

Behavioral thermoregulation and associated mortality trade-offs in migrating adult steelhead (*Oncorhynchus mykiss*): variability among sympatric populations

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Abstract: We used radiotelemetry to assess thermoregulatory behaviors for 14 populations ($n = 3985$) of adult summer steelhead (*Oncorhynchus mykiss*) as they passed through the Columbia River migration corridor. Steelhead use of small cool-water tributaries (“thermal refugia”) rapidly increased when the Columbia River reached a temperature threshold of about 19 °C. When main stem temperatures were warmest (i.e., >21 °C), more than 70% of the tagged fish used refugia sites and these fish had median refugia residence times of 3–4 weeks. Thermoregulatory responses were similar across populations, but there were large among-population differences in the incidence and duration of refugia use likely linked to population-specific migration timing patterns. In survival analyses using 1285 known-origin steelhead, fish that used thermal refugia were significantly less likely to survive to natal basins, were harvested at relatively high rates in refugia tributaries, and had greater unknown mortality in the main stem. These results highlight the trade-off between the presumed physiological benefits of thermal refugia use and a likely increase in harvest and other mortality risks that arise when preferred thermal habitats are severely constricted.

Résumé : La radiotélémetrie nous a servi à évaluer le comportement thermorégulateur de 14 populations ($n = 3985$) de truites arc-en-ciel anadromes (*Oncorhynchus mykiss*) adultes d'été lors de leur passage à travers le corridor de migration du fleuve Columbia. L'utilisation par les truites arc-en-ciel anadromes de petits tributaires d'eau froide (« refuges thermiques ») augmente rapidement quand la température du Columbia atteint un seuil d'environ 19 °C. Lorsque les températures du cours principal sont maximales (c'est-à-dire >21 °C), plus de 70 % des poissons marqués utilisent les sites de refuge et la durée médiane du séjour de ces poissons dans les refuges est de 3–4 semaines. Les réactions de thermorégulation sont les mêmes dans les diverses populations, mais il y a d'importantes différences entre les populations en ce qui concerne la fréquence et la durée de l'utilisation des refuges, vraisemblablement liées aux patrons temporels de migration spécifiques à chaque population. Des analyses de survie impliquant 1285 truites arc-en-ciel anadromes d'origine connue montrent que les poissons qui utilisent les refuges thermiques sont significativement moins susceptibles de survivre jusqu'à leur retour à leur bassin versant de naissance, qu'ils sont récoltés à des taux relativement élevés dans les tributaires refuges et qu'ils ont une mortalité de cause inconnue plus forte dans le cours principal. Ces résultats mettent en évidence le compromis entre les bénéfices physiologiques présumés de l'utilisation des refuges thermiques et une vraisemblable augmentation de la récolte et des autres risques de mortalité qui apparaissent lorsque les habitats thermiques préférés sont grandement réduits.

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Introduction

Water temperature is a controlling factor in the distribution, ecology, physiology, and behavior of poikilothermic fishes (Brett 1971; Angilletta et al. 2002; Perry et al. 2005), and most species have relatively narrow thermal preferences where physiological and metabolic processes are optimized (Beitinger and Fitzpatrick 1979; Magnuson et al. 1979). Many also have well-defined thermal tolerance thresholds where exposure marks dramatic reductions in performance, survival, and fitness (Eaton et al. 1995; Beitinger et al. 2000; Pörtner and Knust 2007). Some fishes regularly encounter thermal thresholds, particularly in temperate systems where large seasonal temperature fluctuations constrict or eliminate preferred habitats. These fish must balance use of favored thermal niches with other biological needs such as feeding, predator avoidance, reproduction, and migration (e.g., Fischer et al. 1987; Baird and Krueger 2003).

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One of the principal strategies for living in marginal or complex thermal environments is behavioral thermoregulation, where animals actively avoid stressful temperatures or seek preferred thermal habitats (Reynolds and Casterlin 1979; Adolph 1990; Holland et al. 1992). In fishes, behavioral thermoregulation has been documented for a diverse group of saltwater (e.g., Holland et al. 1992; Hight and Lowe 2007) and freshwater species (e.g., Magnuson et al. 1979; Schaefer et al. 2003). There has been particular research interest in the coldwater Salmonidae (e.g., Biro 1998; Torgersen et al. 1999; Sutton et al. 2007) both because they are vulnerable at relatively moderate temperatures and because climate warming may rapidly constrict suitable habitats for many populations (Eaton and Scheller 1996; Hari et al. 2006; Battin et al. 2007). As a group, anadromous salmonids can confront temperature challenges throughout their complex life cycle, with thermoregulatory behaviors reported during freshwater rearing (Ebersole et al. 2001; Breau et al. 2007), juvenile outmigration (Sauter et al. 2001), and ocean residency (Tanaka et al. 2000), along adult migration corridors (Newell and Quinn 2005; Goniea et al. 2006), and in spawning tributaries (Berman and Quinn 1991; Torgersen et al. 1999).

In all environments, behavioral thermoregulation is adaptive and presumably results in beneficial fitness outcomes. However, the behavior has inherent mortality risks because fish often become spatially or temporally concentrated in otherwise marginal habitats. Such aggregations are vulnerable to a variety of threats, including predation, disease transmission, and human harvest. A dramatic fisheries example occurs in the lower Columbia River where thousands of adult summer steelhead (anadromous rainbow trout) (*Oncorhynchus mykiss*) move into small, cool-water tributaries as the main migration corridor warms (Keefer et al. 2004). Many steelhead use these thermal refugia for days to months during summer (High et al. 2006) and attract intensive recreational and tribal fisheries. Harvest from these aggregations is controversial because the steelhead are seeking refuge from stressful conditions and because most fish derive from upriver populations (i.e., from river basins distant from the harvest sites). These include dozens of genetically distinct steelhead populations (e.g., Brannon et al. 2004) and several metapopulations (Snake River, mid-Columbia River, and upper Columbia River) that are listed as threatened under the US Endangered Species Act (National Marine Fisheries Service 1997; Good et al. 2005). Despite likely impacts on protected fish, uncertainty about the demographics of the thermoregulating group has restricted management options.

To investigate the relationships between behavioral thermoregulation, population demographics (i.e., fish size and origin), and mortality risks, we reconstructed adult migration histories for several thousand radio-tagged summer steelhead. The study had four basic objectives. First, the telemetry data were used to identify main stem water temperatures associated with thermoregulatory responses in migrating steelhead. Second, we assessed among-population differences in thermal refugia use, including residency times and percentages of each population recorded in refugia sites. Third, we tested for associations between refugia use and fish fate (i.e., main stem harvest, unknown main stem mor-

tality, nonnatal tributary harvest/mortality, and successful return to spawning tributaries). Fourth, we examined potential delayed effects of refugia use on fish fate in upstream river reaches. The last two objectives were addressed using a subsample of the tagged fish for which juvenile origin was known. This was a prerequisite for differentiating harvest of thermoregulating fish from harvest of returning local stocks. The combined objectives tested two hypotheses: (1) that the degree and duration of behavioral thermoregulation differ among Columbia River steelhead populations as a function of stock-specific migration timing and migration corridor temperatures and (2) that mortality risks associated with thermoregulation vary among populations, with greater risk for populations with proportionately greater refugia use and longer refugia residency times.

