North American Journal of Fisheries Management 28:81–96, 2008

DOI: 10.1577/M07-011.1

[Article]

Overwintering Distribution, Behavior, and Survival of Adult Summer Steelhead: Variability among Columbia River Populations

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Abstract.—Unlike most anadromous salmonids, summer steelhead *Oncorhynchus mykiss* overwinter in rivers rather than the ocean for 6–10 months prior to spring spawning. Overwintering in rivers may make summer steelhead more vulnerable to harvest and other mortality sources than are other anadromous populations, but there has been little systematic study of this life history strategy. Here, we used a large-scale radiotelemetry study to examine the overwintering behaviors and distributions of 26 summer steelhead stocks within the regulated lower Columbia–Snake River hydrosystem. Over 6 years, we monitored 5,939 fish, of which 3,399 successfully reached spawning tributaries or the upper Columbia River basin and were assigned to specific populations. An estimated 12.4% of fish that reached spawning areas overwintered at least partially within the hydrosystem (annual estimates = 6.8–19.6%), while the remainder overwintered in tributaries. Across all populations, later-arriving fish were more likely to overwinter in the hydrosystem; overwintering percentages ranged from less than 1% for fish tagged in June to over 40% for those tagged in October. Proportionately more interior-basin steelhead (Clearwater, Salmon, and Snake River metapopulations) overwintered in the hydrosystem than did fish from lower-river populations. Steelhead were distributed in mixed-stock assemblages throughout the hydrosystem during winter, usually in reservoirs closest to their home rivers but also in nonnatal tributaries. Overwintering fish moved upstream and downstream between reaches in all months; a nadir occurred in early January and peak egress into spawning tributaries was in March. The estimated survival to tributaries was higher for fish that overwintered in the hydrosystem (82%) than for fish that did not (62%); this difference was largely attributable to low winter harvest rates. Our results suggest that large main-stem habitats, including reservoirs, may be widely used by overwintering summer steelhead. The complex migration behaviors of steelhead indicate both the potential for adaptation and possible susceptibility to future river environment changes.

The life history strategy of summer steelhead *Oncorhynchus mykiss* (anadromous rainbow trout) is unique among anadromous Pacific salmonids in that returning adults enter freshwater from spring through late fall, overwinter, and then spawn during the subsequent spring (Busby et al. 1996; Quinn 2005). Extended river residence prior to spawning (up to 11 months: Busby et al. 1996) is thought to be an adaptation to long-term environmental conditions in migration corridors and on spawning grounds. Robards and Quinn (2002), for example, hypothesized that seasonal temperature or discharge barriers historically prevented summer-run fish from reaching spawning sites during the season in which they began reproductive migrations. Many interior summer steelhead stocks also migrate from several hundred to more than 1,500 km to reach high-elevation spawning tributaries, and early migration may allow fish to move long distances and achieve large elevation gains that would be impossible at low winter and spring temperatures (Brett 1995; Trudel et al. 2004).

The approximate current geographic center of steelhead distribution in the eastern Pacific is the Columbia River basin (Brannon et al. 2004; Augerot 2005). Annual runs of more than 500,000 steelhead were estimated to have returned to the Columbia River near the end of the 19th century (Chapman 1986), but a variety of well-documented human activities decimated populations during the 20th century (National Research Council 1996; Lichatowich 2001; McClure et al. 2003). Several Columbia River steelhead populations were listed as threatened under the U.S. Endangered Species Act (ESA) in 1997–1999, including all interior-basin summer-run fish (National Marine Fisheries Service 1997; Good et al. 2005). These include mid- and upper-Columbia River populations as well as Snake River steelhead, which have among the longest inland steelhead migrations in the world (Busby et al. 1996). Since receiving ESA listing, some Columbia River steelhead populations have increased in size through hatchery supplementation, conservation efforts, harvest reform, and—in recent years—improved

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Received January 18, 2007; accepted May 15, 2007

dam operations and ocean conditions. Approximately 315,000 steelhead (on average) were counted annually at Bonneville Dam from 1995 to 2004 (U.S. Army Corps of Engineers 2005), making it the second-most abundant anadromous salmonid run during this period after fall Chinook salmon *O. tshawytscha* (1995–2004 average ≈ 328,000). Notably, however, returns of wild fish remain depressed (Good et al. 2005), and hatchery fish have made up approximately 75% of recent Columbia River steelhead runs.

The migration environment for summer steelhead in the Columbia River has been radically altered over the last seven decades by the construction and operation of a series of large hydroelectric dams (National Research Council 1996). Main-stem migration corridors have largely been converted from free-flowing lotic environments to run-of-river reservoir habitats by the construction of 10 hydroelectric dams (part of the federal Columbia River power system [FCRPS], also referred to here as the hydrosystem) and several additional dams owned by public utility districts. In response, water temperatures have increased, especially in fall, and flow regimes have been moderated, as indicated by lower runoff peak flows and higher winter base flows (Quinn and Adams 1996; Quinn et al. 1997; Peery et al. 2003). These physical and environmental changes, combined with substantial hatchery effects and loss of native stock diversity, have resulted in complex shifts in steelhead migration timing (Robards and Quinn 2002) and altered migration behaviors (Evans et al. 2004; Keefer et al. 2004a; High et al. 2006).

