

## Temporary Staging of Columbia River Summer Steelhead in Coolwater Areas and Its Effect on Migration Rates

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**Abstract.**—We used radiotelemetry to evaluate the temporary staging of adult migrating steelhead *Oncorhynchus mykiss* into nonnatal tributary rivers of the Columbia River and to determine the effects of staging behavior on migration rate. By monitoring the movement patterns of 2,900 individual steelhead over 3 years (1996, 1997, and 2000), we determined that an average of 61% of the steelhead destined for upstream areas temporarily staged in one or more tributaries in the lower Columbia River for durations from less than 1 h to 237 d. Median residence time varied significantly by tributary used and year and, based on canonical correlation analysis, was correlated with main-stem Columbia River water temperature. Steelhead that temporarily staged in tributary rivers migrated through the lower Columbia River significantly more slowly than steelhead that did not use tributaries. Use of coolwater tributaries as thermal refugia during warm summertime conditions significantly influences the migratory behavior of Columbia River adult steelhead. Our results highlight the need to preserve the water quality parameters of existing cooler-water Columbia River tributaries and to rehabilitate watersheds that historically maintained cooler-water tributaries as sources of thermal refugia for adult summer steelhead returning to the basin.

Summer steelhead *Oncorhynchus mykiss* in the Columbia River basin are highly prized for their commercial, sport, and cultural values, but many wild stocks are in peril. The National Marine Fisheries Service has identified five steelhead evolutionarily significant units (ESUs) in the Columbia River basin: the Lower Columbia River, Willamette River, Middle Columbia River, Upper Columbia River, and Snake River basin ESUs. All five ESUs are currently protected under the Endangered Species Act, and efforts are underway to curtail recent trends of diminishing returns (Busby et al. 1996; National Research Council 1996). While adult anadromous salmonid migratory behavior may be largely genetically regulated (Wagner 1974), environmental factors such as photoperiod, temperature, and flow are influential (Banks 1969; Quinn and Adams 1996; Trépanier et al. 1996; Quinn et al. 1997). Water temperature and flow are the two most commonly cited exogenous cues affecting migration initiation (Jensen et al. 1986; Trépanier et al. 1996; Workman et al. 2002), and these cues may continue to influence the migratory behavior of adult salmonids after entry into freshwater.

Because salmonids are considered to be coldwater species, water temperature is of particular concern (Hokanson 1977).

Though less pronounced than that of historical returns of summer steelhead, a bi-modal pattern characterizes the distribution of returning steelhead in the Columbia River: an early group (A run) enters freshwater beginning in early summer, and a later group (B run) begins entry in late summer (Busby et al. 1996; NOAA 2001). Currently, summer steelhead runs are delineated according to dates of passage past Bonneville Dam, which is the first dam encountered by adult steelhead returning to the Columbia River basin; A-run steelhead pass Bonneville Dam from 1 June through 25 August, and B-run steelhead pass the dam from 26 August through October. Summer steelhead remain in the system until the following spring, when they spawn. Thus, the majority of summer steelhead occupy freshwater in late summer and early fall, during the period of peak summertime water temperatures in the Columbia River basin. Additionally, conversion of the once free-flowing Columbia River into a series of reservoirs by means of dam construction and river flow attenuation has significantly altered the river environment (Quinn and Adams 1996; Quinn et al. 1997). Currently, Columbia River water temperatures reach higher maximums and remain warm longer into the fall relative to the period prior to most of the dams' construction (Quinn and Adams 1996; Quinn et al.

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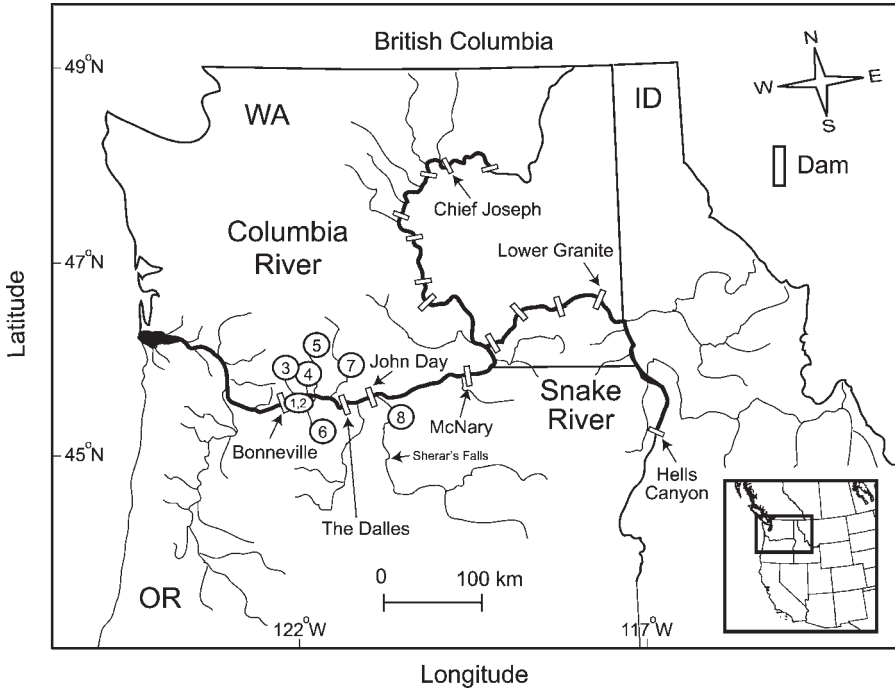


