely arrival at spawning sites. With this strategy, even brief delays in cool-water refuges may increase the likelihood of warm-water exposure later in their migration due to seasonal warming.

Our lack of evidence for behavioral thermoregulation by spring- and summer-run Chinook salmon along their migration routes may reflect low vertical heterogeneity in main stem river temperatures and the relatively moderate river temperatures fish encountered in 2000 and 2002. Exposure and behaviors, including thermoregulatory behavior, may be appreciably different in warmer years. However, our findings do align with results from several other adult salmon studies. Sockeye salmon migrating in the comparably large Fraser River (British Columbia; Donaldson et al., 2009) and Chinook salmon in the Klamath River (California-Oregon; Strange, 2012) and Willamette River (Oregon; Keefer et al., 2015) had body temperatures that rarely deviated from main stem river temperatures, despite availability of cooler water at tributary confluences and near groundwater sources. Importantly, behavioral thermoregulation appears to be much more common for adult salmon near spawning sites. Chinook and sockeye salmon from many populations select water ~ 2–10 °C cooler than ambient river or lake epilimnion temperatures during prespawn staging, an apparently adaptive behavior that conserves energy and regulates maturation processes (e.g., Berman and Quinn, 1991; Newell and Quinn, 2005; Roscoe et al., 2010; Armstrong et al., 2016).

4.3. Bioenergetics simulations

Given the importance of energy allocation to adult Chinook salmon migration and reproductive success, there are surprisingly few empirical bioenergetics studies for the species. Recent efforts to parse the total costs of upstream migration, maturation, prespawn holding, and spawning have used sequential proximate analysis (Mesa and Magie, 2006; Bowerman et al., 2017) or modeling exercises (Geist et al., 2000; Connor et al., 2018; Plumb, 2018) like our simulations. These models require a number of assumptions about metabolic parameters, Chinook salmon behavior, and their thermal experience. In our study, the temperature data were precise, but there was considerable uncertainty about several other model elements, including the metabolic parameters inferred from other species and life stages (e.g., Stewart and Ibarra, 1991; Rand et al., 2006; Deslauriers et al., 2017), and the potential for standard metabolic costs to decrease as a result of organ atrophy (Armstrong and Bond, 2013) after adult salmon cease feeding during migration. Additional uncertainties include the effects of water-for-muscle exchange, the reallocation of energy to gonads and secondary sexual traits, and how to capture varying (and unknown) swim speeds and aerobic activity. Given these uncertainties, the simulation results are best viewed as an index of relative costs. Furthermore, the estimates do not include most of the prespawn holding period and are therefore underestimates of the total energy that would be used by spawn time. Typical spring- and summer-run fish in our samples would have spent an additional ~ 50–100 days before spawning.

Our estimates of total lost energy of 24–40% for spring Chinook salmon are slightly lower than the empirically estimated 46% (females) and 41% (males) decline in initial energy for South Fork Salmon River fish over their ~ 920-rkm migration (Bowerman et al., 2017). In the other most directly relevant bioenergetics study, Mesa and Magie (2006) reported that spring Chinook salmon used 10–17% (females) and 6–10% (males) of their energy content during a 510-rkm migration from Bonneville Dam to Roza Dam on the Yakima River, Washington. Our estimates of lost mass were ~ 16–24% for spring Chinook salmon, a range that was comparable to the 21–24% loss in somatic mass (excluding gonad mass) measured by Bowerman et al. (2017). Lethal sampling and proximate analysis in the Bowerman study allowed estimation of lost mass and energy density in constituent body parts, and so the decrease in somatic mass can be adjusted for an increase in gonad mass, resulting in an estimated ~ 19% loss in total mass. Mesa and Magie (2006) reported declines in total mass of 12% (females) and 2% (males). Importantly, the methods in Bowerman et al. (2017) and Mesa and Magie (2006) differed from each other and from our model simulations and so comparisons should be interpreted cautiously.

