ASSOCIATIONS BETWEEN ADULT SALMON AND STEELHEAD BODY TEMPERATURE DURING UPSTREAM MIGRATION AND ESTIMATED WATER TEMPERATURES IN LOWER GRANITE RESERVOIR DURING COLD WATER RELEASES FROM DWORSHAK RESERVOIR, 2004

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by

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Abstract

Water is released from Dworshak Reservoir, Clearwater River, Idaho, during summer to improve flows for outmigrating anadromous salmonid smolts *Oncorhynchus* spp., and to cool summer water temperatures in the lower Snake River for smolts and returning adults. Complex mixing of Clearwater and warmer Snake River water masses results in vertical and lateral temperature gradients below the confluence of these two rivers and persists into the Lower Granite Reservoir. These gradients represent variation in the thermal environment from which adult salmonids may potentially select to regulate body temperature during upstream migration (behavioral thermoregulation). In a previous study during 2001 and 2002, 216 adult Chinook salmon *O. tshawytscha* and 250 steelhead *O. mykiss* were tagged with acoustic Multiple Array Processor (MAP) tags which indicated fish position and transmitted temperatures and depths of fish. Results indicated mean fish temperatures were cooler than mean modeled river temperatures supporting the hypothesis that fish were behaviorally thermoregulating by selecting cooler water originating from Dworshak Reservoir.

In 2004, 120 adult salmon and 128 steelhead were tagged with MAP tags at Lower Granite Dam. Temperature and depth information from mobile tracked fish (89) and fish recorded on a fixed MAP receiver site (168) were analyzed and compared to fixed field temperature sites (modeled river data was not available). The results from the 2004 study were consistent with results from 2001-2, where we observed consistent evidence that fish selected and used cool water when available. Individual fish temperatures were frequently below the mean field river temperatures and decreased as individuals neared the Snake-Clearwater confluence. Comparisons of fish depth between Dworshak Dam release and non-release periods supported the hypothesis that individual fish used cool-water masses originating from Dworshak Reservoir found at deeper depths during release periods. Overall, these data support the hypothesis that upstream migrating adults use the cool water released from Dworshak Reservoir and that these releases reduce thermal stress during warm summer months.
Introduction

Returning adult salmonids require cool water for successful migration, and coldwater refuges appear to be increasingly important for adult salmonids in the Columbia Basin as regional conditions warm in response to changing land- and water-use patterns, regional climate, and hydropower impoundment (Quinn and Adams 1996; Quinn et al. 1997). In general, the run timing of salmonids coincides with periods of suitable thermal conditions in mainstem rivers, and both differences among stocks and within stocks over time suggest that river temperature has been and continues to be a major evolutionary force shaping salmonid life histories (Quinn and Adams 1996; Robards and Quinn 2002; Brannon et al. 2004; Newell and Quinn 2005). At fine scales, fish may behaviorally thermoregulate during migration by using pools, groundwater discharge, and tributary inflows as thermal refugia (Snucins and Gunn 1995; Biro 1998; Torgersen et al. 1999; Baigun 2003; Baird and Krueger 2003). High et al. (2006) found 61% of steelhead temporarily strayed into lower Columbia River tributaries for thermal refuge during their upstream migration to spawning areas. Fall Chinook salmon were also found to temporarily stray into tributaries, which were on average 2-7 °C cooler than the main stem Columbia River (Goniea et al. 2006). Adult salmon also appear to thermoregulate by altering swimming depth in lakes that are thermally stratified (Newell and Quinn 2005).

Since 1991, the cool water release schedule from Dworshak Dam has been modified in an attempt to decrease water temperatures and augment flows for juvenile salmon passing the Snake River (Karr et al. 1998). However, the potential benefits of cooler water in the lower Snake River for adult migrants had not been evaluated, and importantly, there are few other potential thermal refuges in the lower Snake River (e.g. cold-water tributaries), highlighting the potential benefit of the Dworshak releases to summer- and fall-run adult salmon and steelhead.

In a separate study during 2001 and 2002, adult salmon and steelhead with multiple array processor (MAP) tags that transmitted depth and temperature in order to determine if fish were using the cooler water in Lower Granite Reservoir (Clabough et al. 2006). The objectives of that study were to determine the temperatures and depths of Chinook
salmon and steelhead migrating through Lower Granite Reservoir and determine temperature use compared to availability. “Available” water temperature data from three fixed reservoir sites and geographically extensive simulated water temperature data from an Environmental Fluids Dynamic Code (EFDC) model were evaluated and compared to the temperatures “selected” by individual fish as estimated by temperature and depth recorders integrated into telemetry tags. Thermal stratification in Lower Granite Reservoir occurred during the cold water release period (July 2-August 29 in 2001; July 8-September 11 in 2002), resulting from both the subduction of the Dworshak water masses under the warmer Snake River water masses and solar heating. Near the confluence, the EFDC model indicated that Clearwater River plume also created lateral gradients in temperature (Rakowski et al. 2003). Collectively, these vertical and lateral gradients in temperature represented variation in the thermal environment available to adult salmonids as they migrated upstream, and individual fish had the potential to select among available temperatures to thermoregulate. A lack of thermoregulation would result in mean fish temperatures being equal to mean environmental temperatures. Through our analysis in 2001 and 2002, we found mean fish temperature to be close to or cooler than the mean modeled river temperature (Clabough et al. 2006). Fish spent 76 to 81 % of their time in 12 to 15 °C water during the cold water release period near the confluence, while the model river temperature ranged from 9.5 to 23.0 °C. We also found evidence of behavioral thermoregulation of adult salmon and steelhead as their depth of migration became deeper during the cold water release period compared to the pre-release and post-release depths. Finally, we found evidence of temperature-dependent thermoregulation, where individuals did not appear to select cool water at temperatures less than approximately 14°C, but the difference between mean environmental and fish temperatures increased as environmental temperatures increased.

