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To: David Clugston, USACE Portland District

From: Matthew Keefer, Chris Caudill (University of Idaho) and Chris Peery (USFWS)

RE: Temperature regimes during upstream migration and the use of thermal refugia by adult salmon and steelhead in the Columbia River basin.

Date: 15 December 2011 (Note: this is an updated version of the report provided on 6 May 2010)

Introduction

Summertime water temperatures in the lower Columbia River have steadily increased over the last several decades (Figure 1). Annual peak temperatures have exceeded 21 °C in most recent years and have been as high as 24 °C. The warmest period typically occurs in late July to early September, coincident with late-migrating summer Chinook and sockeye salmon and with substantial portions of the fall Chinook salmon and summer steelhead runs (Figure 2). Water temperatures in the 19-22 °C range, like those that routinely occur in the Columbia River main stem, are a significant management concern for adult migrants because large proportions of adults currently can experience thermal conditions thought to be stressful. Such temperatures have been associated with behavioral changes and a variety of sub-lethal effects on physiology, disease susceptibility, reproductive development, gamete quality (i.e., over-ripening), survival, and fitness (e.g., Flett et al. 1996; Lee et al. 2003; Naughton et al. 2005; Richter and Kolmes 2005; Wagner et al. 2005; King et al. 2007; Mann 2007; Reid 2007; Farrell et al. 2008; Keefer et al. 2008a, 2010; Eliason et al. 2011). Based on these and other studies, we assume that temperatures above ~18-19 °C induce stress in adult migrants and that higher temperatures are associated with stronger negative costs. This issue may become more acute if warmer regional temperatures predicted by climate models come to pass.

Many adult salmon and steelhead temporarily use thermal refugia when Columbia and Snake River water temperatures are high (Goniea et al. 2006; Keefer et al. 2009). These sites appear to be critically important mid-migration holding habitats for some populations. A series of cool-water refugia are located along the migration corridor at tributary confluences with the main stem rivers. Many of the most-used refugia sites are located between Bonneville and John Day dams in the lower Columbia River, where cool-water tributaries draining the Cascade Range enter reservoirs. These sites are often 2-7 °C cooler than the main stem (High et al. 2006; Goneia et al. 2006). Additional sites that may be thermal refugia for adult migrants include

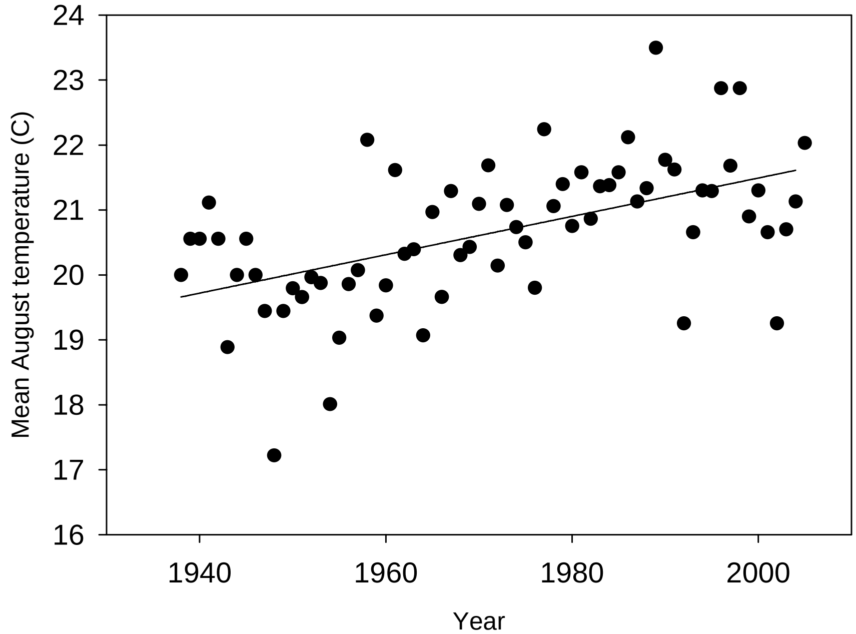

Figure 1. Mean August water temperature (°C) at Bonneville Dam, 1938-2005. Source: Columbia River DART.

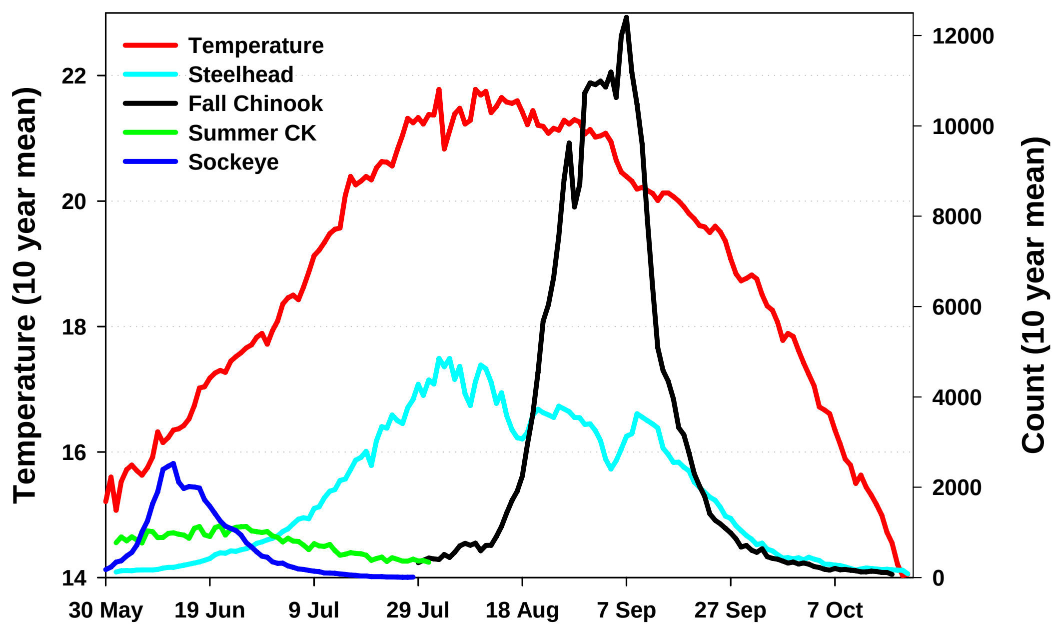

Figure 2. Ten-year (1996-2005) mean lower Columbia River water temperature (°C) and mean run size and timing of adult summer Chinook salmon, fall Chinook salmon, sockeye salmon, and summer steelhead at Bonneville Dam. Thermal refugia use by many adult populations has been associated with water temperatures greater than 19-20 °C.

tributary confluence areas downstream from Bonneville Dam, upstream from the Columbia River-Snake River confluence in the mid-Columbia River, and in the Snake River upstream from Lower Granite reservoir. The lower Snake River contains little in the way of cool water refugia but there is evidence that fish will use the limited cool water sources when available. In addition, managers have seasonally reduced Snake River reservoir water temperatures by releasing cool water from Dworshak reservoir on the Clearwater River, and adult migrants do use the cooler water (Clabough et al. 2007a, 2007b). Salmonid use of specific refugia sites other than in the Bonneville-John Day reach has not been well documented, but there is anecdotal evidence that adult aggregations occur seasonally at several locations. Groundwater-based refugia in the main stem have not been identified, but may be present in reaches not dominated by bedrock. Potential locations include areas downstream of dams such as tailraces where there is a potential for groundwater input (above the dam) and expression (below the dam). The ecological significance of such areas would depend on the discharge rate and temperature of groundwater. The latter would be strongly influenced by groundwater residence time.

