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Water Temperatures in Adult Fishways at Mainstem Dams on the Snake and Columbia Rivers: Phase 2 — Biological Effects.

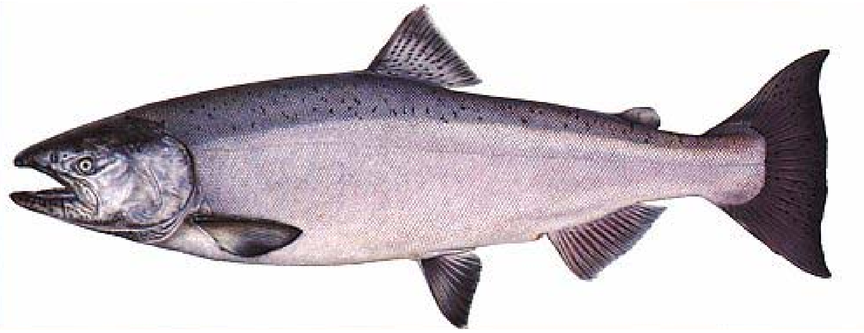
by

Christopher C. Caudill, Tami S. Clabough, George P. Naughton, Christopher A. Peery

Idaho Cooperative Fish and Wildlife Research Unit &
Department of Fish and Wildlife Resources
University of Idaho
Moscow, ID 83844-1141

and

Brian J. Burke
NOAA Fisheries
2725 Montlake Blvd. East
Seattle, WA 98112



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Abstract

Impoundments on the Columbia, Snake and Clearwater rivers have strong effects on the environment encountered by adult salmonids as they migrate upstream. Reservoirs influence seasonal temperature regimes and spatial heterogeneity in temperature, key factors affecting salmonid behavior. We hypothesized that temperature gradients in fish ladders caused by thermal layering in reservoirs and dam forebays represent potential thermal barriers impeding passage of adult salmonids. As a preliminary step in quantifying the biological effects of ladder temperature gradients on adult salmonids, we examined associations between fish passage behaviors and the difference between fish ladder exit and transition pool temperatures (ΔT) at the time of the first detection of fish at the base of fishways. Study sites included McNary Dam and the four lower Snake River dams and this report includes data collected from 2000 to 2003.

Throughout the run season, ladder ΔT values frequently exceeded 1˚C during fish passage events. Ladder temperature differences increased in frequency and magnitude during the warmest periods of the year and were largest at Lower Granite Dam, with few fish passing during periods of $\Delta T > 4$°C. The proportion of the run experiencing ladder $\Delta T \geq 1.0$ ˚C during the four-year study was lowest for spring Chinook salmon (8.4-15.5%) and highest for summer Chinook salmon (20.3-68.7%), and again, proportions were generally highest at Lower Granite Dam. Importantly, the estimated proportions experiencing $\Delta T \geq 1.0$ ˚C were probably underestimated for summer Chinook salmon and steelhead because of tagging restrictions during warm water temperatures, while the proportions for spring Chinook may represent overestimates.

Passage time estimates consistently suggested that ladder temperature gradients increased ladder passage time, in some cases by a factor of two or more. In many cases, total dam passage time also increased with increasing ladder ΔT. The proportion of fish overnighting—those fish passing one or more days after arriving in the tailrace—also consistently increased with ΔT. Detailed examination of passage routes revealed that more fish switched between ladders prior to passing during periods with ladder temperature gradients at McNary Dam but not Ice Harbor or Lower Monumental dams. The observed effects of ΔT on passage behavior did not appear to be solely caused by correlated factors such as high river temperatures. For instance, tailrace passage times were not related to ladder ΔT. Finally, comparison of ladder exit temperature and adult body temperature at the time of exit demonstrated that adult salmonid body temperature had equilibrated to the surrounding ladder water temperature by the time of ladder exit. Adult salmonids' body temperature increases during ladder passage were also positively, though more weakly, related to ladder ΔT.

Collectively, the results suggest ladder temperature differences represent a migration obstacle that slows adult passage at McNary and the lower Snake River dams, especially at Lower Granite Dam. Passing through ladder temperature gradients may have physiological consequences because fish body temperature increases in proportion to ΔT during passage and many passage events occurred at or near temperatures thought to be stressful to migrating adult salmon and steelhead (> 18-20°C). Improvements to the thermal regime in

ladders, particularly those that reduce temperatures at ladder exits and temperature differences between the tops and bottoms of ladders during warm summer months, could provide improvements to adult passage conditions. However, we recommend that any ladder modification should provide adequate thermal conditions between the ladder exit and cool waters at depth in the forebay during summer to prevent the formation of sharp thermal gradients at the interface between the ladder exits and forebay surface waters.

Acknowledgements

Many people assisted with the field work and data compilation for this report and its successful completion was made possible through their efforts. They include: Rudy Ringe, Steve Lee, and Dennis Quempts for tagging fish, Ken Tolotti, Carol Morat and Travis Dick for downloading receivers, Mark Morasch for downloading and conducting mobile tracking surveys, Kinsey Frick, Ted Bohn, and Alecia Matter for administering the database in Seattle, and Dan Joosten, Cody Williams, and Christine Nauman for interpreting and summarizing the telemetry data. This study was funded by the U.S. Army Corps of Engineers (USACE), Walla Walla District, with assistance provided by Marvin Shutters and Karen Zelch.

Introduction

The impoundment of rivers has strong effects on river corridors used by migrating fishes. The alteration of river temperatures by dams and reservoirs is of particular concern for two reasons. First, temperature plays a central role in regulating fish physiology, behavior, and survival (reviews in Brett 1995; Karr et al. 1998; Coutant 1999; McCullough 1999; Sauter et al. 1999; McCullough et al. 2001). Second, reservoirs alter migration corridors both upstream and downstream of dams (Quinn and Adams 1996; Quinn et al. 1997; Peery et al. 2003; Rakowski et al. 2003; Cook et al. 2006). In the lower Snake River, the thermal regime is modified by the presence of the four lower Snake River dams and also by dam operations at upstream dams, particularly Dworshak Dam on the Clearwater River and the Hells Canyon dam complex. Changes in the thermal regime have the potential to affect adult fish behavior in reservoirs by altering seasonal temperature regimes and spatial patterns in temperature. Vertical temperature gradients in reservoirs can also affect the temperature environment of fish ladders because adults move from relatively cool tailrace waters through water pumped into ladders from one or more locations, and exit into potentially warmer surface waters of forebays (Peery et al. 2003).

In the lower Snake River, impoundment and dam operations have altered the overall hydrosystem thermal environment in several ways. From the limited available pre-dam data, it appears that mean annual temperatures and maximum temperatures have not changed in the lower Snake River as a direct result of construction of the four lower Snake River dams (Peery et al. 2003). Rather, the timing of spring warming and fall cooling have been delayed by increased water residence times (Bennett et al 1997; Peery et al. 2003). The largest alteration of the summer thermal regime in the lower Snake River has resulted from cold water released from the hypolimnion of Dworshak Reservoir on the Clearwater River (Bennett et al. 1997, Rakowski et al. 2003; Cook et al. 2006). The Dworshak releases have been conducted since 1991 in an effort to improve passage conditions for migrating juvenile and adult salmonids. These releases have been effective at reducing summer mean temperatures.

Temperature conditions in ladders are most affected by vertical temperature conditions in dam forebays. Vertical temperature differences may develop in reservoirs during summer, causing thermal stratification that prevents mixing between layers or creates less distinct “thermal layering”. At least three processes contribute to vertical temperature differences in reservoirs of the lower Snake River hydrosystem, one of which (Dworshak releases) has unique effects on the Lower Granite reservoir. In all reservoirs, increased water residence times and solar heating causes thermal layering (Bennett et al 1997) with distinct layering present mid-pool and most defined in the dam forebay (Cook et al. 2006). Prevailing upstream summer winds can reinforce the layering by further slowing, or even reversing the movement of surface water masses and causing weak upwelling at the dams. Such wind setup events can result in complete stratification and net transport of warm masses *upstream* over a hypolimnetic water mass moving downstream (e.g., Figure 5.5 in Cook et al. 2006). The strongest stratification has been observed at Lower Granite Dam, where incoming water is composed of a warm layer consisting primarily of Snake River water on top of a cool layer originating from the Clearwater River/Dworshak Reservoir.

Solar heating and wind setup probably increase stratification as water moves toward Lower Granite Dam. In contrast, water in the Lower Granite Dam tailrace (and tailraces of other downstream dams) is well mixed vertically and thermally homogenous because most if not all flow is via powerhouse turbines during summer period. The depth of turbine intakes means that potentially cooler water is pulled from lower layers in the forebay and passed to the tailrace of dams.

Thermal stratification or layering in dam forebays create temperature differences in fish ladders that may represent migration obstacles to adult salmonids. Warm surface waters entering fishway exits mixes with tailrace water at one or more diffusers along the length of the fish ladder before mixing with tailrace water added to the base of ladders in transition pools (Peery et al. 2003; USACE 2004). Temperature differences between the top and bottom of ladders may exceed several degrees Celsius because forebay surface water enters ladder exits whereas tailrace water has been vertically mixed (see results from Phase I of this study, USACE 2004),

Phase II of this study was initiated to estimate the biological effects of ladder temperature differences. At least two aspects of temperature are important to the behavior and physiology of salmonids. First, adults acclimate to a broad range of ambient temperatures, and ambient temperatures have strong effects on fish behavior, swimming speed, and migration rate (Brett 1995). For instance, salmonid migration rates and dam passage times increase with increasing temperature until ~15-18˚C, an increase thought to result from faster and more efficient metabolic processes. Above these temperatures, swim speeds and migration rates decline (Brett 1995, Salinger and Anderson 2006). High temperatures are of particular concern for salmonids. Many adult salmonids slow or stop migration at temperatures > 21˚C (reviewed in Karr et al. 1998; Coutant 1999; McCullough 1999; Sauter et al. 1999; McCullough et al. 2001; see also Richter and Kolmes 2005 for a review of temperature tolerances of adult salmonids). Stabler (1981, cited in McCullough 1999) reported that spring-summer Chinook salmon temporarily held in the relatively cool Clearwater River during July and August until mainstem Snake River temperature dropped below 21˚C. Peery et al. (2003) reported some evidence of slowed migration through the lower Snake River by radio-tagged adult Chinook salmon and steelhead during unfavorable high temperature conditions. Based on ladder counts, they also reported later run timing in years with high summer temperatures. More recently, Keefer et al. (2004), Goniea et al. (2006) and High et al. (2006) reported extensive slowed migration and temporary use of non-natal cool water tributaries in the lower Columbia River by fall Chinook salmon and steelhead during warm periods. Second, rapid changes in temperature from the acclimation temperature have strong effects on adult physiology and behavior.(Beitinger and Bennett 2000; Beitinger et al 2000; Lund et al. 2003; Quinn 2005), suggesting the potential for temperature differences in ladder to affect passage behavior and adult physiology across a wide range of ambient river (i.e., acclimation) temperatures.

Here, we examined the relationship between ladder temperature differences and passage behavior of radio-tagged salmon and steelhead at McNary Dam and the four lower Snake River Dams to determine whether passage slowed when temperature gradients were present in fish ladders. **The primary objectives of this study were to 1) examine the**

relationships between ladder temperature difference (ΔT) and river temperature during fish passage events, 2) to test for associations between passage time and ΔT, 3) to test for associations between ΔT and other behaviors indicating slowed migration (overnighting, ladder switching), and 4) to test associations between changes in fish body temperature (estimated with radio-data storage tags) and ladder ΔT. Overall, the results support the hypotheses that ΔT > 1˚C occurs over a wide array of river environmental conditions, that ΔT > 1˚C increases fish passage times, and that fish body temperature increases during ladder passage during periods of high ΔT. The results also reveal important differences among fish runs, dams, and ladders at individual dams.

Methods

Study system

The Columbia River is the third largest river system in North America, draining an area of 671,000 km^2 including nearly all of Idaho and large areas of Oregon, Washington, Montana, and British Columbia. The Snake River is the largest tributary in the Columbia System, draining much of Idaho, and parts of Wyoming, Montana, Oregon, and Utah. Currently, Snake River adult salmonids must pass four dams on the lower Columbia River and the four lower Snake River dams (Figure 1). Those returning to Columbia River sites upstream from the Snake River confluence pass a total of four to nine dams. The heads of reservoirs transition to 1-2 km long tailraces below dams with turbulent flow caused by discharge from dam turbines and spillways. Fish must distinguish relatively low volume attraction flows leading to fishway entrances at dam faces from the large discharge of turbines and spillways. Once in collection channels, fish pass through transition pools and into ladders, which may be up to 1300 m long, gain 35 m in elevation, and contain 75 or more weirs and pools.

Most interior Columbia spring and summer Chinook salmon are ‘stream’ type Chinook, spending their first year rearing in freshwater before migrating seaward in the spring and summer of their second year. Most adults return after three winters at sea with some returning after two and four winters (‘jacks’, precocious males returning after one winter, were not included in this study). Adult fall Chinook salmon return in late summer and early fall and most spawn in the mainstem Columbia and Snake rivers, especially the 70 km Hanford Reach below Priest Rapids Dam, the only remaining unimpounded stretch of the Columbia River accessible to anadromous fishes upstream from Bonneville Dam. Fall Chinook salmon are ‘ocean’ type salmon, migrating to sea in their first year (age 0), returning after two to five winters at sea at age three to six. Summer steelhead adults may return in any month, though the majority enter freshwater in summer and fall and spawn in the following spring. Juvenile steelhead remain in freshwater for at least two years before outmigrating in spring. Adult steelhead typically return to spawn after one to two winters at sea and a small proportion (< 10%) are iteroparous.

Radio tagging and telemetry monitoring

The methods used to radio tag and monitor salmonid migration in the Columbia and Snake River basins have been described in detail in Keefer et al. (2004) and (Johnson et al.

2005). Briefly, fish were diverted from the Washington Shore fish ladder at Bonneville Dam (river kilometer [rkm] 235) into a facility where they could be selected by species.