FIGURE 1.—Map of the Columbia River study location, including the migration corridor used by summer steelhead, the fish collection location (Bonneville Dam; rkm 235), and tributaries where temporary straying was monitored. Tributaries are as follows: (1) Eagle Creek; (2) Herman Creek; (3) Wind River; (4) Little White Salmon River; (5) White Salmon River; (6) Hood River; (7) Klickitat River; and (8) Deschutes River.

1997). Concerns of managers leading recovery efforts include (1) the time required for returning adults to navigate through the migration corridor and (2) the effect of summer water temperatures that often exceed upper incipient lethal levels (Coutant 1970). However, the Columbia River's heterogeneous thermal environment provides the potential for fish to use behavioral thermoregulation to compensate for negative effects of exposure to high water temperatures (e.g., Berman and Quinn 1991). Particularly, eight coolwater tributaries in the lower Columbia River could provide thermal refugia to migrating adult steelhead during summer (Figure 1). Groundwater and hyporheic sources may also influence the main-stem thermal environment in the lower Columbia River, although the availability of such coolwater sources is unknown. It has been suggested that changes in Columbia River temperature and flow conditions in the main stem as a whole influence migration timing of some Pacific salmonids, including sockeye salmon *O. nerka* and summer steelhead (Quinn and Adams 1996; Quinn et al. 1997; Robards and Quinn 2002), but the effects of temperature in heterogeneous, thermally influenced areas on adult migrating summer steelhead behavior

have not been thoroughly evaluated. In this paper, we (1) describe the migratory behavior of radio-tagged adult steelhead, including use of coolwater areas in the lower Columbia River, (2) determine the environmental variables with the greatest influence on coolwater area residence times, and (3) compare migration rates of steelhead that did and did not delay migration at coolwater areas.

### Study Area

Adult steelhead were monitored in the Columbia River and its tributaries from Bonneville Dam (river kilometer [rkm] 235) upstream to Chief Joseph Dam (rkm 877) on the Columbia River and Hells Canyon Dam (rkm 919) on the Snake River (Figure 1). During summer and fall, this study focused on data collected from the lower 112 km of the Columbia River from Bonneville Dam upstream to John Day Dam (rkm 347) and tributaries found therein. Seven tributary rivers enter the Columbia River in Bonneville Reservoir: three from the Oregon (south) shore (Eagle Creek, Herman Creek, and Hood River) and four from the Washington (north) shore (Wind, Little White Salmon, White Salmon, and Klickitat rivers) (Figure 1). The

only tributary to the Columbia River that enters the Dalles Reservoir, the Deschutes River, drains 27,195 km<sup>2</sup> of central Oregon east of the Cascade Mountains. Combined, the three largest tributaries (White Salmon, Klickitat, and Deschutes rivers) contributed 6% of the total Columbia River flow during the summers of 1996, 1997, and 2000 (USGS 2003). Monitoring of fish once they reached the middle Columbia River and lower Snake River during winter and spring was used to determine which fish had natal streams upstream of the lower Columbia River.