The extended and often convoluted migrations of Columbia River summer steelhead present many monitoring and management challenges, including considerable uncertainty about wintertime distributions and behaviors. Furthermore, adult migrants were historically not counted at the majority of the system's dams during 1 November–31 March, and count data are still not collected at most projects during December–February. This monitoring gap has made accurate enumeration of Columbia River steelhead difficult and has raised questions about appropriate winter dam operations and fisheries regulations for ESA-listed populations. Our objectives in this summary were to help address these gaps by describing basic summer steelhead overwintering distributions and behaviors within the lower Columbia–Snake River hydrosystem. Using a large-scale, multiyear radiotelemetry database, we screened 5,939 detailed adult migration histories to identify FCRPS-overwintering fish and then assessed their wintertime inter-reach movements, nonnatal tributary use, and distributions. We focused on migrants that successfully returned to spawning tributaries because this allowed for within- and among-population assessment of the effects of migration timing and the relationships between photoperiod, water temperature, discharge, the onset of overwintering, and the resumption of migration in spring. We also examined the seasonal patterns of harvest and unaccounted-for loss within the FCRPS using the larger radio-tagged sample to evaluate the scope and relative contribution of winter mortality in the FCRPS to overall migration mortality.

Methods

Fish collection, tagging, and monitoring.—Adult Columbia River summer steelhead were trapped at Bonneville Dam (river kilometer [rkm] 235, measuring from the mouth of the river; Figure 1) from late May or early June through October in 6 years (1996–1997 and 2000–2003). We collected 5,939 upstream-migrating fish (mean = 990 fish/year; range = 615–1,273) in an adult trapping facility; the fish were radio-tagged and released downstream from the dam or in the dam forebay. Samples represented less than 0.5% of each annual run. Details of the trap facility, fish anesthetization, intragastric radio-tagging methods, types and sizes of radio transmitter used, and rationale for release locations are described by Keefer et al. (2004b, 2005a).

Steelhead were tagged in approximate proportion to the counts at Bonneville Dam each year. However, in an effort to collect adequate samples of Snake River steelhead for Snake River dam passage assessments unrelated to this summary (see Keefer et al. 2004a), we collected relatively larger numbers of late-migrating steelhead in the first four study years. In these years, the median tag dates at Bonneville Dam were 7–14 d later for radio-tagged fish than for the runs at large. Differences were slight (1–4 d) in 2002–2003. Because migration timing is related to stock composition (see Results), we may have oversampled some late-entry stocks. Consequently, we stratified all analyses by tagging date and metapopulation (see the section on data analysis below).

All steelhead that passed through the Bonneville Dam adult trap in 1996–1997 (n = 1,740) and 66% (2,785) of the 4,199 fish passing the trap in 2000–2003 were nonselectively sampled. The only fish rejected from these samples were those with fork lengths less than 50 cm and those with debilitating injuries. The remaining 34% (1,414 fish) of the 2000–2003 samples were selected using an automated system that identified steelhead that had received passive integrated transponder (PIT) tags (Prentice et al. 1990) as juveniles. The majority (n = 905; 64%) of these known-origin fish were PIT-tagged at lower Snake River dams as smolts and were an aggregate of all populations