Much of what is known about adult salmon and steelhead use of thermal refugia in the Columbia basin has been gleaned from the large-scale radiotelemetry studies funded by the USACE and conducted by the UI and NMFS. While these studies focused on monitoring adult salmonid behavior at dams, most major tributaries were also monitored to help estimate Hydrosystem escapement and identify individual populations. The antenna arrays at tributary confluence areas and adjacent reservoir sites allowed us to collect behavioral data at several of the critical refugia sites. The following summary describes some of the basic results of this research.

Thermal refugia summary

Spatial distribution – The thermal refugia sites that have been most studied are located at tributary confluences in the Bonneville and The Dalles reservoirs (Figure 3). These include Herman and Eagle Creeks and the Wind, Little White Salmon, White Salmon, Hood, Klickitat, and Deschutes rivers. The most-used among these have been Herman Creek and the Little White Salmon, White Salmon, and Deschutes Rivers. Upstream from John Day Dam, tributaries draining primarily high-desert landscapes like the John Day, Umatilla, and Yakima rivers may provide periodic cool water refugia, but lower reaches of these rivers are often as warm as or warmer than the Columbia River during summer. A large temperature gradient often exists at the confluence of the Snake and Columbia rivers, with the Snake typically being warmer in summer and fall. Some Snake River adults temporarily hold in the cooler mid-Columbia water during warm periods (e.g., Stuehrenberg et al. 1978; Quinn et al. 1997). For example, some fall Chinook salmon and steelhead tagged at Ice Harbor Dam with thermal recorders delayed reascending the Snake River for 2 to 3 weeks and had noticeably cooler thermal profiles than adults that did not delay their migrations through the lower Snake River (Mann and Peery 2005).

Likely thermal refugia downstream from Bonneville Dam include the confluence areas of the Cowlitz, Lewis, Washougal, and Sandy rivers as well as several smaller tributaries fed by Cascade Range snowmelt or glaciers. Adult use of these sites for thermal refuge is largely anecdotal. Similarly, we are unaware of any quantitative summaries of refugia use in the mid-Columbia River upstream from Priest Rapids Dam, though confluence areas of the Wenatchee, Methow, and Entiat rivers may be seasonally important when main stem Columbia River temperatures reach stressful levels. In the impounded lower Snake River, there are known thermal refugia frequented by fall Chinook salmon and steelhead migrants (Mann 2007) at the outfall from Lyons Ferry hatchery and periodically at the Tucannon River confluence. In Lower Granite reservoir, Chinook salmon and steelhead will select to migrate in cooler water layers that result from releases from Dworshak reservoir when available (Clabough et al. 2007a, 2007b). At the head of Lower Granite reservoir, the confluence of the Clearwater and Snake rivers is an important refugium site for adults *en route* to the Hells Canyon reach of the Snake and to the Salmon, Grande Ronde, and Imnaha rivers. Thermal refugia have also been identified in several Snake River tributaries (e.g., Ebersole et al. 2003; Howell et al. 2010), but these studies have focused on resident salmonids and juvenile anadromous fish. We have observed adult salmon using thermal refugia near spawning grounds in some Salmon River tributaries (e.g., the South Fork Salmon River), but these behaviors have not been quantified. We are also currently examining the relationship between water temperature, adult behavior in relation to water temperature, and prespawn mortality during the migration and prespawn periods for Chinook salmon in the Willamette River basin (Mann et al. 2010; Keefer et al. 2010).

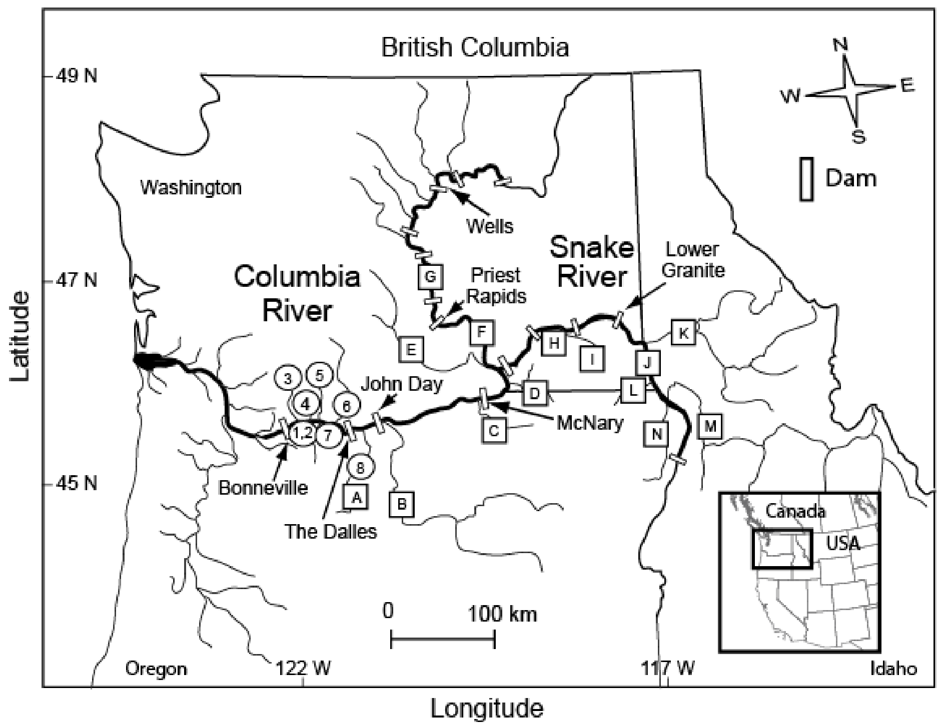

Figure 3. Map of the Columbia and Snake River basins, where radio-tagged adult salmon and steelhead were monitored at dams, in reservoirs, and while using cool water tributaries during migration through the lower Columbia River. Thermoregulatory behaviors were monitored at eight sites: (1) Herman Cr., (2) Eagle Cr., (3) Wind R., (4) Little White Salmon R., (5) White Salmon R., (6) Klickitat R., (7) Hood R., and (8) Deschutes R. Sites A-N were tributary populations used in the steelhead study described in Keefer et al. (2009).