### Methods

*Fish collection and tagging.*—Juvenile steelhead in the Columbia River basin spend an extended period of time rearing in freshwater (up to 4 years but usually 2 years) prior to migrating to the sea, where they usually spend 2 to 3 years (Simpson and Wallace 1982; Meehan and Bjornn 1991). The two types of steelhead populations in the Columbia River basin, winter and summer steelhead, are identified by the time of year of adult freshwater entry, but both groups spawn in the spring. We collected 765 adult wild and hatchery summer steelhead in 1996, 975 in 1997, and 1,160 in 2000. Fish were collected at the Adult Fish Facility trap at Bonneville Dam during June–October of each year and were outfitted with radio transmitters. Three transmitter types (Lotek Engineering, Inc., New Market, Ontario) were used during the study: large (8 × 1.6 cm; 29 g in air), small (4.5 × 1.3 cm; 11 g in air), and radio data storage transmitters (RDST; 9 × 2 cm; 34 g in air; used only in 2000). The tags transmitted unique, digitally coded signals on frequencies from 149.320 to 149.880 MHz at 5-s intervals. Because the adult summer steelhead we studied do not feed while in freshwater, all transmitters were gastrically implanted; this tagging method has minimal impact on swimming performance and behavior relative to other procedures for steelhead (Mellas and Haynes 1985). Summer steelhead averaged 70.3 cm fork length (FL) and ranged from 48.5 to 104.5 cm FL. The smaller radio tags were placed in steelhead with FLs less than 65 cm, and fish of different sizes were observed to react similarly. Approximately equal proportions of male and female summer steelhead were tagged in 1997 and 2000, but relatively more males than females were tagged in 1996. Tagging and subsequent tracking procedures were similar to those described by Keefer et al. (2004b). The combination RDST tag used in a subsample of 181 steelhead during 2000 stored temperature and depth (pressure) data. The RDST was programmed to log temperature every minute and pressure every 5 s, which allowed the tag to store data for approximately 40 d. After 40 d, no additional

temperature and pressure data were collected, although transmission of the radio signal continued. Because data collected by the RDST transmitters were not available unless the tags were retrieved, we preferentially selected steelhead that were expected to return to the Snake River drainage in Idaho. Steelhead destined for the Snake River drainage were identified by the presence of an adipose clip or with passive integrated transponder (PIT) tag data. Some adult steelhead returning in 2000 were PIT-tagged as smolts in the Snake River drainage by multiple state, federal, and tribal agencies for various studies. A portion of these studies were unaffected by the methods used in the present study; thus, we were able to obtain permission from those responsible for originally tagging the smolts to outfit these fish as adults with RDST transmitters. Fish with RDST transmitters were diverted into the adult trap at Lower Granite Dam (Figure 1) for data retrieval.

*Data collection and analysis.*—Movements and locations of radio-tagged steelhead were monitored with a series of fixed-site receivers (Lotek Engineering) and antennas. Scanning receivers attached to aerial antennas sequentially scanned transmitter frequencies at fixed receiver stations near dams and in tributaries and were also used in boats and trucks for mobile tracking. Scanning receivers linked with digital-spectrum processors could scan all frequencies simultaneously and were attached to underwater antennas stationed in and around fishways at dams. Telemetry data downloaded from the receivers were condensed and compiled into general migration databases depicting the first and last occurrences at antennas and stations as radio-tagged steelhead progressed upstream. Each record was accompanied by a date and time stamp, receiver location, river kilometer, antenna, and signal power. Fish detected during mobile tracking were also included in the database according to location, date, and time.

Columbia River temperatures were collected by personnel of the U.S. Army Corps of Engineers at dams and downloaded from a web-based database (<http://www.cqs.washington.edu/dart/dart.html>). The three study years had variable temperature regimes; 1996 was similar to the 10-year (1995–2004) average, 1997 was warmer than the average, and 2000 was slightly cooler during mid- and late summer but warmer during early summer (Figure 2). Tributary river temperature data were obtained by (1) data loggers we deployed during each study year in the Hood and Deschutes rivers, (2) the U.S. Geological Survey in the Wind and White Salmon rivers (2001 only), and (3) the U.S. Forest Service in Herman Creek (2000 only). Stream temperature data from the Little

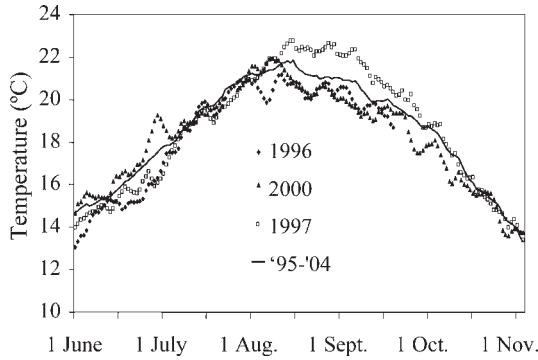


FIGURE 2.—Average daily water temperatures observed at Bonneville Dam on the Columbia River in 1996, 1997, and 2000 and the 10-year average from 1995 to 2004.

White Salmon River and Eagle Creek in 1996, 1997, 2000, and 2001 were obtained from daily records at the Little White Salmon National Fish Hatchery (U.S. Fish and Wildlife Service) and the Cascade Fish Hatchery (Oregon Department of Fish and Wildlife), respectively. Because stream temperature data were available for all of the tributaries in 2001, differences in average daily temperatures between the Little White Salmon River and other tributaries in 2001 were used as correction factors to roughly estimate average daily water temperatures for tributaries when temperature data were not available. In 2000, we conducted field surveys to ascertain the extent of the Little White Salmon River’s coolwater thermal plume in the Columbia River.