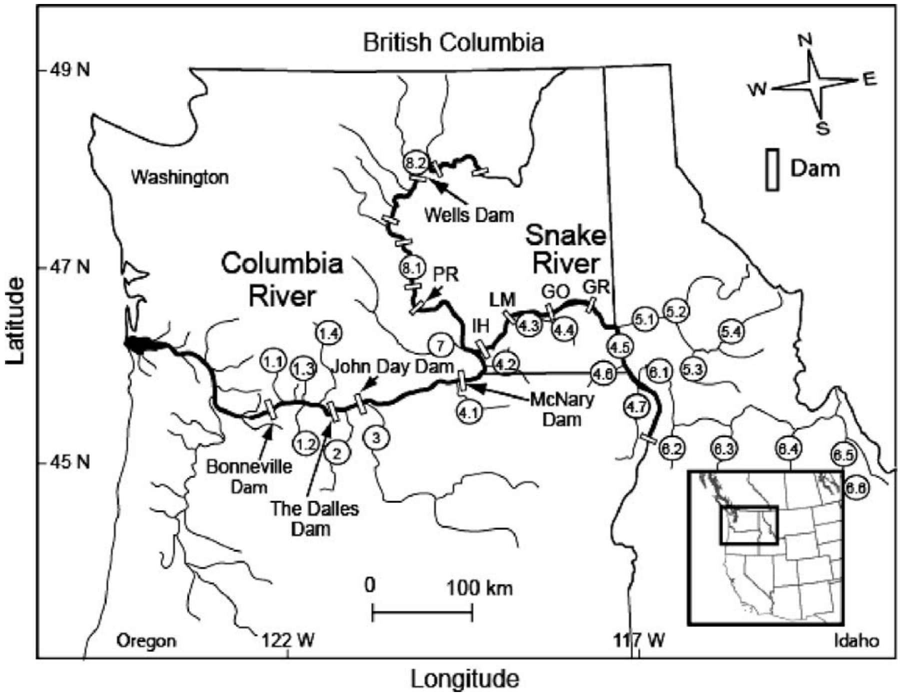

FIGURE 1.—Map of the Columbia and Snake River basins, where overwintering adult steelhead were monitored at eight federal Columbia River power system dams and associated reservoirs: Bonneville, The Dalles, John Day, McNary, Ice Harbor (IH), Lower Monumental (LM), Little Goose (LG), Lower Granite (GR), and at Priest Rapids Dam (PR) of the Grant County Public Utility District. Radio-tagged study fish were assigned to one of eight metapopulations following Brannon et al. (2004): 1 = Lower Columbia River, 2 = Deschutes River, 3 = John Day River, 4 = Snake River, 5 = Clearwater River, 6 = Salmon River, 7 = Yakima River, and 8 = mid-Columbia River, which are the first digits within the circles; the second digits refer to the stocks described in Table 1.

upstream from Lower Granite Dam, including both wild- and hatchery-origin fish. The next-largest group was PIT-tagged at upper Columbia River dams or at Wells Hatchery ($n = 469$; 33%) on the upper Columbia River; the remaining 40 fish (3%) were tagged at a variety of hatchery and natal stream sites throughout the basin.

The movements and locations of adult steelhead in the FCRPS were monitored using a series of about 150–170 fixed aerial and underwater radiotelemetry antenna sites (Lotek Wireless, Inc., Newmarket, Ontario) at main-stem hydroelectric dams on the lower Columbia and Snake rivers (described by Keefer et al. 2004a, 2005a). Antennas at the tops of fish ladders (underwater) and in dam tailraces (aerial) were operated during winter at Bonneville, The Dalles, John Day, and McNary dams on the lower Columbia River, at Priest Rapids Dam on the mid-Columbia River, and at Ice Harbor, Lower Monumental, Little Goose, and Lower Granite dams on the lower Snake River (Figure 1). Coverage at these sites was nearly continuous in all years, except that Lower Monumental and Little Goose dams were not monitored during the winter of 1996–1997. Steelhead movements into and out of major lower Columbia and Snake River tributaries were monitored with aerial antennas located inside of tributary mouths (see Goniea et al. 2006 and High et al. 2006). The main-stem Snake River upstream from Lower Granite Reservoir and several mid-reservoir sites in both the Columbia and Snake rivers were similarly monitored. Data collected at all sites included time and location stamps and were coded to reflect fish movements past each site throughout migration. The monitoring effort upstream from Priest Rapids Dam was intermittent, and therefore we did not examine overwintering above this dam.

Stock and metapopulation assignment.—Questions related to steelhead overwintering in the FCRPS are typically population specific. Therefore, we limited most analyses to fish that returned to known spawning tributaries or to the Columbia River upstream from Priest Rapids Dam. Each steelhead was assigned to 1 of 26 stocks based on final fish location, and these were nested within eight metapopulations. Stock assignments were principally to major tributaries (e.g., the John Day or Yakima River) or to secondary tributaries in large drainages (e.g., the South Fork Clearwater or Middle Fork Salmon River). At this scale, each stock potentially included fish from multiple spawning populations. The two mid-Columbia River stocks (upstream from Priest Rapids Dam) were not tributary based because of the relatively limited monitoring effort in this area. Based on final fish records, the upper group included Wells Hatchery, Okanogan River, and Methow River fish, while the lower group included more Wenatchee and Entiat River steelhead as well as fish that were probably destined for (but not detected at) the upper sites. Metapopulation assignments followed Brannon et al. (2004), who delineated Columbia River steelhead population structure using genetic, life history, and geographic–environmental criteria (Figure 1). Three of the study metapopulations were each composed of a single telemetry-based stock (Deschutes, John Day, and Yakima rivers).

Stock and metapopulation assignment errors were possible when fish from upriver populations were last recorded in lower Columbia River tributaries, either because they were permanent strays or because they were harvested while straying temporarily. Such errors probably inflated sample sizes for lower Columbia, Deschutes, and John Day River metapopulations and stocks because large numbers of upper Columbia and Snake River steelhead use lower-river tributaries as temporary thermal refugia during homing migration (Keefer et al. 2004a; High et al. 2006) and as permanent straying locations (see Keefer et al. 2005b). Refugia use is concentrated in tributaries draining the Cascade Range (the Wind, Little White Salmon, White Salmon, Hood, Klickitat, and Deschutes rivers) during summer and fall, while fish stray into the John Day River during all seasons (Keefer et al. 2005b). Assignment errors were less likely for upriver groups, but we note that the mid-Columbia, main-stem Clearwater, and main-stem Salmon River stocks included fish from multiple sub-basin populations. Some straying also probably occurred between the Snake, Clearwater, and Salmon River metapopulations. In general, however, misclassification should act to increase the variability in behaviors observed within stocks and would be unlikely to create false differences among stocks. Misclassifications of this type were reduced somewhat in years with known-origin samples (i.e., those PIT-tagged as juveniles) because known strays were censored from analyses.