Materials and methods

Study system

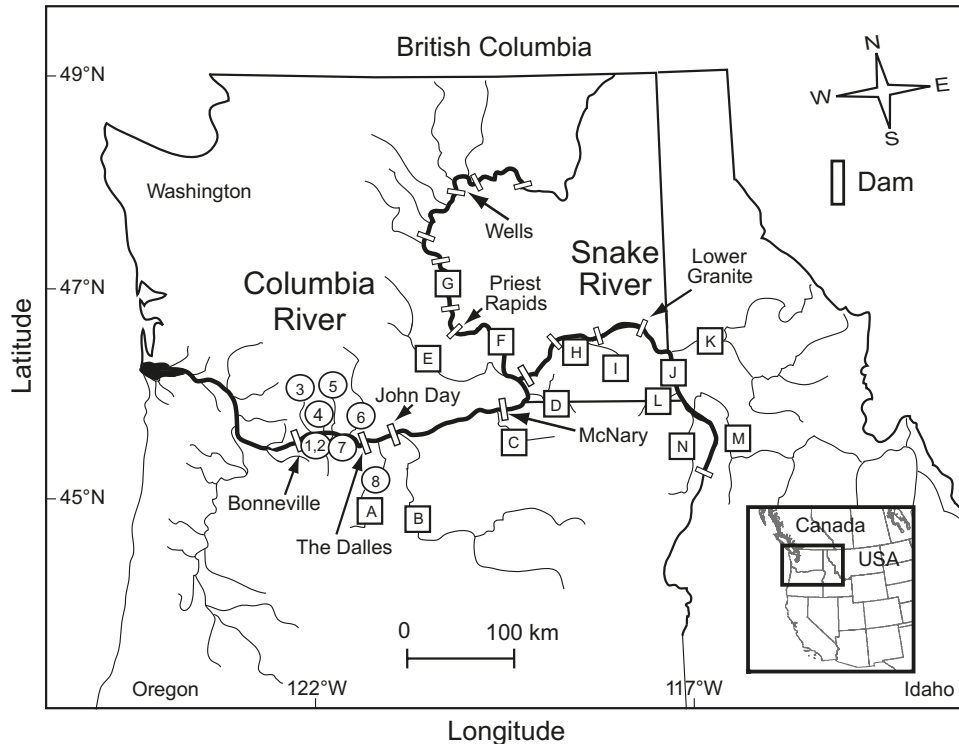
Adult steelhead were monitored at main stem Columbia and Snake River dams (fixed location telemetry sites described in Keefer et al. 2005) and at all major tributaries from Bonneville Dam (river kilometre (rkm) 235) upstream to Priest Rapids Dam (rkm 639) on the Columbia River and Hells Canyon Dam (rkm 919) on the Snake River (Fig. 1). Additional tributaries were monitored continuously in the Snake River Basin and intermittently in the upper Columbia River Basin. Thermoregulatory behaviors were studied at the confluence areas of eight Columbia River tributaries to the two most downstream reservoirs. Bonneville reservoir (~73 rkm long) extends to the tailrace of The Dalles Dam (rkm 308), and The Dalles reservoir (~38 rkm long) extends to the tailrace of John Day Dam (rkm 346). The eight tributaries (Wind, Little White Salmon, White Salmon, Klickitat, Hood, and Deschutes rivers and Herman and Eagle creeks) drain the Cascade Range and are routinely 2–7 °C cooler than the main stem Columbia River in summer and fall (Goniea et al. 2006).

The summer steelhead run is protracted at Bonneville Dam, with the earliest fish arriving in April and continuous passage through November (Busby et al. 1996; Robards and Quinn 2002). Most fish pass Bonneville Dam from June to September, coincident with seasonally high main stem water temperatures as recorded at dams (Fig. 2). Columbia River temperatures typically reach 20 °C in mid- to late July and remain at 20–23 °C until early to mid-September. In the study years, a mean of ~370 000 steelhead (range = ~204 000 – 636 000) were counted at Bonneville Dam and ~281 000 (range = ~154 000 – 481 000) were counted at John Day Dam (available from www.cbr.washington.edu/dart/). At a minimum, these data indicate that about 75% of the steelhead that passed Bonneville Dam were from interior populations (i.e., from Idaho and eastern Oregon and Washington). Actual interior population percentages were likely higher because fish counts at John Day Dam were truncated on 31 October in most years and harvest removed a portion of the interior runs in the Bonneville to John Day reach.

Collection, tagging, and monitoring

Adult steelhead were trapped and intragastrically implanted with radiotransmitters at Bonneville Dam from late

Fig. 1. Map of the Columbia and Snake River basins where radio-tagged adult summer steelhead (*Oncorhynchus mykiss*) were monitored at dams, in reservoirs, and while using cool-water tributaries during migration. Tagged fish were assigned to one of 14 populations upstream from The Dalles Dam: Deschutes River (A), John Day River (B), Umatilla River (C), Walla Walla River (D), Yakima River (E), Hanford Reach (F), upper Columbia River (G), Lyons Ferry Hatchery (H), Tucannon River (I), Snake River upstream from Lower Granite Dam (J), Clearwater River (K), Grande Ronde River (L), Salmon River (M), and Innaha River (N). Thermoregulatory behaviors were monitored at eight sites: Herman Creek (1), Eagle Creek (2), Wind River (3), Little White Salmon River (4), White Salmon River (5), Klickitat River (6), Hood River (7), and Deschutes River (8).



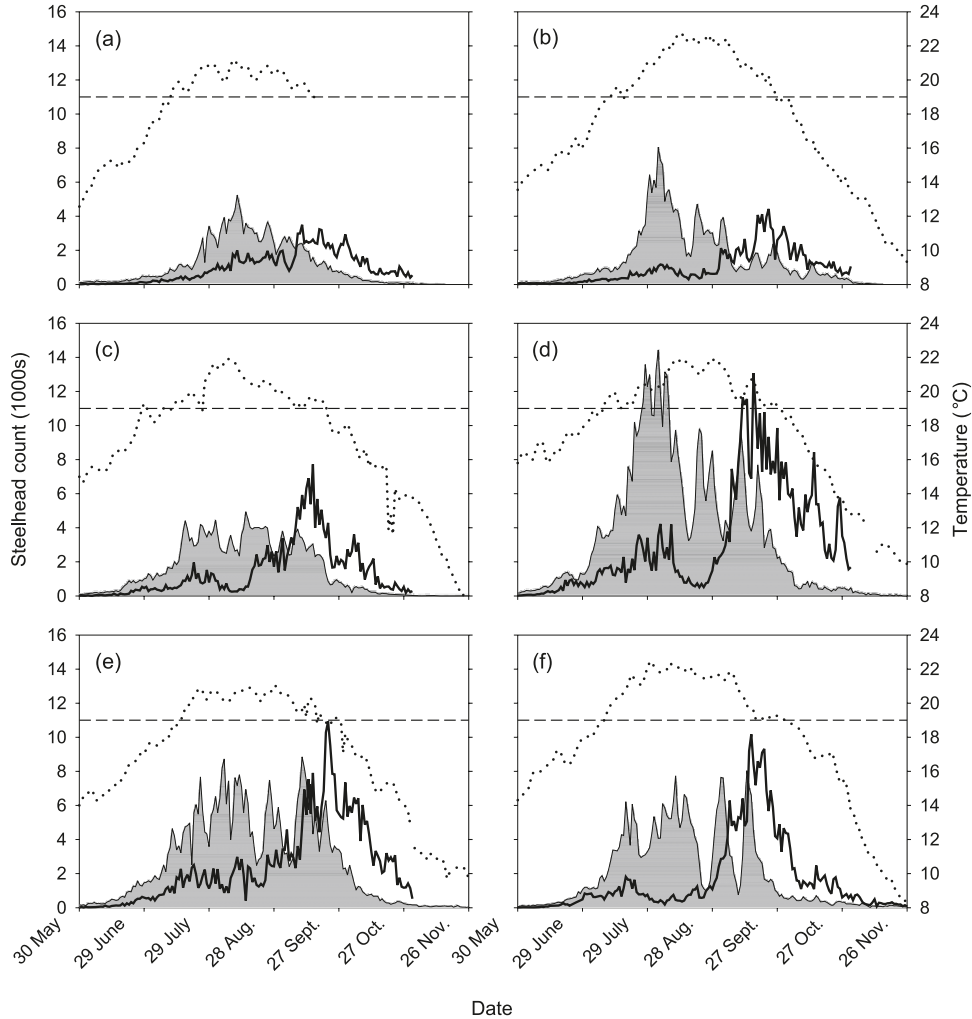
May or early June through October during 6 years (1996–1997 and 2000–2003). Details of the trap facility, tagging methods, and types and sizes of radiotransmitters are described in Keefer et al. (2004, 2005). In 1996, 1997, and 2000, steelhead were nonselectively sampled in approximate proportion to the runs, with a slight bias for later timed fish to ensure adequate samples for evaluations at Snake River dams (see Keefer et al. 2004). Total samples in these years were 765 (1996), 975 (1997), and 1160 (2000); 200 fish (7%) were excluded from analyses because they never passed Bonneville Dam or they lost transmitters during migration and refugia use could not be evaluated (Table 1).