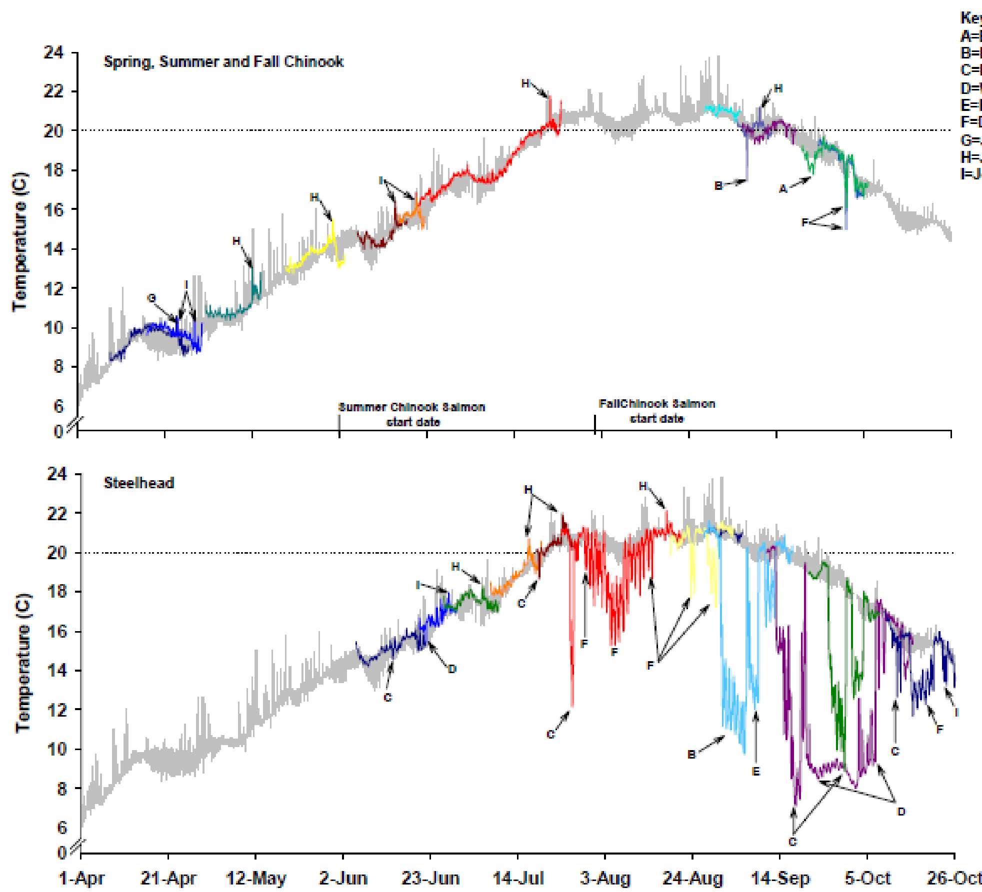

Figure 4. Examples of migration temperatures adult Chinook salmon (top) and steelhead (bottom) experienced during their migration from Bonneville Dam to McNary Dam, 2002. Gray bars represent the range (min to max) of daily mean water temperatures recorded at the four lower Columbia River dams. Colored lines represent fish body temperatures as recorded by internal temperature tags. Body temperatures below the gray bars indicate thermal refugia use: specific migration locations are noted in the key at the upper right. Figure from Caudill et al. *in prep*. Also see Clabough et al. (2008).

Refugia use by summer steelhead – The incidence and duration of thermal refugia use differs widely among species as a function of migration timing and basic life history. In our research, summer steelhead had both the greatest incidence (~70%) and longest duration (up to several weeks or more) of refugia use among species studied in the lower Columbia River (Figure 4).

Initiation of thermal refugia use by steelhead in the lower migration corridor has been associated with main stem water temperatures of about 19 °C (Figure 5). For example, only about 10% of steelhead that entered the Bonneville reservoir when temperatures were <19 °C were detected on antennas at refugia sites, and these fish only briefly used the sites. In contrast, almost half the steelhead that entered the reservoir when temperature were 19-21 °C used refugia tributaries, and >70% used tributaries when temperatures were > 21 °C (Keefer et al. 2009). Duration of use rapidly increased as temperature increased, and extended to weeks during the warmest times (Figure 5). The summary of refugia use by upper Columbia River steelhead shown in Figure 6 is typical of the observed behavior in the Bonneville-John Day reach: fish that entered the

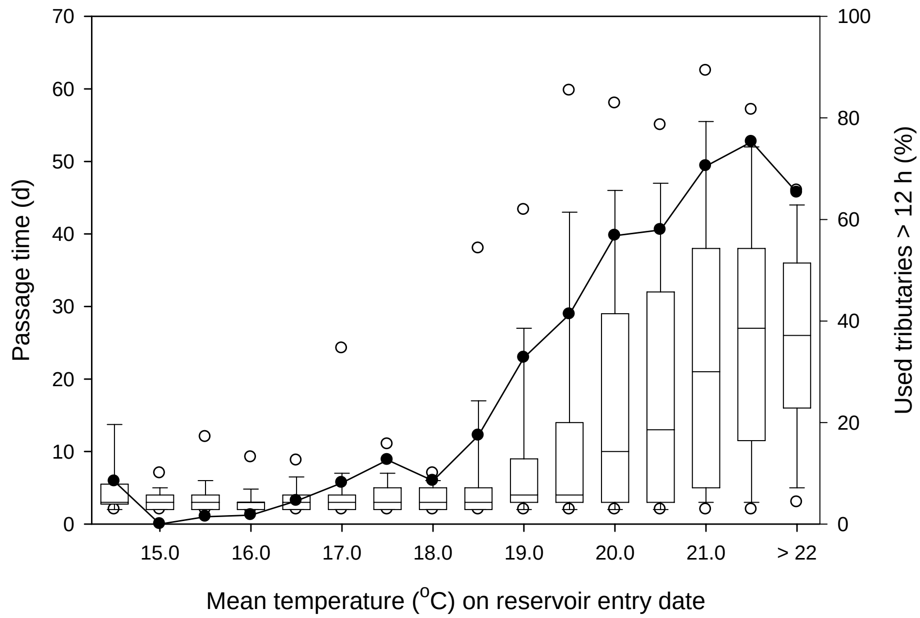

Figure 5. Steelhead passage times (d) from the top of Bonneville Dam to the top of The Dalles Dam, by water temperature at the Bonneville WQM site on the date each fish entered the Bonneville reservoir. Box plots show median, quartile, 10th, and 90th percentiles, pooled across study years; 5th, and 95th percentiles are marked by open circles. Solid line with solid circles shows the percent of steelhead recorded in cool water Bonneville reservoir tributaries for > 12 h. Figure from Keefer et al. (2009).

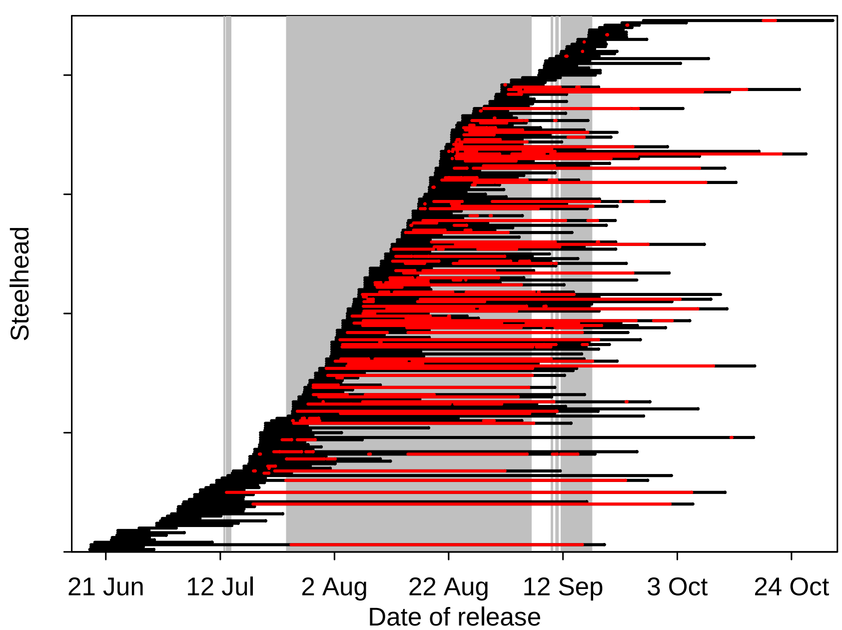

Figure 6. Cool-water refugia use recorded in the lower Columbia River (Bonneville Dam-John Day Dam) for 235 summer steelhead that eventually migrated to the upper Columbia River in 2001. Gray shading represents days when the mean Columbia River water temperature was ≥20 C. Black lines represent time when steelhead were in the main stem and red lines represent time in refugia tributaries.