Data analysis.—Operationally, summer steelhead tagged at Bonneville Dam during May–October of a given year were considered to have at least partially overwintered within the FCRPS if they passed one or more of the monitored main-stem dams or were first recorded as exiting a reservoir into a spawning tributary after 1 January of the next year. The selected date was arbitrary but coincides with nadirs in steelhead passage counts at dams and the period of coldest main-stem water temperatures (see Results). We stratified all analyses by tagging date and metapopulation to examine the differences in behavior among groups and to account for the potential oversampling of late-run stocks. Overwintering estimates should therefore be reliable within strata, particularly for upriver populations that are relatively unaffected by interbasin straying.

The individual probability of overwintering for each metapopulation was assessed by multiple logistic regression (Hosmer and Lemeshow 2000) using the model

$$\begin{aligned}\text{overwintering(yes, no)} &= \text{date} + \text{origin}\\ &\quad + (\text{date} \times \text{origin}),\end{aligned}$$

where date = tagging date at Bonneville Dam and origin = hatchery or wild. We were unable to include year as a predictor because of missing cells (i.e., some categories had no overwintering fish). Hatchery fish were identified by missing adipose fins or other fin clips, and those without fin clips were presumed to be wild. It is unknown how many unclipped hatchery fish were in the samples, but their misclassification should act to minimize detectable differences between origin groups.

The relationships between water temperature, total discharge, initiation of overwintering, and resumption of migration were qualitatively assessed using estimated dates for steelhead movement cessation and resumption. Temperature and discharge data were from the U.S. Army Corps of Engineers (archived by the University of Washington 2006). The summaries were qualitative because (1) temperature data were not consistently collected at any Columbia or Snake River sites during winter for the 1996 and 1997 migrations and (2) there were intercorrelations between potential environmental cues such as date (as a proxy for photoperiod), flow, and temperature.

Seasonal patterns of mortality within the monitored FCRPS, including harvest and unaccounted-for loss, were also assessed. Although the date of harvest was typically reported as part of a reward program for transmitter returns, accurately assigning final dates for unaccounted-for loss was more difficult in late fall or winter, when fish moved infrequently and there were often large spans between telemetry records for individuals. At a coarse scale, we believe the mortality data were appropriate for qualitatively comparing steelhead survival prior to and during winter. We did not statistically test for mortality differences between overwintering and non-overwintering fish because the likelihood of overwintering differed seasonally and among populations and the majority of unsuccessful migrants could not be assigned to populations. A more complete full-migration summary of steelhead escapement, harvest, and unaccounted-for loss by steelhead run year is presented by Keefer et al. (2005a).

Results

Overwintering Estimates

Ten percent (598) of the 5,939 radio-tagged steelhead were removed from the data set prior to any analyses, primarily because transmitters were lost or removed during migration or because the fish were last recorded in tributaries without known spawning populations (e.g., the Little White Salmon River) or downstream from Bonneville Dam. Another 63 known-origin steelhead (1% of 5,939) were removed because they were known strays. Most known strays were last recorded in the Deschutes ($n = 22$; 35% of all strays), John Day ($n = 16$; 25%), and White Salmon ($n = 14$; 22%) rivers, and 6 (10%) were last recorded in other lower Columbia River tributaries. Before removal, known-origin strays represented 6–9% of the fish assigned to the lower Columbia, Deschutes, and John Day River metapopulations; the true straying rates were probably higher because samples almost certainly included unidentified strays (i.e., strays of unknown origin that could not be censored). Overwintering rates may have been underestimated for tributary groups receiving a disproportionately high number of unidentified strays, which would inflate the total observed sample size. Such underestimation was possible, for example, for the Wind River stock or the John Day River metapopulation. Upriver overwintering rates were less likely to be biased by permanent straying because these tributaries received fewer strays.

Of the remaining 5,278 steelhead, 3,399 (64%) were considered to be successful migrants that could be confidently assigned to stocks and metapopulations (i.e., with a presumed low level of incorrect assignment due to unidentified straying), and we focused on this group for the analysis of overwintering behavior. Successful migrants either passed and remained upstream from Priest Rapids Dam or entered tributaries with known spawning populations. Overall, 14.6% (497) of the 3,399 successful migrants met criteria for overwintering within the monitored FCRPS (Table 1); annual overwintering estimates ranged from 7.9% to 18.8% (mean = 14.0%; SD = 3.7%). Weighting by monthly dam counts within years to account for the potential oversampling of late-entry groups in some years produced adjusted estimates of 12.4% overall and from 6.8% to 19.6% for individual years. Similar percentages were obtained when known-origin fish were excluded: unweighted estimates were 14.8% overall and ranged from 7.9% to 24.5% annually, and weighted estimates were 13.0% overall and ranged from 6.8% to 21.5%. Similarly, inclusion or exclusion of known-origin fish had little effect on overwintering estimates within metapopulations, and we therefore combined the two groups for all subsequent analyses.