Use of tributary rivers by upriver-migrating steelhead was primarily monitored by fixed receivers located at tributary confluence areas in Bonneville and the Dalles reservoirs. Tributary receivers were located near the mouths of the Wind, Little White Salmon, White Salmon, Hood, Klickitat, and Deschutes rivers. Receivers were located 0–2.0 km downstream from the mouth of each tributary river as well as within tributary rivers. Additional receivers were located 0.2 and 0.6 km upstream of the White Salmon and Little White Salmon rivers, respectively (Figure 1). The receiver site at the Wind River was moved upstream between 1997 and 2000, which caused it to record fewer fish in 2000. Eagle and Herman creeks were not outfitted with receivers but were monitored daily by mobile tracking in 2000. Steelhead were classified as using a particular tributary if they (1) had a spawning or final location somewhere other than that tributary or the reservoir reach entered by the tributary and (2) had calculated residence times longer than 12 h in or near the mouth of that tributary. For tributaries with one receiver site upstream from their mouths (Hood and Klickitat rivers), steelhead

were considered to use the tributary as long as they met the first criterion. The time period during which radio-tagged steelhead resided within the influence of cooler water was calculated by summing the duration of time at and between the downstream and instream receivers at tributaries. Half of the elapsed time between instream and upstream receiver records was added as well to account for coolwater exposure as fish left tributaries and continued migration upstream.

Pearson’s chi-square tests were used to test for differences between the proportions of the all radio-tagged steelhead that used one or more tributaries in Bonneville or the Dalles reservoirs in 1996, 1997, and 2000. Chi-square tests ( $\alpha = 0.05$ ) were also used to evaluate (1) differences between observed and expected proportions of the earlier-arriving A-run and the later-arriving B-run steelhead that used tributaries and (2) differences in observed and expected proportions of steelhead that used tributaries among years, because the B-run steelhead can avoid the higher main-stem water temperatures that A-run steelhead are likely to experience. Observed values were the number of radio-tagged A- and B-run steelhead that did or did not use tributaries, while expected values were based on the proportion of A- or B-run steelhead in the entire tagged sample, namely,

$$E = (\text{Trib} \times \text{Run}) / \text{Total},$$

where Trib = the total number of radio-tagged A- and B-run steelhead that were observed to use no tributaries or one or more tributaries, Run = the total number of radio-tagged steelhead of either the A or B run, and Total = the total number of radio-tagged A- and B-run steelhead combined. Residence times of steelhead that used tributaries were compared between A- and B-run fish by use of a Kruskal–Wallis test. A product multinomial log-linear model (Bishop et al. 1975) was used to test the equality of the proportions of

radio-tagged adult steelhead that used the Little White Salmon, White Salmon, Klickitat, and Deschutes rivers among the 3 years of study. Analysis of variance was used to compare median residence times for steelhead that used the Little White Salmon, White Salmon, Klickitat, and Deschutes rivers during 1996, 1997, and 2000. Nonparametric median tests were performed when the underlying distribution of the data was nonnormal. Tukey's method was used to compare residence times across years and across tributaries and years when a significant difference occurred (Kleinbaum et al. 1998). Median tests were also used to compare residence times of female versus male steelhead.

Steelhead body temperatures obtained from RDST tags were assessed in coordination with radiotelemetry data for evidence of the use of coolwater refuges other than tributaries (i.e., mid-channel groundwater upwelling) in the Columbia River. Of the 181 steelhead outfitted with RDSTs in 2000, 110 were recaptured and provided temperature data. These tags were downloaded, and data sets describing the duration for which RDST-tagged steelhead occupied the lower river (between Bonneville and John Day dams) were compiled according to the times each fish passed the top of the ladder receiver sites at Bonneville Dam and one of several antennas at entrances to John Day Dam. These data sets were reviewed, and blocks of temperature records for the times when individual steelhead were known to be in or near coolwater tributary areas, as determined by records from fixed receivers, mobile tracking efforts, or recapture information, were removed. The remaining steelhead body temperatures were averaged on an hourly basis and were compared with Columbia River water temperatures recorded hourly at Bonneville Dam. Telemetry records were used to identify steelhead locations at which mean hourly body temperature was more than 2°C cooler than the Columbia River.

