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Thermal biology and bioenergetics of different upriver migration strategies in a stock of summer-run Chinook salmon

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ABSTRACT

By combining biotelemetry with animal-borne thermal loggers, we re-created the thermal histories of 21 summer-run Chinook salmon (*Oncorhynchus tshawytscha*) migrating in the Puntledge River, a hydropower impacted river system on Vancouver Island, British Columbia, Canada. Daily maximum water temperatures in the Puntledge River during the summer-run adult Chinook salmon migration and residency period frequently exceeded 21 °C, a value that has been observed to elicit behavioral thermoregulation in other Chinook salmon populations. We therefore compared river temperatures to body temperatures of 16 fish that migrated through the river to understand if cool-water refuge was available and being used by migrants. In addition, we used thermal histories from fish and thermal loggers distributed in the river to model the effect of thermal habitat on energy density using a bioenergetics model. In general, we found no evidence that cool-water refuge existed in the river, suggesting that there is no opportunity for fish to behaviorally thermoregulate during upriver migration through the regulated portion of the river. Of the thermal histories used in the bioenergetics model, fish that reached an upstream lake were able to access cooler, deeper waters, which would have reduced energy consumption compared to fish that only spent time in the warmer river. Consequently, the Puntledge River water temperatures are likely approaching and in some cases exceeding the thermal limits of the summer-run Chinook salmon during the spawning migration. Further warming may cause more declines in the stock.

1. Introduction

Understanding the thermal biology of fish has become increasingly important due to global climate change and the rise in water temperatures in some regions (Pörtner, 2002; Pörtner and Farrell, 2008; Farrell et al., 2008; Hofmann and Todgham, 2010). Pacific salmon (*Oncorhynchus* spp.) are cold-water species and are at particular risk to increases in ambient water temperature throughout their life cycle (McDaniels et al., 2010), but especially during their spawning migration (Crozier et al., 2008; Farrell et al., 2008, 2009). Pacific salmon have a thermal preferenda between 4 and 18 °C (Brett, 1971) and many migratory routes, such as the Fraser River in Canada, routinely experience temperatures greater than 18 °C during time periods when salmon are migrating upstream (Patterson et al., 2007; Hague et al., 2010; Martins et al., 2010). Temperature is considered the “master” abiotic factor for fish (Fry, 1968) and influences the behavioral ecology and most physiological processes of Pacific salmon (see reviews by Brett, 1995; Quinn, 2005).

Fish can select their surrounding temperature by using behavioral thermoregulation to exploit thermal habitats at either a coarse- (e.g., lake versus river) or fine-scale (e.g., groundwater inputs or cool water from a tributary). Migrating adult salmon can avoid warm temperatures by delaying or advancing upriver migration times (Berman and Quinn, 1991; Newell and Quinn, 2005; Keefer et al., 2008, 2009) though most stocks have limited flexibility in migration timing because spawning times tend not to vary regardless of migration initiation dates (Cooke et al., 2004a). Pacific salmon can also thermoregulate when faced with water temperatures that exceed their tolerance by seeking cool water in lakes, tributaries, or regions of groundwater input (e.g., Newell and Quinn, 2005; Keefer et al., 2008, 2009).

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In addition to aiding in survival, exploiting cooler water offers a trade-off between reproductive development and energy savings (Berman and Quinn, 1991). Cooler water will conserve energy, which is important as adult Pacific salmon have stopped feeding and rely on energy reserves to mature gametes and to complete migration and spawn; however, cooler water can slow gamete development, which could impair spawning success.

Hydropower infrastructure and operations can affect the thermal regime of rivers (Angilletta et al., 2008) and thus, may impact the behavioral thermoregulation of salmonids. Controlled releases of cool hypolimnetic water, the presence of deep pools near dams, and water release sites that salmon can exploit as cool-water refuge (Nickel et al., 2004) may facilitate behavioral thermoregulation. Dams, diversion structures, natural barriers, and inefficient fish passage ways may prevent fish from accessing thermal refuges, such as lakes and/or reservoirs located upriver. Furthermore, water drawdowns and low flows associated with hydropower operations can lead to elevated river temperatures (Angilletta et al., 2008), potentially reducing the availability of riverine thermal refuges.

The purpose of this study was to assess the thermal biology and associated bioenergetics of adult upriver migrating summer-run Chinook salmon (*Oncorhynchus tshawytscha*) in the Puntledge River, British Columbia. The stock typically arrives at the mouth of the river between late May and late July and has a spawning window between late September and late October (E. Guimond, private consultant, personal communication). Fish can either hold in the river or move through a number of fishways to gain access to cool hypolimnetic water in Comox Lake, though migration through the river typically takes between 3 weeks and 4 months (Hasler et al., provisionally accepted). In addition, it is unknown whether cool-water refuge exists in the river, and because the stock can be present in the river for over 4 months during warm weather conditions (compared to other runs of salmon [i.e., fall-run Chinook salmon]), there is potential for the exposure to high temperatures to have negative consequences on fish energetics, health, condition and survival. The summer-run population of Puntledge Chinook salmon has declined over the last few decades as a result of several factors including overexploitation, habitat alteration and thermal conditions during upriver migration (Darcy Miller, DFO Restoration Ecologist, Personal Communication). Although the population is not officially listed on any threat lists at the provincial or federal level, a recovery strategy exists and significant funds are spent annually on trying to enhance the stock. Elevated water temperature has been identified as a potential important factor influencing the recovery potential for this imperiled stock so this study has the opportunity to inform management and conservation efforts.