Overwintering Movements

The nadir for upstream movement within the FCRPS by overwintering steelhead occurred in the first half of January, when only 2.3% were recorded as moving upstream past one or more dams (Figure 2). Mean water temperatures during this period were 3.8–4.7°C at Bonneville, McNary, and Lower Granite dams. The lowest overall movement rate (neither upstream nor downstream movement between reaches) was detected in the second half of December, when 94.7% of the fish remained within individual reaches. Mean temperatures during this time were 6.1–6.2°C at Bonneville and McNary dams and 4.8°C at Lower Granite Dam. There was no evidence of a clear threshold temperature for the onset of overwintering, as some fish stopped moving in November (temperature range = 8–12°C), while others continued to migrate at the lowest recorded temperatures.

Some overwintering steelhead moved upstream in all months, but the largest numbers resumed active upstream migration during March with the onset of warmer temperatures (Figure 2). This pattern was consistent across years. Mean temperatures (2000–2004) at the three dams were 4.4–5.6°C during the first half of March and 6.7–7.2°C during the second half of March (Figure 2). Warming in March was accompanied by rapidly increasing day length and typically by increased flow; mean daily water temperatures from 1 February to 30 April were positively correlated with discharge ($r \geq 0.79$ at Lower Granite Dam) in study years with available temperature data (2000–2004). Correlations at Bonneville and McNary dams ($0.71 < r < 0.87$) were similar to those at Lower Granite Dam except in 2001 ($-0.25 < r < -0.23$), a near-record low-flow year. Increased upstream movement by steelhead may therefore have been a response to temperature, photoperiod, discharge, or some combination of these and other cues. However, steelhead generally did not reinitiate migration during or immediately after winter freshets in any year.

On average, almost 2% of successful overwintering fish moved downstream past dams during each semimonthly period (Figure 2). In total, 102 fish (20.5%) fell back below dams 161 times after 1 November but prior to postspawn out-migration (as

TABLE 1.—Monthly stock- and metapopulation-specific estimates of the percentages of radio-tagged steelhead (n = number tagged) that overwintered in the federal Columbia River power system before successfully returning to spawning tributaries (all years combined). Percentages are based on the month of tagging at Bonneville Dam and demonstrate the increasing likelihood of overwintering for fish with later migration timing. Total percentages show among-population differences across months. Stock numbers correspond to those in Figure 1; metapopulations follow Brannon et al. (2004). Known-origin strays (n = 63) are excluded.

	May		Jun		Jul		Aug		Sep		Oct		Total[a]	
Metapopulation and stock	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%	*n*	%
1. Lower Columbia River														
1.1 Wind River			7	0.0	5	0.0	17	0.0	8	12.5	1	0.0	38	2.6
1.2 Hood River	2	0.0	23	0.0	9	0.0	4	0.0	5	0.0	2	50.0	45	2.2
1.3 White Salmon River[b]			4	0.0	13	0.0	21	0.0	12	8.3			50	2.0
1.4 Klickitat River	1	0.0	44	0.0	27	0.0	31	3.2	9	0.0	8	0.0	120	0.8
Total	3	0.0	78	0.0	54	0.0	73	1.4	34	5.9	11	9.1	253	1.6
2. Deschutes River			22	0.0	71	5.6	130	0.8	64	4.7	34	17.6	321	4.4
3. John Day River			5	0.0	31	12.9	62	14.5	43	23.3	15	13.3	156	16.0
4. Snake River														
4.1 Umatilla River			4	0.0	17	29.4	17	35.3	10	30.0	1	0.0	49	28.6
4.2 Walla Walla River			4	0.0	15	26.7	22	22.7	5	0.0	1	0.0	47	19.2
4.3 Lyons Ferry			6	0.0	15	0.0	9	0.0	2	0.0			32	0.0
4.4 Tucannon River			7	0.0	10	0.0	12	16.7	2	0.0			31	6.5
4.5 Snake River			14	14.3	88	9.1	177	2.8	69	5.8	12	16.7	360	5.8
4.6 Grande Ronde River			9	0.0	66	6.1	109	13.8	37	2.7	2	50.0	223	9.4
4.7 Imnaha River					11	0.0	17	5.9	2	0.0	2	50.0	32	6.3
Total			44	4.6	222	9.5	363	9.4	127	6.3	18	22.2	774	8.9
5. Clearwater River														
5.1 Clearwater River	1	0.0	10	0.0	16	12.5	85	22.4	254	38.6	65	50.8	431	35.3
5.2 Dworshak Hatchery							9	33.3	97	69.1	27	77.8	133	68.4
5.3 South Fork Clearwater River					1	100.0	18	55.6	66	54.5	23	73.9	108	59.3
5.4 Lochsa River			1	0.0			11	72.7	56	42.9	7	85.7	75	50.7
Total	1	0.0	11	0.0	17	17.6	123	32.5	473	47.6	122	63.1	747	46.2
6. Salmon River														
6.1 Salmon River			5	0.0	59	1.7	178	2.2	123	5.7	22	22.7	387	4.4
6.2 Little Salmon River					10	0.0	20	0.0	16	43.8	5	80.0	51	21.6
6.3 South Fork Salmon River					1	0.0	6	0.0	15	0.0	1	100.0	23	4.4
6.4 Middle Fork Salmon River					5	0.0	27	3.7	12	0.0	2	0.0	46	2.2
6.5 Upper Salmon River			1	0.0	12	8.3	48	0.0	26	3.8	7	28.6	94	4.3
6.6 Pahsimeroi Hatchery					6	0.0	21	0.0	10	0.0	2	0.0	39	0.0
Total			6	0.0	93	2.2	300	1.7	202	7.4	39	30.8	640	5.3
7. Yakima River			6	0.0	13	15.4	5	0.0	6	33.3	1	100.0	31	16.1
8. Mid-Columbia River[c]														
8.1 Priest Rapids—Wells Dam			15	0.0	88	0.0	164	0.0	36	2.8	2	0.0	305	0.3
8.2 Above Wells Dam			13	0.0	54	0.0	85	0.0	20	0.0			172	0.0
Total			28	0.0	142	0.0	249	0.0	56	1.8	2	0.0	477	0.2
All stocks	4	0.0	200	1.0	643	5.6	1,305	6.9	1,005	26.5	242	42.6	3,399	14.6