In 2001–2003, we used an automated system to identify fish with passive integrated transponder (PIT) tags as they passed through the Bonneville adult trap. PIT tags indicated where fish were tagged as juveniles and we refer to this group as “known-origin” fish. Radio-tagging of known-origin fish allowed for direct tests of thermoregulation effects on fish fate because harvested fish and those with unknown fate could be assigned to specific populations, unlike for the unselective samples in earlier years. The availability of known-origin steelhead depended on unrelated juvenile tagging projects and so these groups were not random with respect to population. The largest known-origin sample ($n = 684$) (Table 1) was for two steelhead groups PIT-tagged at Lower Granite Dam on the Snake River as part of an ongoing National Marine Fisheries Service project (e.g., Bu-

chanan et al. 2006). As juveniles, these fish were either transported downstream in barges or migrated in-river. There were year-to-year differences in juvenile selection protocols at Lower Granite Dam, but all wild and hatchery populations upstream from the dam should have been represented. Adult distributions of the sampled barged and in-river groups were nearly identical among those fish that passed Lower Granite Dam, with about 16% last recorded in the Clearwater River, 10% in the Grande Ronde River, 22%–26% in the Salmon River, and ~50% last recorded in the main stem Snake River. The second largest known-origin group was PIT-tagged at Wells Hatchery (near Wells Dam) (Fig. 1) or collected and tagged at other upper Columbia River dams ($n = 465$). The remaining 136 known-origin fish were PIT-tagged in Snake River tributaries (Table 1).

Adult radio-tagged steelhead movements were monitored at a series of approximately 170 receiver sites that operated from April through late fall, with some tributary and dam sites in place all year (see Keefer et al. 2008a). Aerial antennas were used in reservoirs, in the tailraces of dams, and in tributaries; underwater antennas monitored passage inside dam fishways and at fish ladder exits. In all years, the six larger tributary rivers in the Bonneville to John Day reach (Wind, Little White Salmon, White Salmon, Klickitat, Hood, and Deschutes) had fixed aerial antennas within 2 km of their confluences with the Columbia River. These sites were far enough upstream so that fish passing in the

Fig. 2. Numbers of adult summer steelhead (*Oncorhynchus mykiss*) counted passing fish ladders at Bonneville (shaded area) and John Day (solid line) dams on the Columbia River. (a) 1996; (b) 1997; (c) 2000; (d) 2001; (e) 2002; (f) 2003. Dotted lines represent mean daily Columbia River water temperatures at the water quality monitoring site at Bonneville Dam. Dashed horizontal lines at 19 °C represent a possible thermoregulatory threshold.



main Columbia River channel would rarely be detected. Additional aerial antennas were used to monitor fish entries and exits from tributary plumes and confluence areas at the Wind, Little White Salmon, White Salmon, and Deschutes rivers. An aerial antenna was installed inside the low-discharge Herman Creek in 2001–2003 and this site was also monitored daily (2000) or periodically (1996–1997) using truck- or boat-mounted aerial antennas (see High et al. 2006). The low-discharge Eagle Creek was periodically monitored with mobile antennas in all years. The lower monitoring effort at the creeks relative to the larger tributary rivers resulted in some underestimation of thermoregulatory behavior.

Tributary use and passage time estimation

The time that steelhead spent in cool-water tributaries along the Bonneville to John Day reach was calculated from the first to last telemetry records at antennas inside tributaries, and multiple times were summed when individuals exited and reentered one or more tributaries. At the

creeks without fixed aerial antennas, repeated mobile records of fish were required to establish use of the site. Each of these measures were conservative estimates of the time that fish spent inside cool-water refugia because tracking with mobile antennas indicated that many fish were also in tributaries downstream from fixed antennas, in tributary plumes where temperatures were lower than the main stem (High 2002), and in confluence areas for extended periods. For analyses, steelhead were considered to have “used” tributaries if their cumulative time inside tributaries was >12 h. This cutoff was selected to minimize the number of fish that used tributaries only incidentally (e.g., during exploratory movements or at night). Passage times through three study reaches (Bonneville to The Dalles, Bonneville to John Day, and The Dalles to John Day) were calculated from the dates fish passed each dam. Times were calculated using passage dates determined from telemetry records; use of dates rather than dates plus times allowed us to include fish that passed top-of-ladder sites during receiver outages but had other telemetry records that clearly identified passage date.

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Table 1. Numbers of adult steelhead (*Oncorhynchus mykiss*) that were collected and radio-tagged at Bonneville Dam during 6 study years.

	Unknown-origin samples				Known-origin samples			
	1996	1997	2000	Total	2001	2002	2003	Total
Total tagged	765	975	1160	2900	655	548	82	1285
Used in analyses	712	904	1084	2700	655	548	82	1285
Hatchery (%)	84	86	73	80	68	34	22	51
Wild (%)	16	14	27	20	32	66	78	49
Populations: based on final fish locations (unknown-origin) or juvenile tag site (known-origin)								
Deschutes River	86	78	69	265				
John Day River	21	33	36	90				
Umatilla River	4	8	12	24				
Walla Walla River	8	17	16	41				
Yakima River	4	5	8	17				
Hanford Reach	12	15	18	45				
Upper Columbia River	18	25	46	89	324	140	1	465
Lyons Ferry Hatchery	8	10	6	24				
Tucannon River	9	9	1	19				
Snake River above Lower Granite Dam	92	81	92	265				
Clearwater River	65	84	166	315	20	34	2	56
Grande Ronde River	18	38	30	86	3	18	2	23
Salmon River	72	92	114	278	16	10	4	30
Imnaha River					14	7	6	27
Lower Granite Dam (barged) ^a					160	213	51	424
Lower Granite Dam (in-river) ^a					118	126	16	260

Note: "Unknown-origin" fish were randomly collected. Natal basins for "known-origin" fish were identified from PIT tags implanted when fish were juveniles. Population assignment for unknown-origin fish was by final recorded location outside the monitored Columbia–Snake River Hydrosystem.

^aIncludes fish from Clearwater, Grande Ronde, Salmon, and Imnaha rivers and from the Snake River and its smaller tributaries upstream from Lower Granite Dam.