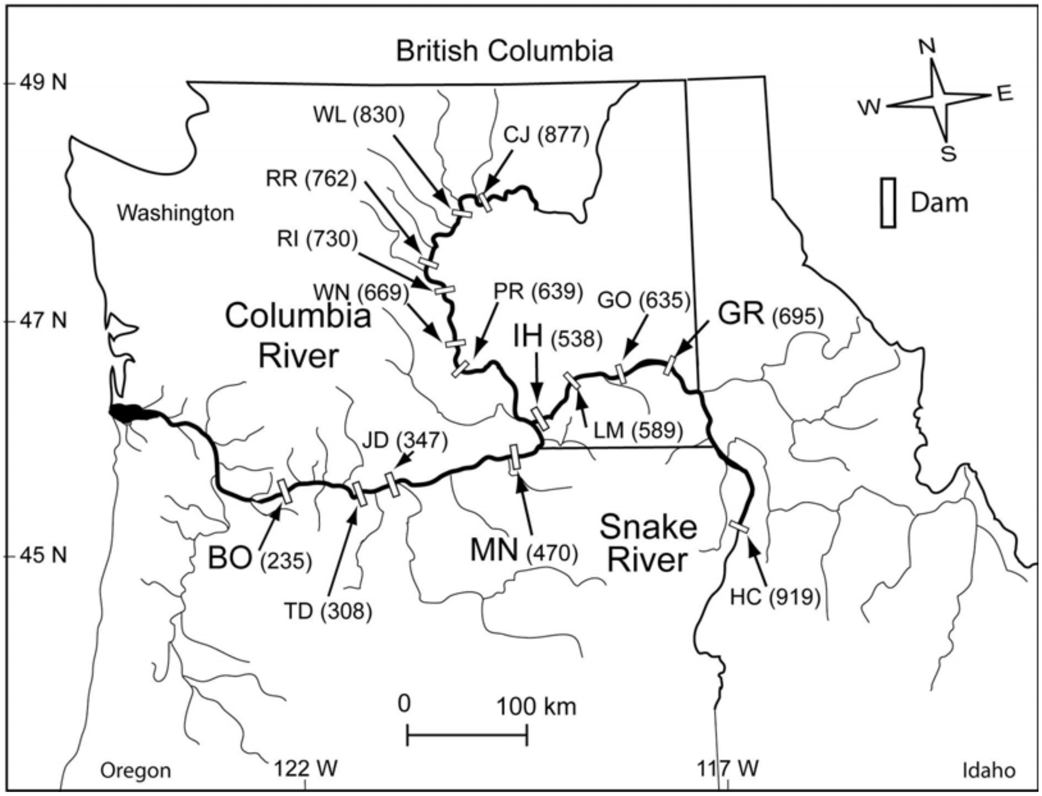


Figure 1: Map of the study region, including location of dams. Fish were collected and tagged at Bonneville dam. Upstream migration to spawning sites was monitored as far upstream as river km (rkm) 1300 in the Snake River basin or Wells dam on the Columbia River using 150-170 fixed site antennas and mobile tracking in boats and trucks. Distances from the Columbia River mouth are given parenthetically as river kilometers (rkm). Dam abbreviations for Lower Columbia River dams: BO = Bonneville, JD = John Day, TD = The Dalles, MN = McNary; mid-Columbia River dams: PR = Priests Rapids, WN = Wanapum, RI = Rock Island, RR = Rocky Reach, WL = Wells, CJ = Chief Joseph (impassible); Snake River dams: IH = Ice Harbor, LM Lower Monumental, GO = Little Goose, GR = Lower Granite, HC = Hells Canyon (impassible).

Diverted fish were anesthetized, sexed, measured for fork length, and inspected for the presence of injuries and hatchery fin clips. All fish were tagged with a gastrically implanted radio transmitter (Lotek Wireless, Inc., Newmarket, Ont). During 2000-2002, 23.2% of spring Chinook, 23.9% of summer Chinook, 35.1% of fall Chinook, and 27.9% of steelhead were released to the Bonneville forebay to meet other study objectives; the remainder were released at the downstream sites. Adult migration behavior in the Columbia basin was monitored using an extensive array of approximately 160 radio receiver sites at dams and in tributaries (detailed in Moser et al. 2002; Reischel and Bjornn 2003; Naughton et al. 2005). Behavior at dams was monitored using fixed aerial and underwater antennas in tailraces and fishways. Individual Chinook salmon were assigned to spring, summer, and fall stocks using date of tagging and USACE criteria for passage date at Bonneville Dam.

Environmental data sources

Hourly temperature data from multiple locations within fishways at the lower Snake River dams and McNary Dam were provided by the U.S. Army Corps of Engineers for the years 2000-2003 (see USACE [2004] for details of data collection). Data on other aspects of river condition were obtained from water quality monitoring stations operated by the USACE and archived on DART (2005).

Data analysis

Temperature difference (ΔT, ˚C) was calculated as Ladder Exit Temperature – Transition Pool Temperature. Transition pool loggers were at the base of fish ladders (see USACE 2004 for placement details; referred to as junction pools in USACE 2004). At McNary Dam, two loggers were present in each transition pool, at 3.3 m and 6.6 m depth. We used data from the shallow logger in all analyses because differences between the two transition pool loggers were small, the shallow logger locations was most comparable to loggers at other dams, and because swimming depths of salmonids in this system (Johnson et al. 2005) suggest the shallow logger best represented temperatures encountered by fish. We classified observed ΔT for each passage event into one of three categories when examining passage behavior: $\Delta T < 1.0$ ˚C (“ΔT < 1”), 1.0 ˚C $\leq \Delta T < 2.0$ ˚C (“ΔT = 1-2”), and $\Delta T > 2.0$ ˚C (“ΔT = 2+”).

We examined three aspects of passage time using ΔT categories at all five dams: (1) mean passage times for several passage segments and (2) the proportion of fish passing the same day they entered the fishway. Adult salmonids typically orient to shorelines during upstream migration, occasionally crossing the channel, apparently in response to orientation cues and conditions encountered at dams (Keefer et al. 2006). Therefore, (3) we also tested whether the proportions of fish that moved from one ladder to the other before passing increased at higher ΔT categories for the three dams (McNary, Ice Harbor, and Lower Monumental dams) with fishways on both the north or south shores. Little Goose and Lower Granite dams have single fishways on the south shore.

We used the telemetry data to identify the following passage events: entrance into the tailrace, 0.5 – 1.0 km downstream of the dam face (F1), first approach to a fishway entrance (A1), first detection inside a fishway (E1), the first detection at a transition pool, located at the bottom of a fish ladder (FP), and the last detection at a fishway exit (LT). Our primary interest in this study was the passage time of the fish ladder segment (FP-LT). We also calculated tailrace passage times (F1-A1) to assess whether any observed differences in passage time were associated with any confounding environmental conditions that both slowed migration in the tailrace and created large ladder ΔT. Analyses of F1-E1 passage times produced qualitatively identical results to the F1-A1 data. Finally, we compared mean total dam passage times (F1-LT) among ΔT categories to assess the overall effect on dam passage time of ΔT at ladders and to facilitate comparisons to previous analyses. All passage time analyses excluded passage attempts after fallback events (the downstream movement past dams after ascension, Boggs et al. 2004). We also excluded a small number of fish that passed more than seven calendar days after their first detection at the dam, including steelhead that overwintered in the tailrace of Lower Granite Dam or Little Goose Reservoir. We conservatively excluded individuals that switched ladders before passing at those dams with two ladders.

In all cases, we matched ΔT categories to the FP record, though the use of FP did not qualitatively affect the outcome of tests because ΔT conditions were relatively constant during most passage events (see **Results** Figure 6; Caudill unpublished analyses). We used ANOVA to test for differences in mean passage time among ΔT categories, followed by preplanned contrasts that tested for differences between the <1 vs. 1-2 and the <1 vs. 2+ ΔT categories. We pooled across years because of limiting sample size at higher ΔT. Passage times were $\log_e$ transformed prior to analysis to improve normality and homogeneity of the error terms. Note that back transformation of means calculated from $\log_e$ transformed data and associated CIs represent estimates of the true population medians with CIs for the median, and are not equivalent to the mean and CI calculated from the original, untransformed data (McArdle and Anderson 2004), but were very similar to the observed medians.

We also tested whether ΔT category was associated with ladder passage by classifying individual fish as having passed on the same day as the first fishway entrance (E1) or one or more calendar days later. We refer to this metric as *overnighting.*

We tested for associations between ΔT and ladder switching because 14.5-29.9% of individuals in each run were detected at the base of more than one ladder prior to passing each year at McNary Dam. For example, some fish were first detected at the south shore transition pool but ascended the north shore ladder. We evaluated the association of this behavior with ΔT category by performing 2x2 chi-square tests on the categories (same ladder, switched) and (FP $\Delta T < 1^\circ$ C, FP $\Delta T \geq 1\ ^\circ$C). We pooled the $\Delta T \geq 1^\circ$C with the $\Delta T > 2^\circ$C observations to achieve adequate sample size in all cells of the contingency table. Similar analyses were conducted at Ice Harbor and Lower Monumental Dams.

We also estimated how fish body temperature changed while passing through thermal gradients in ladders using a subset of fish tagged in 2000 and 2002 that carried combination radio/data storage tags (RDST). RDST tags recorded depth every 5s and fish body temperature every 1 min. RDST fish were tagged at Bonneville and RDST tags were retrieved by diverting fish at the Lower Granite Dam fish trap, where the RDST tag was exchanged with a normal radiotag and the fish was returned to the Snake River to continue migration (for additional details on the tagging protocol for the RDST population, see Johnson et al. 2005). The Lower Granite adult trap is in the lower portion of the fish ladder, and consequently, we did not examine patterns of fish body temperature at this location. We used these data to examine how fish body temperatures changed as individual fish passed fishways across the range of observed ΔT. Specifically, we tested the hypothesis that body temperature would increase during ladder passage as ΔT increased. To test this hypothesis, we correlated ladder ΔT at the time of the first transition pool record with the change in fish body temperature between the first transition pool record and ladder exit (FP-LT) records. We restricted this analysis to passage attempts occurring on the same day because we were primarily interested in how fish body temperature changed over the short-term as fish moved through thermal gradients within ladders. Similarly, for dams with two ladders, we performed analyses on data from each ladder. We also examined the association between ladder ΔT and body temperature change between the F1 and A1 records to test for confounding effects of overall river environment on body changes at dams. Specifically, a lack of association between ladder ΔT and body temperature changes during tailrace passage would support the hypothesis that changes in body temperature were caused by ladder temperature gradients rather than by river conditions that were also correlated with ladder ΔT.

Results

Radio-tagging and the run-at-large

We compared the frequency distributions of radio-tagged adults to dam counts at Ice Harbor Dam for each year and run to assess how well the radio tagged population represented the Snake River run-at-large in terms of run timing and potential exposure to high ladder ΔT (Figures 2-5). Spring Chinook salmon were overrepresented during the late portion of the run and during the warmest temperatures experienced by this group during 2000 and 2001. Summer Chinook salmon were underrepresented during the late portion of the run during all years, particularly in 2000 and 2003. Fall Chinook sample sizes were low throughout all years and generally followed the trends in dam counts. Steelhead were consistently undersampled during the early portion of the run (i.e., A-run steelhead). B-run steelhead were slightly under represented in 2000 and 2002. Most undersampling was caused by stoppages in tagging due to temperatures in excess of fish handling guidelines, and suggest that the summer Chinook salmon and steelhead runs-at-large may have experienced ΔT > 1˚C more frequently than reported here, while spring Chinook salmon may have experienced high ΔT less frequently than reported.

Patterns of temperature and ΔT during fish passage events:

The frequency and magnitude of ladder temperature differences increased with spring warming, was highest during summer months, and declined with fall cooling. At Lower Granite Dam, for example, the greatest ΔT values were highly correlated with increases in summer temperature in the forebay (Figure 6). Ladder temperature differences at the time of fish passage events were greatest at Lower Granite Dam, declined at downstream dams, and in some cases, the pattern of ΔT differed strongly between ladders at the same dam, especially at Ice Harbor Dam. In general, there was an increase in ΔT at higher river temperatures, presumably reflecting the higher degree of thermal stratification or layering within dam forebays during summer. At Lower Granite Dam, some salmon encountered high exit pool temperature and high temperature differences during summer, with ΔT values exceeding 5˚C in some cases (Figure 7). Though high ΔT values were clearly associated with high summer temperatures, moderate temperature differences (1-3˚C) occurred throughout the run season (Figure 7). Temperature differences at Little Goose Dam were less than 3˚C during the study period, though again ΔT ≥ 1 ˚C conditions occurred through most of the run season (Figure 8).

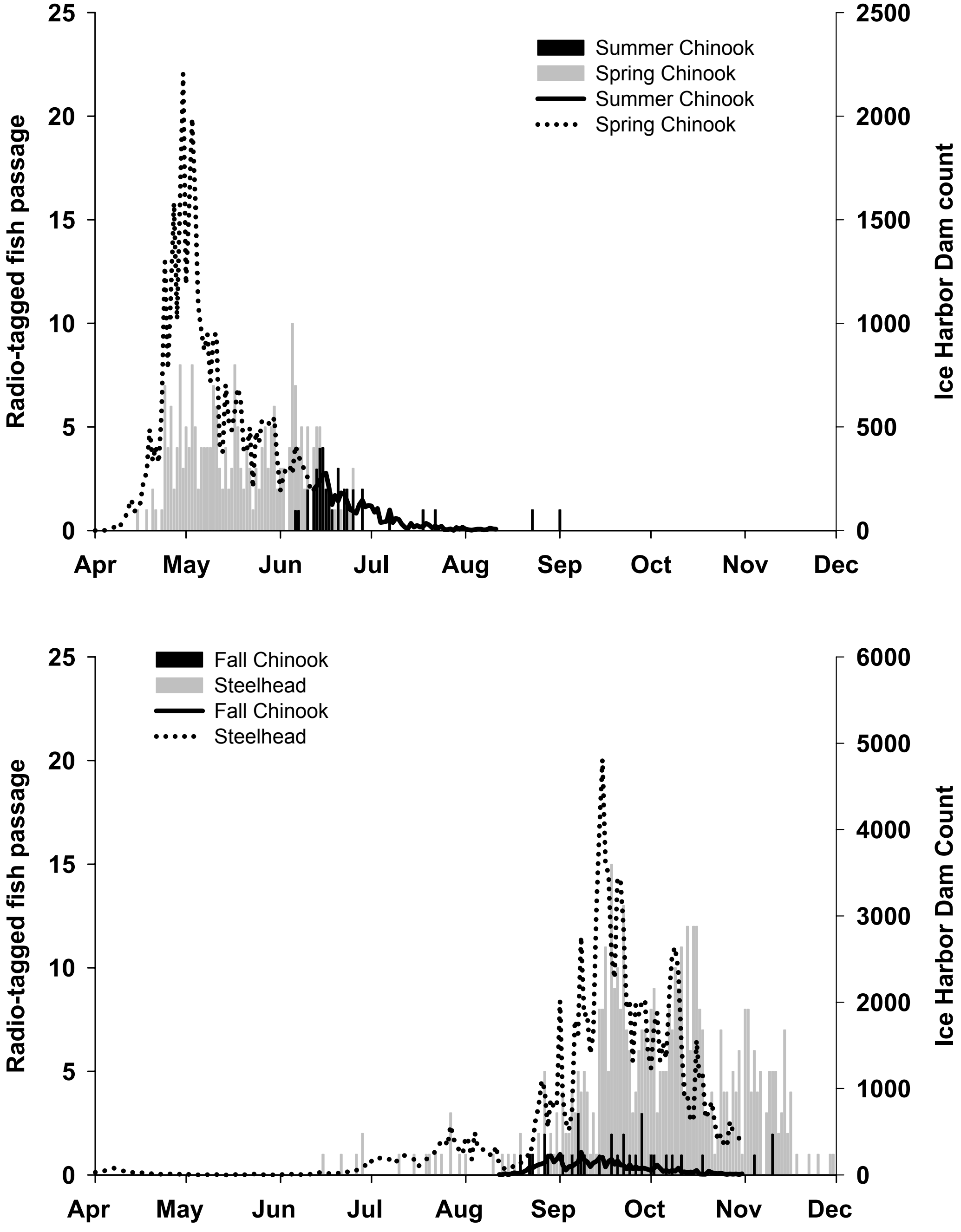


Figure 2: Frequency of dam passages by radio tagged fish (bars) compared to daily dam counts (lines) for spring and summer Chinook (top) or steelhead and fall Chinook salmon (bottom) at Ice Harbor Dam in 2000. Late-run spring Chinook were slightly overrepresented by radio-tagged fish. Late-run summer Chinook salmon were underrepresented by the radio-tagged group, and early-run steelhead were also underrepresented.