[a] See text for discussion of possible sample-based bias in totals.

[b] There is limited evidence for recent natural reproduction in the White Salmon River.

[c] The mid-Columbia River of Brannon et al. (2004) is synonymous with the upper Columbia River.

indicated by telemetry records inside spawning tributaries at traditional spawning times); 64 fell back once and 38 fell back two or more times. Fallbacks were recorded at all dams, but the largest number of events occurred at The Dalles ($n = 45$; 28%), McNary ($n = 33$; 20%), and John Day ($n = 32$; 20%) dams. Forty-six wintertime fallbacks (29%) were distributed among the four lower Snake River dams, and five (3%) fallbacks occurred at Bonneville Dam. About 25% of fish that fell back subsequently entered tributaries downstream from a fallback site. This behavior, termed overshoot fallback by Boggs et al. (2004), was most common at McNary and John Day dams.

Patterns within Metapopulations

There was strong variation in the proportion of overwintering among stocks and metapopulations (<1.0% to 68.4%; Table 1) but little variability within metapopulations among years. Some metapopulations were composed of stocks with consistently low (e.g., lower and mid-Columbia River) or consistently high (e.g., Clearwater River) overwintering rates, while others (e.g., Snake and Salmon rivers) were composed primarily of stocks with low overwintering proportions along with one or two stocks with high overwintering proportions.