We used *in situ* biologgers and biotelemetry to understand whether fish were exposed to high temperatures and if fish were able to located fine-scale cool-water refuges. We then assessed the ability of the tagged fish to behaviorally thermoregulate and whether this varied by river location, water temperature, and river discharge. Lastly, we assessed how choice of thermal habitats could influence spawning success. Using a bioenergetics model, we estimated energy use of fish that were exposed to different thermal conditions and strategies during the spawning migration, and determined which migratory conditions were most likely to result in fish surviving to historical spawning dates.

2. Methods

2.1. Study area and sampling locations

The Puntledge River is located on the east coast of Vancouver Island Canada (Fig. 1). The river is approximately 16.9 km long and drains Comox Lake into the Comox Estuary. A hatchery located near the river supplements the natural populations of

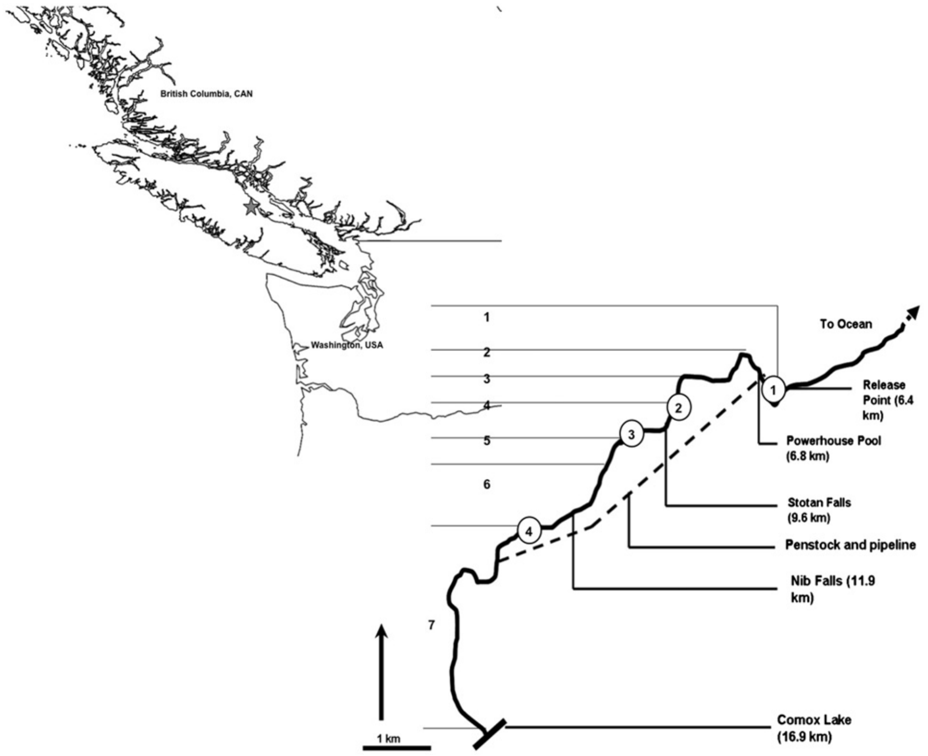

Fig. 1. The location of the study area in the Pacific Northwest (gray star) and a schematic of the study area with each study segment labeled, (1) Powerhouse, (2) Island pocket, (3) Upper side-channel, (4) Stotan Falls, (5) Highway crossing, (6) Nib Falls, (7) Upper hatchery site. The white circles represent river temperature sampling locations (1, Lower Hatchery Site; 2, Upper Side-Channel; 3, Highway Crossing; 4, Upper Hatchery Site).

Pacific salmon in the river, but the summer-run of Chinook has experienced continuous declines in returning adults since the development of a hydroelectric facility, despite much effort from both Fisheries and Oceans Canada and the hydroelectric utility (Hirst, 1991). The hydroelectric facility consists of a storage dam at the output of Comox Lake that releases water from near the surface of Comox Lake and has been outfitted with a vertical slot fishway. Approximately 3.0 river km downstream, another dam diverts water through a penstock that funnels water through the turbine 7.2 rkm downstream. A fishway is also located at the diversion dam. The diversion results in the river having relatively lower flows between 6.8 rkm and 14.0 rkm (rkm measured starting at the estuary). Within this reach there are two natural barriers, Stotan and Nib Falls. Both falls are three-tiered waterfalls with habitat enhancement to aid in the upstream movement of adult fish (i.e., concrete baffle fishways). The penstock output at the power station is located at 6.8 rkm and our capture and release point was located at 6.4 rkm. River temperature was measured at 4 locations throughout the river using Stowaway Tidbit Temperature Loggers (Model TBI32-05+37; Onset Computer Corporation, MA, USA; Temperature accuracy$= \pm 0.20$ °C, Temperature resolution$=\pm 0.16$ °C), Upper Hatchery, Highway Crossing, Upper Side Channel, and the Lower Hatchery (Fig. 1; Fig. 2). The thermologgers had a sampling rate of 15 min and were located in areas continuously wetted and exposed to typical river flow conditions.