In 2004, we continued to study the temperatures and depths of adult Chinook salmon and steelhead as they migrated upstream through Lower Granite Reservoir. Our objectives were to evaluate temperature use compared to availability, as in the previous two years. However, in 2004 EFDC modeling data of river temperatures were not available. Instead, data from thirty temperature data loggers at four fixed sites were used to evaluate cold water use of adult salmon and steelhead.
**Study Area**

Our study area included the segment of the lower Snake River from Lower Granite Dam (695 river kilometers [rkm] from the mouth of the Columbia River; Figure 1) upstream to the confluence of the Snake and Clearwater rivers (rkm 746.0). Lower Granite Reservoir is approximately 0.5 km wide and extends 63 km upstream to near the town of Asotin, WA, approximately 7 km upstream of the Snake-Clearwater confluence. During flow-augmentation releases from Dworshak Dam, which typically occur in July and August, average Snake River flows from 1995-2004 were 1105 m$^3$/s. During this same period, flows from Dworshak averaged 312 m$^3$/s during July and August, or about 28% of the Snake River flow (Columbia River DART 2006).

![Study area map](image)

Figure 1. Shaded area represents study area for MAP tracking from Lower Granite Dam through the reservoir to the confluence of the Snake and Clearwater rivers. Cold water is released from Dworshak Dam (DW) on the North Fork of the Clearwater River.
Methods

Study Period

The study period was from 6 June through 25 October 2004. Average flows from 1 June until 31 October at Lower Granite Dam (1020 m$^3$/s) were below the 10 year average (1995 to 2004) of 1246 m$^3$/s, while average temperatures during the study period at Lower Granite Dam (18.7 ºC) were above the 10 year average of 17.7 ºC (Columbia River DART 2006).

Water Temperature Monitoring

Field measurements: Water temperatures were monitored at selected sites within the reservoir using either Onset Optical StowAways or SeaBird SBE39 temperature loggers as described in Cook et al. (2006). Temperature loggers were placed at six locations: Site 1 at rkm 709.0 ~ 9 rkm above Wawawai Landing, Site 2 at rkm 722.0 ~ 6 rkm below Steptoe Creek, Site 3 at rkm 734.1 near Silcott Island, Site 5a at rkm 742.8 near Red Wolf Crossing Bridge, Site 9 at rkm 749.3 near the Southway Bridge above Lewiston, and Site 11 at rkm 748.7 near the Clearwater Memorial Bridge (Figure 2; Table 1). Water temperature data from 30 temperature loggers at four of the temperature locations (Sites 1-3 and 5a) in Lower Granite Reservoir were used to evaluate individual fish behavior.

Data from Site 11 on the Clearwater River were only available from July 28 until December 2 in 2002; therefore, data from the U. S. Army Corps of Engineers station in Lewiston (LEWI) were used from June 1 to July 27, 2004 to supplement the missing data at this site (Columbia River DART 2006). Temperature recordings were downloaded three times during the study period. We refer to these data as the “field temperature data”.

Tagging procedures

Adult Chinook salmon and steelhead were trapped and tagged from 06 June through 21 October at the Lower Granite Dam trap. A screened gate in the main fish ladder directed fish toward the trap where fish passed over a weir into an attraction pool and
then passed over two false weirs into pipes containing coded wire (CWT) and passive integrated transponder (PIT) tag detectors (Harmon 2003).

Figure 2. Lower Granite Reservoir showing the six field temperature monitoring sites.

Table 1. Field temperature sites showing number of loggers deployed and logger depths.

<table>
<thead>
<tr>
<th>Location</th>
<th>Number of loggers</th>
<th>Logger depths (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Site 1</td>
<td>9</td>
<td>0.07, 2.7, 6.1, 9.1, 12.6, 17.1, 21.6, 26.6, 31.6</td>
</tr>
<tr>
<td>Site 2</td>
<td>8</td>
<td>0.7, 2.7, 8.5, 12.0, 16.0, 20.0, 24.5, 29.5</td>
</tr>
<tr>
<td>Site 3</td>
<td>7</td>
<td>0.7, 2.7, 5.6, 8.6, 12.1, 16.1, 20.1</td>
</tr>
<tr>
<td>Site 5a</td>
<td>6</td>
<td>0.7, 3.3, 5.3, 7.3, 9.8, 12.3</td>
</tr>
<tr>
<td>Site 9</td>
<td>2</td>
<td>0.6, 4.4</td>
</tr>
<tr>
<td>Site 11</td>
<td>2</td>
<td>0.4, 4.5</td>
</tr>
</tbody>
</table>
After the diversion gate was opened manually or triggered by a tag (CWT or PIT), fish were diverted into a holding area. Fish then passed over a dewatering screen into a 378.5-L box where they were anesthetized (16-mg/L solution of clove oil). A ~5mm piece of latex surgical tubing (3mm thick; 12-mm inside diameter) was placed on each transmitter to reduce regurgitation and then tags were glycerin-coated and inserted gastrically (Eiler 1990; Winter 1996; see Keefer et. al 2004 for more details). Fish were released into a recovery area which leads back to the fish ladder. Uniquely encoded acoustic MAP tags (76 KHz multiple array processor, 149 MHz 3-volt radio transmitter Lotek Wireless, Newmarket, Ontario; 1.6 x 5.4 cm, 24 g in air) transmitted a radio signal every 5 sec and temperature (C) and depth (m), alternately every 2.5 sec. Tag accuracy for temperature was +/-0.8 °C and for depth was +/-0.7 m and transmitter life expectancy was ~150 days.

Tracking and monitoring

Once in the reservoir, tagged fish were tracked with a 6.4 m boat that was equipped with two hydrophones, a MAP_600 receiver, a laptop computer, and a GPS unit. Median and average GPS coordinate error measured by the GPS unit were both 7 m. Hydrophones were mounted on 3.0 m long metal poles, one on either side of the boat and each were covered with 45 degree baffles. When extended laterally, the hydrophones were approximately 2.6 meters apart and approximately 2.7 m deep in the water column.