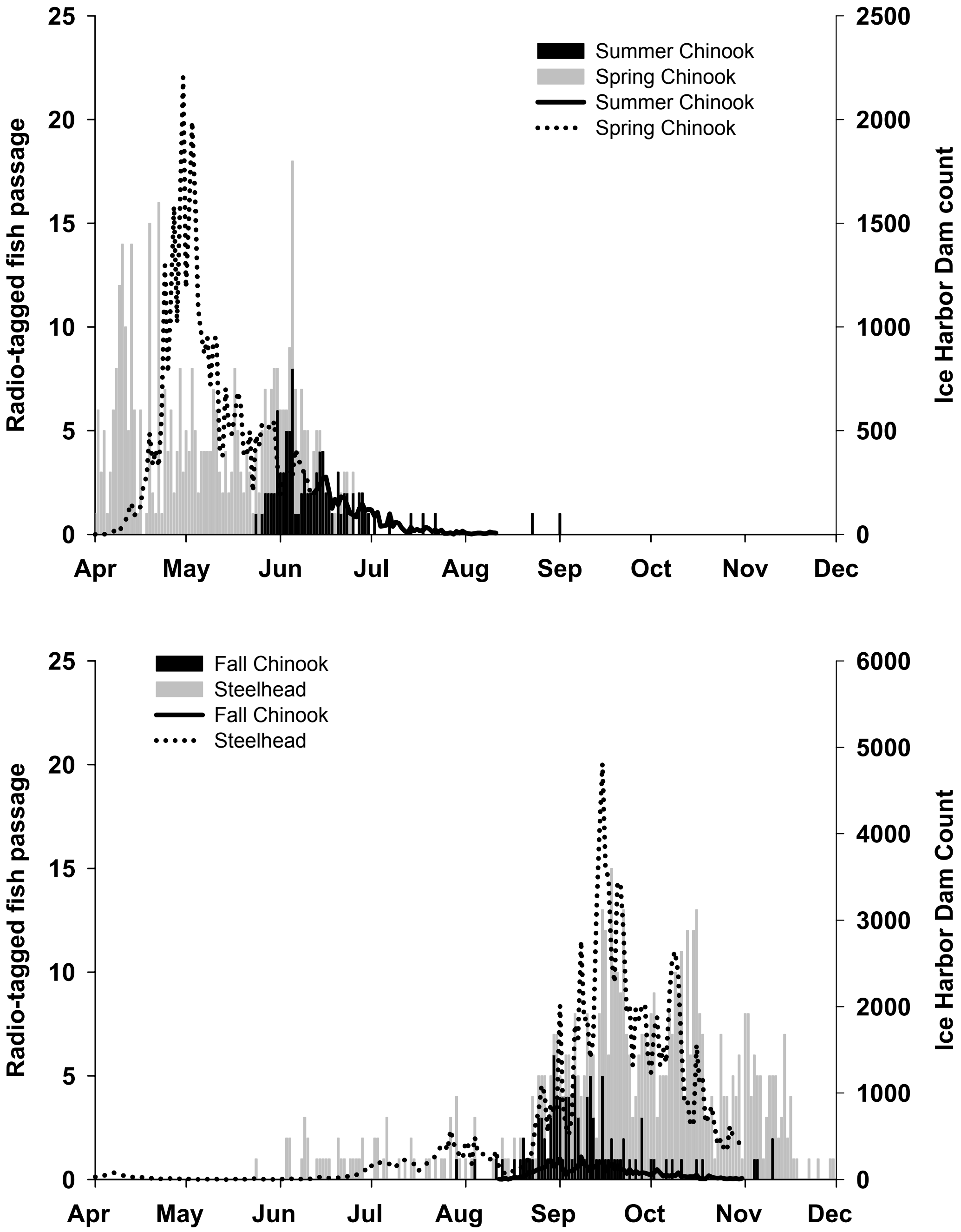


Figure 3: Frequency of dam passages by radio tagged fish (bars) compared to daily dam counts for spring and summer Chinook (top) or steelhead and fall Chinook salmon (bottom) at Ice Harbor Dam in 2001. Late-run spring Chinook were overrepresented by radio-tagged fish. Late-run summer Chinook salmon were slightly underrepresented by the radio-tagged group. Very early-run steelhead were slightly overrepresented.

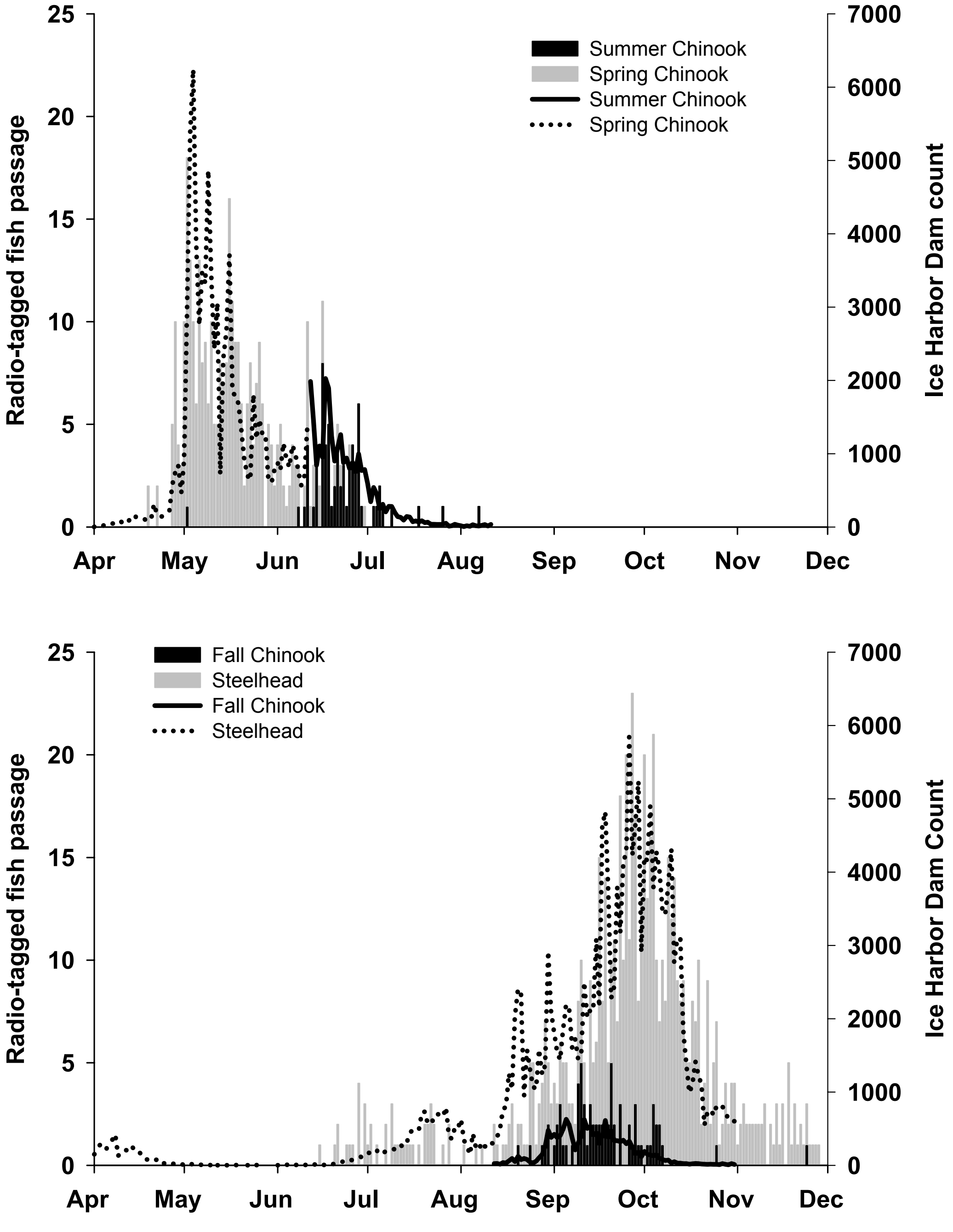
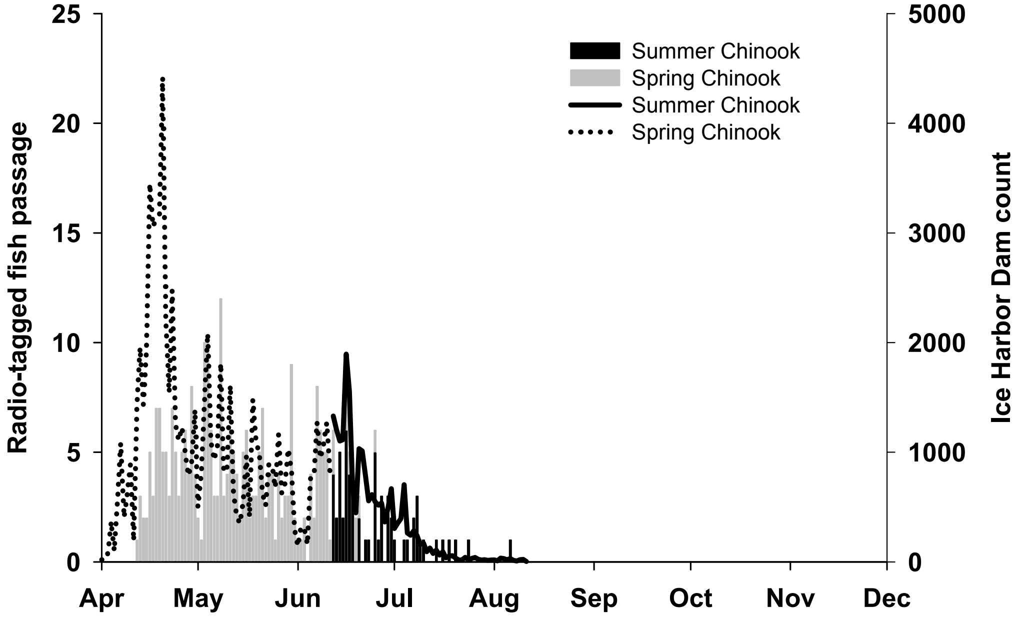


Figure 4: Frequency of dam passages by radio tagged fish (bars) compared to daily dam counts for spring and summer Chinook (top) or steelhead and fall Chinook salmon (bottom) at Ice Harbor Dam in 2002. Late-run summer Chinook salmon were underrepresented by the radio-tagged group, and early-run steelhead were also underrepresented.



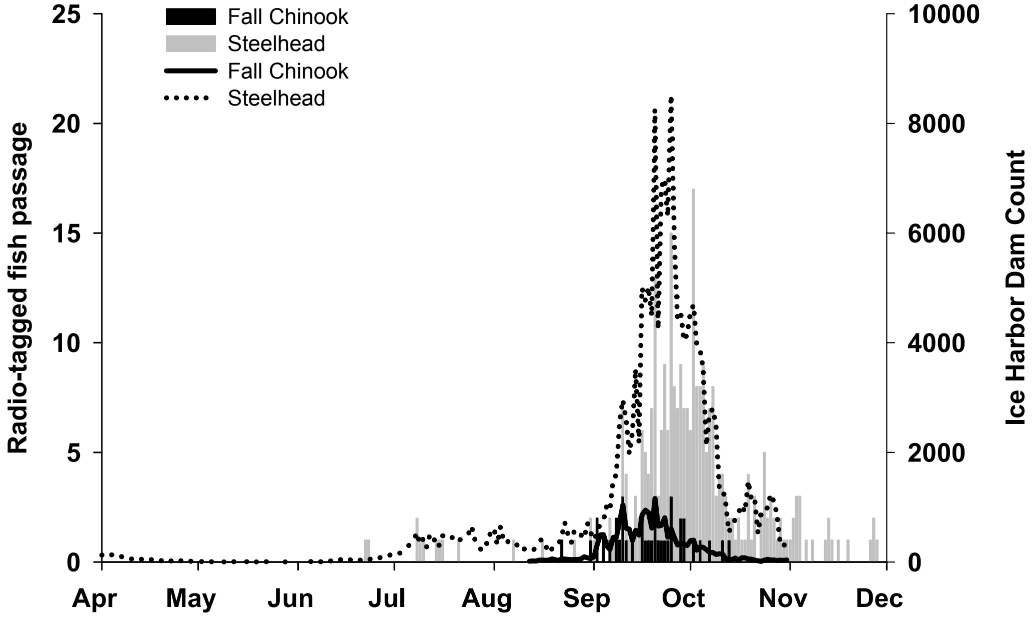


Figure 5: Frequency of dam passages by radio tagged fish (bars) compared to daily dam counts for spring and summer Chinook (top) or steelhead and fall Chinook salmon (bottom) at Ice Harbor Dam in 2003. Late-run summer Chinook salmon were underrepresented by the radio-tagged group, and early-run steelhead were also underrepresented.