2.2. Study animals and telemetry methods

Between June 25 and July 20 2007 and 2008, and between June 2 and June 26 2009, 133 adult male summer-run Chinook salmon were diverted into raceways at the Lower Puntledge River Fish Hatchery (Fisheries and Oceans Canada; Size distribution [2007, 38 fish; TL$=727\pm14$ mm [S.D.]; 2008, 26 fish, TL$=663\pm11$ mm; 2009, 39 fish, TL$=646\pm56$ mm]; Fig. 1) for transmitter implantation. The conservation status of the stock restricted us to only tagging male fish, which is admittedly a limitation, but at this point we are unaware of studies that have documented sex-specific behavioral thermoregulation or thermal tolerances in adult Pacific salmon. Of the 133 fish, thirty-seven fish (16 in 2007, 11 in 2008, and 10 in 2009) were implanted with coded electromyogram (CEMG) transmitters (CEMG2-R16-25 [2007, 2009] and CEMG2-R11-25 [2008], Lotek Wireless, Inc., Newmarket, Ontario; surgical methods outlined in Cooke et al., (2004b)), and sixty-six fish (22 in 2007, 15 in 2008, and 29 in 2009) had a conventional radio transmitter (MCFT-3A, Lotek Wireless, Inc., Newmarket, Ontario) gastrically inserted with the antenna protruding from the oral cavity. The additional 30 fish (2007, 10 fish; TL$=672\pm5$ mm [S.D.]; 2008, 10 fish, TL$=638\pm4$ mm; 2009, 10 fish, TL$=629\pm4$ mm) were implanted with conventional radio transmitters (MCFT-3 A, Lotek Wireless, Inc., Newmarket, Ontario) and transported *via* a tanker truck and released directly into Comox Lake. The entire confinement and transportation time was <30 min and there was no more than 100 kg of fish in a 1600 L of oxygenated freshwater. Temperature loggers (iButton DS1921Z; factory-stated resolution$=\pm 0.1$ °C, accuracy$=\pm1$ °C; Maxim Integrated Products, Inc., Sunnyvale, California) were attached to each transmitter using a hot glue gun and Plasti Dip® (Performix Brand, Blaine MN) and were programmed to record temperature at 2 h intervals (Donaldson et al., 2009). Similarly plasticized temperature loggers were tested in a laboratory setting to have an accuracy of 0.4 ± 0.3 °C and a temperature precision of 0.2 ± 0.3 °C (Donaldson et al., 2009).

Fish were manually tracked from shore at least twice a day to estimate location (time varied from 30 s to 15 min) between June and early October using a telemetry receiver (SRX-600 or SRX-400, Lotek Engineering, Inc., Newmarket, Ontario) and a 3-element Yagi antenna. Fish locations (approximate rkm) were determined using zero point tracking, as the river is narrow and there are a minimum number of possible locations fish can inhabit, meaning individual fish could be readily found. Transmitter tracking is impossible at depths greater than 10 m, and the river has no pools greater than this depth. The tracking period encompassed the time period that summer-run Chinook salmon enter the river and post-spawning die-off. River temperatures were assigned to each ‘fish’ temperature based on the closest river temperature sampled. Fish released directly into the lake occupied water depths in the main body of the lake where they could not be effectively tracked, and were only located during the spawning period once they moved into the lake outlet and upper reach of the river (Reach 7, Fig. 1).