reservoirs during warm periods quickly moved into cool-water tributaries and many remained until the onset of fall cooling. Notably, individual steelhead often exited refugia tributaries into the main stem, but then quickly re-entered either the same refugia or another cool-water site if the main stem was warm. There did not appear to be differences in which tributaries were used that were associated with main stem temperatures or refugia-main stem temperature differentials, though these hypotheses were not explicitly tested.

In the Bonneville reservoir reach, radio-tagged steelhead were most likely to use the Little White Salmon (i.e., Drano Lake), White Salmon, and Wind rivers along with Herman Creek (Figure 7). Eagle Creek was also frequented by steelhead, though monitoring at that site was limited. Use of the Klickitat and Hood rivers was less than at the other tributaries, perhaps because of the extensive shallow flats near the mouths of these rivers (High et al. 2006). Above The Dalles Dam, about 25% of steelhead that passed John Day Dam were recorded in the Deschutes River. Fewer steelhead used the Deschutes (relative to the combined Bonneville sites) primarily because steelhead entered The Dalles reservoir about three weeks later, on average, than they entered the Bonneville reservoir and therefore encountered cooler main stem temperatures.

In all of the monitored lower Columbia River tributary refugia sites, rates of use and temporary residence times varied among steelhead populations (Figure 8). Population-specific refugia use was predictably associated with migration timing (Figure 9), with early- and late-timed populations less likely to use the cool-water sites. Groups with lower use included Hanford Reach, Tucannon, Clearwater and some Salmon River populations. The highest use rates and

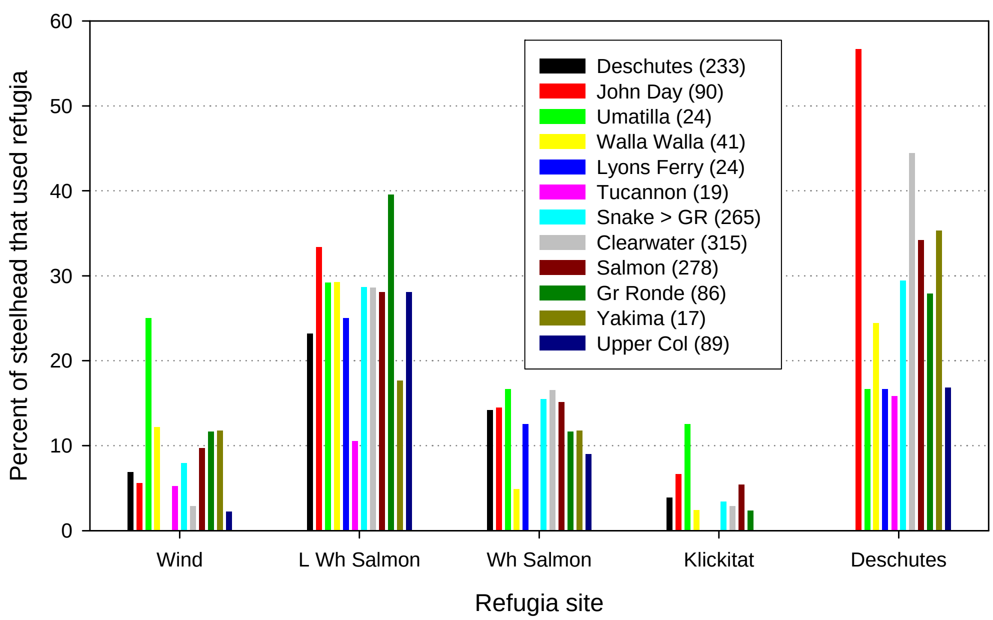

Figure 7. Population-specific use of selected cool-water refugia tributaries in the Bonneville-John Day reach by radio-tagged summer steelhead in 1996-1997 and 2000. Bar colors represent upriver populations, with sample sizes in parentheses. Steelhead additionally used Herman and Eagle creeks, but these small sites were inconsistently monitored in these study years. A small number of steelhead temporarily used the Hood River (not shown).

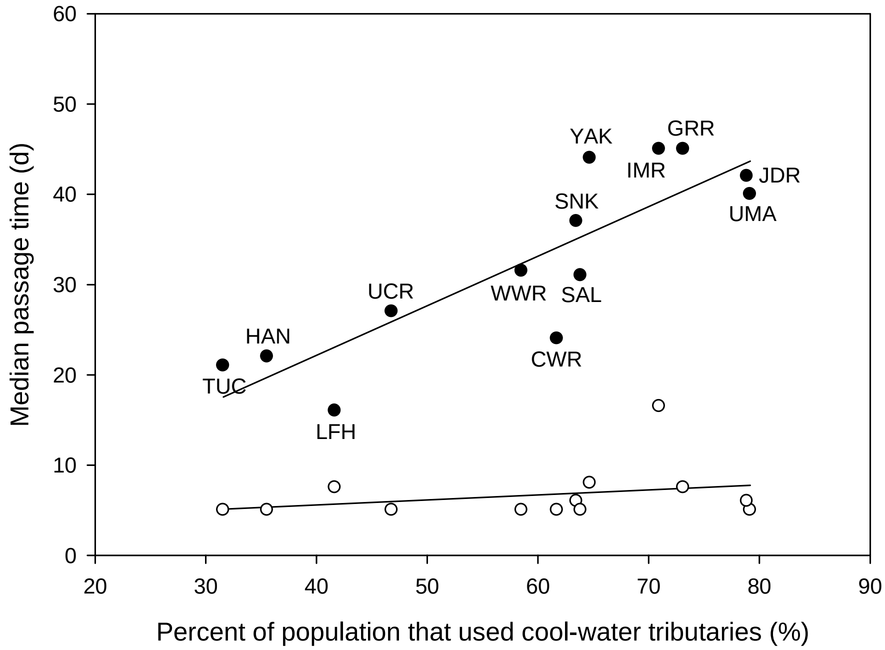

Figure 8. Relationships between median population-specific steelhead passage times from the top of Bonneville Dam to the top of John Day Dam and the percentages of steelhead that were (●) or were not (○) recorded in cool-water tributaries for > 12 h. Labels represent specific upriver populations. From Keefer et al. (2009).