The relative influences of river conditions on tributary use by steelhead in the lower Columbia River were evaluated by use of a Hotelling's  $T^2$  test and subsequent canonical variable structure (Bishop et al. 1975). For this analysis, we used the difference between tributary and main-stem daily temperatures, spill, turbidity, discharge, and main-stem temperature as independent variables. Spill, turbidity, discharge, and main-stem temperature data were measured by U.S. Army Corps of Engineers personnel at the Dalles Dam on the date each steelhead entered Bonneville Reservoir. For steelhead that used the Deschutes River in the Dalles Reservoir after passing through Bonneville Reservoir without stopping, we used river

environment variables recorded on dates of entry into the Dalles Reservoir.

Migration rates between Bonneville and the Dalles dams and between the Dalles and John Day dams were compared for tagged steelhead that did and did not use coolwater tributaries during 1996, 1997, and 2000. Migration rates were calculated from the time fish exited the top of the ladder at Bonneville Dam or the Dalles Dam until they first entered the tailrace of the Dalles Dam or John Day Dam. Analysis of variance ( $\alpha = 0.05$ ) was used to compare migration rates between the two groups among years. Analysis of covariance was used to test effects of Columbia River discharge, spill, turbidity, and temperature on migration rates.

The effect of temporary delays at lower Columbia River tributaries on migration timing was evaluated based on the median dates that radio-tagged steelhead passed McNary (rkm 470) and Lower Granite (rkm 695) dams. The median dates of passage of radio-tagged steelhead that did and did not use tributaries were compared by use of nonparametric median tests ( $\alpha = 0.05$ ) on data from both dams.

## Results

Tributary usage by radio-tagged adult steelhead varied significantly among tributaries and years ( $P < 0.0001$ ), and this behavior was closely linked to migration speed. In all years, the majority of migrating steelhead—from 57% to 66% of the radio-tagged fish that migrated upstream of the Dalles Dam—temporarily staged in at least one downstream tributary. Tributary use was highest in 2000 and lowest in 1996, when water temperatures were close to average (Table 1). The frequency of tributary usage corresponded to the general pattern of summertime water temperatures in both Bonneville and the Dalles reservoirs (Figures 2, 3). In all 3 years, a relatively larger proportion of radio-tagged A-run steelhead than B-run steelhead used tributaries, although the difference was statistically significant only in 2000 ( $P < 0.025$ ). When data from Eagle and Herman creeks and the Wind River were excluded, as warranted by the moving of the receiver site at Wind River and differences in monitoring effort among years, none of the years yielded significant differences in proportions of A- and B-run steelhead that used tributaries ( $P > 0.10$ ). However, the average residence time in tributaries was significantly greater (Kruskal-Wallis test:  $P < 0.001$ ) for A-run than B-run steelhead in all 3 years (Figure 4).

Two tributary rivers (Little White Salmon and Deschutes) were used preferentially over others available during the 3 years studied ( $P < 0.001$ ). Approximately 25% to 30% of the tagged steelhead

TABLE 1.—Total number of radio-tagged steelhead released at Bonneville Dam (Columbia River) that passed the Dalles Dam, the proportion passing the Dalles Dam that used tributaries, the number that used single and multiple tributaries, and the number and percentage of adult A- and B-run steelhead migrating upstream of the Dalles Dam that used one or more coolwater tributaries for over 12 h in Bonneville and the Dalles reservoirs in 1996, 1997, and 2000 (data were not collected at Eagle and Herman creeks in 1996 and 1997).

Variable	1996	1997	2000
Total released at Bonneville Dam	765	975	1,160
Total that passed the Dalles Dam	575	668	864
Percentage that used tributaries ( <i>n</i> )	57% (328)	61% (410)	66% (574)
Number of A run tagged (1 Jun–25 Aug)	323	323	444
Percentage of A run that used tributaries ( <i>n</i> )	61% (196)	63% (202)	74% (329)
Number of B run tagged (26 Aug–23 Oct)	252	345	420
Percentage of B run that used tributaries ( <i>n</i> )	52% (130)	60% (208)	58% (245)
Number that used single tributaries	211	296	372
Eagle Creek			1
Herman Creek			33
Wind River	21	38	20
Little White Salmon River	57	104	144
White Salmon River	27	29	30
Hood River		2	
Klickitat River	13	23	15
Deschutes River	93	100	129
Number that used multiple tributaries	117	114	202
Including Little White Salmon River	80	65	113
Including Deschutes River	73	71	124
Including Little White Salmon and Deschutes rivers	45	37	62

that migrated upstream of the Dalles Dam were observed in at least one of these two rivers, and these two tributaries accounted for 78% to 83% of all tributary usage (Table 1). In July 2000, we documented that the measurable thermal plume (water at least 2°C cooler than the main-stem Columbia River) from the Little White Salmon River extended downstream into the Columbia River approximately 500 m after flowing through a large, man-made backwater area.