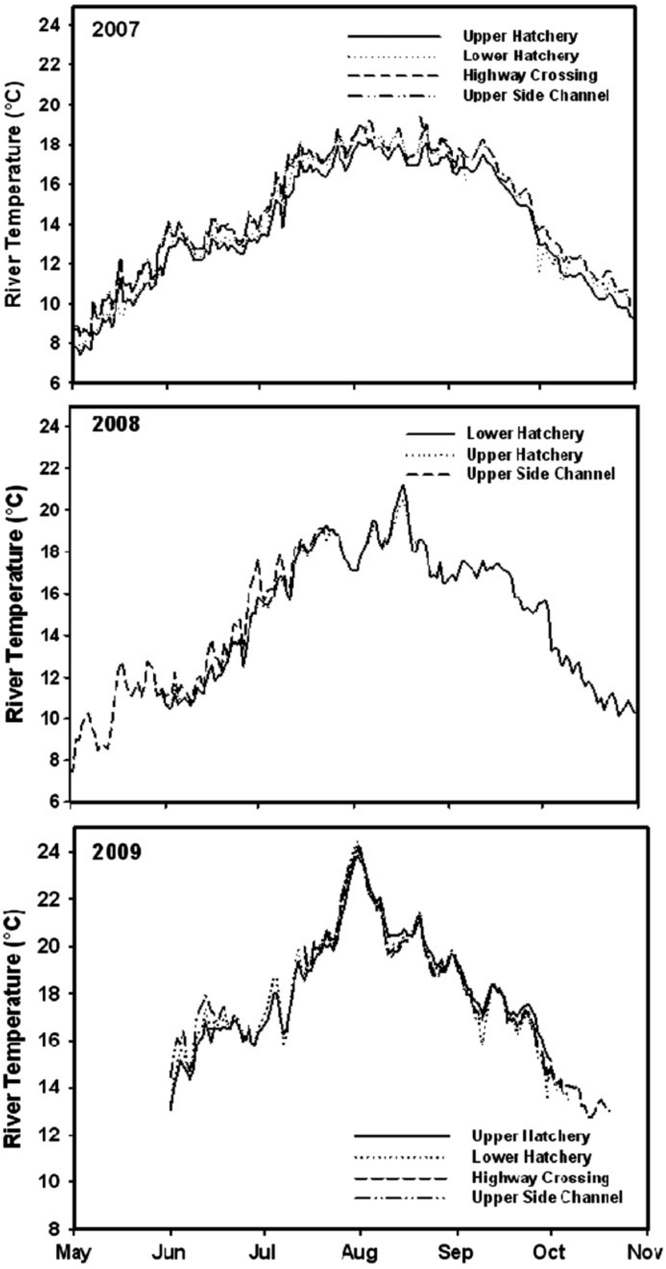

Fig. 2. River temperatures (°C) recorded at multiple sites along the Puntledge River during 2007, 2008, and 2009.

2.3. Recovery of transmitters and thermal loggers

Of the 133 deployed transmitters affixed with thermal loggers, 21 were haphazardly recovered and contained data that were used in this study (Fig. 3; low recovery rates were due to tags being washed out of the system during periods of high flow and tags being located in areas unsafe for tag retrieval). Transmitters and thermal loggers were recovered throughout the study period and most searching and collection occurred after the spawning period when fish were decomposing. Fish that were observed by radio-tracking to be moving upstream prior to the spawning period were classified as spawners ($n=8$) and fish that were visually confirmed to have died prior to the spawning period (but spent greater than one month in the river) were classified as pre-spawn mortalities ($n=8$). The remaining 5 fish had held in the lake and then spawned in the river below the lake (Reach 7). A further 23 transmitters with affixed thermal loggers were recovered but either contained no data, or were from fish observed to have been dead (dates of death unknown) after only a few weeks in the river. Although our sample size is not that large, the sample size was similar to that of another recently published study (i.e., Donaldson et al., 2009). Moreover, we have no reason to believe that the thermal logger data analyzed for this study was derived from fish that behaved in different manners than the entire population (Hasler et al., provisionally accepted) so we believe that it is possible to make population-level inferences.

2.4. Behavioral thermoregulation

Mean body temperature was calculated for each fish (using all thermal records) and a Wilcoxon's sign-rank test was used to assess whether or not body temperature predicted spawning fate. The study area was divided into study segments to understand if fish location influenced body temperature and ΔT (body temperature–river temperature). In order to assess the body temperature versus the river temperature, body temperature and river temperature were compared within each study segment using a Wilcoxon's sign-rank test. Telemetry data were used to determine positions of the fish. ΔT was compared among study segments using a Kruskal–Wallis non-parametric ANOVA. The slope of the relationships between each fish in each segment was calculated using a linear regression and then compared to a hypothetical slope of 1 using a Wilcoxon's sign-rank test, which enabled us to test the hypothesis that there may be an influence of increased river temperatures on body temperatures if behavioral thermoregulation were occurring (Donaldson et al., 2009). A significant difference between the slopes would indicate temperature-dependent selection by the individuals. Linear regressions were also used to estimate if river discharge, total length of fish, or distance from the river temperature sensor had significant effects on ΔT. All statistical analyses were done using JMP 7.0.2 (SAS Institute Inc., Cary NC, USA) and significance was tested at $\alpha=0.05$.

2.5. Energy density and thermal habitat

In order to predict energy density based on thermal habitat use, we developed a model using the software Fish Bioenergetics 3.0 (Hanson et al., 1997) and the physiological parameters found in Stewart and Ibarra (1991) for Chinook salmon. In 2007 we used a handheld microwave energy meter (Crossin and Hinch, 2005) to estimate somatic energy concentration of the 38-tagged summer-run Chinook salmon (TL$=727\pm14$ mm [S.D.]). Using a species-specific length–weight relationship, we transformed total length of each fish into weight (Jasper and Evenson, 2006), and then converted the energy meter values into somatic energy concentrations using the equation ($R^2=0.94$) for sockeye salmon presented in Crossin and Hinch (2005). The estimate of somatic energy density used in the bioenergetics model was 9.00 ± 0.57 (S.D.) MJ kg^{-1}. Energy density was also modeled using 8.43 and 9.57 MJ kg^{-1} to account for possible variations in outcomes due to differences in the initial somatic energy density value. The bioenergetics model allowed for the calculation of routine daily energy use (in MJ kg^{-1}).

In the model we varied temperature using four different hypothetical thermal regimes based on the experiences of the Puntledge River summer-run Chinook salmon as recorded by the temperature loggers attached to the transmitters. Thermal regimes were based on temperatures experienced by fish in the river during 2007 (River Cool), fish in the river during 2009 (River Hot), fish that were transported to the Lake in 2009 (Lake), and fish that used both the river and the lake in 2009 (River and Lake [note that this is the River Hot year but fish were tagged earlier and the fish used in this scenario had migrated through the river before temperatures became warm]; Fig. 4). These thermal regimes represent all the possible outcomes for the migrating salmon once they reached the tagging site.