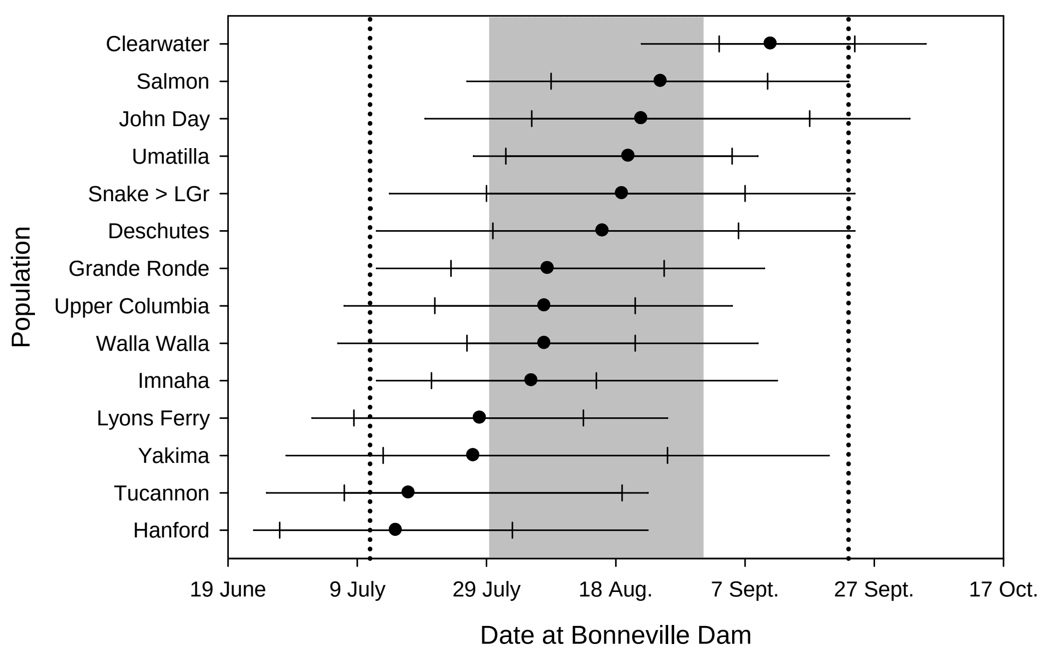

Figure 9. Migration timing distributions (median, quartiles, and 10^{th} and 90^{th} percentiles) at Bonneville Dam for steelhead that successfully returned to tributaries or hatcheries across study years. Vertical dotted lines show mean first and last dates that Columbia River water temperature was 19 °C; the shaded area shows dates with mean temperature ≥21 °C. From Keefer et al. (2009).

residence times were for populations that migrated during the warmest period, including Grande Ronde, Imnaha, Umatilla, Yakima, and John Day River populations (Figure 8).

Extended refugia residence times for summer steelhead resulted, at least in part, from the relatively flexible migration timetable for steelhead. Many of the summer-run fish enter the Columbia River study area at the warmest time but have 6-10 months to reach springtime spawning areas. In our research, steelhead populations with relatively early (i.e., May) and relatively late (i.e., late September to October) migration past Bonneville Dam tended to encounter lower main stem temperatures and used lower Columbia River refugia at substantially lower rates than populations that migrated in mid-summer. It is certainly plausible – even probable – that the early-timed groups used other, unmonitored cool water sites further upstream, including sites in secondary tributaries. We have anecdotal evidence for this behavior, but temperature monitoring outside the Hydrosystem was not an objective of the original research.

Refugia use by Chinook salmon – In contrast with summer steelhead, about 20% of fall Chinook salmon and 15% of late summer Chinook salmon were recorded in one or more lower Columbia refugia sites in the radiotelemetry studies (e.g., Goneia et al. 2006). Summer and fall Chinook salmon have typically used refugia sites on a scale of days rather than weeks and mostly when main stem temperatures were highest (Figure 4). Even shorter temporary residence times in refugia sites were recorded for spring and early summer Chinook salmon (i.e., minutes to hours), suggesting to us that many of these populations enter lower river tributaries while searching for olfactory or other orientation cues (i.e., ‘proving’), or as a result of conspecific behavior rather than as a result of thermoregulatory activity. Keefer et al. (2008b) includes a summary of temporary, non-natal tributary use by spring–summer Chinook salmon.
Initiation of thermal refugia use in the lower Columbia River by upriver fall Chinook salmon was associated with main stem water temperatures between 20 and 21 °C and rapidly increased as temperatures rose above 21°C (Figure 10). In our studies, 9% of radio-tagged fall Chinook salmon used migration corridor refugia for ≥12 h and the mean residence time for this group was 5.1 d (median = 2.9 d; Goniea et al. 2006). A fairly distinct temperature threshold was evident in both the initiation of refugia use (Figure 10) and the reduction in salmon passage rates through the Bonneville-John Day migration reach (Figure 11).

The Little White Salmon and White Salmon rivers were the most-used refugia sites for upriver fall Chinook salmon (i.e., those that passed John Day Dam), followed by the Deschutes and Klickitat rivers. Detections at antennas near the mouths of the Wind and Deschutes rivers also indicated that many salmon used the cool-water plumes from these rivers without moving out of the main stem and passing the in-stream antennas.

The upriver bright fall Chinook salmon run is numerically dominated by Hanford Reach fish, with additional populations in the Snake, Yakima, Deschutes, and upper Columbia rivers (Jepson et al. 2010). As with summer steelhead, among-population differences in run timing among the upriver bright Chinook salmon results in differences in temperature exposure and refugia use patterns among populations. On average, stocks that return to spawning areas upstream from Priest Rapids Dam and Deschutes river stocks are relatively abundant in August (Figure 12).

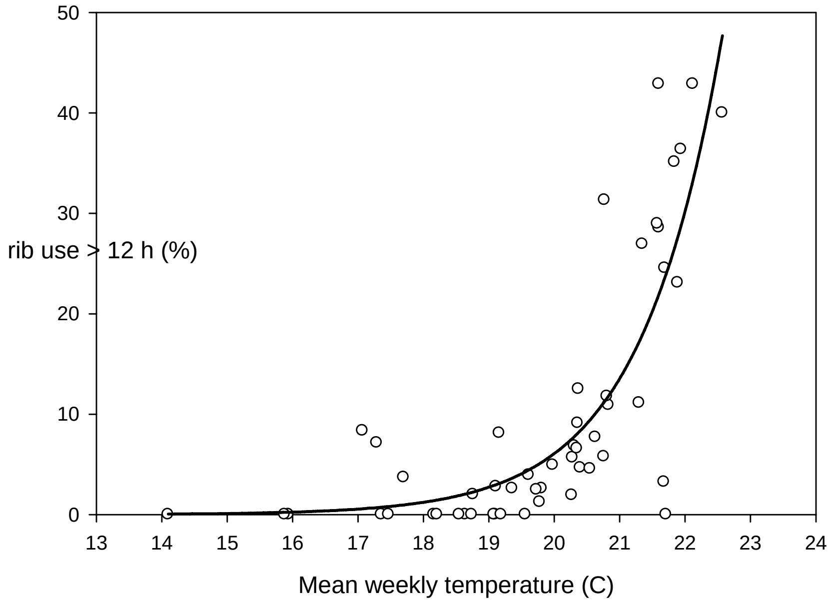

Figure 10. Relationship between the percent of fall Chinook salmon that used (> 12 h) cool-water tributaries and mean weekly water temperatures at Bonneville Dam. Symbols (○) represent 52 weekly bins (*mean* = 41 fish/bin; *range* = 4-122 fish/bin). Curve (▬) is the exponential regression line that best fits the data ($r^2 = 0.80$; $P < 0.0001$; percent = $6.558^{-7} e^{0.802*\text{temperature}}$. Asterix indicates data point with < 10 fish. Figure from Goniea et al. (2006).