We tracked fish 6 days a week between 8 June and 25 October. We systematically searched sections of the river until a fish was located. Usually, we first detected fish on a single hydrophone and maneuvered the boat closer in order to receive a signal on both hydrophones (stereo reception). Once stereo reception was achieved, the MAP software would indicate the direction of the fish with respect to the boat. The acoustic signal received by the hydrophones would be translated by the MAP receiver and the real-time data would be displayed and recorded on a laptop computer. Depths and temperatures of tracked fish would be displayed and stored on the laptop screen along with the date, time stamp, and a power reading. We were able to detect a tag within 500 meters and fish were tracked within a range of approximately 10 to 50 m.
Once located, we would track a fish until contact was lost or until it had moved into the Clearwater River or up the Snake River to the Southway Bridge (rkm 749.3). A fixed receiver site was established at rkm 742.0 below Red Wolf Crossing Bridge at the Port of Wilma to verify when fish first reached the confluence area. We also compared temperature data from fish recorded at the fixed MAP receiver site to field temperature data recorded at Site 5a (rkm 742.8, 0.8 rkm upstream of the MAP receiver site).

Movements of salmon and steelhead were monitored with aerial and underwater antennas at Lower Granite Dam. Aerial antennas were used with sequentially scanning receivers (6 s per frequency) while underwater antennas were used in combination with SRX/DSP receivers capable of simultaneously monitoring several radio transmitter frequencies and antennas. Fixed radio receivers (aerial antennas) located in the reservoir and tributaries monitored fish as they moved upstream and were used to evaluate final distribution.

**Data processing**

Data on fish location, depth and temperature were obtained by acoustic MAP tags combined with radio tags with horizontal resolutions of approximately 30 m, vertical resolutions of 0.6 m, and high temporal resolution (every 5 seconds for depth and temperature). The experimental unit or replicate in the study was individual fish. MAP temperature and depth data were matched spatially to field temperature data throughout each individual fish track as each fish passed each temperature location site. Only data from fish records that were within a kilometer downstream or upstream of each field temperature site were used in temperature comparisons. We chose this scale to provide adequate sample size at each location, and because horizontal differences in temperature were relatively small, even over kilometer scales, but differed strongly among depths.

Prior to analysis, we screened the fish tracks for adequate duration and resolution, and 89 of the 110 intensively tracked fish (≥ 0.5 hour tracking duration) were subsequently used for temperature data comparisons and behavioral thermoregulation analysis. Some fish were excluded because of insufficient data, problems with movement patterns (i.e. movements downstream or in a circle) and/or extremely large distances between data points. We classified adults into groups according to whether water was being released.
from Dworshak Reservoir. We refer to the intervals before, during, and after Dworshak Dam water releases as “pre-release,” “release,” and “post release” periods. In 2004, the pre-release period was from June 6 until June 30, the release period was from July 1 until September 20, and the post release period was from September 21 until October 25.

**Testing for Selection Behavior**

We tested for temperature selection behavior by comparing the observed temperature of individual fish recorded (n=168) at the fixed MAP receiver site to the closest field river temperature site (Site 5a, ~0.8 rkm upstream from fixed MAP receiver site). We also compared mobile tracked fish (n=89) temperatures to field river temperatures as individuals passed each reservoir temperature site (4 sites). Fifty-six fish had temperature records that were within one river kilometer downstream and/or upstream of each fixed temperature site were used for comparisons. Eighteen fish were mobile tracked past two different fixed temperature sites. There was no evidence that individual behaviors were correlated between the sites (unpub. data), and due to the small sample sizes available, we included all of these records in the analysis at each site. Only temperature records of the first time a fish was recorded on the fixed site receiver were used in the analysis (some fish were recorded on multiple days or on more than on occasion).

To statistically test for selection behavior at each site, we calculated the mean field temperature across all depths at each site, and ran regression models to determine whether observed mean fish temperatures deviated significantly from the mean available field temperature. The null hypothesis of nonselective (random) behavior predicted that, on average, the observed fish temperatures and average field temperatures would be similar (Figure 3, left panel). Constant selection for cool water would result in consistently lower fish temperatures than field temperatures (Figure 3, middle panel). Temperature-dependent selection would be indicated by a slope that differed significantly from one, with greater selection for cooler water at higher temperatures, and potentially no evidence of selection at cooler environmental temperatures (e.g. the regression line and the 1:1 line overlap at cool temperatures; Figure 3, right panel). Temperature-
dependent selection could occur from stronger selection at higher temperatures, a greater range of temperatures to select from at higher temperatures, or both.

Prior to testing for the selection behavior as described above, we used a model to test for species-specific responses to temperature: average_fish_temperature = constant + average_field_temperature + species + species*average_field_temperature. In this model, a significant species effect would indicate a difference in mean selection behavior across all temperatures (e.g., under constant selection), while the species*average_field_temperature term tested for species-specific differences in the selection across temperatures. In other words, the interaction term tested whether one species exhibited stronger selection at higher temperatures than the other species. There was evidence of species-specific responses when we tested data from the fixed MAP receiver site; therefore, each species was tested separately for selection behavior (see Results). We were unable to test for species-specific responses to temperature in mobile tracked fish due to extremely small sample sizes and we combined species to maximize statistical power.

A General Linear Model (GLM) was then used to calculate the slope coefficient of the regression of average fish temperature versus average field temperature and its 95% confidence interval. The analyzed model was: average_fish_temperature=constant + average_field_temperature where average_fish_temperature was the mean temperature.
from records as the fish passed the field temperature site under analysis and the 
average_field_temperature was the mean temperature across all data logger points 
(depths) at the time the fish passed. Significant constant selection would be indicated by 
a slope of 1.0 and an intercept (constant) significantly different than zero. Temperature-
dependent selection behavior would be indicated by a slope different than 1.0.