The winter behaviors of hatchery and presumed wild

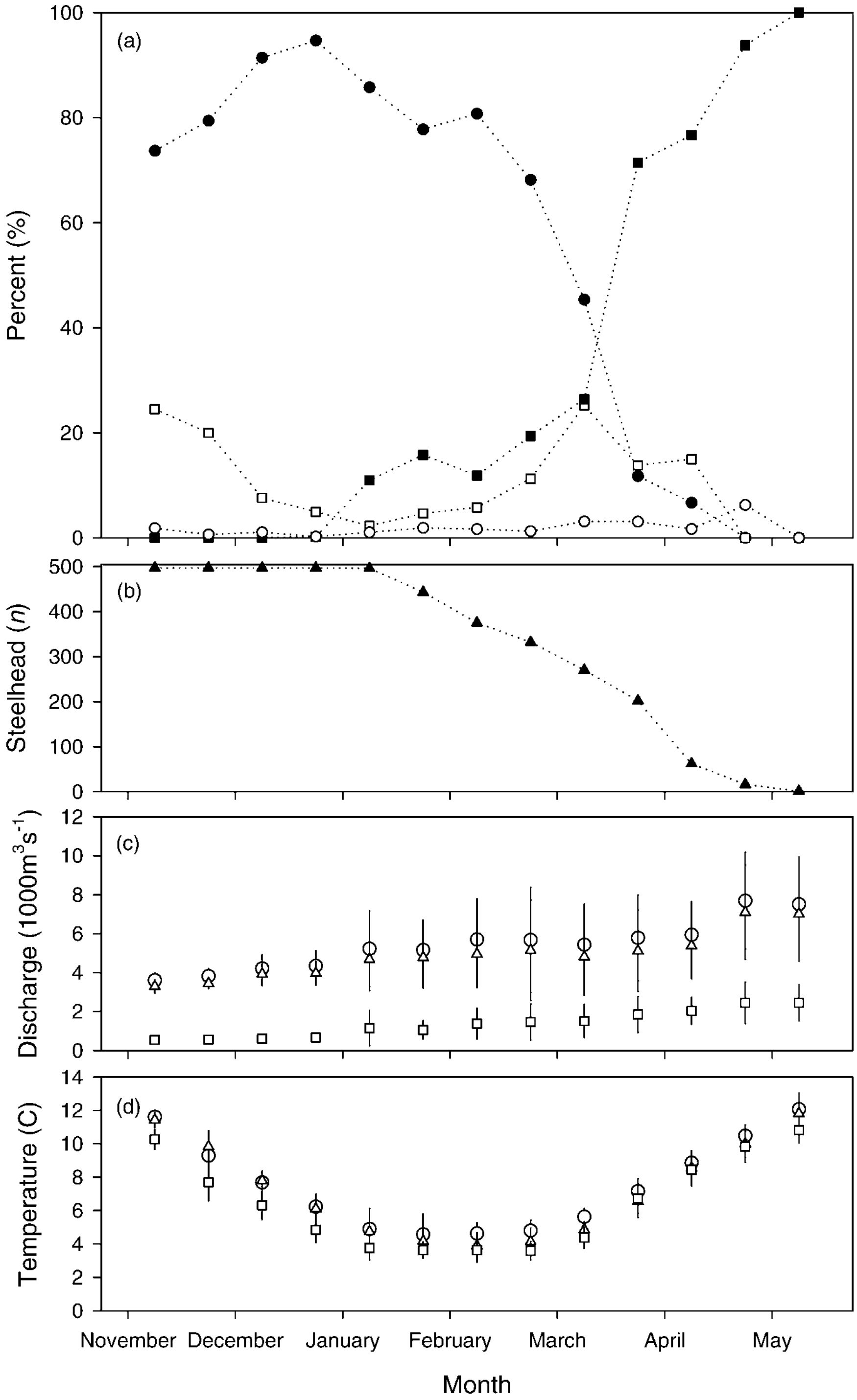

FIGURE 2.—Movements by overwintering steelhead and environmental attributes in the Columbia–Snake River basins, by semimonthly block during November–May 1996–1998 and 2000–2004. Panel **(a)** shows the percentages of fish that moved upstream (open squares), moved downstream (open circles), entered final spawning tributaries (filled squares), or did not move (filled circles); panel **(b)** shows the number remaining in the monitored portion of the federal Columbia River power system; panel **(c)** shows the mean ± SD discharge at Bonneville (circles), McNary (triangles), and Lower Granite (squares) dams; and panel **(d)** shows the mean water temperature at the above three dams.

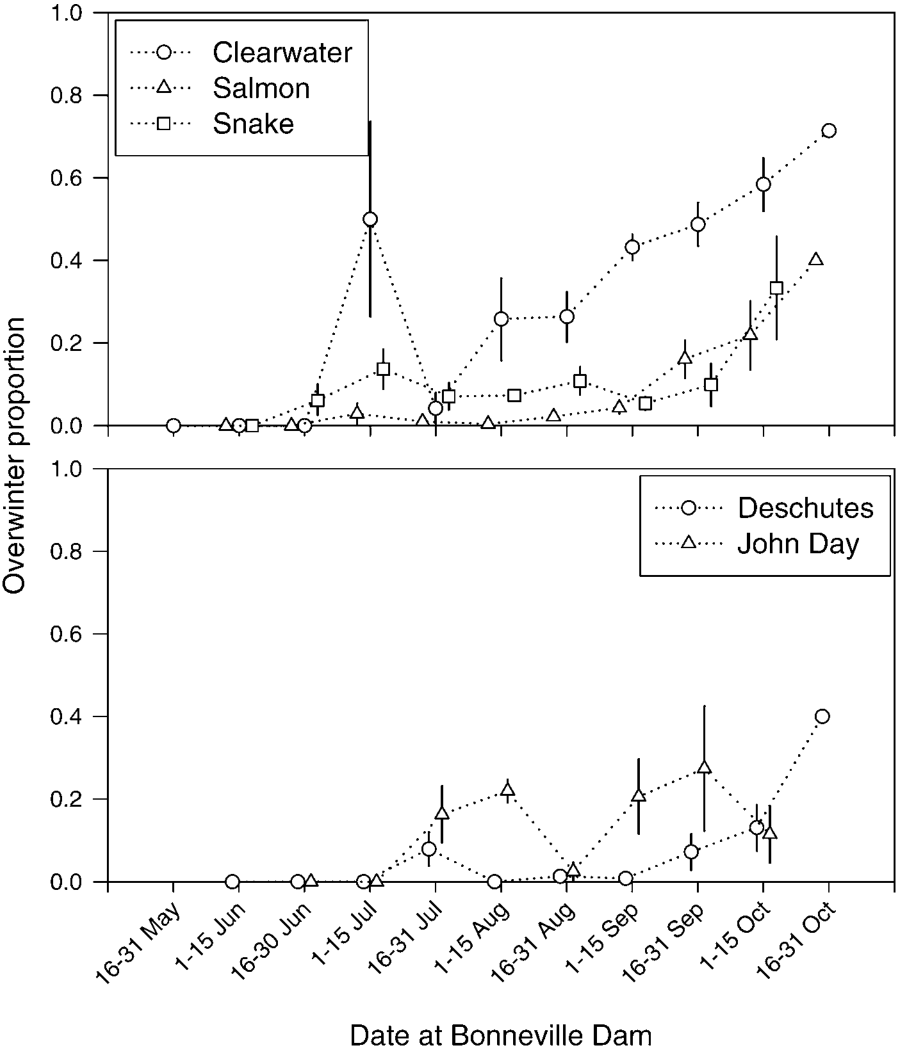

FIGURE 3.—Mean ± SE annual proportions of Columbia–Snake River basin steelhead metapopulations that were recorded as overwintering within the federal Columbia River power system during 1996–1998 and 2000–2004, presented by semimonthly block based on tagging at Bonneville Dam. Metapopulations with small numbers of overwintering fish ($n \leq 5$) are excluded.