Residence times for radio-tagged steelhead in tributaries entering Bonneville and the Dalles reservoirs were highly variable; individual median residence times ranged from 0.02 to 16.1 d (means = 3–23 d; Figure 5). Overall median residence times of radio-tagged adult steelhead (over the 3 years) ranged from 15.1 d (Little White Salmon River) to 0.2 d (Hood River). Residence times of radio-tagged steelhead in the Little White Salmon River were greater than those of steelhead in other tributaries in all significant pairwise comparisons ( $P < 0.05$ ). Median residence times of female steelhead in tributaries were not statistically different than those of male steelhead ( $P > 0.05$ ). When data from males and females were combined, median residence times differed significantly among years when data from the Little White Salmon, White Salmon, Klickitat, and Deschutes rivers were pooled (1996: 6.2 d; 1997: 9.8 d; 2000: 8.2 d;  $F = 3.56$ ,  $P = 0.0287$ ). Median residence times for steelhead in 1997, the warmest of the three study years, were significantly longer than those in 1996 ( $P =$

0.0084) but not significantly different than those in 2000 ( $P = 0.2827$ ). Within years, residence times of radio-tagged adult steelhead were not significantly different for the Little White Salmon, White Salmon, Klickitat, and Deschutes rivers ( $P = 0.1168$ ).

Main-stem river temperature and the difference between main-stem and tributary temperatures were the most influential variables affecting when adult steelhead were recorded in or near coolwater tributaries of the lower Columbia River. In 1996, 1997, and 2000, main-stem temperature, total dissolved gas (%), and the differences between main-stem and tributary average temperatures were significantly different among (1) periods when radio-tagged steelhead that used tributaries migrated through the lower Columbia River and (2) periods when radio-tagged steelhead that did not use tributaries migrated through the lower Columbia River ( $T^2 = 320.109$ ,  $df_1 = 6$ ,  $df_2 = 1,909$ ,  $P < 0.0001$ ; canonical variables were  $-0.859$  for main-stem temperature,  $-0.641$  for temperature differences,  $0.521$  for river discharge,  $-0.307$  for total dissolved gas,  $-0.290$  for turbidity, and  $0.250$  for spill). The positive or negative signs of canonical variables indicated that increasing main-stem temperature, differences between main-stem and tributary temperatures, and total dissolved gas influenced the periods of coolwater tributary use in a manner opposite to that of increasing river discharge and spill.

Body temperatures for most (82%;  $n = 90$ ) adult steelhead, as recorded on archival tags, were similar to

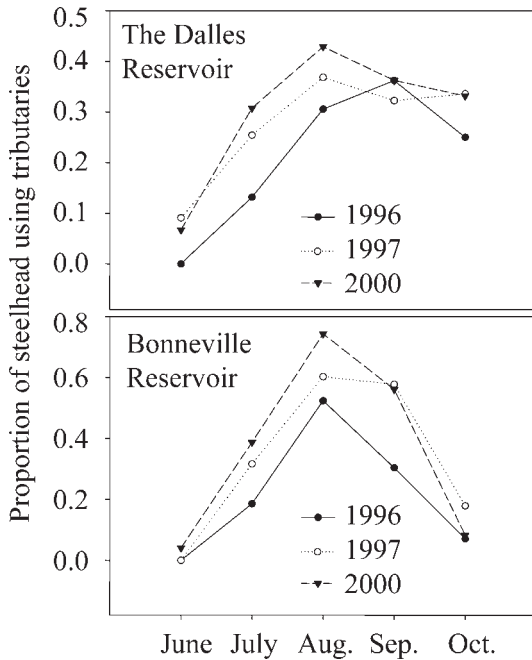


FIGURE 3.—Proportion of radio-tagged adult steelhead that entered Bonneville and the Dalles reservoirs on the Columbia River each month and that used one or more coolwater tributaries in 1996, 1997, and 2000.

those for the Columbia River when we removed tributary-influenced data recorded during the migration between Bonneville and John Day dams. The difference between hourly Columbia River water temperature and hourly mean steelhead body temperature without tributary influence ranged from  $-1.8^{\circ}\text{C}$  to  $9.8^{\circ}\text{C}$  and averaged  $0.1^{\circ}\text{C}$  ( $\text{SE} = 1.0$ ). The range of differences in temperature was relatively wide and may have been unduly inflated because 20 steelhead (18%) had average body temperatures at least  $2^{\circ}\text{C}$  cooler than the main-stem Columbia River for 1 h or more. Although the lower body temperatures could not be directly associated with detections at tributary receiver sites, based on the closest receiver and mobile tracking records before and after the times of cooler body temperature we believe those 20 steelhead were indeed in areas influenced by tributary discharge. These tributaries were Herman and Eagle creeks and the Wind and Klickitat rivers, which accounted for 18 of the 20 RDST-tagged steelhead. The other two RDST-tagged steelhead each had a single hour of cooler body temperature near the Deschutes River.