**Results**

*Radio Tracking*

Two hundred and forty-eight adult salmon and steelhead (72 spring-summer Chinook 
salmon, 48 fall Chinook salmon, and 128 steelhead) were tagged with MAP transmitters 
at Lower Granite Dam (Figure 4). During tracking, we located 190 (76%) of the tagged 
salmon and steelhead and intensively tracked (≥ 0.5 hour) 110 fish (44%; 37 spring-
summer Chinook salmon, 16 fall Chinook salmon, and 57 steelhead). The average time 
fish were intensively tracked was 2.5 h (range: 0.5 to 7.5 h) and the average distance was 
5.4 rkm (0.6 to 32.7 rkm). A total of 144 (58%) fish (30 spring-summer Chinook salmon, 
33 fall Chinook salmon, and 81 steelhead) were located at the mouth of the Clearwater 
River during the tracking period. Average temperatures between species were similar, 
and average fish temperatures remained below 19°C throughout the study (Table 2).

<table>
<thead>
<tr>
<th>Species</th>
<th>N</th>
<th>Pre-Release</th>
<th>N</th>
<th>Release</th>
<th>N</th>
<th>Post Release</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spring-summer Chinook</td>
<td>17</td>
<td>16.50 (0.62)</td>
<td>16</td>
<td>18.7 (0.32)</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Fall Chinook</td>
<td>-</td>
<td>-</td>
<td>9</td>
<td>16.9 (0.33)</td>
<td>5</td>
<td>15.6 (0.53)</td>
</tr>
<tr>
<td>Steelhead</td>
<td>-</td>
<td>-</td>
<td>22</td>
<td>16.6 (0.52)</td>
<td>20</td>
<td>14.8 (0.42)</td>
</tr>
</tbody>
</table>

Ninety-three tags were recovered and returned to us by anglers and from hatcheries 
from the following locations: Clearwater River (28), the Grande Ronde River (5), the 
Imnaha River (3), the Snake River (22), and the Salmon River (22). The final 
distribution (percent) of all tagged fish in 2004 based on radio telemetry records and
recaptures for spring-summer Chinook salmon (n=72), fall Chinook salmon (n=49), and steelhead (n=127) respectively, was: Clearwater River (17%, 19%, 26%), Snake River (12%, 58%, 36%), Grande Ronde River (4%, 3%, 5%), Imnaha River (9%, 3%, 1%), and Salmon River (51%, 0%, 16%).

Reservoir temperatures

During June through October, Snake River water temperatures (near Asotin) reached a maximum daily average of 23.0 °C in July while the maximum temperature in the Clearwater River occurred in June at 18.5 °C (Columbia River DART 2006; Figure 4). When cold water was released from Dworshak Dam, the Snake and Clearwater rivers reached minimum daily average temperatures of 17.1 and 10.7 °C and daily averages of 21.6 °C and 12.5 °C, respectively. The greatest single day difference in average daily temperatures between the Snake and Clearwater rivers was 12.2 °C in August.

Figure 4. Dworshak Dam outflow, Dworshak Dam, Clearwater River (near Clearwater Memorial Bridge; rkm 748.7), and Snake River (near Southway Bridge; rkm 749.3) average daily temperatures, and number of fish tagged per day in 2004.
Field temperature data

Water temperatures were monitored at four fixed sites in the reservoir during the study period. Minor differences occurred between the surface and bottom depths at these sites during the pre-release and post-release periods. However, a pronounced stratification in temperature occurred during the release period and the strength of stratification increased moving upstream toward the confluence (Figure 5). Associated with stratification was an increase in the range of temperatures observed among the loggers at each location, with a greater range of available temperatures at higher mean water column temperatures (Figures 6-7).

Water temperatures monitored at Site 1 (rkm 709.0; ~ 9 rkm above Wawawai Landing) indicated pronounced summer stratification in July, August, and most of September, with the surface (0.7 m) 1-6°C warmer than the middle layer (17.1 m; Figure 8). The average daily maximum temperature occurred in August at 20.4 °C across all depths (9 levels) with the minimum temperature occurring in October at 11.2 °C. The average daily temperature (across all depths) near Wawawai during the cold water release period was 19.1 °C with a maximum average daily temperature of 20.4 °C and a minimum average daily temperature of 16.8 °C (Figure 8). The greatest single day difference in temperatures between depths occurred in August with a 7.6 °C difference. During the cold water release period, the maximum temperature occurred near the surface (0.7 m) in August at 24.3 °C and the minimum temperature occurred in September near the bottom (31.4 m) at 16.2 °C.

Water temperatures monitored at Site 2 at (rkm 722.0; ~ 6 rkm below Steptoe Creek) indicated pronounced summer stratification in July, August, and most of September, with the surface (0.7 m) 1-8°C warmer than the middle layer (15.8 m; Figure 9). Temperatures reached an average daily maximum of 19.8 °C in June across all depths (8 levels) with the minimum temperature occurring in October at 11.0 °C (Figure 9). The average daily temperature (across all depths) during the cold water release period near Steptoe Creek was 18.0 °C with a maximum average daily temperature at 19.6 °C and a minimum average daily temperature at 16.1 °C. The greatest single day difference in temperatures between depths occurred in August with a 5.7 °C difference. During the cold water release period, the maximum temperature occurred near the surface (0.7 m) in August at
24.5 °C and the minimum temperature occurred near the bottom (29.3 m) at 14.8 °C in August.

Figure 5. Average field temperatures by reservoir site for 3 strata: the surface (top 1/3 of water column), middle (middle 1/3 of water column), and bottom (bottom 1/3 of water column) by site during the pre-release period (June 6 - June 30; top panel), release period (July 1 - September 20; middle panel), and post release period (September 21 - October 25; bottom panel) in 2004. Note data were not available for Site 11 during pre-release period.
Figure 6. Range of fixed site temperatures (°C) among depths versus mean fixed site temperatures (°C) at sites 1 and 2 during all months in 2004.
Figure 7. Range of fixed site temperatures (°C) among depths versus mean fixed site temperatures (°C) at sites 3 and 5a during all months in 2004.
Figure 8. Average daily Snake River water temperatures at Site 1 (rkm 709.0) in 2004 (DWR=Dworshak Dam outflow).