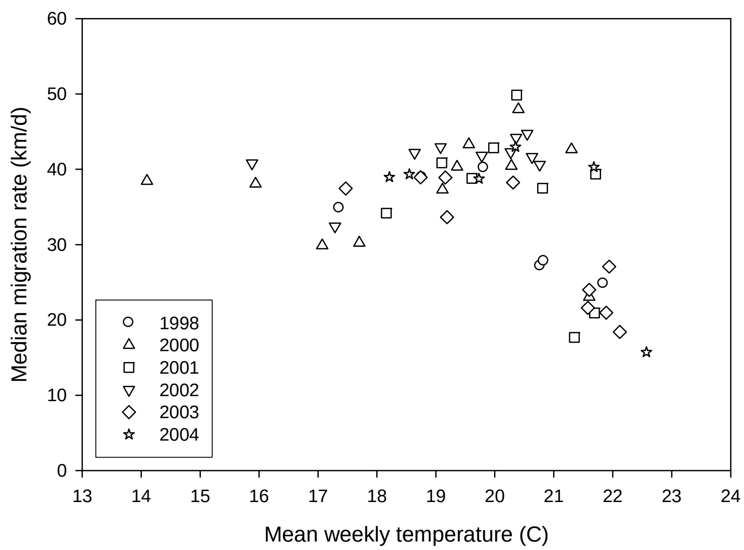

Figure 11. Relationship between median fall Chinook salmon migration rates (Bonneville to John Day Dam and mean weekly water temperatures at Bonneville Dam. Symbols represent week bins (*mean* = 41 salmon/bin; range = 4-122 salmon/bin). From Goneia et al. (2006).

Snake and Yakima River populations pass through the lower river corridor at low levels through much of August and September, while the Hanford Reach group increases in relative abundance as the fall season progresses. Refugia use by the radio-tagged fall Chinook salmon reflected these among-population differences in abundance and migration timing. A total of 161 salmon used refugia sites in the lower river for ≥12 h and could be confidently assigned to an upriver population. Of these, 80 (50%) were Hanford Reach fish, 30 (19%) were upper Columbia River fish, 18 (11%) returned to Priest Rapids Hatchery, 16 (10%) entered the Snake River, and 11 (7%) entered the Yakima River. Small numbers were last recorded in the Deschutes, Umatilla, and White Salmon rivers and at the Little White Salmon Hatchery, all after passing John Day Dam (i.e., some fell back downstream). Overall, the upriver fall Chinook salmon that used refugia sites were in approximate proportion to the overall escapement for these populations. We also note that Chinook salmon from headwater-spawning spring and summer runs have been recorded using thermal refugia in secondary tributaries to the Columbia and Snake rivers (e.g., Berman and Quinn 1991; Pinson 2005; Mann et al. 2008).

The comparatively limited thermal refugia use by Chinook salmon (versus summer steelhead) is presumably because salmon must reach spawning areas by late summer or fall. It is also likely that Chinook salmon populations that have historically migrated through the lower Columbia River corridor during the summer and fall have adapted to higher temperatures. Population-specific thermal tolerances have been explicitly quantified in Fraser River salmon populations (e.g., Lee et al. 2003; Eliason et al. 2011) and are probable in the Columbia River basin as well.

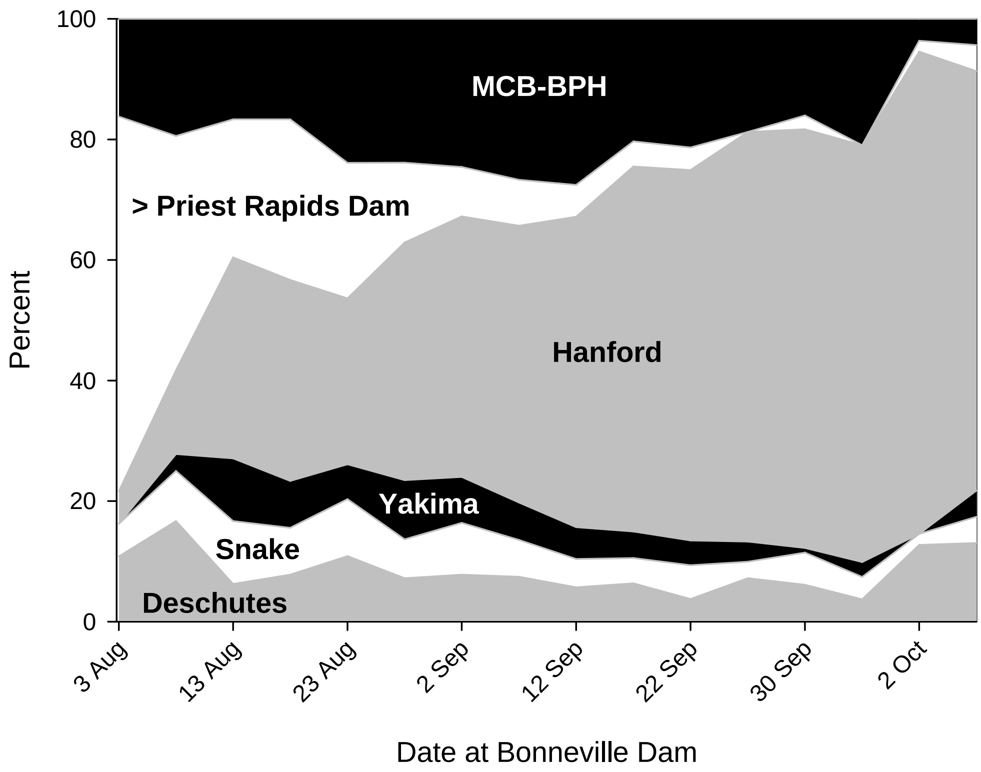

Figure 12. Mean composition of upriver bright fall-run Chinook salmon at Bonneville Dam using 5-day intervals based on release dates of radio-tagged fish, 1998 and 2000-2004. MCB-BPH = mid-Columbia River bright–Bonneville Pool hatchery stock. From Jepson et al. (2010).

Refugia use by sockeye salmon – Sockeye salmon, which mostly pass through the lower Columbia River prior to the warmest temperatures, have had the most limited refugia use in our research, though we emphasize that sockeye salmon have been the least-studied species. About 8% of sockeye salmon that passed through the lower river corridor were recorded in cool water tributaries in our single basin-wide study year (1997). We also recorded limited use of thermal refugia in a small-scale evaluation of Snake River sockeye salmon collected and radio-tagged at Lower Granite Dam in 2000. A few sockeye in that study entered the Clearwater River refugium when the main stem Snake River was > 20.5 °C (Keefer et al. 2008a).