We found no estimates for lost mass or energetic costs during the migration of upper Columbia River summer Chinook salmon. Our simulated costs of ~ 37–60% (lost energy) and ~ 19–29% (lost mass) were substantially higher than our estimates for spring-run fish, which we attribute almost entirely to the warmer body temperatures of summer migrants as all other model parameters were essentially equivalent. On average, summer-run fish were nearly 5 °C warmer than spring-run fish in the impounded reaches. Higher energetic costs for summer Chinook salmon were almost certainly not due to migration difficulty, because summer-run fish migrated shorter distances (*mean = 593 rkm*) and gained far less elevation to reach spawning sites (*mean = 231 m*) than the spring-run group (707 rkm and 1104 m, respectively). Furthermore, a majority of the summer group was collected at Wells or Eastbank hatcheries, where water temperatures were cool and modeled swim speeds (0.5 BL/s) had a low energetic penalty. Our highest estimates of lost mass and energetic costs were for large-bodied (FL ≥ 94 cm) summer-run salmon collected in the Okanogan and Wenatchee rivers, where summer water temperatures can be very warm (Hyatt et al., 2003; Cristea and Burges, 2010). Salmon from these rivers may be at greater risk of energetic exhaustion than many of the other study populations.

4.4. Conclusions

Understanding the thermal experiences and vulnerabilities of *Oncorhynchus* species is a research priority in the Pacific Northwest,

where river warming has increasingly been associated with en route migration mortality (Young et al., 2006; Keefer et al., 2008) and pre-spawn mortality near natal sites (Hinch et al., 2012; Bowerman et al., 2016). In the short term, we think that stream-type Chinook salmon may respond to warming by altering their migration phenology to minimize exposure to stressful temperatures or increase their reliance on thermal refuges to regulate disease risks and energetic depletion. The opportunity for these types of behavioral responses is likely to vary widely among populations, as demonstrated by the highly divergent thermal regimes the study populations encountered. Over the long term, we expect that there may be natural selection for temperature-tolerant phenotypes, but some of the studied populations are currently near the extremes observed for the species for migration distance and upper thermal exposure. Thus, the scope for such adaptations is uncertain. Informed conservation and management of Columbia River Chinook salmon will require a more quantitative approach to the complex factors that affect survival and fitness. Individual-based bio-telemetry has proven to be an effective generator of useful data for these types of questions (Cooke et al., 2004, 2016; Keefer et al., 2018; Frechette et al., 2018), but significant information gaps must be addressed before we can confidently predict the effects of climate warming on adult Chinook salmon.

References

Armstrong, J.B., Bond, M.H., 2013. Phenotype flexibility in wild fish: dolly Varden regulate assimilative capacity to capitalize on annual pulsed subsidies. J. Anim. Ecol. 82, 966–975.

Armstrong, J.B., Ward, E.J., Schindler, D.E., Lisi, P.J., 2016. Adaptive capacity at the northern front: sockeye salmon behaviourally thermoregulate during novel exposure to warm temperatures. Conserv. Physiol. 4, 039.

Berman, C.H., Quinn, T.P., 1991. Behavioural thermoregulation and homing by spring chinook salmon, Oncorhynchus tshawytscha (Walbaum), in the Yakima River. J. Fish. Biol. 39, 301–312.

Bowerman, T., Keefer, M.L., Caudill, C.C., 2016. Pacific salmon prespawn mortality: patterns, methods, and study design considerations. Fisheries 41, 738–749.

Bowerman, T.E., Pinson-Dumm, A., Peery, C.A., Caudill, C.C., 2017. Reproductive energy expenditure and changes in body morphology for a population of Chinook salmon Oncorhynchus tshawytscha with a long distance migration. J. Fish. Biol. 90, 1960–1979.

Bowerman, T., Roumasset, A., Keefer, M.L., Sharpe, C.S., Caudill, C.C., 2018. Prespawn mortality of female Chinook Salmon increases with water temperature and percent hatchery origin. Trans. Am. Fish. Soc. 147, 31–42.

Brett, J.R., 1995. Energetics. In: Groot, C., Margolis, L., Clarke, W.C. (Eds.), Physiological Ecology of Pacific Salmon. University of British Columbia Press, Vancouver, Canada, pp. 3–68.

Brown, R.S., Geist, D.R., Mesa, M.G., 2006. Use of electromyogram telemetry to assess swimming activity of adult spring Chinook salmon migrating past a Columbia River dam. Trans. Am. Fish. Soc. 135, 281–287.