Stock and fate assignments

All unknown- and known-origin steelhead last recorded in tributaries or hatcheries upstream from The Dalles Dam or that passed Lower Granite Dam or Priest Rapids Dam were assigned to one of 14 populations (Table 1). Ten of the 14 populations were delineated by major tributary basins and one was a hatchery adjacent to the Snake River (Lyons Ferry). The three remaining groups were not tributary based: the "upper Columbia River" included all fish that passed the uppermost Columbia River monitoring site (Priest Rapids Dam), "Snake River above Lower Granite Dam" included fish that passed this dam but were not subsequently recorded in secondary tributaries, and "Hanford Reach" included fish last recorded in the Columbia River between the Snake River confluence and Priest Rapids Dam (Fig. 1). Each of the study populations supports multiple distinct spawning stocks and further separation is possible (e.g., Brannon et al. 2004; Winans et al. 2004; Keefer et al. 2008a). However, we elected to combine stocks within basin to more clearly demonstrate basic patterns. Unknown-origin fish that were harvested or that were last recorded at main stem sites were not assigned to populations. Some steelhead were almost certainly last recorded in nonnatal locations (i.e., they were "strays") and their population assignment was therefore incorrect. In previous analyses, Snake River steelhead were most likely to stray into the Deschutes and John Day rivers (Keefer et al. 2008b), and this should be considered in the interpretation of results. For example, some fish assigned to the Deschutes and John Day rivers were likely from upriver

populations, adding a small bias of unknown direction to thermoregulatory estimates for these stocks.

Each known-origin steelhead was assigned to one of five fate categories. Successful migrants were those that returned to natal tributaries or hatcheries or that passed the uppermost monitored dams (Lower Granite and Priest Rapids). Fish whose transmitters were returned from commercial gillnet, sport, and tribal fisheries through a reward program (US\$10–100) were assigned to either main stem or nonnatal tributary harvest categories based on reported harvest location. Known-origin fish last recorded at antennas in nonnatal tributaries were considered strays, and those last recorded at main stem sites between dams were assigned unknown fate. Both stray and unknown main stem fate categories included unreported harvest as well as nonharvest mortality.

Statistical analyses

To identify potential thermoregulatory threshold temperatures, each fish was assigned a reservoir entry temperature using mean daily Columbia River temperatures from water quality monitoring sites at Bonneville or The Dalles (www.cbr.washington.edu/dart/river.html). Run-of-river reservoirs in the Columbia River have little thermal stratification and temperatures at these sites were strongly correlated. Temperature at date of reservoir entry was selected because fish could easily reach refugia sites within 8–12 h after entering either reservoir. Daily data were also reasonable as steelhead that do not use refugia generally pass through the study reservoirs in <1–3 days (Keefer et al. 2004). Reservoir entry

temperatures were summarized for fish that subsequently did or did not use refugia sites for both the aggregated populations and individual populations (successful migrants) and years separately. Logistic regression was used to model population-specific refugia use probabilities in the Bonneville reservoir.

We tested for associations between refugia use and known-origin steelhead fate (2001–2003 only) using Pearson's χ^2 tests. The four fate classes were successful migrant, main stem harvest, nonnatal tributary, and main stem unknown fate. In these tests, the nonnatal tributary group included strays and fish reported harvested in the tributaries. Approximately a third of the nonnatal tributary group was reported harvest, and unreported harvest was a likely fate for the majority of the remainder because almost no fish were reported on spawning grounds and many transmitter signals ceased, consistent with harvest removal. We note that strays are typically considered a loss from source populations, ecologically equivalent, in this case, to harvest or unknown loss. Within the fate analyses, hatchery and wild fish were evaluated separately and in aggregation, because management implications differ for the two groups.

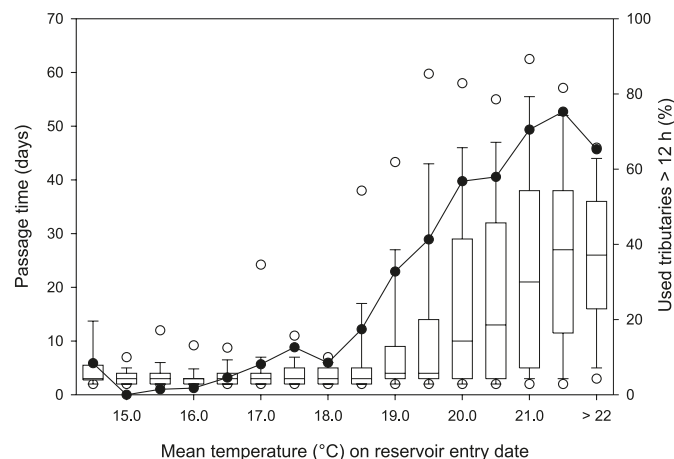
Because harvest tends to be higher for larger fish and both behavior and fate differ seasonally (e.g., Keefer et al. 2005; Hard et al. 2008), steelhead length and migration timing at Bonneville Dam were compared among fate classes using ANOVA. Models used to evaluate potential delayed effects upstream were similar to the Pearson tests described above for overall fish fate, except that steelhead had to pass the dam upstream from refugia sites (The Dalles Dam for Bonneville tributary sites and John Day Dam for all study sites) to be included in comparisons. In other words, fish in these comparisons had survived their initial thermoregulatory behavior and resumed upstream migration. Importantly, tests for delayed effects did not include premature mortality (harvest or otherwise) that occurred upstream from Lower Granite Dam or Priest Rapids Dam because monitoring of these areas was spatially and temporally limited.

Results

Thermoregulatory behavior

Across all study years, steelhead use of thermal refugia in Bonneville reservoir tributaries rapidly increased after mean daily main stem water temperatures reached $\sim 19^\circ\text{C}$ (Fig. 3). Fish that entered the reservoir when temperatures were $< 19^\circ\text{C}$ passed from Bonneville Dam to The Dalles Dam in a median of 3 days ($n = 689$), with 10% recorded in cool-water tributaries. At reservoir entry temperatures of $19\text{--}21^\circ\text{C}$, the median passage time was 6 days ($n = 1802$) and 49% used tributaries. Above 21°C , the median time was 25 days ($n = 731$) and 71% used tributaries. The telemetry data from tributary and confluence antennas strongly indicated that steelhead with passage times > 3 days spent most of the additional migration time inside refugia tributaries or in tributary plume areas where cool tributary water mixed with the main stem near confluences. Notably, Columbia River temperature profiles varied among years (Fig. 2), but steelhead behavior in relation to temperature was consistent (i.e., annual cool-water refugia use increased severalfold as temperatures rose above $\sim 19^\circ\text{C}$).

Fig. 3. Steelhead (*Oncorhynchus mykiss*) passage times from the top of Bonneville Dam to the top of The Dalles Dam (~ 73 rkm) by water temperature at the Bonneville water quality monitoring site on the date that each fish entered the Bonneville reservoir. Box plots show median, quartile, and 10th and 90th percentiles pooled across study years; 5th and 95th percentiles are marked by open circles. The solid line with solid circles shows the percentage of steelhead recorded in cool-water Bonneville reservoir tributaries for > 12 h.