Historically, it is believed that fish would migrate through the river and enter the lake and hold in the cool waters; thus, the River and Lake thermal regime represents the historical normal,

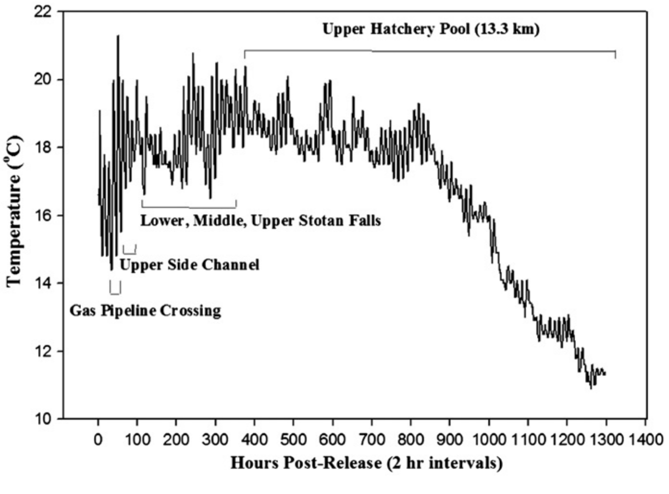

Fig. 3. An example of a thermal history recorded by the thermal logger attached to the radio transmitter. The location of the tagged-fish is indicated.

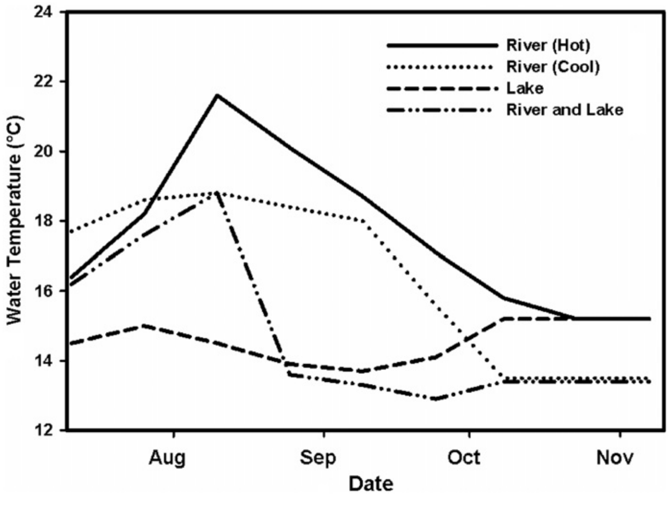

Fig. 4. The thermal regime scenarios used in the bioenergetics model to understand the effect of temperature on energy density depletion.

the River (Hot and Cold) regimes represent annual variation during post-hydropower development, and the Lake regime represents a possible management directive. Post-spawned salmon die when energy density is <4.0 MJ kg^{-1} (Hendry and Berg, 1999, Geist et al., 2000; Crossin et al., 2004b); therefore, we used this energy density value as a benchmark to assess spawning success. Fish for which our modelling simulations indicate would be reduced to this energy level prior their historical spawning dates would be classified as dying unspawned. The simulation day start date was set at July 11 (the mean date of energy density sampling). Because all of our sampled fish were males, and males allocate only a small fraction of total energy into gonads (e.g., 31–45% of total energy and remains relatively unchanged (0–2%) between river entry and spawning grounds; Crossin et al., 2004b), we did not account for energy partitioning to gonads in our modeling.

3. Results

3.1. Behavioral thermoregulation

Mean body temperature for the 8 fish that spawned was 17.7 °C (individual fish means ranged from 16.9 to 18.3 °C; Fig. 5a) and did not differ from the mean body temperature for the 8 fish that did not spawn (17.8 °C; individual fish means ranged from 17.0 to 18.6 °C; Fig. 5b; Wilcoxon's sign-rank test, $Z=0.053$, $P=0.958$). Mean ΔT did not differ between spawning fates (Wilcoxon's sign-rank test, $Z=0.473$, $P=0.637$).

In total, 2145 of 10,988 body temperature observations were warmer than river temperatures by $>=1.0$ °C and 419 of 10,988 body temperature observations were cooler than river temperature by <1.0 °C. Within each study segment, mean body temperature did not differ from the mean river temperature (Wilcoxon's sign-rank tests, all $P<0.56$) and mean ΔT did not vary among study segments (Kruskal–Wallis test, $\chi^2=0.544$, df$=6$, $P=0.997$; Fig. 6). The mean regression coefficients of body temperature and river temperature did not differ from a hypothetical slope of 1 in any of the study segments (Table 1).

River discharge did not affect the mean ΔT (Table 2) nor did total length have an effect on mean ΔT (linear regression; $R^2=0.003$; sum of squares$=3.540$; df$=15$; $P=0.836$). In addition, the mean distances between the river sampling location and the location of the fish (body temperature) was -802 m (upper 95%$=-773$; lower 95%$=-860$). Mean ΔT was not related to the mean river distance from the river temperature sensors that the body temperature was assigned to (linear regression; $R^2=0.045$; sum of squares$=3.54$, DF$=1$, 14, $P=0.484$).