Burnett, N.J., Hinch, S.G., Braun, D.C., Casselman, M.T., Middleton, C.T., Wilson, S.M., Cooke, S.J., 2014. Burst swimming in areas of high flow: delayed consequences of anaerobiosis in wild adult sockeye salmon. Physiol. Biochem. Zool. 87, 587–598.

Caudill, C.C., Keefer, M.L., Clabough, T.S., Naughton, G.P., Burke, B.J., Peery, C.A., 2013. Indirect effects of impoundment on migrating fish: temperature gradients in fish ladders slow dam passage by adult Chinook salmon and steelhead. PLoS One e85586.

Connor, W.P., Tiffan, K.F., Chandler, J.A., Rondorf, D.W., Arnsberg, B.D., Anderson, K.C.,

2018. Upstream migration and spawning success of Chinook salmon in a highly developed, seasonally warm river system. Rev. Fish. Sci. Aquac. https://doi.org/10.1080/23308249.2018.1477736.

Cooke, S.J., Brownscombe, J.W., Raby, G.D., Broell, F., Hinch, S.G., Clark, T.D., Semmens, J.M., 2016. Remote bioenergetics measurements in wild fish: opportunities and challenges. Comp. Biochem. Physiol. A Physiol. 202, 23–37.

Cooke, S.J., Hinch, S.G., Farrell, A.P., Patterson, D.A., Miller-Saunders, K., Welch, D.W., Donaldson, M.R., Hanson, K.C., Crossin, G.T., Mathes, M.T., Lotto, A.G., Hruska, K.A., Olsson, I.C., Wagner, G.N., Thomson, R., Hourston, R., English, K.K., Larsson, S., Shrimpton, J.M., Van Der Kraak, G., 2008. Developing a mechanistic understanding of fish migrations by linking telemetry with physiology, behavior, genomics and experimental biology: an interdisciplinary case study with adult Fraser River sockeye salmon. Fisheries 33, 321–338.

Cooke, S.J., Hinch, S.G., Wikelski, M., Andrews, R.D., Kuchel, L.J., Wolcott, T.G., Butler, P.J., 2004. Biotelemetry: a mechanistic approach to ecology. Trends Ecol. Evol. 19, 334–343.

Cristea, N.C., Burges, S.J., 2010. As assessment of the current and future thermal regimes of three streams located in the Wenatchee River basin, Washington State: some implications for regional river basin systems. Clim. Change 102, 493–520.

Crossin, G.T., Hinch, S.G., Cooke, S.J., Welch, D.W., Patterson, D.A., Jones, S.R.M., Lotto, A.G., Leggatt, R.A., Mathes, M.T., Shrimpton, J.M., Van Der Kraak, G., Farrell, A.P., 2008. Exposure to high temperature influences the behaviour, physiology, and survival of sockeye salmon during spawning migration. Can. J. Zool. 86, 127–140.

Crozier, L.G., Bowerman, T., Burke, B.J., Keefer, M.L., Caudill, C.C., 2017. High stakes steeplechase: a behavior-based model to predict individual travel time through diverse migration segments. Ecosphere 8, e01965.

Crozier, L.G., Hendry, A.P., Lawson, P.W., Quinn, T.P., Mantua, N.J., Battin, J., Shaw, R.G., Huey, R.B., 2008. Potential responses to climate change in organisms with complex life histories: evolution and plasticity in Pacific salmon. Evol. Appl. 1, 252–270.

Deslauriers, D., Chipps, S.R., Breck, J.E., Rice, J.A., Madenjian, C.P., 2017. Fish bioenergetics 4.0: an R-based modeling application. Fisheries 42, 586–596.

Donaldson, M.R., Cooke, S.J., Patterson, D.A., Hinch, S.G., Robichaud, D., Hanson, K.C., Olsson, I., Crossin, G.T., English, K.K., Farrell, A.P., 2009. Limited behavioural thermoregulation by adult upriver-migrating sockeye salmon (Oncorhynchus nerka) in the Lower Fraser River, British Columbia. Can. J. Zool. 87, 480–490.

Døving, K.B., Stabell, O.B., 2003. Trails in open waters: sensory cues in salmon migration. In: Collin, S.P., Marshall, N.J. (Eds.), Sensory Processing in Aquatic Environments. Spring-Verlag, New York, pp. 39–52.