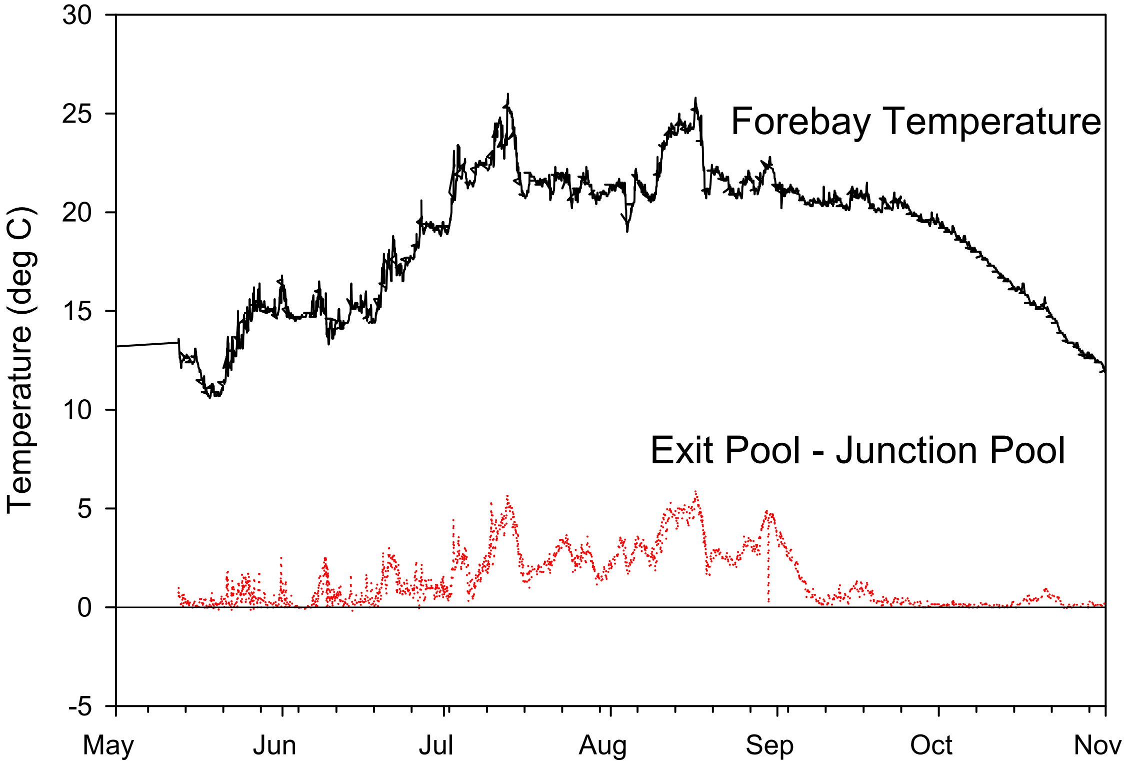


Figure 6: Example of the seasonal pattern of forebay temperature and ΔT (Lower Granite Dam in 2001). ΔT values ≥ 1˚C were recorded during much of the run season, with the highest ΔT recorded in summer months.

Temperature differences between ladders at those dams with two ladders frequently differed. The temperature differences at the two ladders at Lower Monumental Dam were similar at ladder exit temperatures below 20˚C (Figure 9). The north ladder, where 82.2% of fish exited, exhibited higher ΔT values than the south ladder when ladder exit temperatures were greater than 20˚C. At Ice Harbor Dam, the two ladders differed in the magnitude of ΔT, with small ΔT values at the north ladder throughout the season and higher ΔT values at the south shore ladder (Figure 10). The warmer south ladder passed the majority (88.3%) of fish at this dam. At McNary Dam, the two ladders exhibited similar patterns in ΔT, with ΔT values ≥ 1˚C common throughout the run season (Figure 11). The south ladder at McNary Dam did exhibit more exit pool temperatures ≥ 23˚C and associated high ΔT values. The south ladder also frequently exhibited ΔT values that were slightly negative, possibly caused by the intake of primarily Snake River water into the fish ladder exit during fall cooling and winter when the Snake River was running cooler than the mainstem Columbia. The proportion of fish passing each ladder was more equitable at McNary Dam than at Ice Harbor or Lower Monumental Dams (McNary south ladder = 60.9% of all fish).

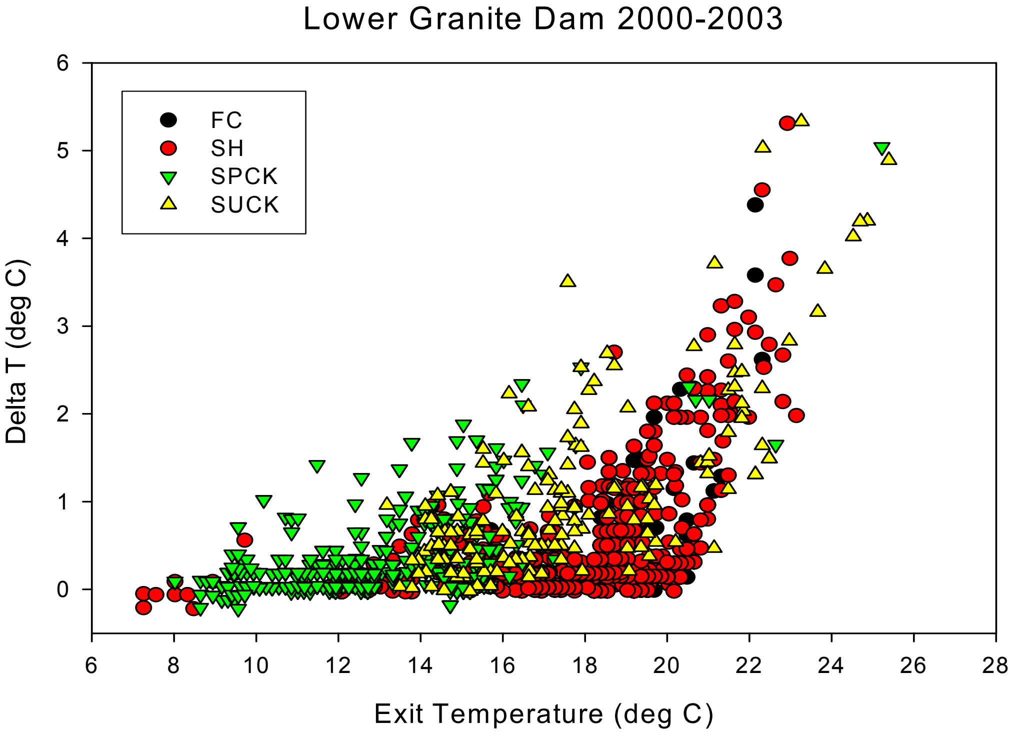


Figure 7: Temperature in the exit pool (˚C) at the time of passage compared to the difference in temperature between the exit and transition pools (ΔT, ˚C) at Lower Granite Dam. All runs combined for the years 2000-3. Species abbreviations: SPCK = Spring Chinook salmon, SUCK = Summer Chinook Salmon, FC = Fall Chinook salmon, SH = Steelhead. N = 1,948 passage events.

The proportion of radio-tagged fish that reached the base of fish ladders when ΔT was ≥ 1.0˚C (as indicated by the first transition pool record, FP) ranged from 4.11-68.7% among species and dams (Table 1). Much of this variability appeared to be tied to differences among dams and run timing/seasonality. Among dams, a greater proportion of fish experienced ΔT ≥ 1˚C at Lower Granite Dam for all species, probably reflecting the greater degree of thermal stratification in the Lower Granite Pool compared to downstream dams receiving water masses vertically mixed at upstream dams. Among species, summer Chinook salmon consistently had the highest proportion of adults experiencing temperature differences at ladders. As expected from run timing and seasonal temperature patterns, spring Chinook salmon and Steelhead had lower proportions of adults reaching ladders with ΔT ≥ 1˚C.

Relationship between fish ladder passage time and ΔT:

Estimated median ladder passage was rapid (FP-LT < 10 hours) when ΔT was < 1˚C for all species at all dams. Median passage times generally increased at higher ΔT for those species passing during warm periods (summer and fall Chinook, and steelhead; Figure 12). In some cases, passage times were more than four times longer for fish passing when ΔT > 2

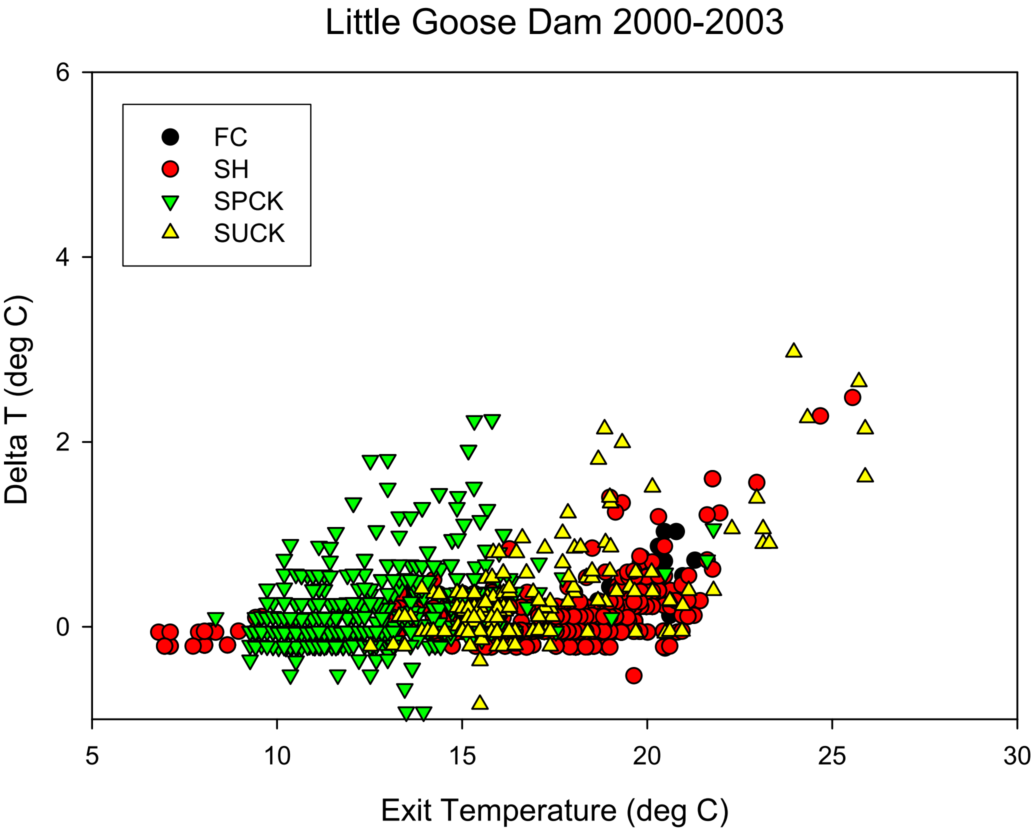


Figure 8: Temperature in the exit pool (˚C) at the time of passage compared to the difference in temperature between the exit and transition pools (ΔT, ˚C) at Little Goose Dam. All runs combined for the years 2000-3. Species abbreviations: SPCK = Spring Chinook salmon, SUCK = Summer Chinook Salmon, FC = Fall Chinook salmon, SH = Steelhead. N = 2,413 passage events.

˚C compared to ΔT = 0 - 1˚C (fall Chinook salmon at Little Goose and Lower Monumental dams). Within species, the magnitude of the ΔT effect was largest at upstream dams and was smaller at downstream dams, consistent with the more frequent and higher ΔT at upstream dams.

The largest effects of ΔT on passage time were observed in summer Chinook at Lower Granite, Little Goose, and Lower Monumental Dams, fall Chinook at Lower Granite Dam, and steelhead at Lower Granite and Little Goose Dams ($P < 0.05$, Figure 12). In other cases, passage times were not significantly different, but point estimates suggested longer passage times at ΔT > 0˚C. In many of these cases, sample sizes were low, especially for ΔT ≥ 2 ˚C (Table 2). Spring Chinook ladder passage times were not significantly different ($P > 0.05$) in any case except at Little Goose Dam for the ΔT = 0-1˚C vs. 1-2˚C comparison, perhaps because very few spring Chinook passed during periods of large ladder temperature differences and high absolute temperatures (i.e. ≥ 20˚C), and because of higher swimming speeds at warmer late-spring temperatures.

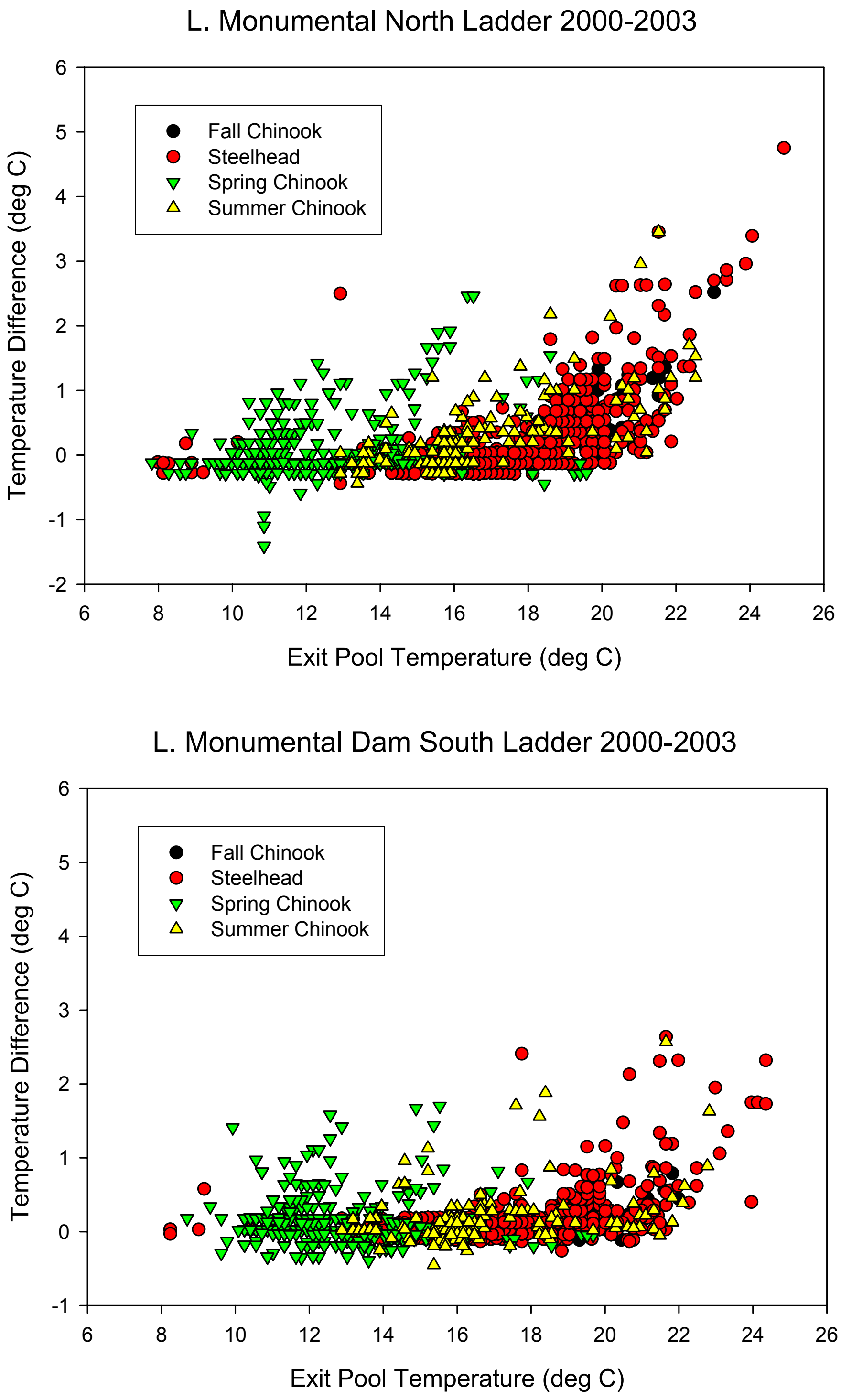


Figure 9: Temperature in the exit pool (˚C) at the time of passage compared to the difference in temperature between the exit and transition pools (ΔT, ˚C) at Lower Monumental Dam North Ladder (upper panel) and South Ladder (lower panel). All runs combined for the years 2000-3. Species abbreviations: SPCK = Spring Chinook salmon, SUCK = Summer Chinook Salmon, FC = Fall Chinook salmon, SH = Steelhead. N_{north} = 1,546, N_{south} = 333 passage events.