Figure 9. Average daily Snake River water temperatures at Site 2 (rkm 722.0) in 2004 (DWR=Dworshak Dam outflow).
Water temperatures monitored at Site 3 (rmk 734.1; near Silcott Island) indicated pronounced summer stratification in July, August and most of September, with the surface (0.7 m) 1-6°C warmer than the middle layer (8.6 m; Figure 10). Temperatures reached an average daily maximum of 19.8 °C in June across all depths (7 levels) with the minimum temperature occurring in October at 10.7 °C (Figure 10). The average daily temperature (across all depths) during the cold water release period near Silcott Island was 17.5 °C with a maximum average daily temperature at 19.4 °C and a minimum average daily temperature at 14.8 °C. The greatest single day difference in temperatures between depths occurred in August with a 6.8 °C difference. During the cold water release period, the maximum temperature occurred near the surface (0.7 m) in August at 21.6 °C and the minimum temperature occurred near the bottom (12.1 m) at 14.1 °C in September.

Figure 10. Average daily Snake River water temperatures at Site 3 (rmk 734.1) in 2004 (DWR=Dworshak Dam outflow).
Water temperatures monitored at Site 5a (rkm 742.8, near Red Wolf Crossing Bridge) indicated pronounced summer stratification in July, August and most of September, with the surface (0.7 m) 1-7°C warmer than the middle layer (7.2 m; Figure 11). Temperatures reached an average daily maximum of 19.6 °C in June across all depths (6 levels) with the minimum temperature occurring in October at 10.7 °C (Figure 11). The average daily temperature (across all depths) during the cold water release period near Red Wolf Bridge was 17.5 °C with a maximum average daily temperature at 18.9 °C and a minimum average daily temperature at 14.7 °C. The greatest single day difference in temperatures between depths occurred in August with an 8.2 °C difference. During the cold water release period, the maximum temperature occurred near the surface (0.7 m) in July at 22.4 °C and the minimum temperature occurred near the bottom (12.2 m) at 13.8 °C in August.

![Graph showing average daily temperatures at Site 5a](image)

Figure 11. Average daily Snake River water temperatures at Site 5a (rkm 742.8) in 2004 (DWR=Dworshak Dam outflow).
General Patterns of Fish Behavior

Examination of individual mobile-tracked fish depth and temperature in relation to field temperatures revealed that most fish traveled deeper during the cold release period than during the pre- and post-release periods, body temperatures declined as fish neared the confluence, and most fish temperatures were below the average available water temperature. During the pre-release period, fish temperatures remained fairly constant as they moved upstream. In contrast, fish body temperatures declined as they moved towards the confluence during the coldwater release period (Figure 12-14). During the early post release period, warm river temperatures were present and fish temperatures were still observed declining as fish moved upstream until the reservoir cooled and then fish temperatures were fairly constant (Figure 12). For example, one steelhead (MAPID 48900) was tracked on July 22 (during the coldwater release period) from Silcott Island (rm 729.0) to the confluence of the Snake and Clearwater rivers. The fish’s beginning average body temperature was about 20.4 ºC and its ending body temperature was approximately 14.8 ºC (Figure 14). Mobile tracked fish near the fixed reservoir temperature sites and fish recorded on the fixed MAP receiver site were deeper in the water column at cooler temperatures during the cold release period (Figures 15-19). Fish body temperatures were usually below the average available temperature as estimated from fixed field temperature sites (e.g., Figure 20).

Behavioral Thermoregulation

Fish tended to move along the shorelines in the lower and middle parts of the reservoir and occasionally traveled through the center of the river near the confluence, as in previous years (Clabough et al. 2006). We found fish crossing from one side of the river to the other throughout the reservoir; sixty percent (n=53) of the intensively tracked fish crossed from one side of the river to the other, and fish depth changed constantly (Figures 13-14), suggesting the potential for “sampling” of water temperatures across the channel as fish moved upstream.

In the lower reservoir (Site 1) average fish temperature during the cold water release period was 0.1 ºC colder than the average field river temperature. In the middle reservoir
(Sites 2-3) average fish temperature during the cold water release period was 0.1 °C warmer at Site 2 and 0.6 °C colder at Site 3 than the average field river temperature.

Figure 12. Difference between fish temperature and average field temperature by site during the pre-release period (June 6 -June 30; top panel), release period (July 1-September 20); middle panel), and post release period (September 21 -October 25; bottom panel). Boxplot symbols: means (crosses within boxes), medians (horizontal lines within boxes), quartiles (upper and lower bounds of boxes), and 10th and 90th percentiles (ends of whiskers).
Figure 13. Depth and temperature of a spring-summer Chinook salmon mobile tracked in the lower and middle part of the reservoir past temperature sites 1 and 2 during the cold water release period (July 1 –September 20) in 2004 (upper panel). Map depicting mobile track locations of the fish as it moved upstream (bottom panel).
Figure 14. Depth and temperature of a steelhead mobile tracked in the middle and upper part of the reservoir past temperature sites 3 and 5a during the cold water release period (July 1 –September 20) in 2004 (upper panel. Map depicting mobile track locations of the fish as it moved upstream (bottom panel).
Figure 15. Average daily Snake River water temperatures at Site 5a (rkm 742.8) showing average temperatures of fish recorded at the fixed MAP receiver site in 2004 (DWR=Dworshak Dam outflow).
Figure 16. Average daily Snake River water temperatures at Site 1 (rmk 709.0) showing average temperatures of mobile tracked fish as they passed Site 1 in 2004 (DWR=Dworshak Dam outflow).

Figure 17. Average daily Snake River water temperatures at Site 2 (rmk 722.0) showing average temperatures of mobile tracked fish as they passed Site 2 in 2004 (DWR=Dworshak Dam outflow).
Figure 18. Average daily Snake River water temperatures at Site 3 (rkm 734.1) showing average temperatures of mobile tracked fish as they passed Site 3 in 2004 (DWR=Dworshak Dam outflow).

Figure 19. Average daily Snake River water temperatures at Site 5a (rkm 742.8) showing average temperatures of mobile tracked fish as they passed Site 5a in 2004 (DWR=Dworshak Dam outflow).
Figure 20. Temperatures differences between average fish temperatures recorded at the MAP receiver fixed site and average field temperatures at Site 5a during all months in 2004.