Dowd, W.W., King, F.A., Denny, M.W., 2015. Thermal variation, thermal extremes and the physiological performance of individuals. J. Exp. Biol. 218, 1956–1967.

Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., Gale, M.K., Patterson, D.A., Hinch, S.G., Farrell, A.P., 2011. Differences in thermal tolerances among sockeye salmon populations. Science 332, 109–112.

Eliason, E.J., Clark, T.D., Hinch, S.G., Farrell, A.P., 2013. Cardiorespiratory performance and blood chemistry during swimming and recovery in three populations of elite swimmers: adult sockeye salmon. Comp. Biochem. Physiol. A 166, 385–397.

Eliason, E.J., Farrell, A.P., 2016. Oxygen uptake in Pacific salmon Oncorhynchus spp.: when ecology and physiology meet. J. Fish. Biol. 88, 359–388.

Frechette, D.M., Dugdale, S.J., Dodson, J.J., Bergeron, N.E., 2018. Understanding summertime thermal refuge use by adult Atlantic salmon using remote sensing, river temperature monitoring, and acoustic telemetry. Can. J. Fish. Aquat. Sci. 75, 1999–2010.

Fullerton, A.H., Torgersen, C.E., Lawler, J.J., Faux, R.N., Steel, E.A., Beechie, T.J., Ebersole, J.L., Leibowitz, S.G., 2015. Rethinking the longitudinal stream temperature paradigm: region-wide comparison of thermal infrared imagery reveals unexpected complexity of river temperatures. Hydrol. Process. 29, 4719–4737.

Geist, D.R., Abernethy, C.S., Blanton, S.L., Cullinan, V.I., 2000. The use of electromyogram telemetry to estimate energy expenditure of adult fall chinook salmon. Trans. Am. Fish. Soc. 129, 126–135.

Gilhousen, P., 1990. Prespawning mortalities of sockeye salmon in the Fraser River system and possible causal factors. Int. Pac. Salmon Fish. Comm. Bull. 26.

Goniea, T.M., Keefer, M.L., Bjornn, T.C., Peery, C.A., Bennett, D.H., Stuehrenberg, L.C., 2006. Behavioral thermoregulation and slowed migration by adult fall Chinook salmon in response to high Columbia River water temperatures. Trans. Am. Fish. Soc. 135, 408–419.

Hammerschlag, N., Gallagher, A.J., Lazarre, D.M., 2011. A review of shark satellite tagging studies. J. Exp. Mar. Biol. Ecol. 398, 1–8.

Hasler, C.T., Cooke, S.J., Hinch, S.G., Guimond, E., Donaldson, M.R., Mossop, B., Patterson, D.A., 2012. Thermal biology and bioenergetics of different upriver migration strategies in a stock of summer-run Chinook salmon. J. Therm. Biol. 37, 265–272.

Hayes, S.A., Bond, M.H., Wells, B.K., Hanson, C.V., Jones, A.W., MacFarlane, R.B., 2011. Using archival tags to infer habitat use of central California steelhead and coho salmon. Am. Fish. Soc. Symp. 76, 1–22.

Hess, M.A., Hess, J.E., Matala, A.P., French, R.A., Steele, C.A., Lovtang, K.C., Narum, S.R., 2016. Migrating adult steelhead utilize a thermal refuge during summer periods with high water temperatures. ICES J. Mar. Sci. 73, 2616–2624.

Hewett, S.W., Johnson, B.L., 1987. A Generalized Bioenergetics Model of Fish Growth for Microcomputers. University of Wisconsin Sea Grant Institute, Madison, Wisconsin.

Hinch, S.G., Cooke, S.J., Farrell, A.P., Miller, K.M., Lapointe, M., Patterson, D.A., 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.

Hinch, S.G., Rand, P.S., 2000. Optimal swimming speeds and forward-assisted propulsion: energy-conserving behaviours of upriver-migrating adult salmon. Can. J. Fish. Aquat.

Sci. 57, 2470–2478.