In all 3 years, migration rates of radio-tagged adult steelhead that delayed migration at tributary rivers within Bonneville and the Dalles reservoirs were

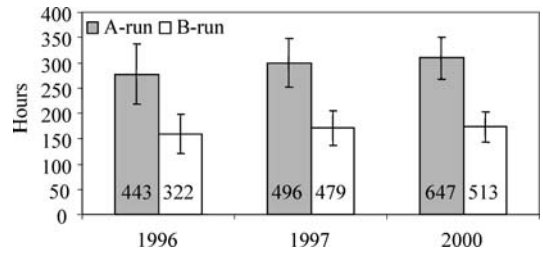


FIGURE 4.—Average residence times  $\pm$  95% confidence intervals of radio-tagged A- and B-run steelhead that used nonnatal tributaries in the lower Columbia River in 1997, 1998, and 2000. Numbers within the bars are sample sizes.

significantly lower ( $F = 252.03$ ,  $P < 0.0001$ ) than those of steelhead that were not recorded in or near tributaries (Figure 6). None of the river environment covariates contributed to the variation observed among migration rates during these 3 years. Significant differences between migration rates of radio-tagged steelhead that did and did not use tributaries were due to a three-way interaction between year, tributary use, and reservoir. Migration rates of steelhead that did not use tributaries were significantly different between reservoirs ( $P < 0.0001$ ) but not among years ( $P = 0.53$ ). Multiple pairwise comparisons indicated that the migration rates of steelhead that did not use tributaries were significantly greater in 2000 than in 1996 or 1997 ( $P < 0.05$ ).

## Discussion

The majority of upriver summer steelhead, regardless of sex, delayed migration at one or more coolwater tributaries to the lower Columbia River, and the proportion of fish that staged in tributaries was highest during periods corresponding to the warmest main-stem Columbia River water temperatures. Our results indicate that adult steelhead temporarily staged in lower tributary rivers as a way to obtain coolwater refuge during periods of warm temperatures in the main-stem Columbia River. When temporary staging in coolwater areas is sufficiently long to affect overall migration rates (see below), it probably offers benefits such as reduced potential of infection by harmful pathogens, reduced metabolic demand on energy reserves, timely maturation of gametes, and possibly higher survival rates (Bjornn and Reiser 1991). The fact that median residence times for steelhead in 1997 (warmest year) were significantly longer than those in 1996 (near-average year;  $P = 0.0084$ ) but not significantly different than those in 2000 ( $P = 0.2827$ ) suggests that there may be a temperature threshold above which adult steelhead are more likely

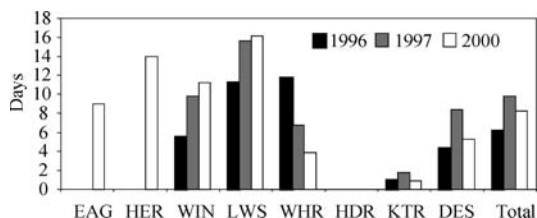


FIGURE 5.—Median residence times of radio-tagged adult steelhead in coolwater tributaries of Bonneville and the Dalles reservoirs on the Columbia River during 1996, 1997, and 2000. The tributaries are Eagle Creek [EAG], Herman Creek [HER], the Wind River [WIN], Little White Salmon River [LWS], White Salmon River [WHR], Hood River [HDR], Klickitat River [KTR], and Deschutes River [DES]. Information for Eagle and Herman creeks was only available during 2000 and is based on daily mobile tracking.

to detect and make use of thermal refugia during their upstream migration.

In our study, radio-tagged steelhead were observed to use certain tributary rivers, notably the Little White Salmon and Deschutes rivers, in greater proportions than other tributaries, independent of year. This finding can be explained by the relative amounts and temperatures of these rivers' attractive flow. The Little White Salmon River provided a large area of thermal refugia in its thermal plume and the manmade backwater area near its mouth. The Deschutes River also provided a large area of thermal refugia in the plume and main-stem river. Of the 591 upriver steelhead that delayed migration in the Deschutes River, 17.0% were recorded in the Deschutes River 5 km or more upstream from its mouth and nearly 7% were recorded at a receiver site at Sherars Falls, located 67.9 km upstream. The Deschutes River may also be more attractive to steelhead because it is the only coolwater refuge in the Dalles Reservoir, which is warmer than Bonneville Reservoir. In 2000, water temperatures at the Dalles Dam averaged nearly 1.0°C warmer than those at Bonneville Dam during June–October.