In other river systems, sockeye salmon have shown thermoregulatory behavior in lakes (Newell and Quinn 2005; Roscoe et al. 2009), and Columbia River populations do occasionally stop migration when they encounter high Columbia River temperatures (Major and Mighell 1967; Hyatt et al. 2003). These examples suggest that sockeye salmon may use thermal refugia along the migration corridor to a greater degree than we have identified in our studies. Notably, we have found evidence for temperature-dependent mortality in sockeye salmon related to late run timing and high temperature exposure (Naughton et al. 2005). This temperature-survival relationship has been confirmed for Columbia River sockeye salmon in more recent studies (e.g., Crozier et al. 2011), and warrants further investigation.

General effects of refugia use – Adult salmonid use of thermal refugia potentially has both positive and negative effects on upstream migrants. These effects have rarely been quantified in field studies because fish fate, reproductive success, survival of progeny, and other fitness measures are difficult to measure and to link to thermoregulatory behavior or thermal experience. Presumed benefits of refugia use include reduced metabolic costs, reduced physiological stress, reduced negative temperature effects on maturation and gamete quality, and increased survival. An obvious direct negative effect is increased harvest risk because fish are spatially and temporally concentrated in refugia, attracting intensive fisheries. We found that Snake River and upper Columbia River steelhead that used refugia in the lower Columbia River were significantly less likely to survive to spawning tributaries, primarily because harvest rates in and near the refugia sites were high (Keefer et al. 2009). We have been unable to assess this harvest effect in Chinook salmon because the proportions using refugia were lower and relatively few fish were of known origin (i.e., with juvenile PIT tags that identified natal sites). The latter distinction is necessary to differentiate harvest of returning local fish from harvest of upstream migrants taken while holding in refugia.

Potential indirect negative effects of refugia use include migration delay, exposure to pathogens, permanent straying (i.e., loss from the source population), predation risk, and delayed effects from fisheries contact (i.e., catch and release, gill net fallout, etc.). Refugia sites are typically shallow, and intensive human use of the sites presumably can elevate fish stress levels. With the exception of estimating migration delay, these effects have not been measured.

Typical migration delays for fall Chinook salmon using refugia sites have ranged from hours to about 5 d, though some salmon used refugia for several weeks (Goniea et al. 2006). For most Chinook salmon, upstream passage delays on the order of several days likely have limited negative biological consequences, though this has not been explicitly tested with Columbia River populations. The delays potentially affect arrival timing at spawning grounds and consequently may have fitness effects, but it is certainly possible that the physiological benefits of refugia use outweigh potential negative effects of migration delay.

It is less clear what constitutes a migration ‘delay’ for summer steelhead given the considerable flexibility in migration timing and rate exhibited by fish in this run. The mean refugia residence times for steelhead in the radiotelemetry studies have ranged from 5-15 d (High et al. 2006; Keefer et al. 2009), but times have varied widely among populations and many fish use refugia sites for 3-4 weeks (see Figures 5 and 6). As with Chinook salmon, it is not clear whether steelhead migration delays in refugia affect migration success or fitness (except for the harvest effects mentioned above).

Overall, it is currently unclear whether thermal refugia occasionally function as ecological traps for adult salmonids, where holding was adaptive under historic conditions but now results in a net mortality cost due to increased mortality factors (e.g., fishing), or whether they primarily provide fitness benefits.

Potential for reducing negative harvest effects in thermal refugia – As shown in Keefer et al. (2009), the concentration of summer steelhead in lower Columbia River refugia sites (e.g., at Drano Lake at the Little White Salmon confluence and the Deschutes River mouth) can result in high exploitation rates. Harvest impacts on upriver populations are also probable for Chinook salmon (especially summer and fall runs) and at sites other than those studied by the UI and NMFS. Harvest management at these sites may become increasingly important, particularly if impacts on threatened populations are determined to significantly reduce escapement.

The temperature thresholds shown in Figures 5 and 10 may be useful as predictors of refugia use by upriver populations in the lower Columbia River corridor. Importantly, the timing and duration of warm water periods in the main stem varies considerably among years (Figure 13). If managers seek to reduce harvest of upriver populations in lower river refugia sites or in the cool-water plumes created by these tributaries, main stem temperature thresholds may be useful for identifying times of greatest risk. The among-year differences shown in Figure 13 suggest that temperature-based management criteria would more effectively balance protection of thermoregulating fish with harvest of local stocks than would date-based restrictions.

Temperature-related harvest management that is population- specific or ESU-specific will require relatively detailed estimates of migration timing. Figures 9 and 12 show some of the best current migration timing data for summer steelhead and fall Chinook salmon. Population-specific migration timing distributions are also available for spring–summer Chinook salmon (Keefer et al. 2004) and sockeye salmon (e.g., Fryer 2009). We expect that lower river refugia use for these earlier migrants is most likely for upper Columbia River summer-run Chinook salmon, relatively late-timed Snake River Chinook salmon populations like those from the South Fork Salmon River and Imnaha River, and late-timed sockeye salmon.

Temperature variation in the main stem Columbia and Snake rivers

Adult salmon and steelhead can also exploit spatial heterogeneity in water temperature within the migration corridor. In addition to the cool-water plumes associated with tributaries, areas of cooler summer temperatures occur as a result of thermal stratification. Because most of the lower Columbia and lower Snake River reservoirs are flow-through projects, stratification is limited relative to some managed river systems, but vertical temperature gradients routinely occur. Lower Granite reservoir has some of the most heterogeneous temperature profiles in the Hydrosystem, with summer temperatures ranging from >23 °C at the surface to ~11 °C at depth (Clabough et al. 2007b; Tiffan et al. 2009). This variability is related, in large part, to different temperature profiles from the Snake River (~20-24 °C in much of the summer and early fall) and the much cooler Clearwater River (~10-14 °C during the same time frame). Fish managers have exploited this temperature differential by increasing cold (~6 °C) water releases from Dworshak reservoir on the North Fork Clearwater River during the warmest summer periods in an effort to reduce temperatures in lower Snake River reservoirs. The Dworshak temperature effect is most pronounced in Lower Granite reservoir but does extend to downstream reaches in some cases. The research by Clabough et al. (2007a, 2007b) demonstrated that adult migrants preferentially use the cooler layers in the Lower Granite reservoir.

Thermal layering in reservoirs is most typically characterized by the warmest water at the surface due to solar heating and wind events. This can directly affect the water temperature inside