Hyatt, K.D., Stockwell, M.M., Rankin, D.P., 2003. Impact and adaptation responses of Okanagan River sockeye salmon (Oncorhynchus nerka) to climate variation and change effects during freshwater migration: stock restoration and fisheries management implications. Can. Water Res. J. 28, 689–713.

Independent Scientific Advisory Board, 2007. Climate Change Impacts on Columbia River Basin Fish and Wildlife (ISAB-2007-2). Northwest Power and Conservation Council, Portland, Oregon.

Isaak, D.J., Luce, C.H., Horan, D.L., Chandler, G., Wollrab, S., Nagel, D.E., 2018. Global warming of salmon and trout rivers in the Northwestern U.S.: road to ruin or path through purgatory? Trans. Am. Fish. Soc. 147, 566–587.

Isaak, D.J., Young, M.K., Nagel, D.E., Horan, D.L., Groce, M.C., 2015. The cold-water climate shield: delineating refugia for preserving salmonid fishes through the 21st century. Glob. Chang. Biol. 21, 2540–2553.

Jeffries, K.M., Hinch, S.G., Sierocinski, T., Pavlidis, P., Miller, K.M., 2014. Transcriptomic responses to high water temperature in two species of Pacific salmon. Evol. Appl. 7, 286–300.

Johnson, E.L., Clabough, T.S., Bennett, D.H., Bjornn, T.C., Peery, C.A., Caudill, C.C., Stuehrenberg, L.C., 2005. Migration depths of adult spring and summer Chinook salmon in the lower Columbia and Snake Rivers in relation to dissolved gas supersaturation. Trans. Am. Fish. Soc. 134, 1213–1227.

Johnson, E.L., Clabough, T.S., Caudill, C.C., Keefer, M.L., Peery, C.A., Richmond, M.C., 2010. Migration depths of adult steelhead (Oncorhynchus mykiss) in relation to dissolved gas supersaturation in a regulated river system. J. Fish. Biol. 76, 1520–1528.

Johnson, E.L., Clabough, T.S., Bennett, D.H., Bjornn, T.C., Peery, C.A., Caudill, C.C., Richmond, M.C., 2007. Estimating adult Chinook salmon exposure to dissolved gas supersaturation downstream of hydroelectric dams using telemetry and hydrodynamic models. Riv. Res. Appl. 23, 963–978.

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.

Keefer, M.L., Caudill, C.C., 2014. Homing and straying by anadromous salmonids: a review of mechanisms and rates. Rev. Fish. Biol. Fish. 24, 333–368.

Keefer, M.L., Caudill, C.C., 2016. Estimating thermal exposure of adult summer steelhead and fall Chinook salmon migrating in a warm impounded river. Ecol. Freshw. Fish. 25, 599–611.

Keefer, M.L., Clabough, T.S., Jepson, M.A., Johnson, E.L., Peery, C.A., Caudill, C.C., 2018. Thermal exposure of adult Chinook salmon and steelhead: diverse behavioral strategies in a large and warming river system. PLoS One 13 (9), e0204274.

Keefer, M.L., Clabough, T.S., Jepson, M.A., Naughton, G.P., Blubaugh, T.J., Joosten, D.C., Caudill, C.C., 2015. Thermal exposure of adult Chinook salmon in the Willamette River basin. J. Therm. Biol. 48, 11–20.

Keefer, M.L., Peery, C.A., Bjornn, T.C., Jepson, M.A., Stuehrenberg, L.C., 2004. Hydrosystem, dam, and reservoir passage rates of adult Chinook salmon and steelhead in the Columbia and Snake rivers. Trans. Am. Fish. Soc. 133, 1413–1439.

Keefer, M.L., Peery, C.A., Daigle, W.R., Jepson, M.A., Lee, S.R., Boggs, C.T., Tolotti, K.R., Burke, B.J., 2005. Escapement, harvest, and unknown loss of radio-tagged adult salmonids in the Columbia River - Snake River hydrosystem. Can. J. Fish. Aquat. Sci. 62, 930–949.

Keefer, M.L., Peery, C.A., Heinrich, M.J., 2008. Temperature-mediated *en route* migration mortality and travel rates of endangered Snake River sockeye salmon. Ecol. Freshw. Fish. 17, 136–145.