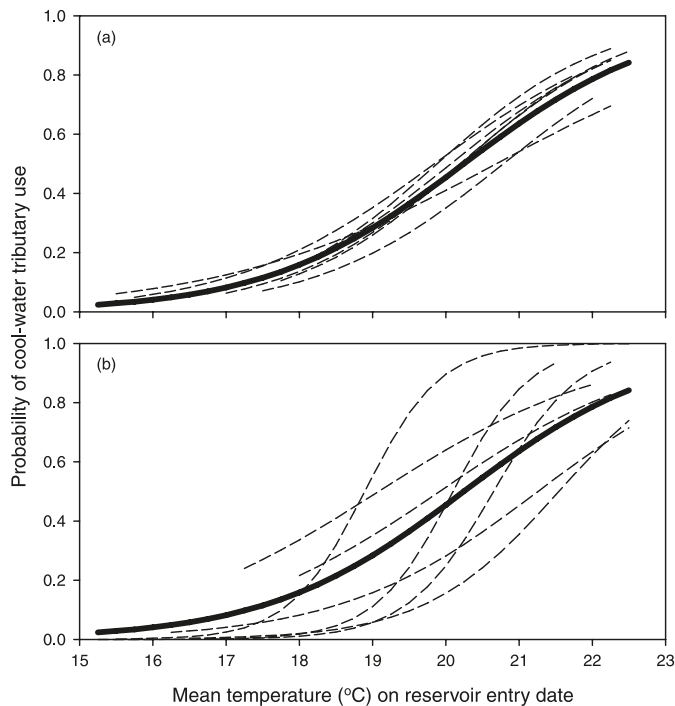


Steelhead use of the Deschutes River where it enters The Dalles reservoir similarly increased as Columbia River temperatures rose. However, fewer fish had thermoregulatory behaviors in The Dalles reservoir because most entered the reach relatively later in the migrations and encountered cooler conditions. Across years, median steelhead reservoir entry dates were 24 August at Bonneville Dam near peak temperatures versus 13 September, when temperatures were decreasing, at The Dalles Dam (Fig. 2). Overall, 27% of steelhead that entered The Dalles reservoir ($n = 3222$) and 28% of those that eventually passed John Day Dam ($n = 2762$) were recorded in the Deschutes River. Median passage times through the 38 rkm reach were 15 days for fish that used the Deschutes River ($n = 744$) versus 2 days for fish that did not ($n = 1953$). Median passage times through the combined Bonneville to John Day reach were five times longer for fish recorded using cool-water tributaries (32 days, $n = 1662$) than for fish not recorded in tributaries (6 days, $n = 1046$).

Stock-specific refugia use patterns by successful migrants paralleled those for the aggregate runs, with consistent evidence for a thermoregulatory threshold near 19°C and rapidly increasing duration of use at higher temperatures. Stock-specific logistic regression models of refugia use in the Bonneville reservoir were consistent for the seven stocks with the largest sample sizes (Fig. 4a). Predicted use probabilities were more variable among stocks with small sample sizes and lower statistical power, although the overall response was similar (Fig. 4b). The two populations with the greatest modeled difference from the aggregate sample had the smallest sample sizes (Tucannon River, $n = 23$; Yakima River, $n = 26$).

Both the percentage of fish that used refugia and the duration of use differed more than twofold among populations (Fig. 5). Differences were related to stock-specific migration

Fig. 4. Population-specific refugia use probabilities estimated by logistic regression models. The predictor variable was water temperature at the Bonneville water quality monitoring site on the date that steelhead (*Oncorhynchus mykiss*) entered the Bonneville reservoir and the dependent variable was use of a Bonneville refugia tributary for >12 h. (a) Populations with large sample sizes: Deschutes River, John Day River, upper Columbia River, Snake River upstream from Lower Granite Dam, Clearwater River, Grande Ronde River, and Salmon River. (b) Populations with small sample sizes: Umatilla River, Walla Walla River, Yakima River, Hanford Reach, Tucannon River, Lyons Ferry Hatchery, and Imnaha River. Solid lines show modeled probabilities for all 14 populations combined and dashed lines show population-specific probabilities.



timing and associated seasonal warming and cooling (Fig. 6). On average, stocks migrating earliest (Tucannon, Hanford Reach, and Lyon's Ferry) encountered the lowest mean daily temperatures in the Bonneville reservoir, were least likely to use refugia, and passed through the Bonneville to John Day reach fastest. The latest timed stock (Clearwater) also encountered relatively cool main stem temperatures and had migration rates most similar to those of early migrants. In contrast, stocks with the longest passage times and highest rates of refugia use (Grande Ronde, Imnaha, John Day, and Umatilla) had migration timing distributions that coincided with the warmest migration conditions (Figs. 5 and 6). Migration times for fish not recorded in tributaries were consistent across populations, with median Bonneville to John Day passage times of 5–8 days. The single exception was the small sample of Imnaha steelhead (median = 16.5 days, $n = 9$).

Fish fate

Final fates of known-origin steelhead in 2001–2003 indicated lower overall migration success for fish that used thermal refugia (Fig. 7). With all groups combined, mean annual

Fig. 5. Relationships between median population-specific steelhead (*Oncorhynchus mykiss*) passage times from the top of Bonneville Dam to the top of John Day Dam (~112 rkm) and the percentages of steelhead that were (solid circles) and were not (open circles) recorded in cool-water tributaries for >12 h. Results pooled for successful migrants across study years. TUC, Tucannon River; HAN, Hanford Reach; LFH, Lyons Ferry Hatchery; UCR, Upper Columbia River; WWR, Walla Walla River; CWR, Clearwater River; SAL, Salmon River; SNK, Snake River above Lower Granite Dam; YAK, Yakima River; IMR, Imnaha River; GRR, Grande Ronde River; UMA, Umatilla River; JDR, John Day River.

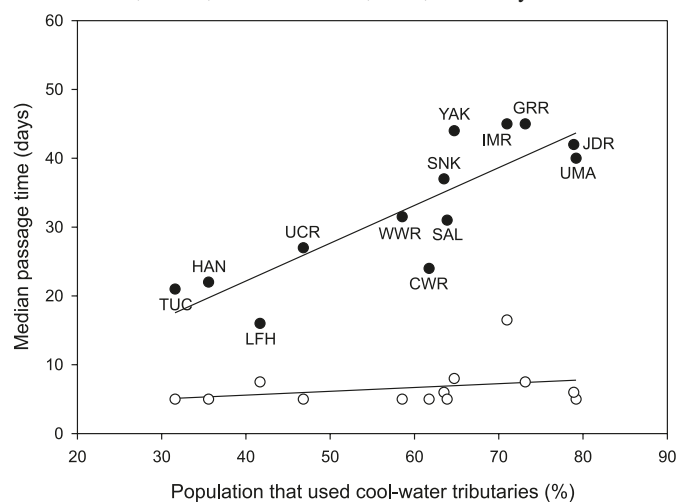
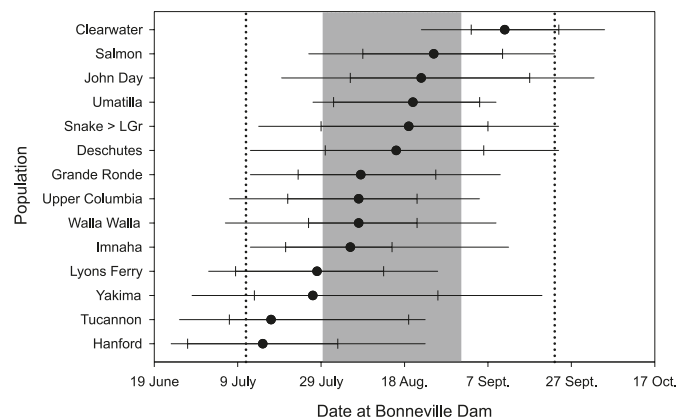
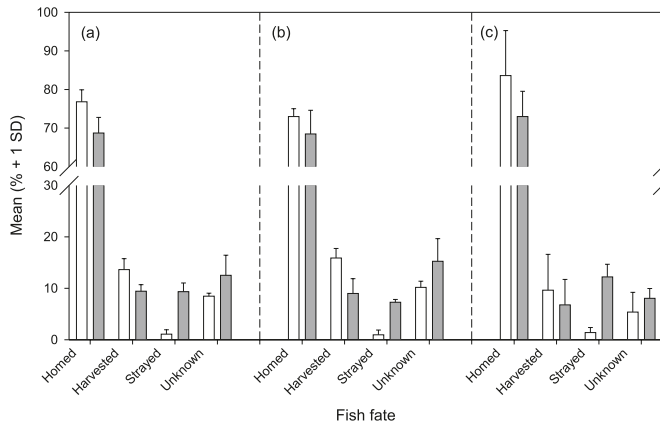


Fig. 6. Migration timing distributions (median, quartiles, and 10th and 90th percentiles) at Bonneville Dam for steelhead (*Oncorhynchus mykiss*) that successfully returned to tributaries or hatcheries pooled across study years. Populations were identified by final fish locations. The vertical dotted 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.