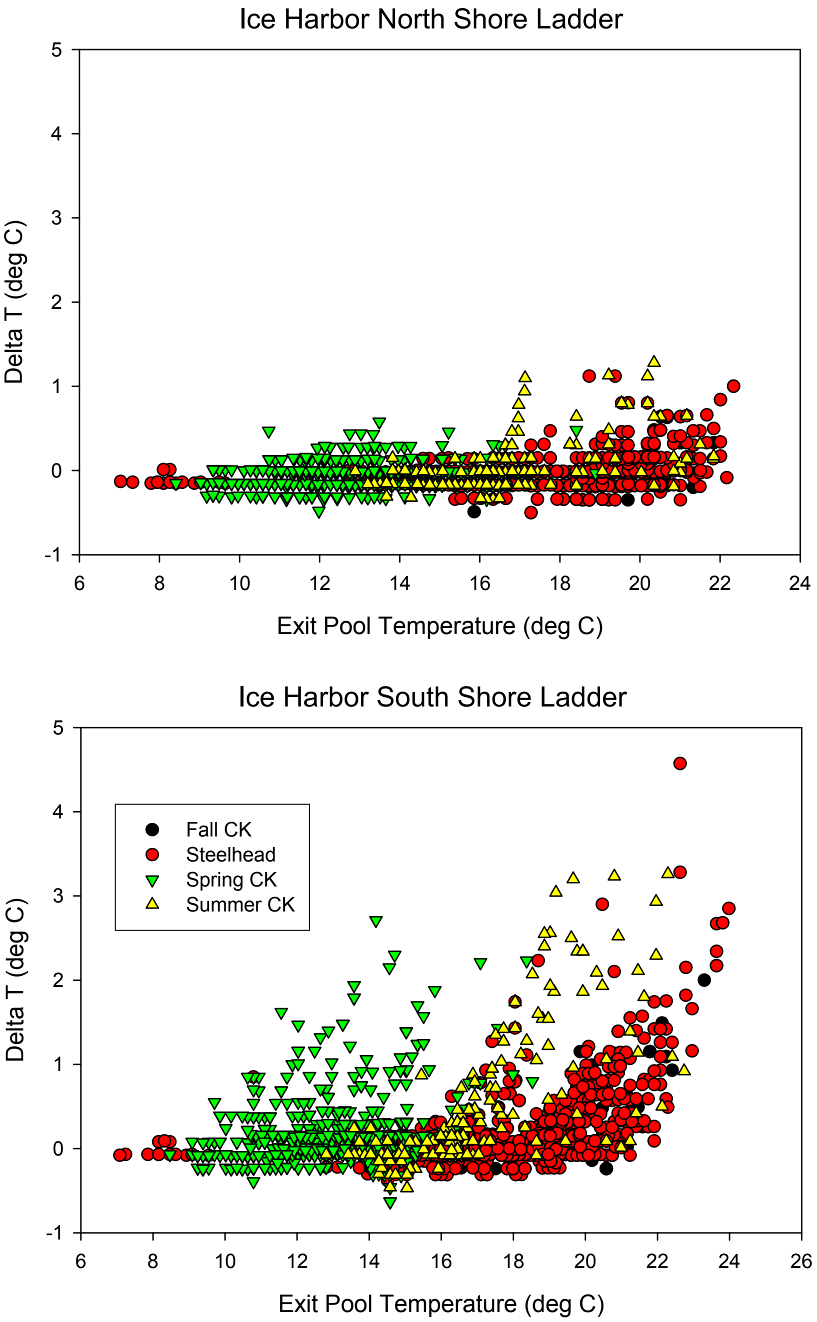


Figure 10: Temperature in the exit pool (˚C) at the time of passage compared to the difference in temperature between the exit and transition pools (ΔT, ˚C) at Ice Harbor Dam North Ladder (upper panel) and South Ladder (lower panel). All runs combined for the years 2000-3. Species abbreviations: SPCK = Spring Chinook salmon, SUCK = Summer Chinook Salmon, FC = Fall Chinook salmon, SH = Steelhead. $N_{north} = 237$, $N_{south} = 2,574$ passage events.

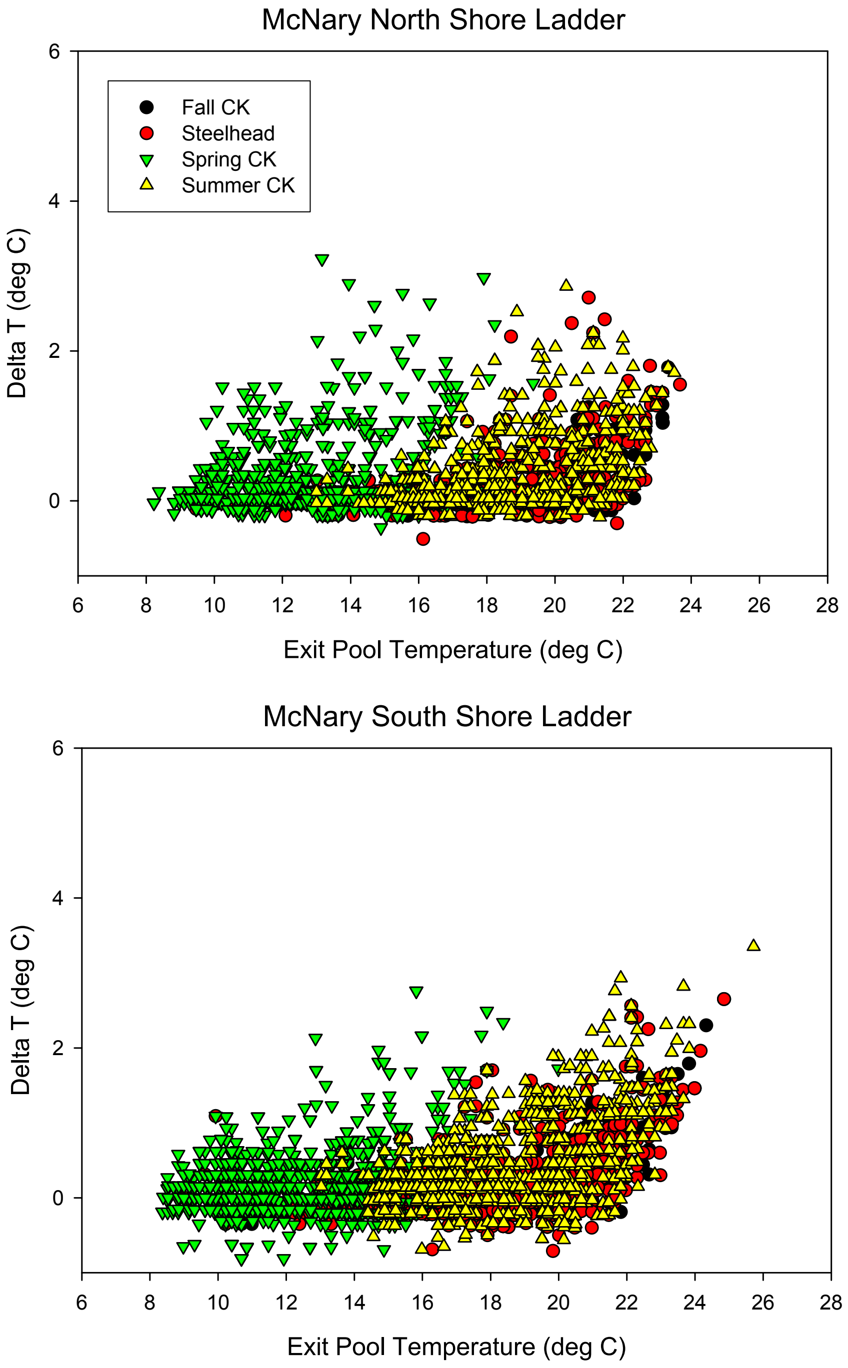


Figure 11: Temperature in the exit pool (˚C) at the time of passage compared to the difference in temperature between the exit and transition pools (ΔT, ˚C) at McNary Dam North Ladder (upper panel) and South Ladder (lower panel). All runs combined for the years 2000-3. Species abbreviations: SPCK = Spring Chinook salmon, SUCK = Summer Chinook Salmon, FC = Fall Chinook salmon, SH = Steelhead. N_{north} = 2,180, N_{south} = 3,397 passage events.

Table 1: Percent of passage events that occurred when ladder ΔT was ≥ 1.0 ˚C. Total sample sizes are given parenthetically.

Dam	Spring Chinook	Summer Chinook	Fall Chinook	Steelhead
Lower Granite	15.5 (645)	68.7 (185)	36.7 (147)	22.2 (970)
Little Goose	13.6 (882)	23.3 (176)	11.0 (164)	4.11 (1191)
L. Monumental	9.87 (598)	20.3 (182)	29.0 (124)	13.4 (988)
Ice Harbor	8.33 (1032)	23.4 (214)	16.6 (223)	10.8 (1375)
McNary	13.8 (1675)	26.7 (1080)	7.26 (1130)	9.82 (1772)

Relationship between total passage time and ΔT:

Total dam passage times (F1-LT) were significantly longer for ΔT = 1-2 ˚C and/or ΔT > 2˚C at several dams (Lower Granite, Little Goose, and Ice Harbor Dams) in steelhead (Figure 13). A similar, but non-significant pattern was observed in summer Chinook salmon, except for ΔT = 0 - 1 ˚C vs. ΔT > 2˚C at Lower Monumental Dam. Median passage times did not differ among ΔT categories for spring and fall Chinook, consistent with the high variability typical of total passage time (Keefer et al. 2004) and relatively small sample sizes for fall Chinook salmon.

Relationship between tailrace passage time and ΔT:

Median tailrace passage times (F1-A1) were not significantly higher for ΔT > 1 in any case, suggesting that the slowed passage observed in the ladders was not caused by correlated river environmental factors that were both slowing passage and creating higher ΔT (Figure 14). In two cases, spring Chinook salmon at Little Goose Dam and fall Chinook salmon at McNary Dam, median tailrace passage times were *shorter* at ΔT =1 compared to ΔT = 0, probably reflecting the general increase of ΔT > 1˚C at warmer river temperatures and higher metabolic rate and swimming speeds of adults at warmer temperatures (Brett 1995).

Relationship between overnighting and ΔT:

In addition to the relationship between ΔT and passage time, we also examined the relationship between ΔT and overnighting—events where individual fish were detected in the tailrace, but did not pass until one or more nights had passed. Specifically, we compared the frequencies of individuals passing on the same day they reached a dam to those passing after one or more nights for each ΔT category (Figure 15, Table 3).

Patterns of overnighting were generally consistent among dams and across species, where the majority of individuals passed on the same day as arrival when ΔT < 1.0 ˚C and the proportion overnighting increased as ΔT increased. When proportions were significantly different among ΔT categories, the percent overnighting for ΔT 0-1˚C ranged from 10.2-46.3 %. At Lower Granite Dam, proportionately more individuals overnighted when ΔT > 2˚C (range 56.3-80.0%) and this proportion was frequently near or above 50% at other dams (range 22.2-68.13%; Figure 15). The proportion of individuals overnighting increased by a factor of 0.321-1.62 and 0.352 – 2.56 when comparing ΔT = 0-1˚C to ΔT = 1-2˚C, and ΔT = 0-1˚C to ΔT > 2 ˚C categories, respectively. The differences in proportions were not significant for fall Chinook at three of the Snake River dams, where sample sizes were the smallest (Little Goose, Lower Monumental, and Ice Harbor; Table 3).

Table 2: Total number of fish used in analysis of passage time by dam, species, and ΔT category. Actual sample sizes for individual tests were slightly lower in some cases due to missed detections at the endpoint antenna (i.e., the FP or LT antenna).

	McNary	Ice Harbor	Lower Monumental	Little Goose	Lower Granite
Spring Chinook Salmon ΔT = 0-1˚C	1161	855	539	761	537
Spring Chinook Salmon ΔT = 1-2˚C	145	74	49	111	82
Spring Chinook Salmon ΔT > 2˚C	19	11	10	9	16
Summer Chinook Salmon ΔT = 0-1˚C	584	142	45	135	55
Summer Chinook Salmon ΔT = 1-2˚C	154	21	31	32	83
Summer Chinook Salmon ΔT > 2˚C	20	23	6	9	37
Fall Chinook Salmon ΔT = 0-1˚C	727	156	84	136	88
Fall Chinook Salmon ΔT = 1-2˚C	47	32	34	17	30
Fall Chinook Salmon ΔT > 2˚C2	0	0	0	0	5
Steelhead ΔT = 0-1˚C	1364	1164	854	1133	719
Steelhead ΔT = 1-2˚C	126	122	111	41	152
Steelhead ΔT > 2˚C	8	15	19	5	49

Relationship between ladder switching and ΔT:

In all runs except fall Chinook, ΔT category was significantly associated with ladder switching at McNary Dam (P < 0.0012). Adults were 1.72-1.83 times more like to switch ladders before exiting when ΔT was ≥ 1 ˚C compared to when ΔT was < 1˚C. The pattern in fall Chinook was similar but was not significant (odds = 1.68, *P* = 0.081). At Ice Harbor Dam, no ladder switching was observed. At Lower Monumental Dam 13.11-23.08% of each run switched ladders, but there was no evidence that this behavior was associated with ΔT (*P* = 0.1052-0.8638).

Relationship between ladder temperature and adult body temperature:

Adult body temperatures were closely associated with ladder exit temperatures at the time of exit (LT) and increased during ladder passage during periods of high ladder ΔT. The relationships exhibited nearly a 1:1 correspondence, demonstrating that, on average, adult body temperatures had equilibrated with the ladder environment by the end of the passage event (e.g., Little Goose Dam, Figure 16). Relationships at other projects were similar to those observed at Little Goose Dam ($R^2_{spring\ CK}$ = 0.895 - 0.964, $R^2_{summer\ CK}$ = 0.880 - 0.942; $R^2_{fall\ CK}$ = 0.973 - 0.983; $R^2_{steelhead}$ = 0.743 - 0.972).