Near the confluence (Site 5a) average fish temperature during the cold water release period was 1.8 °C colder than the average field river temperature (Figure 12). The range in temperature was larger at the upstream sites (Table 3), suggesting that the greater difference between fish and available temperatures at site 5a may have been related in part to a greater potential for selection. In other words, the lower range in available temperatures may have limited the choices available to fish at downstream sites.

Average fish body temperature cooled by more than 3°C between the lower part of the reservoir (Site 1) and the upper part of the reservoir near the confluence (Site 5a) during the cold water release period (Table 3). Fish spent the majority of their time between 14 and 17 °C (80%) during the cold water release period downstream from the confluence at Site 5a. The single highest percent of time was spent at 16 °C (26.5%) where field temperature at Site 5a averaged 17 °C and ranged from 12.5 to 23.5 °C during the cold water release period.
Table 3. Intensive mobile tracked fish temperatures (°C) by reservoir location before, during, and after coldwater releases compared to field temperatures in 2004 (lower includes Site 1, middle includes Site 2 and 3, and upper includes Site 5a).

<table>
<thead>
<tr>
<th>Location</th>
<th>Average fish</th>
<th>Average field temperatures</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Surface</td>
<td>Middle</td>
</tr>
<tr>
<td>Lower</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre</td>
<td>17.3</td>
<td>15.6</td>
</tr>
<tr>
<td>Release</td>
<td>18.6</td>
<td>21.2</td>
</tr>
<tr>
<td>Post</td>
<td>15.9</td>
<td>12.8</td>
</tr>
<tr>
<td>Middle</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre</td>
<td>16.2</td>
<td>15.8</td>
</tr>
<tr>
<td>Release</td>
<td>17.3</td>
<td>20.2</td>
</tr>
<tr>
<td>Post</td>
<td>15.9</td>
<td>12.4</td>
</tr>
<tr>
<td>Upper</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre</td>
<td>16.5</td>
<td>16.1</td>
</tr>
<tr>
<td>Release</td>
<td>15.3</td>
<td>20.7</td>
</tr>
<tr>
<td>Post</td>
<td>14.0</td>
<td>12.5</td>
</tr>
</tbody>
</table>

Comparisons of depth use among release and pre- and post-release periods were consistent with the hypothesis that fish were finding and using deeper, cooler water from the Clearwater River during release periods because the average fish depth increased during the release period (Table 4). Fish were, on average, 6.1 meters deeper in the water column during the cold water release period compared to the post-release period in the lower and middle parts of the reservoir (Sites 1-3; Table 4). Fish were on average 2.5 meters deeper in the water column during the cold water release period compared to the pre-release period in the lower and middle parts of the reservoir (Sites 1-3).

A central aim of this study was to test for evidence of temperature selection or behavioral thermoregulation—evidence that individual fish were finding and using cool water masses at or near optimal temperatures (~14-15°C). We tested for two aspects of temperature selection using general linear models and bivariate regression plots of fish temperature versus field temperature as fish were recorded on a fixed MAP receiver site (close to field temperature Site 5a) and as mobile tracked fish moved past Sites 1, 2, 3, and 5a (Figures 21-23). First we examined plots to assess whether individuals were on average cooler than the average water temperature (i.e., did most points fall below the 1:1
These analyses were generally consistent with those above that suggested fish used cool water. Second, we explicitly tested for temperature-dependent selection for cool water—that selection would become stronger as water temperatures increased—by testing whether the slope of the fish-field temperature relationship was below 1.0 (Table 5, Figures 21-23).

Table 4. Intensive mobile tracked fish depths (m) by reservoir location before, during, and after coldwater releases in 2004 (lower includes Site 1, middle includes Site 2 and 3, and upper includes Site 5a; 95 % confidence intervals shown in parentheses).

<table>
<thead>
<tr>
<th>Location</th>
<th>N</th>
<th>Average</th>
<th>Avg. minimum</th>
<th>Avg. maximum</th>
<th>Avg. stdev.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lower</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre</td>
<td>6</td>
<td>7.8 (4.3-11.4)</td>
<td>0.9 (0.2-1.6)</td>
<td>20.3 (13.2-27.4)</td>
<td>1.6</td>
</tr>
<tr>
<td>Release</td>
<td>27</td>
<td>12.0 (9.2-14.7)</td>
<td>1.5 (0.6-2.4)</td>
<td>23.9 (20.4-27.3)</td>
<td>4.7</td>
</tr>
<tr>
<td>Post</td>
<td>13</td>
<td>4.4 (3.0-5.8)</td>
<td>0.8 (-0.1-1.7)</td>
<td>15.8 (9.9-21.6)</td>
<td>2.8</td>
</tr>
<tr>
<td>Middle</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre</td>
<td>12</td>
<td>7.7 (5.2-10.1)</td>
<td>2.5 (0.5-1.2)</td>
<td>19.6 (15.0-23.6)</td>
<td>4.5</td>
</tr>
<tr>
<td>Release</td>
<td>20</td>
<td>8.3 (6.6-10.1)</td>
<td>0.9 (0.6-1.2)</td>
<td>17.3 (14.1-20.5)</td>
<td>3.6</td>
</tr>
<tr>
<td>Post</td>
<td>9</td>
<td>3.7 (2.5-4.9)</td>
<td>1.0 (0.2-1.9)</td>
<td>9.4 (3.3-12.6)</td>
<td>1.6</td>
</tr>
<tr>
<td>Upper</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pre</td>
<td>7</td>
<td>6.9 (4.3-9.4)</td>
<td>2.4 (-0.9-5.7)</td>
<td>12.9 (9.0-16.8)</td>
<td>2.4</td>
</tr>
<tr>
<td>Release</td>
<td>15</td>
<td>7.3 (6.3-8.4)</td>
<td>1.8 (1.0-2.7)</td>
<td>12.0 (9.9-14.1)</td>
<td>2.3</td>
</tr>
<tr>
<td>Post</td>
<td>13</td>
<td>6.0 (4.8-7.2)</td>
<td>2.1 (1.1-3.2)</td>
<td>10.6 (8.1-13.0)</td>
<td>1.7</td>
</tr>
</tbody>
</table>

Table 5. The sample size, r-squared, intercept, and coefficient of the slope with 95% confidence interval from the general linear models.