Keefer, M.L., Peery, C.A., High, B., 2009. Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (Oncorhynchus mykiss): variability among sympatric populations. Can. J. Fish. Aquat. Sci. 66, 1734–1747.

Mantua, N., Tohver, I., Hamlet, A., 2010. Climate change impacts on streamflow extremes and summertime stream temperature and their possible consequences for freshwater salmon habitat in Washington State. Clim. Change 102, 187–223.

Mathes, M.T., Hinch, S.G., Cooke, S.J., Crossin, G.T., Patterson, D.A., Lotto, A.G., Farrell, A.P., 2010. Effects of water temperature, timing, physiological condition and lake thermal refugia on migrating adult Weaver Creek sockeye salmon. Can. J. Fish. Aquat. Sci. 67, 70–84.

McCullough, D.A., 1999. A review and synthesis of effects of alterations to the water temperature regime of freshwater life stages of salmonids, with special reference to Chinook salmon. U.S. Environmental Protection Agency Report EPA 910-R-99-010.

Mesa, M.G., Magie, C.D., 2006. Evaluation of energy expenditure in adult spring Chinook salmon migrating upstream in the Columbia River basin: an assessment based on sequential proximate analysis. Riv. Res. Appl. 22, 1085–1095.

Murdoch, A.R., Pearsons, T.N., Maitland, T.W., 2009. The number of redds constructed per female spring Chinook salmon in the Wenatchee River basin. N. Am. J. Fish. Manag. 29, 441–446.

Myers, J.M., Kope, R.G., Bryant, G.J., Teel, D., Lierheimer, L.J., Wainwright, T.C., Grant, W.S., Waknitz, F.W., Neely, K., Lindley, S.T., Waples, R.S., 1998. Status Review of Chinook Salmon from Washington, Idaho, Oregon, and California. NOAA Fisheries, Washington, D.C.

Naik, P.K., Jay, D.A., 2011. Distinguishing human and climate influences on the Columbia River: changes in mean flow and sediment transport. J. Hydrol. 404, 259–277.

National Marine Fisheries Service, 2011. Endangered and threatened species: 5-year reviews for 17 evolutionarily significant units and distinct population segments of Pacific salmon and steelhead. Fed. Reg. 76 (157), 50448–50449.

NOAA Fisheries, 2016. 2015 adult sockeye salmon passage report. Report of NOAA Fisheries in collaboration with U.S. Army Corp of Engineers and Idaho Department of Fish and Game.

Naughton, G.P., Keefer, M.L., Clabough, T.S., Knoff, M.J., Blubaugh, T.J., Sharpe, C., Caudill, C.C., 2018. Reservoir provides cool-water refuge for adult Chinook salmon in a trap-and-haul reintroduction program. Mar. Freshw. Res. https://doi.org/10.1071/MF18124.

Newell, J.C., Quinn, T.P., 2005. Behavioral thermoregulation by maturing adult sockeye salmon (Oncorhynchus nerka) in a stratified lake prior to spawning. Can. J. Zool. 83, 1232–1239.

Pankhurst, N.W., King, H.R., 2010. Temperature and salmonid reproduction: implications for aquaculture. J. Fish. Biol. 76, 69–85.

Payne, N.L., Taylor, M.D., Watanabe, Y.Y., Semmens, J.M., 2014. From physiology to physics: are we recognizing the flexibility of biologging tools? J. Exp. Biol. 217, 317–322.

Plumb, J.M., 2018. A bioenergetics evaluation of temperature-dependent selection for the spawning phenology by Snake River fall Chinook salmon. Ecol. Evol.

Pörtner, H.O., Farrell, A.P., 2008. Physiology and climate change. Science 322, 690–692.

Quinn, T.P., Hodgson, S., Peven, C., 1997. Temperature, flow, and the migration of adult sockeye salmon (Oncorhynchus nerka) in the Columbia River. Can. J. Fish. Aquat. Sci. 54, 1349–1360.

Rand, P.S., Hinch, S.G., Morrison, J., Foreman, M.G.G., MacNutt, M.J., Macdonald, J.S., Healey, M.C., Farrell, A.P., Higgs, D.A., 2006. Effects of river discharge, temperature, and future climates on energetics and mortality of adult migrating Fraser River sockeye salmon. Trans. Am. Fish. Soc. 135, 655–667.