homing success was 8.1% lower for steelhead that used tributaries (68.7%) than for those that did not (76.8%). Differences were 4.5% for wild steelhead (68.5% versus 73.0%) and 10.6% for hatchery steelhead (73.0% versus 83.6%). Allocations among unsuccessful categories (main stem harvest, unknown fate, and harvest in refugia/permanent straying) showed higher unknown loss for fish that used tributaries and relatively high harvest rates in refugia sites (Fig. 7). In contrast, main stem harvest (which included both gillnet and recreational fisheries) tended to be higher for fish not re-

Fig. 7. Mean annual estimates of homing, main stem harvest, straying, and unknown fate for known-origin steelhead (*Oncorhynchus mykiss*) that were (shaded bars) or were not (open bars) recorded using tributary thermal refugia in the lower Columbia River during the 2001–2003 migrations. (a) All fish; (b) wild fish; (c) hatchery fish. The “strayed” category includes permanent strays to nonnatal basins and fish reported harvested inside monitored tributary refugia.



corded in refugia. Distributions among the four fate classes differed significantly for wild fish in 2001 ($\chi^2 = 7.9$, $df = 3$, $P = 0.048$, $n = 208$) and 2002 ($\chi^2 = 17.0$, $df = 3$, $P < 0.001$, $n = 357$) but not in 2003 ($\chi^2 = 1.9$, $df = 3$, $P = 0.591$, $n = 63$). Similarly, differences were significant for hatchery fish in 2001 ($\chi^2 = 17.5$, $df = 3$, $P < 0.001$, $n = 447$) and 2002 ($\chi^2 = 11.5$, $df = 3$, $P = 0.009$, $n = 185$) but not in 2003 ($\chi^2 = 1.8$, $df = 3$, $P = 0.403$, $n = 20$). We note that many fish harvested in the main stem were reported captured near tributary mouths where they may have been using cool-water tributary plumes. Treating these fish as “not using” refugia sites likely reduced the power to detect statistical differences among categories.

Fate patterns for individual populations were more mixed (Table 2), at least in part due to among-stock migration timing and demographic differences that affected harvest. For the predominantly (96%) hatchery origin upper Columbia group, steelhead last recorded in refugia were larger (75.0 cm) than fish harvested in the main stem (72.2 cm), fish that homed (70.6 cm), and fish with unknown fate (70.0 cm) (ANOVA: $F = 5.18$, $df = 464$, $P = 0.002$). Mean migration timing at Bonneville Dam was latest for upper Columbia fish harvested in the main stem (13 August) and progressively earlier for fish that homed (7 August), that were last recorded in refugia (6 August), and with unknown fate (3 August) ($F = 2.52$, $df = 464$, $P = 0.057$). Sample sizes were limiting for several of the Snake River known-origin groups. However, with all Snake River wild fish combined, main stem harvested fish were largest (74.4 cm) followed by fish that homed (72.3 cm), fish with unknown fate (69.7 cm), and fish last recorded in refugia (68.7 cm) ($F = 3.57$, $df = 613$, $P = 0.014$). Both Snake River wild and hatchery steelhead last recorded in refugia migrated earlier (8–14 days on average) than fish in other fate classes; these timing differences were not statistically significant ($P > 0.26$).

Snake River steelhead fates did differ ($\chi^2 = 13.1$, $df = 3$, $P = 0.004$) for wild versus hatchery fish. With all Snake River groups combined, wild fish were twice as likely to

have unknown fate (12.9%, $n = 614$) as hatchery fish (6.3%, $n = 206$). Further, more wild (10.8%) than hatchery fish (8.3%) were reported harvested in main stem fisheries, more hatchery (9.7%) than wild fish (4.7%) were last recorded in refugia sites, and more hatchery (75.7%) than wild fish (71.5%) returned to Lower Granite Dam or Snake River tributaries.

Delayed effects

There was little evidence that steelhead survival upstream from The Dalles and (or) John Day dams was affected by thermoregulatory behavior in reservoir reaches downstream from these sites. For example, of all known-origin fish that passed The Dalles Dam, those that used refugia downstream in Bonneville reservoir homed and were harvested at similar rates as fish that did not use Bonneville refugia (Table 3). Similarly, fates of fish that passed John Day Dam did not differ with downstream refugia use in Bonneville or The Dalles reservoirs. Nonsignificant ($P > 0.05$) results were consistent for hatchery and wild fish separately and for individual years. In delayed effects tests using individual populations, upstream fates differed with thermoregulatory behavior only for the Snake River barged group that passed John Day Dam (all fish pooled across years). In this case, barged fish recorded in tributaries were less likely to home (76.3%) and were more likely to be harvested (4.7%), to last be recorded in nonnatal tributaries (8.8%), and to have unknown fate (10.2%) than fish not recorded in tributaries (home = 87.3%, harvest = 1.4%, nonnatal tributary = 2.8%, and unknown = 8.5%) ($\chi^2 = 9.1$, $df = 3$, $P = 0.028$, $n = 357$). Results were nonsignificant ($P > 0.05$) when the barged group was separated into groups based on origin (hatchery or wild) or year.

Discussion

Behavioral thermoregulation

The first study objective was to identify temperatures that provoked behavioral thermoregulation in adult steelhead. An apparent threshold for the initiation of refugia use was associated with Columbia River warming to $\sim 19^\circ\text{C}$, when about a third of the telemetered migrants were recorded in cool-water tributary areas. By comparison, $<10\%$ were detected in refugia when main stem temperatures were between 14 and 18°C . With continued warming, the likelihood of thermoregulation rapidly increased, with $>70\%$ of the aggregate run using refugia at the warmest times (i.e., $\geq 21^\circ\text{C}$). Typical refugia residence times were on the scale of hours to days at 19°C but increased to weeks and even months when temperatures were 20°C and higher. Temperatures associated with the initiation of refugia use were relatively constant across populations, and large percentages of all groups used refugia when main stem temperatures were highest.

Steelhead thermoregulatory behaviors differed substantially from those of Columbia River fall-run Chinook salmon (*Oncorhynchus tshawytscha*) that comigrate with steelhead in August–October. In a concurrent study by Gonia et al. (2006), fall Chinook salmon experienced similar peak temperatures and used the same refugia as steelhead, but only 9% stayed more than 12 h and typical residence times were 3–5 days. A fall Chinook salmon thermoregula-

Table 2. Summary of known-origin steelhead (*Oncorhynchus mykiss*) fates by natal basin, rearing type (hatchery, wild), and use of cool-water tributaries in the Bonneville or The Dalles reservoir.

Stock	Rearing type	Tributary use	n	Fate				χ^2	P		
				Successful	Main stem harvest	Nonnatal tributary ^a	Main stem unknown				
UpperColumbia	All	No	234	76.5	14.1	1.3	8.1	25.3	<0.001		
		Yes	228	63.6	13.2	12.7	10.5				
	Hatchery	No	226	76.1	14.2	1.3	8.4			25.1	<0.001
		Yes	217	64.1	12.4	13.4	10.1				
	Wild	No	8	87.5	12.5					2.7	0.263
		Yes	11	54.6	27.3		18.2				
Snake (barged)	All	No	170	72.9	12.9	2.4	11.7	17.6	<0.001		
		Yes	248	66.1	6.5	11.7	15.7				
	Hatchery	No	24	83.3	4.2	4.2	8.3			2.8	0.424
		Yes	42	66.7	7.1	16.7	9.5				
	Wild	No	146	71.2	14.4	2.1	12.3			16.3	0.001
		Yes	206	66.0	6.3	10.7	17.0				
Snake (in-river)	All	No	114	75.6	17.5	0.9	7.0	10.6	0.014		
		Yes	144	79.9	8.3	6.9	4.9				
	Hatchery	No	28	75.0	14.3	3.6	7.1			6.8	0.077
		Yes	48	83.3	2.1	12.5	2.1				
	Wild	No	86	74.4	18.6		7.0			5.3	0.154
		Yes	96	78.1	11.5	4.2	6.3				
Snake (other ^b)	All	No	50	78.0	14.0	2.0	6.0	2.3	0.514		
		Yes	86	77.9	8.1	5.8	8.1				

Note: Steelhead in the Snake River barged and in-river groups were PIT-tagged at Lower Granite Dam and either transported downstream or released back to the river. Those in the Snake River (other) group were PIT-tagged in tributaries or at hatcheries upstream from Lower Granite Dam. Statistical results from Pearson χ^2 tests.