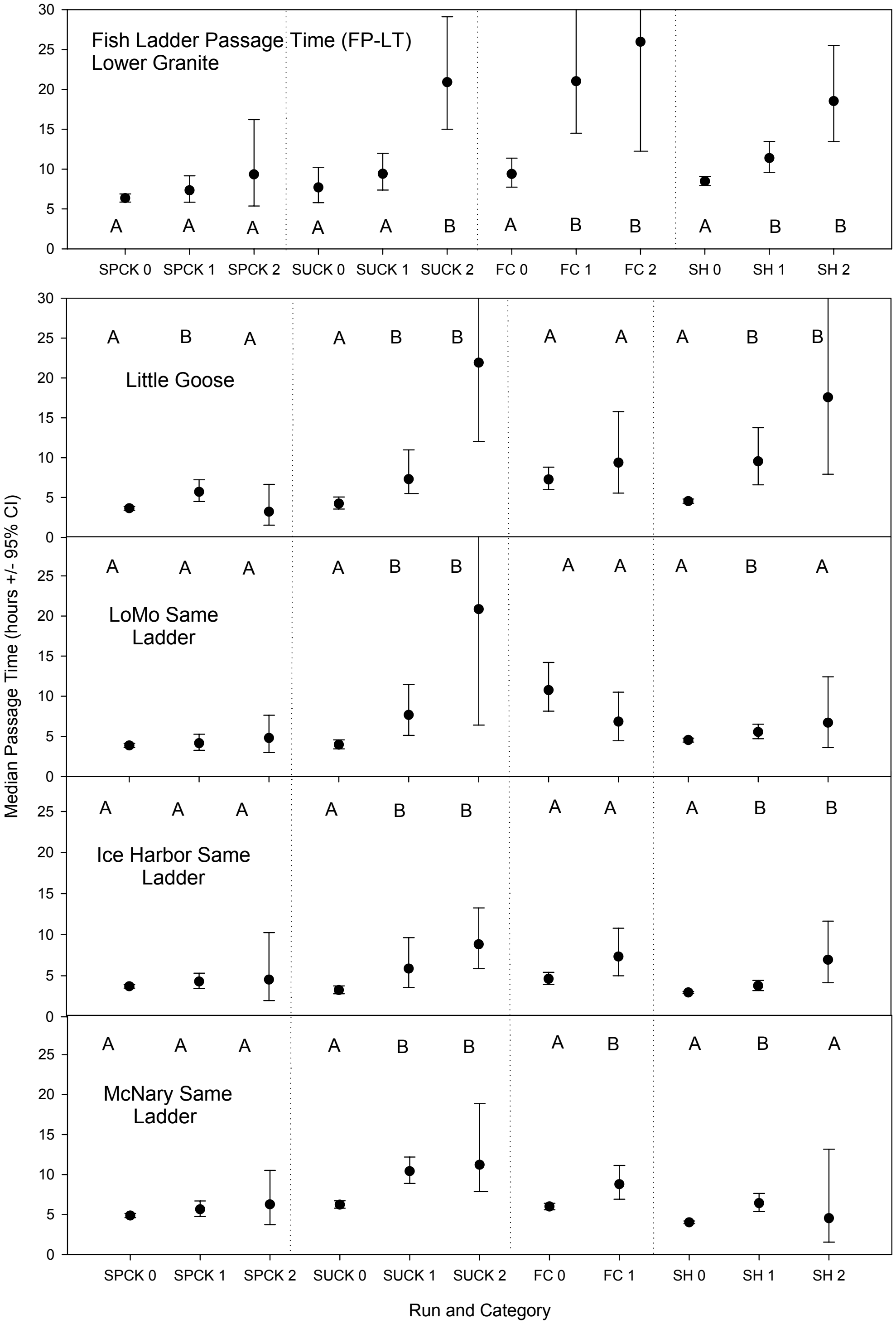


Figure 12: Ladder passage times (FP-LT) by dam and species for individuals encountering ladder ΔT of <1˚C (0), 1-2˚C (1) or > 2˚C (2). Different letters indicate significantly different median passage times within species and dam for contrasts between ΔT categories 0 vs. 1 and 0 vs. 2 (*P* < 0.05, ANOVA with Tukey's correction for pairwise comparisons). Individuals switching ladders were excluded, indicated by "Same ladder".

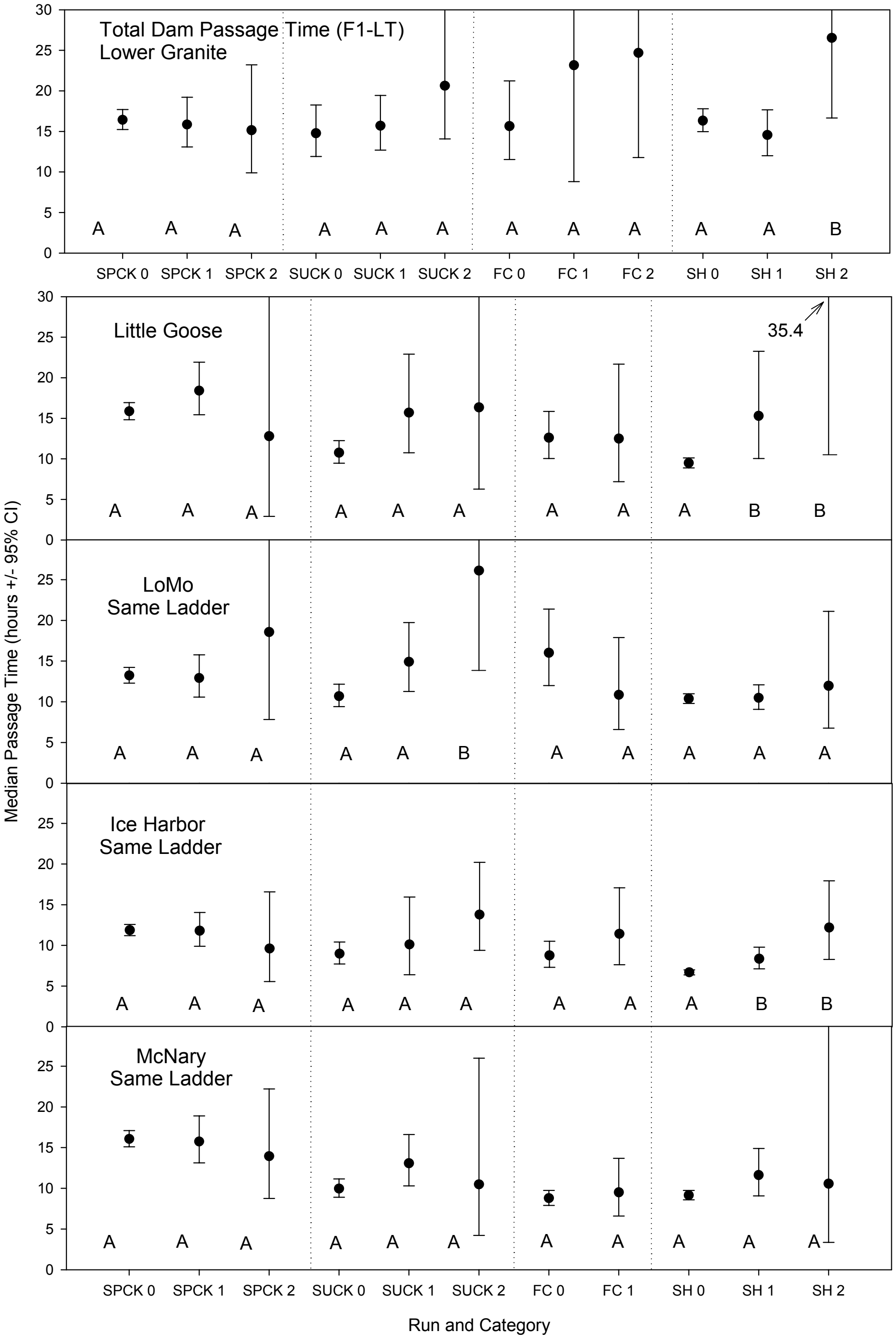


Figure 13: Total dam passage times (F1-LT) by dam and species for individuals encountering ladder ΔT of <1˚C (0), 1-2˚C (1) or > 2˚C (2). Different letters indicate significantly different median passage times within species and dam for contrasts between ΔT categories 0 vs. 1 and 0 vs. 2 ($P < 0.05$, ANOVA with Tukey's correction for pairwise comparisons). Individuals switching ladders were excluded, indicated by "Same ladder".

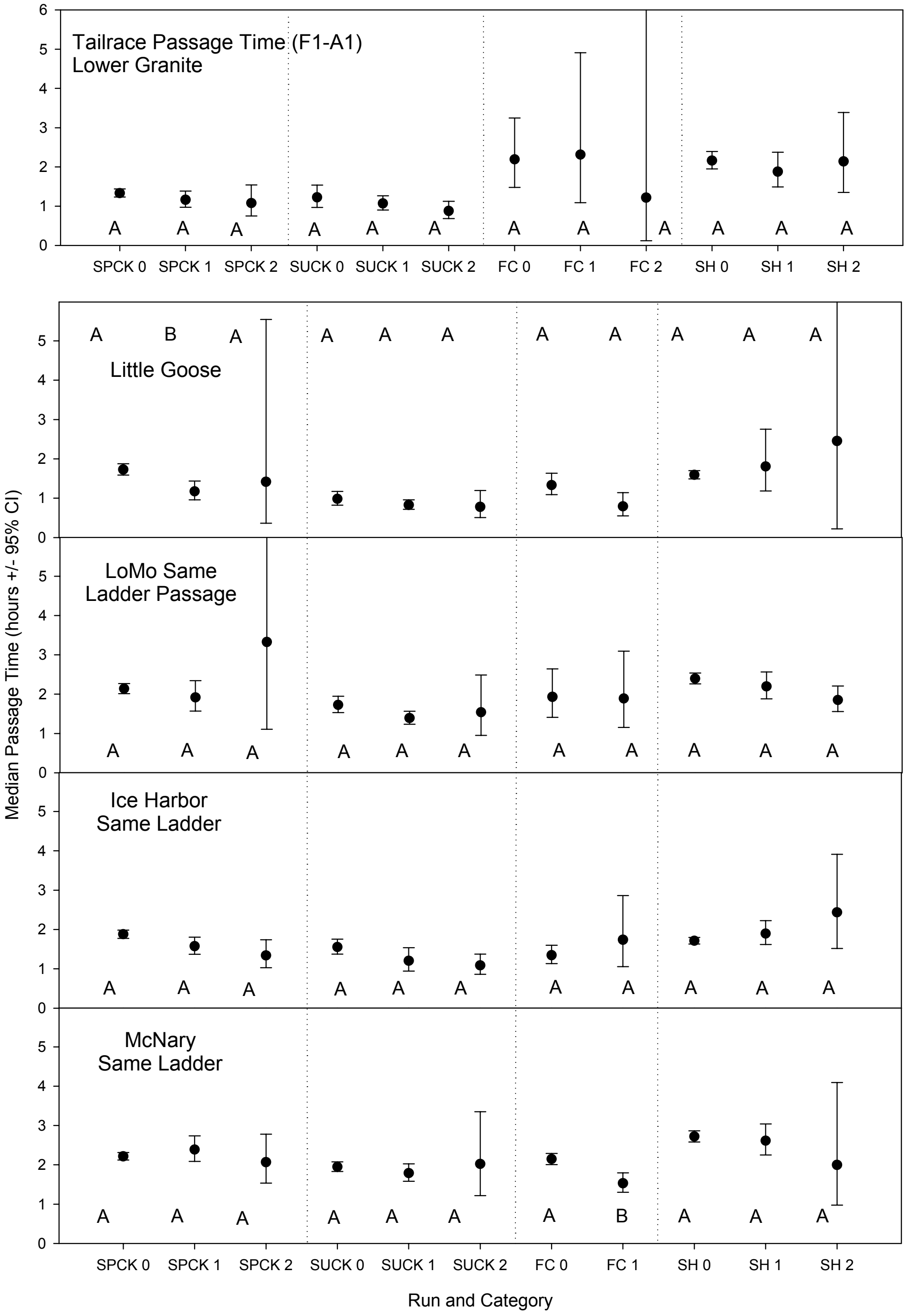


Figure 14: Tailrace passage times (F1-A1) by dam and species for individuals encountering ladder ΔT of <1˚C (0), 1-2˚C (1) or > 2˚C (2). Different letters indicate significantly different median passage times within species and dam for contrasts between ΔT categories 0 vs. 1 and 0 vs. 2 ($P < 0.05$, ANOVA with Tukey's correction for pairwise comparisons). Individuals switching ladders were excluded, indicated by "Same ladder".

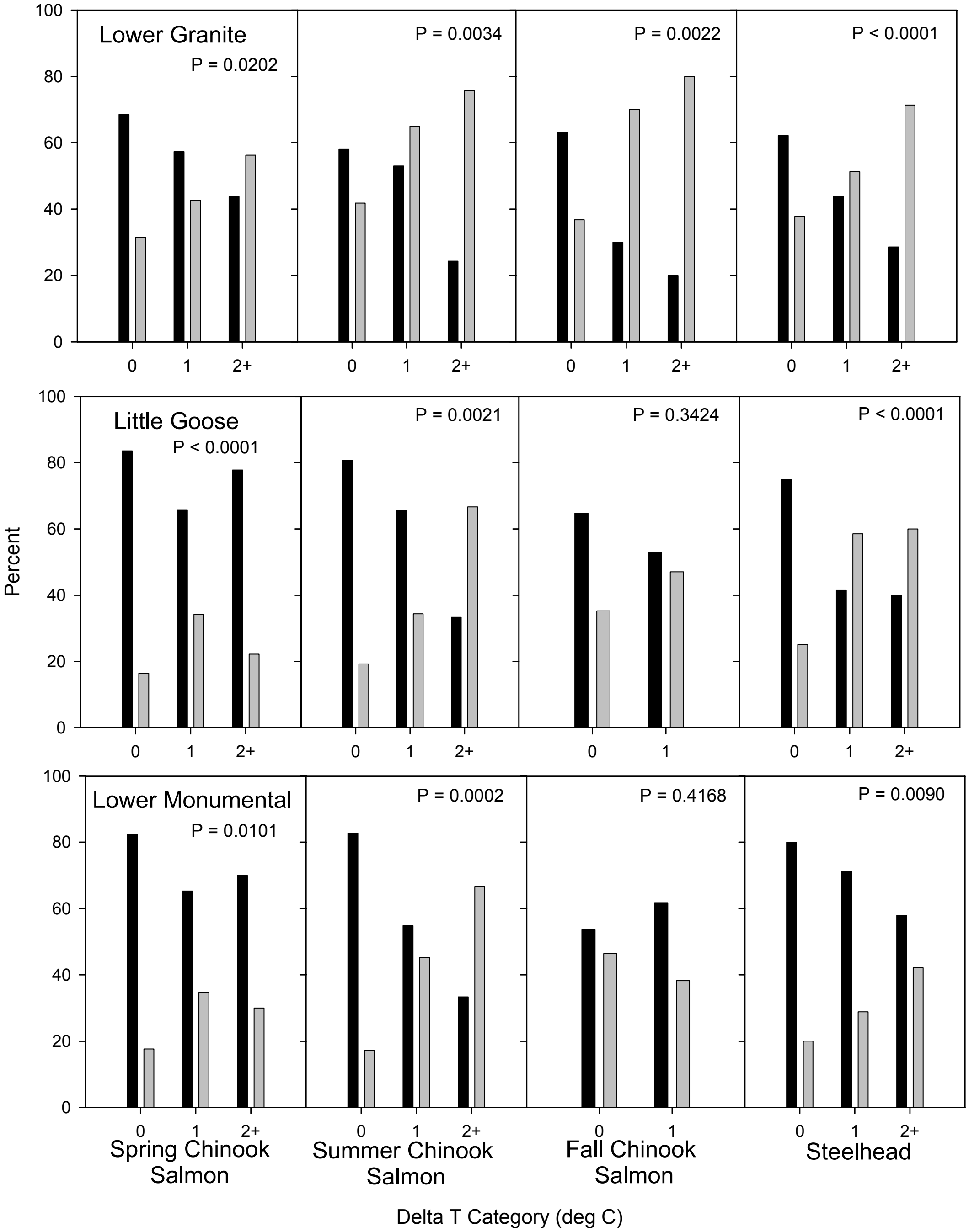


Figure 15: Proportion of individual fish that passed on the same day as reaching each tailrace (indicated by an F1 detection) (black bars) or one or more days later (gray bars) for fish passing during each ΔT category. P-values represent results of χ^2 tests of association (see Table 3).