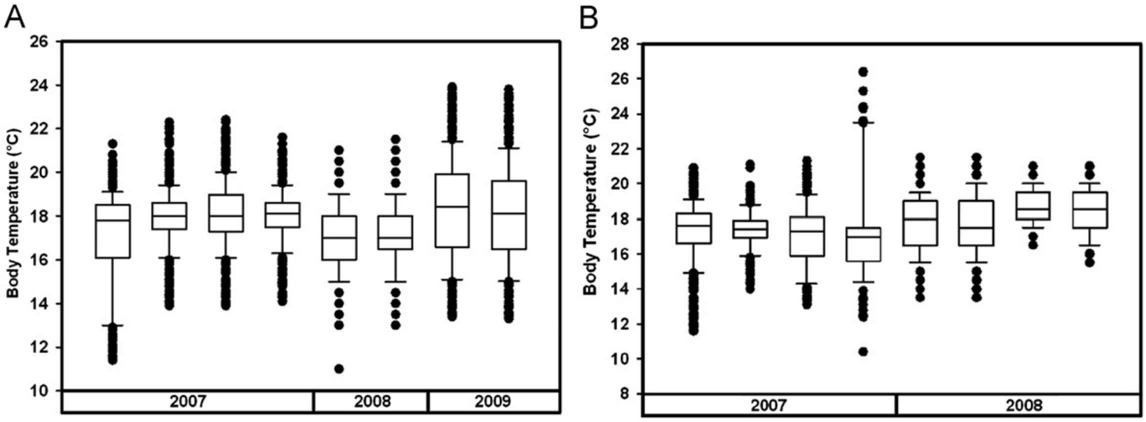

Fig. 5. Whisker plots of the body temperatures of each fish classified as a spawner (A) and as a pre-spawn mortality (B).

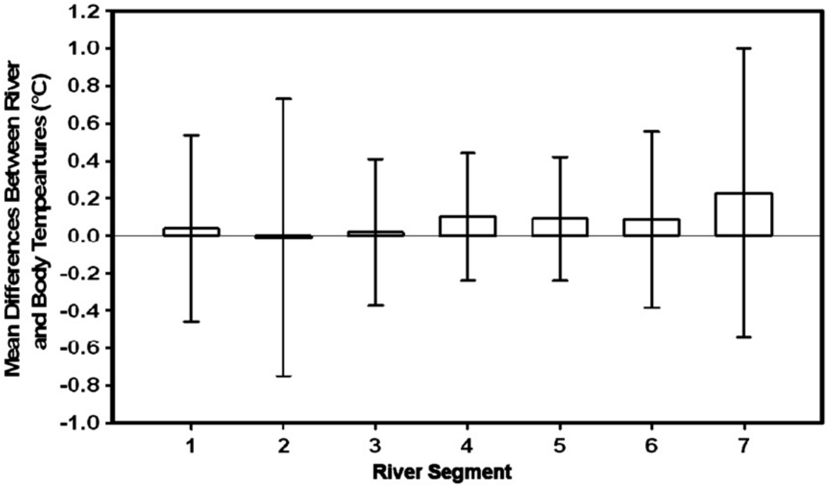

Fig. 6. Mean ΔT (T_B–T_R; and standard deviation) at each study segment, (1) Powerhouse ($n=11$), (2) Island pocket ($n=9$), (3) Upper side-channel ($n=11$), (4) Stotan Falls ($n=15$), (5) Highway crossing ($n=10$), (6) Nib Falls ($n=13$), (7) Upper hatchery site ($n=8$).

3.2. *Bioenergetics modeling*

The mean temperature for the River Cool group was 16.4 °C (13.5–18.8 °C min.–max.), River Hot was 17.6 °C (15.2–21.6 °C min.–max.), Lake was 14.6 °C (13.7–15.2 °C min.–max.), and River and Lake was 14.7 °C (12.9–18.8 °C min.–max.) (Fig. 4). When the thermal regimes were entered into the bioenergetics model to assess the effect of temperature on energy density, it was found that by late September energy had depleted to <4.0 MJ kg^{-1} for the River (Hot) and River (Cold) thermal regimes (Fig. 7). The model outcome varied by 11 days for River (Hot), 15 days for River (Cold), 20 days for Lake, and 25 days for River and Lake depending on the initial energy value (varied ± standard deviation).

4. Discussion

4.1. *Cool-water refuge*

Multiple studies have shown that migrating adult Pacific salmon will exploit cool water refuge to avoid warmer water temperatures during the freshwater migration, likely to conserve energy and to develop healthy gametes (Berman and Quinn, 1991; Newell and Quinn, 2005; Hyatt et al., 2003; Goniea et al., 2006; Keefer et al., 2009; Mathes et al., 2010). In our study, we found no evidence that the Puntledge River summer-run Chinook salmon were able to find and use cool water refugia, which may indicate that the river is generally well mixed. Interestingly, fish were at times exposed to higher temperatures than recorded by river temperature loggers. This may suggest that in-river characteristics or flow-dynamics may be causing areas used by the fish to be warmer, possibly representing tradeoffs between the various habitat features that collectively influence habitat choice (e.g., flow characteristics, proximity to cover; Caissie, 2006).