^aPermanent strays to nonnatal basins and fish reported harvested inside monitored tributary refugia.

^bClearwater ($n = 56$), Grande Ronde ($n = 23$), Salmon ($n = 30$), and Imnaha ($n = 27$).

Table 3. Tests for delayed effects of cool-water tributary use on main stem fates of known-origin steelhead (*Oncorhynchus mykiss*) after they passed over The Dalles and (or) John Day dams.

Dam passed	Rearing type	Tributary use	n	Fate				χ^2	P		
				Successful	Main stem harvest	Nonnatal tributary ^a	Main stem unknown				
The Dalles	All	No	622	81.4	7.2	3.4	8.0	0.5	0.919		
		Yes	517	80.1	7.4	4.1	8.5				
	Hatchery	No	321	81.9	8.1	3.4	6.5			0.5	0.930
		Yes	252	81.0	7.5	3.6	7.9				
	Wild	No	301	80.7	6.3	3.3	9.6			0.8	0.856
		Yes	265	79.3	7.2	4.5	9.1				
John Day	All	No	478	89.3	3.1	1.5	6.1	5.5	0.137		
		Yes	574	85.9	4.4	3.5	6.3				
	Hatchery	No	258	89.2	3.9	1.6	5.4			0.7	0.876
		Yes	269	88.1	5.2	1.9	4.8				
	Wild	No	220	89.6	2.3	1.4	6.8			6.0	0.111
		Yes	305	83.9	3.6	4.9	7.5				

Note: Tributary use was limited to tributaries to the Bonneville reservoir for fish that passed The Dalles Dam and to tributaries to the Bonneville or The Dalles reservoir for fish that passed John Day Dam.

^aPermanent strays to nonnatal basins and fish reported harvested inside monitored tributary refugia.

tory threshold was identified at about 20 °C (Gonia et al. 2006). Behavioral differences between these species reflect divergence in life history and migration timetables. The Chinook salmon are obligate fall spawners with a relatively narrow migration window (Dauble and Watson 1997), whereas steelhead have temporally plastic migrations in the seasons preceding spring spawning (Brannon et al. 2004; Quinn

2005). The migration schedule of a third Columbia River salmonid, sockeye salmon (*Oncorhynchus nerka*), overlaps the first half of the steelhead migration and presents a third strategy. Peak adult sockeye passage in the study reach is from mid-June to mid-July when mean daily temperatures are mostly 15–19 °C (Quinn et al. 1997), and the run rapidly passes through the lower river with little evidence of refugia

use (Naughton et al. 2005). Instead, sockeye salmon often encounter high water temperatures at upriver sites closer to spawning grounds where extended migration delays (Major and Mighell 1967; Hyatt et al. 2003) and refugia use (Keefer et al. 2008c) have been reported at temperatures of 20–21 °C.

The behaviors and migration schedules of the three species may reflect alternative evolutionary approaches to avoiding stressful or lethal Columbia River temperatures. Fall-spawning sockeye and fall Chinook salmon migrate mostly before (sockeye) or after (Chinook) historic peak main stem temperatures. Variations of these two patterns are repeated throughout the species' Pacific Rim ranges, with site-specific adaptations to long-term temperature and flow regimes (Groot and Margolis 1991; Myers et al. 1998; Hodgson and Quinn 2002). Historically, Columbia River summer steelhead may have used the same temperature avoidant strategies as both Chinook and sockeye salmon, as their passage distributions in the lower river were bimodal with a nadir in late summer during temperature peaks (Robards and Quinn 2002). However, with development of the Columbia River Hydrosystem, main stem temperatures have significantly increased and bimodality in the steelhead run has shifted to a relatively flat distribution that overlaps the warmest temperatures (Robards and Quinn 2002). Earlier spring warming, higher summer temperatures, and later fall cooling (e.g., Quinn et al. 1997) means that many more steelhead now encounter high water temperatures, and it is likely that a larger proportion of the run thermoregulates during migration compared with historically. It is not clear, however, whether the recent run timing shift can be explained by environmental changes and attendant behavioral responses by steelhead or if other factors (i.e., loss of native stocks and proliferation of hatchery fish (Busby et al. 1996)) are responsible.

Importantly, neither the fitness consequences of cumulative temperature exposure during migration nor the potential for thermal refugia use to ameliorate temperature effects has been directly evaluated for steelhead in unregulated systems. This will be an important next step in the evaluation of the population-level effects of refugia use. For adults, potential negative temperature impacts include elevated physiological and energetic demands (Brett 1995; Lee et al. 2003; MacNutt et al. 2006), greater susceptibility to disease incidence and severity (e.g., Wagner et al. 2005), and higher prespawn mortality (Crossin et al. 2008; Keefer et al. 2008c). High temperature exposure also lowers reproductive success, egg viability, and the fitness of progeny (e.g., Flett et al. 1996; King et al. 2007). Behavioral thermoregulation during migration, like premature and multiphase migrations, may therefore have developed in response to selective constraints on adults and subsequent effects on juveniles (e.g., emergence timing, fry growth, and survival) (Dodson 1997; Quinn 2005).

Variability among populations

In addressing the second objective, we found that the percentage of thermoregulating fish and the duration of thermoregulation significantly varied among study populations. Refugia use patterns strongly supported our first hypothesis, as the behavior appeared to be a function of population-specific migration timing and attendant among-population differences in encountered river temperatures. Relatively early-

and late-migrating populations encountered lower mean water temperatures in the study reach each year. These populations had fewer individuals use refugia sites, and those that did typically remained for relatively shorter periods. On average, the longest refugia use times were for populations with median migration dates in the last week of July or first week of August, coincident with mean Columbia River water temperatures reaching ~21 °C. A third group, the populations with the highest percentages of fish using refugia, had median passage dates in mid-August, or about the time of peak main stem temperatures. We did not attempt to untangle the effects of migration timing (i.e., date effects) from the effects of main stem temperature, as the two were strongly correlated in all years. However, it is possible that timing-related factors unassociated with water temperature, such as river discharge, photoperiod, or conspecific abundance, also affected steelhead behaviors.

Migration timing distributions for the 14 study populations varied considerably, with median passage dates at Bonneville Dam ranging from mid-July to mid-September. The most temporally distinctive distribution was for the relatively late-migrating Clearwater River steelhead, which are part of a Snake River population complex that spends an additional year in the ocean. These larger fish are believed to have been historically abundant in the late mode of the Columbia River run (Busby et al. 1996; Brannon et al. 2004). Among-population timing differences presumably reflect selective pressures that parallel those for the among-species differences in migration timing. For example, it is likely that conditions in spawning tributaries influenced divergence in adult migration timing given the strong organizing effects of environmental conditions during spawning and subsequent juvenile life stages (Quinn et al. 2000; Waples et al. 2004). Migration distance and seasonal migration obstacles (e.g., falls, low flows, temperature barriers, etc.) in both the main stem and tributaries may also have shaped the divergent timing patterns. As additional data become available, it should be possible to better define migration timing distributions for the Columbia's many subbasin steelhead populations. We expect that more nuanced behavioral differences among groups will also be identified. Improving upon our relatively coarse-scale population analyses will be useful for predicting how many fish from either individual or aggregated populations will have thermoregulatory responses within a given year or at specific temperature criteria. Such data can be used to develop appropriate management plans for steelhead with conservation priority.