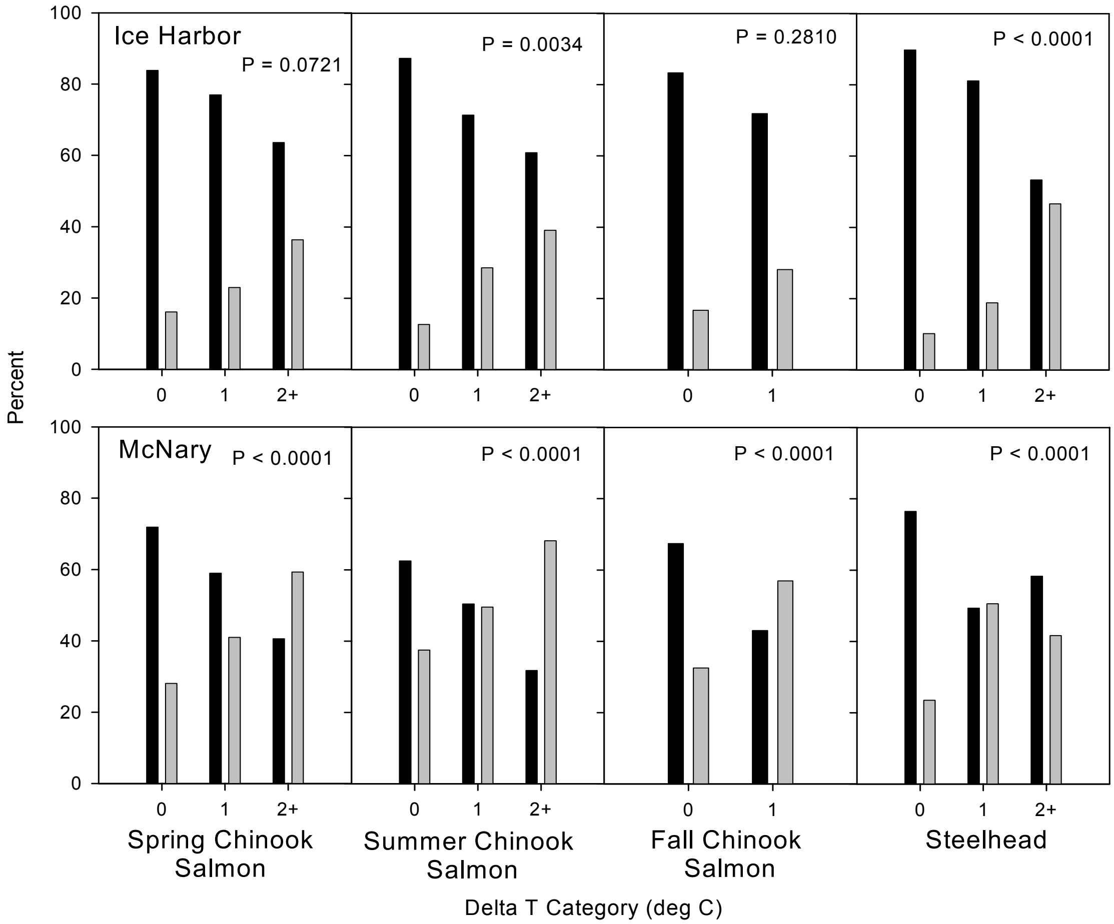


Figure 15 (continued).

Importantly, body temperature changes during passage also appeared to reflect the thermal conditions of the ladder at the time of passage. The comparison of change in adult body temperature during ladder passage (FP-LT) to the ΔT at the time of the first passage (Figure 16, Appendix 1) revealed that body temperatures rose as ladder ΔT increased. The association was strongest in fall Chinook salmon ($R^2 = 0.7231$-0.8666). Associations were weaker or less consistent in other runs, particularly in summer Chinook salmon, though the latter had consistently low sample size (Appendix 1). The weaker association with body temperature change likely reflects inaccuracies in matching water temperatures used by the fishes at the base of the ladder to fish body temperatures as fish swam though the thermally complex transition pools.

The relationship between ladder ΔT and change in body temperature differed between ladders at several dams, the association being highly significant and strong in one ladder, and there being no evidence of an association in the other ladder (e.g. spring Chinook salmon at McNary). These differences were probably related to small sample sizes in many cases, and/or a lower range of ΔT at one ladder compared to the other (e.g., Ice Harbor, Figure 10).

Table 3: (a) Proportion of adults passing on the same day or overnighting by species and dam, (b) and results of $\chi 2$ tests of association between overnighting and ΔT category.

(a)

ΔT Category	Spring Chinook Salmon		Summer Chinook Salmon		Fall Chinook		Steelhead	
L. Granite	Same Day	Next +	Same Day	Next +	Same Day	Next +	Same Day	Next +
0	68.5	31.5	58.2	41.8	63.2	36.8	62.2	37.8
1-2	57.3	42.7	53.0	65.0	30	70	43.7	51.3
2+	43.8	56.3	24.3	75.7	20	80	28.6	71.4
L. Goose								
0	83.6	16.4	80.7	19.3	64.7	35.3	74.9	25.1
1-2	65.8	34.2	65.6	34.4	52.9	47.1	41.5	58.5
2+	77.8	22.2	33.3	66.7			40	60
L. Monumental								
0	82.4	17.6	82.8	17.2	53.6	46.4	80.0	20.0
1-2	65.3	34.7	54.8	45.2	61.8	38.2	71.2	28.8
2+	70	30	33.3	66.7			57.9	42.1
Ice Harbor								
0	83.9	16.1	87.3	12.7	83.3	16.7	89.8	10.2
1-2	77.0	23.0	71.4	28.6	71.9	28.1	81.2	18.9
2+	63.6	36.4	60.9	39.1			53.3	46.7
McNary								
0	71.9	28.1	62.5	37.5	67.4	32.6	76.5	23.5
1-2	59.0	41.0	50.4	49.6	43.0	57.0	49.4	50.6
2+	40.6	59.4	31.8	68.2			58.3	41.7

Table 3 (b)

	Spring CK	Summer CK	Fall CK	Steelhead
Lower Granite				
N	635	175	122	921
d.f.	2	2	2	2
Chi Sq.	7.808	11.397	12.208	28.127
P	0.0202	0.0034	0.0022	<0.0001
Little Goose				
N	881	176	153	1179
d.f.	2	2	1	2
Chi Sq.	20.257	12.365	0.901	25.75
P	<0.0001	0.0021	0.3424	<0.0001
Lower Monumental				
N	598	182	118	984
d.f.	2	2	1	2
Chi Sq.	9.184	17.40	0.659	9.432
P	0.0101	0.0002	0.4168	0.009
Ice Harbor				
N	940	186	189	1301
d.f.	2	2	2	2
Chi Sq.	5.258	11.394	2.539	26.664
P	0.0721	0.0034	0.281	<0.0001
McNary				
N	1647	1061	1110	1753
d.f.	2	2	2	2
Chi Sq.	26.718	24.35	23.181	56.781
P	<0.0001	<0.0001	<0.0001	<0.0001

Adult salmon passing during warm periods must pass multiple dams, suggesting the potential for repeated increases in body temperature during passage through the hydrosystem. We examined whether individual fish experienced increases in body temperature repeatedly during upstream migration by generating correlations between body temperature changes at all pairs of locations. Consistent positive correlations in body temperature change between pairs of locations would suggest chronic body temperature increases during upstream migration. Comparisons of the change in body temperature

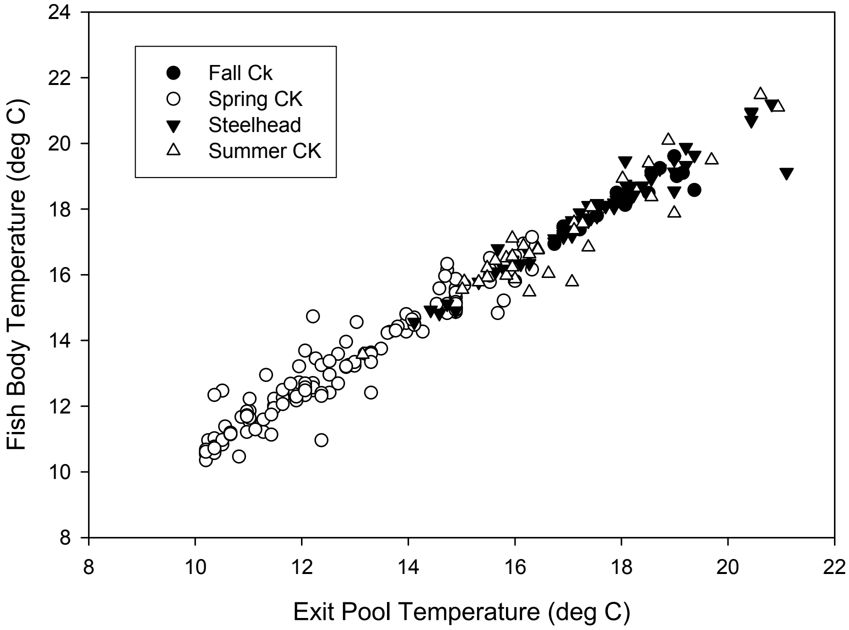


Figure 16. Relationship between body temperature at the time of fish exit and ladder exit temperature at the time of ladder exit (LT) at Lower Goose Dam in 2000 and 2002 for RDST tagged fish. Spring Chinook salmon: N = 128, *F* = 1377.85, $P < 0.0001$, $R^2 = 0.9156$, *slope* = 0.8623, *intercept* = 2.714; Summer Chinook salmon: N = 34, *F* = 231.46, $P < 0.0001$, $R^2 = 0.8714$, *slope* = 0.9328, *intercept* = 1.518; Fall Chinook salmon: N = 18, *F* = 154.45, $P < 0.0001$, $R^2 = 0.9008$, *slope* = 0.9498, *intercept* = 1.137; Steelhead: N = 59, *F* = 856.12, $P < 0.0001$, $R^2 = 0.9355$, *slope* = 0.9956, *intercept* = 0.9367

experienced by individual fish between dams revealed a positive association between body temperature changes at pairs of adjacent dams in steelhead (MN-IH, IH-LMo, etc.), but not between non-adjacent dam pairs (Appendix 2). No such associations were seen in other species with the exception of the IH-LGo comparison for summer Chinook salmon (uncorrected $P = 0.0454$). The lack of association among locations for Chinook salmon may have resulted from an interaction between seasonal changes in temperature and behavior whereby individuals slowed migration when experiencing a high ΔT until the conditions cooled, the high variability and sampling error associated with estimating body temperature precisely at specific migration points, and/ or small sample sizes.

The observed rise in body temperature in ladders did not appear to be caused by correlated river environmental conditions because during conditions causing large ladder ΔT, adults did not experience an increase in body temperature as they passed through the tailrace. There was no evidence of a relationship between ladder ΔT and adult body temperature change during tailrace passage for any dam or species combination (F1-A1; N = 10-82; *F* = 0.30-2.75; *P* = 0.1022-0.9541).

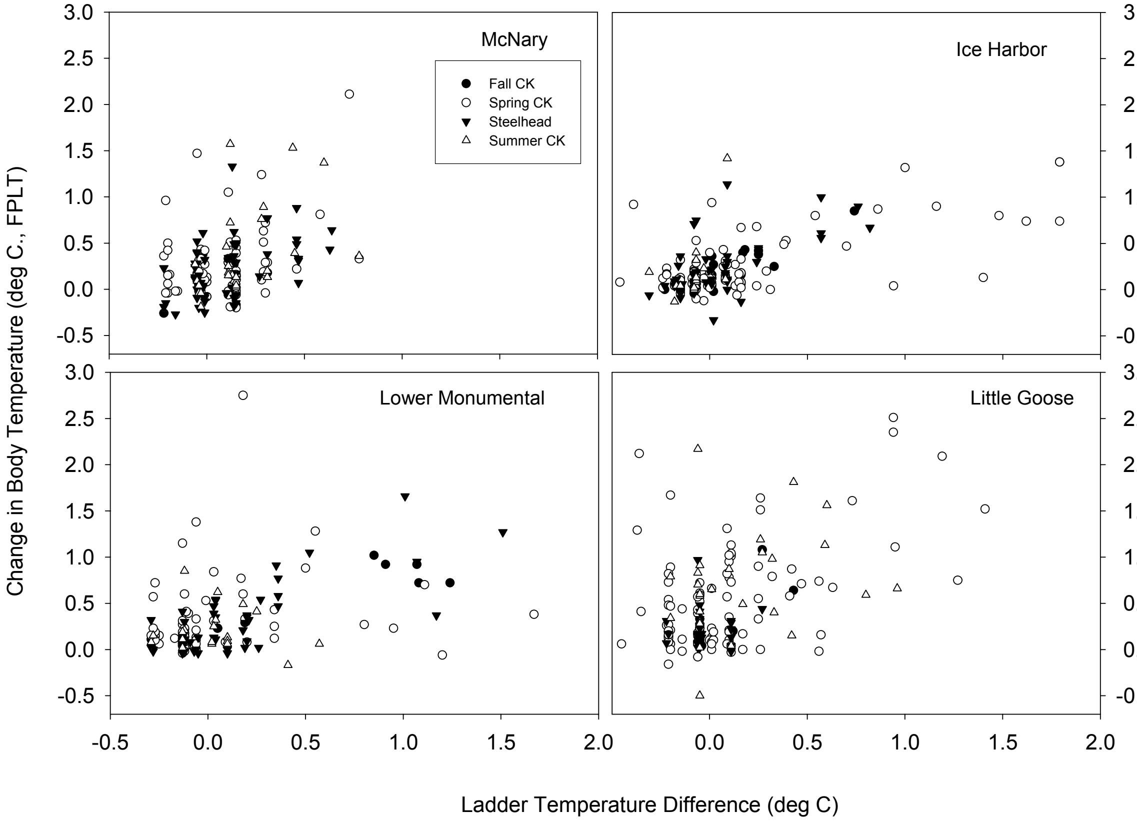


Figure 17: Comparison of the change in adult body temperature during ladder passage to the ladder temperature difference (ΔT) at the time of arrival at the ladder. Only same-day passage events shown. Results of univariate regressions are given in Appendix 1 for each species-dam combination.