Richter, A., Kolmes, S.A., 2005. Maximum temperature limits for Chinook, coho, and chum salmon, and steelhead trout in the Pacific Northwest. Rev. Fish. Sci. 13, 23–49.

Roscoe, D.W., Hinch, S.G., Cooke, S.J., Patterson, D.A., 2010. Behavior and thermal experience of adult sockeye salmon migrating through stratified lakes near spawning grounds: the roles of reproductive and energetic states. Ecol. Freshw. Fish. 19, 51–62.

SAS Institute, 2000. Inc., SAS/STAT User's guide, version 8. SAS Institute, Cary, North Carolina.

Standen, E.M., Hinch, S.G., Rand, P.S., 2004. Influence of river speed on path selection by migrating adult sockeye salmon (Oncorhynchus nerka). Can. J. Fish. Aquat. Sci. 61, 905–912.

Steel, E.A., Sowder, C., Peterson, E.E., 2016. Spatial and temporal variation of water temperature regimes on the Snoqualmie River network. J. Am. Water Resour. Assoc. 53, 769–787.

Steel, E.A., Tillotson, A., Larsen, D.A., Fullerton, A.H., Denton, K.P., Beckman, B.R., 2012. Beyond the mean: the role of variability in predicting ecological effects of stream temperature on salmon. Ecosphere 3 (11), 104.

Stewart, D.J., Ibarra, M., 1991. Predation and production by salmonine fishes in Lake Michigan, 1978–1988. Can. J. Fish. Aquat. Sci. 48, 909–922.

Strange, J.S., 2010. Upper thermal limits to migration in adult Chinook salmon: evidence from the Klamath River basin. Trans. Am. Fish. Soc. 139, 1091–1108.

Strange, J.S., 2012. Migration strategies of adult Chinook salmon runs in response to diverse environmental conditions in the Klamath River basin. Trans. Am. Fish. Soc. 141, 1622–1636.

Teo, S.L.H., Sandstrom, P.T., Chapman, E.D., Null, R.E., Brown, K., Klimley, A.P., Block, B.A., 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. Fish. 96, 175–187.

Wagner, G.N., Hinch, S.G., Kuchel, L.J., Lotto, A., Jones, S.R.M., Patterson, D.A., Macdonald, J.S., Van Der Kraak, G., Shrimpton, M., English, K.K., Larsson, S., Cooke, S.J., Healey, M.C., Farrell, A.P., 2005. Metabolic rates and swimming performance of adult Fraser River sockeye salmon (Oncorhynchus nerka) after a controlled infection with Parvicapsula minibicornis. Can. J. Fish. Aquat. Sci. 62, 2124–2133.

Walker, J.S., Jones, M.W., Laramee, R.S., Bidder, O.R., Williams, H.J., Scott, R., Shepard, E.L., Wilson, R.P., 2015. TimeClassifier: a visual analytic system for the classification of multi-dimensional time series data. Vis. Comput. 31, 1067–1078.

Walker, R.L., Myers, K.W., Davis, N.D., Aydin, K.Y., Friedland, K.D., Carlson, H.R., Boehlert, G.W., Urawa, S., Ueno, Y., Anma, G., 2000. Diurnal variation in thermal environment experienced by salmonids in the North Pacific as indicated by data storage tags. Fish. Oceanogr. 9, 171–186.

Wilmers, C.C., Nickel, B., Bryce, C.M., Sith, J.A., Wheat, R.E., Yovovich, V., 2015. The golden age of bio-logging: how animal-borne sensors are advancing the frontiers of ecology. Ecology 96, 1741–1753.

Yearsley, J.R., 2009. A semi-Lagrangian water temperature model for advection-dominated river systems. Water Resour. Res. 45, W12405.

Young, J.L., Hinch, S.G., Cooke, S.J., Crossin, G.T., Patterson, D.A., Farrell, A.P., Van Der Kraak, G., Lotto, A.G., Lister, A., Healey, M.C., English, K.K., 2006. Physiological and energetic correlates of en route mortality for abnormally early migrating adult sockeye salmon (Oncorhynchus nerka) in the Thompson River, British Columbia. Can. J. Fish. Aquat. Sci. 63, 1067–1077.