We hypothesized that, because of their earlier run timing and longer residence time in the Columbia River prior to spawning, upriver A-run summer steelhead would utilize coolwater tributaries in the lower Columbia River more than the later-arriving B-run steelhead would. We found no evidence of higher proportions of A-run than B-run steelhead utilizing coolwater tributaries. We did, however, find that A-run steelhead had significantly longer residence times than B-run fish. Thus, we conclude that the earlier freshwater entry times of A-run summer steelhead affords them more time to utilize coolwater refugia but that they do not have a higher predilection to this

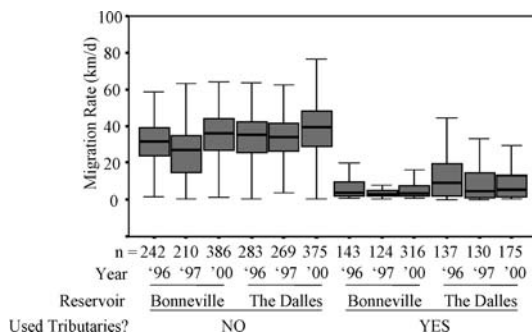


FIGURE 6.—Medians and first through third quartile ranges of migration rates through Bonneville and the Dalles reservoirs for radio-tagged adult steelhead that did and did not use Columbia River tributaries in 1996, 1997, and 2000. Whiskers are 1.5 times the length of the interquartile range and do not extend below 0.

behavior than the later-arriving assemblage of steelhead.

Use of coolwater refugia was most directly related to main-stem Columbia River temperature, followed by the temperature differential between the main-stem and tributaries, which appears to be an adapted behavioral mechanism to avoid potentially stressful conditions in the primary migration corridor. As such, we would have predicted that a higher proportion of steelhead would stage in the cooler tributaries during warmer years. We found that the use of tributaries was higher during 1997 (warmest of the 3 years) than during 1996, but the proportion of steelhead recorded in tributaries during 2000 was higher than during both 1996 and 1997. This apparent lack of a clear pattern between temperature and tributary use may have been related to differences in telemetry coverage and tracking effort among years as well as to the warmer-than-average water temperatures present during the early summer of 2000 (Figure 2). Water temperatures in the lower Columbia River during June 2000 may explain why 2000 was the only year with statistically significant differences between tributary utilization of A- versus B-run steelhead and may explain the differences between our prediction and observations.

We found little evidence that steelhead in the lower Columbia River used mid-channel upwelling sites as coolwater refuges. Upwelling is commonly associated with river channels in broad alluvial floodplains with gravel and cobble substrates (Stanford 1996). The geology of the lower Columbia River floodplain is not conducive to the vertical exchange of water between the river channel and the hyporheos, and this type of coolwater source may not exist in the section of the Columbia River under study (Coutant 1999).

Radio-tagged adult steelhead that used one or more coolwater tributaries migrated significantly more slowly through the lower Columbia River than steelhead that did not use tributaries. Thus, the behavior of delaying migration at coolwater refuge tributaries is sufficient to alter run progression, given that sufficient numbers of steelhead display such behavior. Our findings are consistent with those of other researchers who found several instances where water temperature (Thompson et al. 1958; Liscom et al. 1985; Quinn and Adams 1996; Workman et al. 2002), discharge (Banks 1969; Liscom et al. 1985), and turbidity (Bjornn 1978) negatively affected migration rate and timing, although the mechanism for delay was unknown in those previous studies. For radio-tagged steelhead that did not use tributaries, migration rates were significantly higher in 2000 than in 1996 and 1997. The slower migration during 1996 and 1997 probably is attributable to the higher river discharge that occurred during those years (Banks 1969; Jensen et al. 1986; Trépanier et al. 1996; Keefer et al. 2004a). However, because river flow, turbidity, and temperature variables were all highly correlated, our data do not identify which variables were responsible for the observed differences in migration rates of steelhead that remained in the main-stem lower Columbia River.

This study has demonstrated the need for the conservation of lower Columbia River tributary habitat to ensure the availability of coolwater refugia to listed runs of upriver adult steelhead migrants. The need may be more urgent in the future, as average air temperatures are expected to continue to increase in light of predicted regional climate change. Agencies responsible for setting fishing regulations should be mindful that decisions affecting harvest in downstream tributary areas may potentially affect listed upriver stocks. In warmer years, such effects are potentially greater. In short, provision of coolwater refuge areas to migrating adult steelhead by conserving coolwater tributaries and rehabilitating perturbed tributaries and the wise management of Columbia River basin sport and commercial fisheries in and near coolwater tributaries may prove increasingly necessary to sustain and recover wild populations of summer steelhead in the Columbia River basin.

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