Discussion

Overall, the results were similar to those reported by Peery et al. (2003) for run-years 1996 and 1997. Throughout the run season, ladder ΔT values frequently exceeded 1˚C during fish passage events, particularly at Lower Granite Dam during summer. Ladder temperature differences increased in frequency and magnitude during the warmest periods of the year and were largest at Lower Granite Dam. The proportion of the run experiencing ladder ΔT ≥ 1.0 ˚C during the four year study was lowest for spring Chinook salmon (8.37-15.5%) and highest for summer Chinook salmon (20.3-68.7%). Importantly, the estimated proportions experiencing ΔT ≥ 1.0 ˚C were probably underestimated for summer Chinook salmon and steelhead because of tagging restrictions during warm water temperatures, while the proportions for spring Chinook may represent overestimates. Estimates of passage times consistently suggested that ladder temperature gradients increased ladder passage time, and in many cases, total dam passage time. The proportion of fish overnighting—those fish passing one or more days after arriving in a tailrace—also consistently increased with ΔT. Detailed examination of passage routes revealed that more fish switched between ladders prior to passing during periods with ladder temperature gradients at McNary Dam. Finally, estimates of body temperature during passage demonstrated that adult salmonid body temperature had equilibrated to the surrounding ladder temperature by the time of exit and that increases in fish body temperature during ladder passage were positively related to ladder ΔT, suggesting adults experienced a departure from their acclimation temperature during ladder passage and the potential for physiological heat shock. Collectively, these results suggest that ladder temperature differences represent a migration obstacle which slows adult passage rate at McNary and the lower Snake River dams, especially at Lower Granite Dam. Below, we discuss the data in more detail and suggest potential management actions.

Substantial proportions of each run encountered ladder temperature gradients at lower Snake River dams during 2000-2003. Concerns over fish handling and health prevent tagging during the warmest periods of the year. Unfortunately, this constraint resulted in under-tagging during the warmer summer months for summer and fall Chinook salmon and steelhead in many years (Figures 2-5). Consequently, the values presented in Table 1 probably underestimate the true proportion experiencing ΔT ≥ 1˚C for summer and fall Chinook salmon and steelhead. Conversely, spring Chinook salmon were over-tagged in some years, and the values in Table 1 may slightly overestimate the true proportions. This bias in sampling may have affected the estimated proportion of fish overnighting and ladder switching in parallel ways, whereby estimates for spring Chinook salmon may be liberal and estimates for other runs, especially summer Chinook may be conservative. The bias in sampling was less likely to affect the estimates of differences in median passage time, except to perhaps increase type II error by reducing sample sizes in the higher ΔT categories. Overall, the undersampling during summer probably led to an underestimation of the true effects of ladder ΔT on the migrating adult populations and was unlikely to have created false differences or associations. Comparisons of the relative effects among dams within run were also unlikely to have been compromised, except again, perhaps by increasing type II error in the higher ΔT categories.

Water temperature affects swimming speed (Brett 1995) and dam passage times in salmonids (Caudill et al. *in review*). The general correlation between river temperature and ΔT suggested river temperature rather than ladder ΔT could explain the observed behaviors, i.e., that adults were responding to the overall temperature environment and not to ladder temperature gradients *per se*. Clearly, unequivocally separating these effects in an observational study is impossible; however, at least two lines of evidence suggest that mean river temperature was not solely responsible for the slowed migration rates observed at dams. First, ladder ΔT values frequently exceeded 1˚C at river temperatures thought to be optimal for adult swimming (15-18˚C, Brett 1995, Salinger and Anderson 2006). For example, spring Chinook salmon rarely passed at high river temperatures, yet exhibited patterns of overnighting and ladder switching that were similar to the other runs (Figure 15). Second, examination of tailrace passage times in relation to ΔT provided no evidence of spurious correlations. If high river temperatures were correlated with both large ΔT and slowed swimming/dam passage, we would expect to observe relatively slow tailrace and ladder passage during large ΔT conditions. In fact, the only significant associations between ΔT and tailrace passage time (spring Chinook at Little Goose and fall Chinook at McNary) suggested that during conditions causing higher ΔT, swim speeds increased and passage times decreased.

The combined effects of the Dworshak releases, solar heating, and wind setup events collectively explain why ladder ΔT were greatest in frequency and magnitude at Lower Granite Dam. During summer flow augmentation from Dworshak Reservoir, ~6˚ C water is released from Dworshak reservoir which warms to ~ 10-14˚C in the Clearwater River before reaching the confluence with the Snake River at Lewiston, ID-Clarkston, WA. There, the cool water meets 20-24˚C Snake River water. The warm, relatively light Snake River water flows over the Clearwater River input, and in fact, a cool water plume from the Clearwater may reach 1-3 km upstream into the Snake River portion of the reservoir as the warmer Snake River water flows over it (Cook et al. 2006). The thermal stratification created at the confluence persists throughout the Lower Granite Reservoir, with temperature differences of ≥ 5.0˚C common between surface and bottom waters through the late summer at mid-pool (Cook et al 2006). Solar heating of surface water and wind setup events probably contribute to the stratification in Lower Granite Reservoir. The stratified water column is homogenized in the Lower Granite Tailrace by strong vertical mixing at the dam, and solar heating and wind setup are solely responsible for the more moderate thermal layering observed in downstream reservoirs of the Snake River (Cook et al. 2006). Finer scale circulation patterns in dam forebays also appear to contribute to ladder ΔT, particularly at Ice Harbor Dam (Figure 10), and to a lesser extent at Lower Monumental Dam (Figure 9). It may be possible to alter summer dam operations (e.g., spill pattern) to change forebay circulation and improve input water conditions for ladders at these locations. Operation of the adult trap at Lower Granite Dam may also have affected adult passage behavior at this location. Operation of the Lower Granite adult trap probably does not explain the increase in ladder passage times at higher ΔT because the trap was not operated at the warmest ladder temperatures.

Ladder temperature differences of 1-2˚C had significant biological effects on adult passage behavior and were consistently associated with increased ladder passage times, the proportion of adults overnighting, and adult body temperature during passage. Total passage times consistently increased as well, though these differences were statistically significant only for steelhead at two locations (Little Goose and Ice Harbor Dams). The increases in overnighting suggest that adults entered ladders, but then fell out to the collection channels for some period more frequently during periods of high ladder ΔT. These observations were generally consistent with the increase in exiting behavior observed at John Day Dam in 1997 & 1998 as ladder temperatures increased (Keefer et al. 2003), and such exiting behavior probably contributed to the longer observed ladder and total dam passage times observed there. Keefer et al. (2003) did not find an association between the number of exits per fish per day and ΔT, perhaps because ladder ΔT was not estimated at fine enough a scale at John Day (the only temperature data available for the base of the John Day Dam in 1997-8 were from the tailrace water quality monitoring station) and/or because exits per fish per day responds to increases in ladder temperature and ΔT in complex ways. Regardless, both studies suggest that adults perceive a cost to ascending ladders in the presence of high ladder ΔT and/or high ladder temperatures because they appear to slow migration and search for other routes. Ladder temperature differences ≥ 2˚C had stronger associations with behavior and body temperature, suggesting such perceived costs increase as gradients increase.

How ladder ΔT affected adult physiology, survival, and reproductive success remains unknown, but many passage events occurred at temperatures thought to be physiologically stressful to salmonids (reviewed in Brett 1995, McCullough et al. 2001, Richter and Kolmes 2005). The increased time spent passing dams may have had adverse effects including increased potential for expression of heat shock protein (Lund et al. 2003), disease, impaired ovulation, increased levels of stress hormone (e.g., Young et al. 2006), and decreased migration success (e.g., Naughton et al. 2005). In particular, it remains unknown whether the short-term increases in body temperature or exposures to high temperature at multiple projects affected adult fitness upstream. A first step in assessing the physiological effects of hydrosystem passage during high ambient conditions and ladder passage during large ΔT conditions may be to test for elevated heat shock proteins in adults under different temperature exposure levels (Lund et al. 2003).

The cool water releases from Dworshak reservoir are intended to improve flow and thermal conditions for migrating juvenile and adult salmonids. Indeed, available evidence suggests that the releases reduce summer temperatures throughout the lower river, at least below the surface waters (Cook et al. 2006). Additionally, adult salmonids appear to select cooler temperature water than mean available water during warm summer conditions (Clabough et al in review a, b). How the local negative effects of releases on ladder ΔT at Lower Granite Dam balance against the potential benefits to migrating adults remains unknown, but the period of exposure to high ΔT in ladders compared to total Snake River migration time suggests the benefit of Dworshak releases is positive (excluding other possible negative effects on adults such as high fishing mortality at the confluence caused by Snake and Salmon River fish holding in the Clearwater plume).

Importantly, the local effects of ladder temperature differences may be alleviated by directing cooler water into the ladder exit pools (Peery et al. 2003). However, modification of water sources and temperature in the forebay just upstream of ladder exits will probably be necessary to ensure that a sharp thermal gradient does not form at the ladder exit and cause adults to ‘pile up’ at the ladder exit. One potential strategy would be provide a corridor of cool water from the ladder exit through the immediate forebay using suspended diffusers or a mechanism creating upwelling that would allow adults to exit and sound to deeper, cooler forebay water.

Climate projections for the interior Pacific Northwest suggest higher summer temperatures, less winter snowpack, and consequently, longer, warmer summers with lower stream flows (e.g., Mote et al. 2005, Stewart et al. 2005). These projections suggest that management of the hydrosystem thermal regime will become increasingly important to the recovery of Snake River summer and fall Chinook salmon and steelhead, particularly late spring-early summer runs (e.g., summer Chinook) and early fall run groups that currently experience the highest temperatures (e.g. Snake River A-run steelhead). If current climate predictions hold, modifications to fishways to ameliorate ladder temperature differences could be an important component to the management of the Snake River Hydrosystem thermal regime.

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Appendix 1: Results of univariate regressions of the change in adult body temperature between the first transition pool detection to the last exit record (FP-LT) versus ladder delta T at FP for each dam, ladder, and species. NN denotes use of north shore ladder, SS denotes use of south shore ladder.

Dam	Species	Route	N	Intercept	S.E.	*P*	Δ T ˚C	S.E.	*P*	R^2
MN	Spring CK	NN	27	0.0946	0.063	0.1458	1.8963	0.2556	<0.0001	0.6381
MN	Spring CK	SS	58	0.2227	0.0399	<0.0001	0.02768	0.2045	0.8928	0.0003
MN	Summer CK	NN	15	0.1895	0.1177	0.1314	2.414	0.5105	0.0004	0.6324
MN	Summer CK	SS	11	0.0947	0.0677	0.1967	0.361	0.2109	0.1212	0.2455
MN	Fall CK	NN	1	-	-	-	-	-	-	-
MN	Fall CK	SS	5	-0.0015	0.1349	0.9916	0.4506	0.7028	0.5671	0.1205
MN	Steelhead	NN	8	0.316	0.1885	0.1447	0.8263	1.5298	0.6086	0.4636
MN	Steelhead	SS	52	0.1037	0.03718	0.0075	0.7166	0.1534	<0.0001	0.3039
IH	Spring CK	NN	15	0.0658	0.0243	0.0177	0.2269	0.1801	0.2299	0.1088
IH	Spring CK	SS	81	0.2002	0.0287	<0.0001	0.4381	0.0541	<0.0001	0.4539
IH	Summer CK	NN	3	-	-	-	-	-	-	-
IH	Summer CK	SS	16	0.3251	0.1061	0.0084	1.824	0.9503	0.0756	0.2083
IH	Fall CK	NN	0	-	-	-	-	-	-	-
IH	Fall CK	SS	18	0.1378	0.0272	0.0001	0.9391	0.1199	<0.0001	0.7932
IH	Steelhead	NN	6	0.2188	0.5781	0.0193	0.7881	0.4606	0.1622	0.4226
IH	Steelhead	SS	60	0.1676	0.0281	<0.0001	0.8085	0.1259	<0.0001	0.4152

Appendix 1 (cont.):

Dam	Species	Route	N	Intercept	S.E.	*P*	∆ T ˚C	S.E.	*P*	R^2
LMo	Spring CK	NN	59	0.349	0.06	<0.0001	0.2063	0.1113	0.0691	0.0568
LMo	Spring CK	SS	5	0.2555	0.0674	0.0322	0.5363	0.2964	0.1681	0.5218
LMo	Summer CK	NN	16	0.2095	0.0602	0.0037	-0.1763	0.2593	0.5077	0.03196
LMo	Summer CK	SS	3	-	-	-	-	-	-	-
LMo	Fall CK	NN	12	0.2284	0.0498	0.001	0.5881	0.0729	<0.0001	0.8666
LMo	Fall CK	SS	2	-	-	-	-	-	-	-
LMo	Steelhead	NN	49	0.2196	0.0349	<0.0001	0.7403	0.0885	<0.0001	0.5979
LMo	Steelhead	SS	3	-	-	-	-	-	-	-
LGo	Spring CK	N/A	109	0.4317	0.0465	<0.0001	0.8363	0.1374	<0.0001	0.2572
LGo	Summer CK	N/A	27	0.6299	0.1216	<0.0001	0.4533	0.3564	0.2151	0.0608
LGo	Fall CK	N/A	11	0.1518	0.0578	0.0275	1.7213	0.355	0.0009	0.7231
LGo	Steelhead	N/A	44	0.1816	0.0278	<0.0001	0.1978	0.3002	0.5135	0.0102

Appendix 2: Pairwise correlations between the change in the FPLT body temperature observed by each dam. Note, these analyses include all fish, including those that overnighted. For each comparison, the top value is the Pearson product moment correlation, the middle value is the uncorrected *P*-value, and the bottom value is the correlation sample size.

Spring Chinook

		McNary	Ice Harbor	L. Monumental	L. Goose
McNary	*r*	1	0.05885	0.15686	-0.08977
	P		0.5904	0.162	0.3672
	N		86	81	103
Ice Harbor			1	-0.11087	0.1121
				0.3066	0.2503
				87	107
L. Monumental				1	0.11584
					0.2416
					104
L. Goose					1

Summer Chinook

	McNary	Ice Harbor	L. Monumental	L. Goose
McNary	1	0.07618	-0.1577	0.2742
		0.7639	0.5597	0.242
		18	16	20
Ice Harbor		1	-0.13897	0.37438
			0.5374	0.0454
			22	29
L. Monumental			1	0.22124
				0.2879
				25
L. Goose				1

Fall Chinook Salmon

	McNary	Ice Harbor	L. Monumental	L. Goose
McNary	1	0.12583 0.5868 21	0.26219 0.2509 21	-0.01816 0.9448 17
Ice Harbor		1	0.17218 0.4211 24	0.59304 0.0046 21
L. Monumental			1	0.14728 0.5598 18
L. Goose				1

Steelhead

	McNary	Ice Harbor	L. Monumental	L. Goose
McNary	1	0.42934 0.0004 64	0.15741 0.2603 53	-0.05416 0.7117 49
Ice Harbor		1	0.47046 <.0001 69	0.09125 0.4733 64
L. Monumental			1	0.41275 0.0013 58
L. Goose				1