The overall behavioral consistency among populations suggests exposure to a shared historic selective regime, perhaps during the postglacial period of salmon and steelhead recolonization of the interior basin (e.g., McPhail and Lindsey 1986; Waples et al. 2008). Such a regime potentially predated divergence among Columbia River steelhead populations. Steelhead also may have adapted similar thermoregulatory responses across populations through a process of parallel evolution (e.g., across-population exposure to extreme events or similarity in hydrologic regimes across spatially separated sites; Waples et al. 2004; Beechie et al. 2006).

We note that there was substantial individual variability among steelhead from all identified populations. Some fish showed no thermoregulatory behavior despite migrating at

the warmest times, while others remained in refugia for weeks to months after fall cooling (e.g., Keefer et al. 2008a). Similarly, some steelhead used multiple refugia sites with repeated entries and exits, while others showed high fidelity to single locations (see High et al. 2006). This variability echoes steelhead activities in winter when Columbia River fish hold for varying lengths of time, move up- and downstream past dams, and temporarily enter nonnatal tributaries (Keefer et al. 2008a). Behavioral plasticity across seasons results in mixed stock aggregations that are spatially distributed over long segments of the migration route. Taken together, these behaviors reflect either a remarkable evolutionary legacy of adaptation to stochastic environments (e.g., Hilborn et al. 2003; Dickerson et al. 2005; Wilbur and Rudolf 2006) or a more recent, less adaptive consequence of rapid demographic and environmental changes (e.g., Araki et al. 2008; Hutchings and Fraser 2008).

Mortality trade-offs

Our third objective was to assess associations between refugia use and known-origin steelhead fate. The survival results strongly suggested that use of thermal refugia, a normally adaptive behavior, might carry a relatively high mortality risk in this system. The negative outcome is characteristic of an "ecological trap" where animals respond to a reliable evolutionary cue but then experience reduced survival or reproductive success (Coutant 1987; Schlaepfer et al. 2002; Robertson and Hutto 2006). In our samples, steelhead that used refugia were about 8% less likely to complete migration through the monitored Hydrosystem, and survival costs were significant for both hatchery (~11%) and wild (~5%) fish. The mortality appeared to be most directly related to fisheries inside refugia where reported harvest rates were about 13% for upper Columbia steelhead populations and ranged from 4%–17% for the various Snake River groups. Importantly, a portion of the negative thermoregulatory effect may have been indirect, particularly if steelhead in poor physical condition (i.e., with pathogens or relatively low energetic reserves) were more likely to use refugia sites. Unknown loss in the main stem was also higher for the thermoregulating group in most known-origin populations, likely reflecting unreported harvest near confluence areas and possible indirect effects on natural mortality. Overall, we believe that differences in overall mortality estimates between fish that did or did not use refugia may be conservative for two reasons. First, information returned with transmitters suggested that some "nonthermoregulating" fish harvested in the main stem were almost certainly caught in cool-water plumes from refugia tributaries (i.e., they were incorrectly identified as not using refugia). Second, several dozen known-origin fish were harvested in the main stem before they had an opportunity to enter refugia, a bias that would lead to underestimation of refugia effects.

The mortality and migration timing patterns provided compelling, but indirect, support for our hypothesis that mortality risks associated with thermoregulation differ among populations. Although mortality trade-offs related to refugia use likely vary among populations, we are hesitant to extrapolate results from the known-origin samples to the Columbia's many steelhead stocks given demographic (i.e., hatchery or wild), selective harvest, and migration timing

differences among populations. On balance, we expect that population-level risk of harvest inside thermal refugia is likely greatest for fish that enter the study reach during the peak of thermoregulatory behavior from late July through early September. The presumed mortality for strays that were not reported harvested is also likely highest for those entering during the thermoregulatory peak. Risk of main stem harvest is presumably highest for early and late migrants when fisheries effort is concentrated outside refugia. This early-season harvest hypothesis is supported by the escapement summaries for unknown-origin steelhead reported in Keefer et al. (2005), which showed that Hydrosystem survival was lowest for steelhead that passed Bonneville Dam in late May and June. Low survival during this period was related to both main stem harvest and unknown main stem mortality. Risks also clearly differed for wild and hatchery steelhead because some protection was afforded wild fish (i.e., mandatory release of rod-caught fish with intact adipose fins). However, relatively high percentages of wild fish in the sampled known-origin populations had unknown fates, indicating either illegal harvest, greater susceptibility to "natural" mortality, or possible handling mortality following catch and release (e.g., Bendock and Alexandersdotir 1993). The latter may be of special concern given the combined negative effects of fish handling and high water temperatures (Dempson et al. 2002; Cooke and Suski 2005).

In the fourth objective, we tested for delayed mortality effects with the expectation that steelhead might be targeted after exiting refugia sites as temperatures decreased in the fall. However, we found little evidence that harvest rates in upstream reaches differed between steelhead that did and did not use the studied refugia. Unlike during the onset of high water temperatures, when fisheries in the study area efficiently shifted from main stem to refugia sites, there was no indication of a large-scale shift to main stem fisheries as temperatures decreased. The general lack of delayed effects may have been because fish were not spatially aggregated after exiting refugia or because there was no clear threshold temperature for refugia exit timing. The single statistically significant delayed effect was that Snake River fish that were barged as juveniles had lower upstream survival, consistent with a broader pattern of reduced homing and increased migration mortality for transported fish (Keefer et al. 2008b).

In summary, migrations of Columbia River summer-run steelhead are spatially and temporally complex, in large part because adults encounter a wide range of environmental conditions that include water temperatures near both upper tolerance limits (21–25 °C) and annual minima (1–5 °C). Steelhead have adapted by migrating in phases, with bouts of upstream movement when conditions are favorable and holding or refuge seeking when conditions are stressful. During summer temperature peaks, cool-water habitats are spatially constricted and patchily distributed, resulting in dense adult aggregations in midmigration. The refugia that steelhead used in this study were clustered along the margins of a relatively short (<100 rkm) section of the lower migration corridor, hundreds to more than 1000 km downstream from spawning grounds. Despite their small spatial extent, these few refugia sites were used by >75% of the tagged steelhead from some upriver populations, with many fish holding for weeks to months. The behaviors underscore

the critical importance of thermal refugia in the Columbia River system where decades-long warming of the migration corridor (e.g., Quinn et al. 1997) is forecast to accelerate with regional climate change (Hamlet and Lettenmaier 1999; Battin et al. 2007).

Despite the apparent survival costs, the presumed benefits of steelhead refugia use should not be discounted. Experiments with rainbow trout, Atlantic salmon (*Salmo salar*), and sockeye salmon have all shown that exposure to high water temperature can have large negative effects on fish performance, maturation, survival, and productivity (e.g., Pankhurst et al. 1996; King et al. 2007; Crossin et al. 2008). The recorded steelhead use of refugia almost certainly reduced these effects to varying degrees. The behaviors also presumably helped conserve energy needed to complete migration, compete for redd sites, and spawn (e.g., Berman and Quinn 1991; Newell and Quinn 2005). Future biotelemetry studies that monitor both migration behaviors and reproductive success (e.g., Mann and Peery 2005) or laboratory-based experiments that simulate thermal histories and monitor survival outcomes (e.g., Crossin et al. 2008) will provide a more complete cost-benefit accounting of steelhead refugia use. In the Columbia River system, where many important refugia have already been identified, managers must now balance demands for fisheries with more conservative restrictions in refugia sites to protect populations listed under the Endangered Species Act.

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