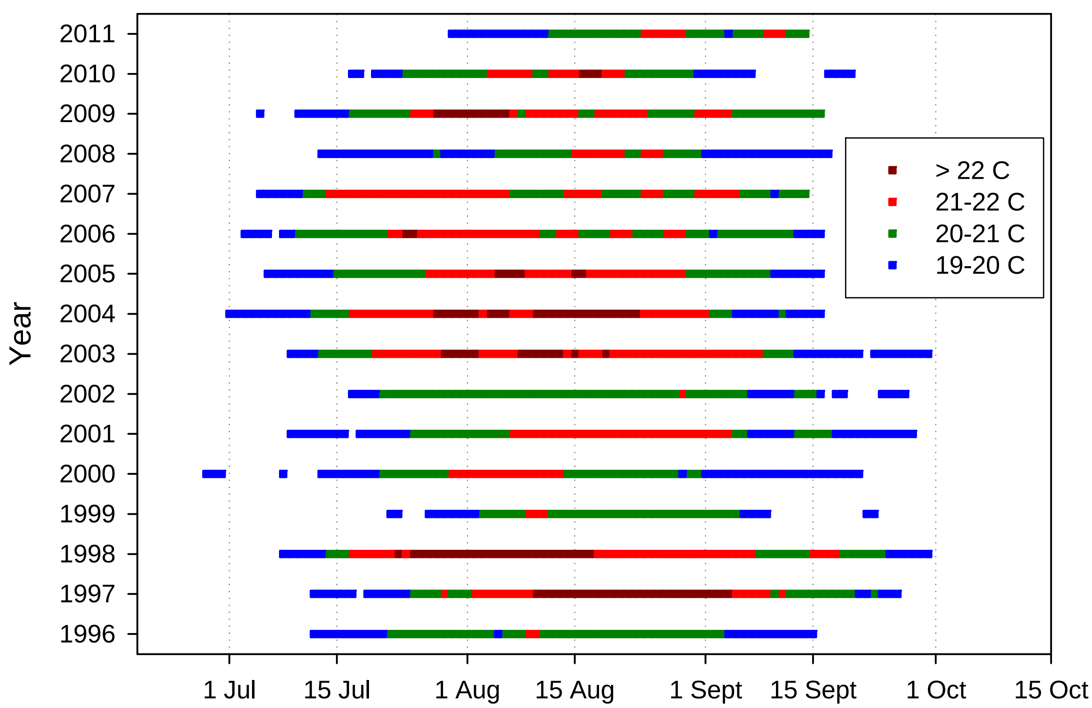

Figure 13. Columbia River water temperature data collected from early July to mid-October, 1996-2011. Colors show dates when mean water temperature was 19-20, 20-21, 21-22, and > 22 °C. Data source: Bonneville Dam water quality monitoring (WQM) site.

fishways at the main stem dams. Peery et al. (2003), Keefer et al. (2003), and Caudill et al. (2006) reported significant temperature discontinuities (>1-2 °C) between upper and lower sections of fishways at Snake River dams and at John Day and McNary dams. This pattern develops when warm reservoir surface water is pumped or gravity fed into the upper fishways while cooler tailrace and turbine outflow water is pumped into the lower fishways. Adult salmonids have responded to the abrupt temperature gradients by exiting fishways more frequently and holding in the cooler water in dam tailraces (often overnight). The overall effect has been slowed dam passage rates and produced migration delays on a temporal scale similar to the thermal refugia use described above for Chinook salmon (i.e., hours to days).

One of the most effective ways to characterize temperature exposure of adult salmonids has been the use of combined radiotelemetry and data storage transmitters (RDST). In 2000 and 2002, two relatively cool years, we monitored several hundred spring–summer and fall Chinook salmon and summer steelhead using RDST tags that collected temperature and depth data (Clabough et al. 2008). These studies confirmed that many adult migrants experience physiologically stressful temperatures. For example, 81% of fall Chinook salmon and 75% of steelhead encountered temperatures >20 °C and these estimates were conservative as a result of tagging restrictions and limits to data storage capabilities. Data from recovered transmitters also corroborated many of the behaviors described in this report, including adult use of tributary refugia, use of cool-water plumes below refugia sites, elevated temperature exposure inside dam fishways, and use of deep water in reservoirs and tailraces (Clabough et al. 2008; Johnson et al. 2005, 2010). The RDST data provided no compelling evidence for cold, groundwater-based refugia (i.e., springs) or that adults found or exploited upwelling hyporheic flows in the main stem rivers.

Information gaps

• ***Spatial distribution*** – Aside from the sites along the margins of the Bonneville and The Dalles reservoirs, there has been little systematic mapping of thermal refugia along the Columbia-Snake River migration corridor or in spawning tributaries. Important gaps along the migration route include downstream from Bonneville Dam, in the mid-Columbia upstream from Priest Rapids Dam, and in the Snake River upstream from the Clearwater River confluence. The presence of potential ground-water inputs to the migration corridor that may provide refuge have been speculated on but not verified or disproven. Tributary refugia may be equally or even more important at upstream sites given the lower overall condition of fish at this stage in the migration.

• ***Temporal distribution*** – Temperature gradients between tributary refugia sites and adjacent migration corridors fluctuate seasonally and make the refugia more or less attractive to adult migrants. Temporal patterns in temperature differentials have not been well described, even for the relatively better studied sites. Similarly, seasonal and daily variability in vertical temperature profiles in reservoirs have not been well described.

• ***Population differences*** – As most clearly demonstrated for steelhead, the incidence and duration of refugia use differs among populations within runs. For steelhead this was largely a function of run timing, but there may be other factors that affect refugia use behavior, including among-population differences in metabolic performance, temperature preferences, or other factors. We still only have a coarse understanding of population-specific use of refugia for steelhead. Identifying population-specific refugia use patterns for Chinook, sockeye, and coho salmon may also help prioritize management strategies.

• ***Physiological benefits*** – Although refugia use is presumably adaptive and confers fitness benefits on adult salmonids, these benefits have not been quantified. Basic physiological metrics such as metabolic rate, stress levels, and reproductive hormone levels have not been measured.

• ***Delayed effects*** – The effects of refugia use on fecundity and fitness have not been quantified, though these are among the most important uncertainties associated with the behavior. Experimental or field testing of the effects of thermal exposure (including simulated or actual refugia use) would help clarify the role that refugia have on Columbia River salmon and steelhead populations. Example studies include Mann and Peery (2005) and Crossin et al. (2008). Discussions on development of effective methods to identify and quantify delayed effects are needed because it remains largely unknown how refugia use relates to reproductive success.

• ***Harvest management*** – As shown in Keefer et al. (2009), the concentration of steelhead in lower Columbia River refugia sites (e.g., at Drano Lake at the Little White Salmon confluence and the Deschutes River mouth) can result in high exploitation rates. Harvest impacts on upriver populations are also possible for Chinook salmon (especially summer and fall runs) and at sites other than those studied by the UI and NMFS. Harvest management at these sites may become increasingly important, particularly if impacts on threatened populations are deemed significant. The population-specific migration timing data, combined with the temperature threshold-refugia use data in this report should be useful for developing criteria for managing fisheries inside refugia sites.

Conclusions

A full understanding of the effects of thermoregulation and thermal refugia use during upstream migration will require a better understanding of several inter-related factors: 1) the behavioral flexibility of adults to find and use refugia; 2) species- and population-specific responses to and use of refugia; 3) the spatial and temporal extent and distribution of refugia; 4) the interaction of refugia use with impacts such as fisheries; 5) the delayed effects of thermal stress and the degree to which these effects are ameliorated by refugia use; 6) the interactions among main stem temperature exposure, pathogen exposure, refugia use, and the conditions adults experience in tributaries during spawning; and 7) the effects of predicted climate change.

In general, the impacts of climate warming are likely to be greater for spring and summer run salmon than for fall-run populations because spring–summer fish hold in tributaries during summer months, with increased metabolic costs and potential for disease expression. Longer, hotter summers predicted under climate change scenarios would also be expected to differentially affect spring-summer run stocks by increasing metabolic costs of migration. The behavioral flexibility observed in summer steelhead suggests the potential for greater benefit of thermal refugia use to steelhead than salmon because they can use the sites for extended periods during the warmest time of the year. However, refugia may become relatively more important for salmon under warmer climate conditions, allowing migration in a “stepping-stone” sequence among refugia sites.

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