The lack of cool-water refuge resulted in no systematic thermoregulation being observed. The study area was only 10.5 km, which is relatively small compared to rivers that have been used in the past to study behavioral thermoregulation (i.e., study segments in previous studies, Yakima River (~344 km; Berman and Quinn, 1991), Columbia River (~404 km; Goniea et al., 2006), the Lower Fraser River (~238 km; Donaldson et al., 2009)). The Puntledge River is lake headed and regulated for power production in a manner typical of most hydropower operations, and results in short-term stable water temperatures during the upstream migration period. There are also no tributaries on the river that appear to provide water that is cooler than the mainstem Puntledge River. It is important to note that there was no relationship between river discharge and the difference between body and river temperatures. These characteristics of the river may indicate that there are few, if any, cold-water refuge sites available for the summer-run Chinook salmon to use when migrating upriver to spawn. Conversely, in the Columbia River, Keefer et al., (2009) found that adult steelhead (*O. mykiss*) exploited cooler tributaries for 3–4 weeks to avoid warmer mainstem temperatures and then resumed migration.

Historically, Comox Lake was likely less difficult for summer-run Chinook salmon to access (i.e., higher river discharge at time of migration such that natural barriers were easier to pass, no fishways to maneuver through, no recreational use of the river by humans, etc.). Comox Lake is a glacier fed, deep-water lake (max. depth = 109 m), and provides ample cool water for sexually maturing summer-run Chinook salmon to use. In fact in this study, fish that used the Lake used cooler water during the warmer spawning migration periods (in comparison to fish using the river during the same period). This phenomenon has been observed in other river-lake systems (e.g., Newell and Quinn, 2005; Mathes et al., 2010) and has direct benefits to reproductive and energetic status of maturing adult salmon (Roscoe et al., 2010). Since the Puntledge River has only recently (~100 years) been impacted by anthropogenic factors, the summer-run stock may not yet have adapted to the habitat

Table 1
Results of a Wilcoxon's sign-rank test (critical $\alpha=0.007$) between the regression slope of river temperature versus body temperature and a hypothetical slope of 1 for each study segment for upriver migrating summer-run Chinook salmon.

Study segment	*n*	Difference (mean ± SD) from hypothetical slope of 1	Test statistic	*P*
Power house	11	−0.03 ± 0.33	−8.0	0.505
Island pocket	9	−0.09 ± 0.22	−7.5	0.406
Upper side-channel	10	−0.23 ± 0.34	−18.0	0.068
Stotan Falls	15	−0.05 ± 0.21	−7.5	0.659
Highway crossing	10	−0.03 ± 0.33	7.5	0.475
Nib Falls	13	0.07 ± 0.19	16.0	0.233
Upper hatchery site	8	0.10 ± 0.10	10.5	0.03

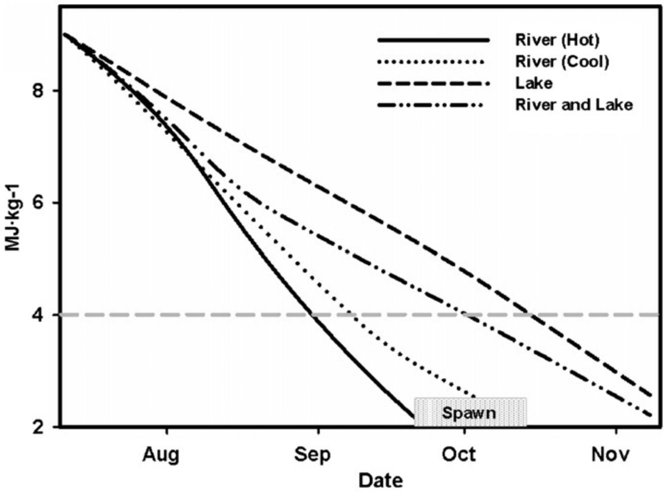

Fig. 7. The bioenergetics output (MJ kg^{-1}) of the 4 thermal regime scenarios used to assess energy density depletion. The horizontal dashed line represents $y=4.0$ MJ kg^{-1}. Spawning window is indicated by the hatched box on the *x*-axis.

Table 2
Results of the mean difference of body temperature and river temperatures versus log-transformed river discharge (log *R*Discharge; m^3 s; $\alpha=0.007$) for each study segment for summer-run Chinook salmon.

Study segment	Regression equation	R^2	df	Sum of squares	*P*
Power house	−1.504 + 1.608 log *R*Discharge	0.372	10	2.320	0.047
Island pocket	1.001–1.021 log *R*Discharge	0.119	8	4.380	0.364
Upper side-channel	0.665 −0.657 log *R*Discharge	0.049	10	1.518	0.512
Stotan Falls	−0.041 + 1.608 log *R*Discharge	0.003	14	1.664	0.851
Highway crossing	−0.536 + 0.690 log *R*Discharge	0.077	9	0.995	0.4391
Nib falls	−0.042 + 0.150 log *R*Discharge	0.002	12	2.679	0.871
Upper hatchery site	6.522–7.305 log *R*Discharge	0.387	7	4.177	0.100

conditions of the river, and may be adapted to use behavioral thermoregulation in the lake. Waples et al. (2008) suggest that if anthropogenic changes to the environment occur at spatial and temporal scales that more closely mimic environmental changes that have occurred during the evolutionary history of Pacific salmon, stocks will be more "well-equipped" to deal with such changes. Evolutionary change and/or extirpation have been shown in large big dam river systems, as thermal regime changes caused by hydropower has been shown to decrease the mean fitness of Chinook salmon (Angilletta et al., 2008).