<table>
<thead>
<tr>
<th>Regression</th>
<th>N</th>
<th>R²</th>
<th>Intercept</th>
<th>95% lower</th>
<th>95% upper</th>
<th>Coefficient</th>
<th>95% lower</th>
<th>95% upper</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fixed site fish</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site 5a</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring-summer</td>
<td>41</td>
<td>0.885</td>
<td>0.075</td>
<td>1.944</td>
<td>2.094</td>
<td>0.985</td>
<td>0.870</td>
<td>1.100</td>
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<tr>
<td>Fall Chinook</td>
<td>38</td>
<td>0.340</td>
<td>5.866</td>
<td>1.345</td>
<td>10.386</td>
<td>0.590</td>
<td>0.312</td>
<td>0.868</td>
</tr>
<tr>
<td>Steelhead</td>
<td>89</td>
<td>0.576</td>
<td>2.171</td>
<td>0.239</td>
<td>4.582</td>
<td>0.803</td>
<td>0.657</td>
<td>0.950</td>
</tr>
<tr>
<td>Tracked fish</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site 1</td>
<td>24</td>
<td>0.675</td>
<td>4.239</td>
<td>0.044</td>
<td>8.521</td>
<td>0.773</td>
<td>0.536</td>
<td>1.010</td>
</tr>
<tr>
<td>Site 2</td>
<td>17</td>
<td>0.890</td>
<td>0.171</td>
<td>3.248</td>
<td>3.590</td>
<td>0.999</td>
<td>0.806</td>
<td>1.193</td>
</tr>
<tr>
<td>Site 3</td>
<td>13</td>
<td>0.821</td>
<td>0.746</td>
<td>3.949</td>
<td>5.440</td>
<td>0.922</td>
<td>0.636</td>
<td>1.208</td>
</tr>
<tr>
<td>Site 5a</td>
<td>20</td>
<td>0.590</td>
<td>3.910</td>
<td>1.038</td>
<td>8.58</td>
<td>0.704</td>
<td>0.413</td>
<td>0.994</td>
</tr>
</tbody>
</table>
Figure 21. Average fish temperature (from fixed MAP receiver records) by species regressed against average field temperature at Site 5a. Thick black line is 1:1 slope ratio and thin middle line is fitted regression line with 95% confidence interval.
Figure 22. Average fish temperature (from mobile track records) regressed against average field temperature at Sites 1 and 2. Thick black line is 1:1 slope ratio and thin middle line is fitted regression line with 95% confidence interval.
Figure 23. Average fish temperature (from mobile track records) regressed against average field temperature at Sites 3 and 5a. Thick black line is 1:1 slope ratio and thin middle line is fitted regression line with 95% confidence interval.
Using the fixed site data, we found a significant interaction between species and the slope of the relationship (F = 3.270; P_{mean_avail_temp*species} = 0.041; N = 168), indicating differing selection by each species, and therefore, we developed separate relationships for each species. These regression relationships revealed temperature-dependent selection in fall Chinook salmon and steelhead, but no evidence of selection in spring-summer Chinook salmon. Sample sizes were low for mobile tracked fish and we were unable to test for species-specific responses between spring and summer Chinook salmon (Table 6). Consistent with the comparison of the mean difference between mean fish and mean available water temperatures (Figure 12), the slope of the regressions for mobile tracked fish pooled across species compared to field temperatures at Sites 1-3 were not significantly different than 1.0, though these sites had relatively low sample sizes (Table 6). In contrast, the regression coefficients were less than one at Site 5a, indicating larger differences between fish and environmental temperatures at higher environmental temperatures.

Table 6. Sample size for regression analysis by species.

<table>
<thead>
<tr>
<th>Location</th>
<th>Spring-summer Chinook</th>
<th>Fall Chinook</th>
<th>Steelhead</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Fixed site fish</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site 5a</td>
<td>41</td>
<td>38</td>
<td>89</td>
<td>168</td>
</tr>
<tr>
<td>Tracked fish</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Site 1</td>
<td>12</td>
<td>1</td>
<td>11</td>
<td>24</td>
</tr>
<tr>
<td>Site 2</td>
<td>10</td>
<td>4</td>
<td>3</td>
<td>17</td>
</tr>
<tr>
<td>Site 3</td>
<td>4</td>
<td>3</td>
<td>6</td>
<td>13</td>
</tr>
<tr>
<td>Site 5a</td>
<td>8</td>
<td>2</td>
<td>10</td>
<td>20</td>
</tr>
</tbody>
</table>
Discussion

During the summer cold water releases from Dworshak Reservoir, pronounced stratification was present and with horizontal gradients present near the confluence (Cook et al. 2006). Comparisons between fish and field temperature measurements revealed evidence of temperature selection behavior by fish, particularly as they neared the confluence. Examination of individual fish tracks revealed that most fish selected cooler than the average available water, and in many cases, appeared to more strongly select cool water as they approached the confluence during release periods. We also found evidence for increasing selection at higher temperatures (temperature-dependent thermoregulation) in fall Chinook salmon and steelhead.

Interestingly, we found no evidence of selection in spring-summer Chinook salmon at the fixed MAP receiver site. During 2001-2, we found evidence of selection behavior in all species, including spring-summer Chinook salmon. This difference between studies may have resulted from random sampling error (especially low sample size in 2004), error associated with using the EFDC model data in 2001-2 versus field temperature data in 2004, or actual differences in the behavior of spring-summer Chinook salmon among years. There may have been greater measurement error associated with estimating selection behavior using the EFDC data because that model did not fully capture the strength of stratification during the release period. Alternatively, assigning estimated field temperatures to mobile tracked fish than fish detected at the fixed site because the mobile track detections were potentially over a greater spatial area. Unfortunately, direct comparison of selection behavior between the 2004 and 2001-2 datasets could not be made using the fixed MAP receiver site because the fixed site was not fully deployed in 2001-2.