There are several potential consequences to adult migrating salmon if they do not use cool-water refuge during their upstream freshwater migration. Exposure to high river temperatures can collapse aerobic scope (Farrell et al., 2008; Mathes et al., 2010), increase infection rate of parasites and disease (Wagner et al., 2005; Crossin et al., 2008; Bradford et al., 2010), slow travel rates (Crossin et al., 2008), and cause energy to be used at an elevated rate (this study), all of which can lead to high levels of migration mortality (Goniea et al. 2006; Caudill et al., 2007; Crossin et al., 2008; Keefer et al., 2008). We found limited evidence that the fish in the study segment were being exposed for prolonged periods of time (>12 h) to temperatures above which migration is halted (21 °C; McCullough, 1999).

4.2. Energy density and thermal habitat

The bioenergetics model predicts that fish behavior with respect to thermal experience clearly influences energy density available at the time of spawning. At the time of spawning fish must be reproductively mature and have enough somatic energy for spawning rituals (i.e., staging, competition, coitus, and minimal brood defense by females) during a window of opportunity when both sexes are present on the spawning grounds (Quinn, 2005). Fish experiencing warmer thermal regimes will have less energy available resulting in a number of fitness-level implications, (1) fish will have lower amounts of energy to develop secondary sexual characteristics (Hendry and Berg, 1999); and (2) males will have fewer energy stores to fight for access to spawning females (Quinn et al., 1996).

Summer-run Chinook salmon had higher energy densities further into the model simulation when they were exposed to the cooler waters in Comox Lake. The bioenergetics model predicts that only fish that use Comox Lake and fish that use the lake and experience early season river temperatures will have a sufficient amount of somatic energy available to potentially use to spawn during the typical spawning period. This finding supports the argument that thermal refuge is beneficial to the spawning success of migrating salmon. Because Pacific salmon do not feed during their upriver migration, energy-use must be optimized to ensure reproductive status is sufficient for spawning during the historic spawning period (Brett, 1995). Mathes et al. (2010) found that of the early-timed Weaver Creek sockeye salmon tagged in the study, only fish that held in Harrison Lake survived to spawn. The other fish held in the warmer Harrison River. Furthermore, Newell and Quinn (2005) found sockeye salmon hold in the cool water of Lake Washington during warm summer months prior to spawning. Likewise, other studies have shown reduced mortality in fish that use coldwater tributaries (Goniea et al., 2006; Keefer et al., 2008). Direct links to energy levels have been found in female sockeye salmon (Roscoe et al., 2010). These studies support our model prediction and further highlight the importance of ensuring migrating salmon have access to thermal refugia during the spawning migration.

The predictive model has limitations. Firstly, we presented only hypothetical thermal regimes of fish based on field obtained temperatures from a few fish (internal temperatures between fish varied little), all of which were male, and in-river thermal loggers. Secondly, only routine activity level was used in the bioenergetics model (Stewart and Ibarra, 1991). The activity level of River fish and Lake fish likely differs, as fish using the river may be exposed to more variable flow conditions which may require increased swimming activity (this would only accentuate the difference between them). Presumably lake fish do not have to expend the same level of activity swimming, although it is worth noting that in the ocean salmon swim up to 40 km/day so it is also possible that swimming activity was not appreciably different between those habitats. There is no research available that provides fine-scale measures of swimming activity of Pacific salmon in lake systems, though Young and Woody (2007) and Roscoe et al. (2010) have measured travel rates in separate lake systems. If activity level were varied in the model (based on the assumption that River fish are more active than Lake fish), it would result in energy density depleting at a faster rate (Brett, 1995). In addition, activity in warmer waters would reduce somatic energy stores faster than at cooler temperatures (Lee et al., 2003). Overall, our model represents a "best case" scenario based on temperature and by manipulating other variables, like activity, energy depletion will occur faster. However, if fish were to have greater somatic energy density at the time of river entry (though current research suggest that energy density at time of river entry is dependent on ocean conditions and may be declining (Crossin et al., 2004a)), energy density would persist to later in the year. Finally, the initial energy values were calculated using a lipid probe calibrated for sockeye salmon because we were unable to sacrifice fish to perform a Puntledge River Chinook salmon calibration. Both Hendry and Beall (2004) and Crossin and Hinch (2005) show positive relationships with high R^2 values between lipid probe measured energy density and laboratory measured energy density in Atlantic salmon (*Salmo salar*) and sockeye salmon, respectively. Furthermore, the standard deviation of our calculated energy density values was low and resulted in deviations in the model predictions that did not change the conclusions.

4.3. Conclusions

We tagged individual fish with both radio transmitters and thermal loggers to link the spatial ecology of individuals with thermal characteristics of the river. To our knowledge, these tools have rarely been combined for the study of the thermal biology of fish (but see Donaldson et al. 2009) but have much potential to reveal basic knowledge about fish thermal biology and to inform management and conservation initiatives. In general we found no evidence for fish choosing habitat based on temperature, which may be due to cold water refuge not existing in the river. Consequently, summer-run Chinook salmon in the Puntledge River may be nearing the thermal limit of the species. Further declines in stock size may be observed if warming occurs in the region. Access to cool-water refuge in the lake *via* modification to fish passageways to enhance upstream movement, or by capture and trucking methods, may benefit the stock. In addition, stock conservation and increased adult returns may be promoted if studies highlighting the in-lake ecology of the stock and their pre-spawning movements are assessed. This study has the potential to reduce uncertainty regarding management options and provides a tool to evaluate thermal consequences of different management scenarios.

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