The lack of selection observed in spring-summer Chinook salmon may have been caused by sampling error, as described above, or may reflect biological processes. Currently, these two possibilities can not be distinguished with the available data or comparisons to the 2001-2 data, but higher temperature tolerances and weaker selection in summer Chinook salmon are plausible. The run timing of summer Chinook salmon implies that this group has historically experienced higher temperatures during migration than spring and fall Chinook salmon or steelhead, which migrate as temperatures are
more moderate. Limited available genetic data suggest that juvenile stream-type Chinook salmon (e.g., Snake River summer Chinook) have higher temperature tolerances than ocean-type Chinook salmon (e.g., Snake River fall Chinook salmon; Beacham and Withler 1991).

Patterns of fish depth supported the hypothesis that fish were using cool water from Dworshak Reservoir for thermoregulation because their depth of migration became deeper during the cold water release period compared to the pre- and post-release periods. Fish traveled 6.1 meters deeper in the water column during the cold water release period compared to the post-release period in the lower and middle parts of the reservoir in 2004. These results were similar to those found in 2001 and 2002 where fish traveled 5.4 (2001) and 4.0 (2002) meters deeper on average in the water column during the cold water release period compared to the post-release period in the lower and middle parts of the reservoir. In the lower and middle parts of the reservoir, fish were 2.5 meters deeper on average during the cold water release period than in the pre-release period in 2004, where in 2002 they were 6.6 meters deeper on average. The deeper migration observed in 2002 could have been caused by warmer June temperatures in that year and likely influenced temperatures experienced by fish; average fish temperatures in all parts of the reservoir in the month of June were warmer in 2004 than in 2002 (16.6 °C versus 13.0 °C). Average fish temperatures during the first part of June (1-17th) in 2004 were 14.2 °C, a little warmer than in 2002 (11.7 °C); however, during the second part of June (18-30th) average fish temperatures were 18.5 °C, compared to 13.0 °C in 2002.

Since we did not have river temperature estimates at the confluence as we did in 2001 and 2002 (transects 7-11 in Clabough et al. 2006) it is difficult to directly compare the temperature selection behaviors among study years. In 2004, we found fish spent the majority (80%) of their time between 14 and 17 °C (single highest percent time = 26.5 % at 16 °C) during the cold water release period downstream from the confluence at Site 5a. The results from 2004 are similar to the previous study years when comparing data just from transect 7, which was equivalent to the location of Site 5a in 2004. At transect 7 in 2001 and 2002, we found fish spent 79 to 85% of their time between 14 to 17 °C (single highest percent at 15 °C) during the cold water release period near the confluence. Although we did not have river temperatures for each tracked fish location in 2004 and
field temperatures near the confluence as we did in 2001 and 2002, we found similar results in selection behavior.

Overall, the results suggest that adults were able to maintain body temperatures near their preferred range during the release period. Fish spent the majority of their time in 12 to 17 °C, values similar to the preferred temperature range suggested by Brett (1952) of 12 to 14 °C for salmon and similar to the 10 to 13 °C preferred temperature range suggested by Bell (1986) for steelhead. Salinger and Anderson (2006) reported maximum swim speeds for adult salmon and steelhead occurred at 16.0 °C and swim speed was reduced when temperatures were above or below this optimum. However, optimal temperatures for swimming are usually higher than optimal temperatures for growth and survival. Body temperatures were consistently 0.1 to 1.8 °C colder than average available temperatures, consistent with behavioral thermoregulation. These patterns were similar to the results reported by Berman and Quinn (1991), where adult spring Chinook salmon holding in the Yakima River, WA prior to spawning had average internal body temperatures 2.5 °C below ambient river temperatures. Similarly, brook trout were found to be 2.3 °C and rainbow trout 1.5 °C cooler than the Adirondack River (New York) temperature during June through September due to cold groundwater discharge and cool tributary influences (Baird and Krueger 2003).

Cool-water releases from Dworshak Reservoir may have conferred a benefit to upstream migrating adults because salmonids face an increased risk of disease, decreased swimming performance, increased energetic costs, and decreased gamete production and viability during warm water temperatures. Colgrove and Wood (1966) reported outbreaks of *Chondrococcus columnaris* in Fraser River sockeye salmon populations in which warm temperatures played a role. Swimming activity used 84% of total energy consumed by upstream migrating sockeye salmon in the Fraser River and areas of difficult passage (Hell’s Gate) and elevated water temperatures (21 °C) were energetically costly (Rand and Hinch 1998). Warm temperatures can delay ovulation (Taranger and Hansen 1993) and cause molecular changes in egg development (Jobling et al. 1995; King et al. 2003). DeGaudemar and Beall (1998) found overripening of gametes in Atlantic salmon where egg retention, egg mortality, egg infertility, and egg malformation increased significantly with the number of days past ovulation. Low hatch rate (42%
compared to 84% of other stocks) of coho salmon from the Fairview stock in Lake Erie was thought to be due to warm water temperatures affecting ovulation and egg maturation (Flett et al. 1996).

The use of fixed field temperature monitoring sites compared to mobile tracked and fixed site fish data presented in this report were sufficient to complete the study objectives. We were able to determine that fish were selecting for cooler than average field temperatures and fish temperatures decreased as individuals neared the Snake-Clearwater confluence. Overall the results and available literature suggest that migrating adult salmon and steelhead find, use, and benefit from the cooler water that is available in Lower Granite Reservoir during the cold water releases from Dworshak Dam. Conflicting results among years for summer Chinook salmon highlights the need for further study of temperature-mediated behavior of adult salmonids. The potential benefit of the Dworshak releases to summer- and fall-run adult salmon and steelhead may be especially important because there are few potential thermal refuges in the lower Snake River (e.g. cold-water tributaries). Consequently, management of Dworshak releases should account for the effects of the releases on adult salmonids as well as juveniles.
References


Bell, M. C. 1986. Fisheries handbook of engineering requirements and biological criteria. U. S. Army Corps of Engineers. Fish Passage Development and Evaluation Program, North Pacific Division, Portland, OR.