steelhead were generally similar, perhaps because many hatchery populations are locally derived. For all stocks combined, 14.3% (143) of 997 successful wild fish and 14.7% (354) of 2,402 successful hatchery fish overwintered in the FCRPS. Without adjusting for migration timing, overwintering differences between hatchery and wild fish within metapopulations were inconsistent and were significant only for the Clearwater River (overwintering percentages of 39.8% for wild fish and 48.6% for hatchery fish; $\chi^2 = 4.7$, df = 1, $P = 0.031$) and Snake River (15.1% for wild, 5.8% for hatchery; $\chi^2 = 18.3$, df = 1, $P < 0.001$) metapopulations. In the Clearwater River metapopulation, hatchery steelhead migrated later on average than did wild fish. The pattern in the Snake River metapopulation was related to differences among stocks and was particularly associated with relatively high FCRPS overwintering for unclipped (presumed wild) Umatilla and Walla Walla River fish.

Migration timing was the best overall predictor of FCRPS overwintering, and this pattern was consistent across years (Figure 3). Overwintering percentages ranged from 1.0% or less for all successful fish tagged in May and June to 42.6% for those tagged in October (Table 1). In multiple logistic regression models of overwintering, the likelihood of FCRPS overwintering

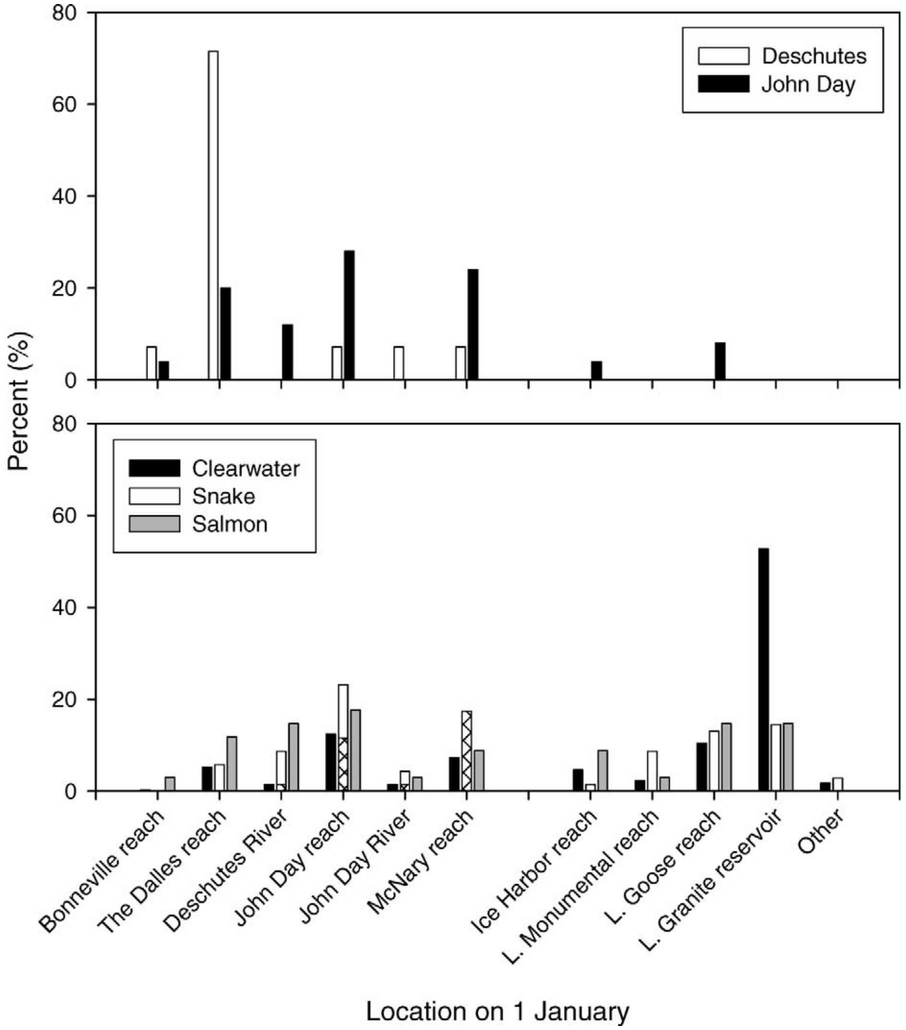

FIGURE 4.—Estimated proportions of radio-tagged overwintering steelhead adults that successfully reached Columbia–Snake River basin spawning tributaries in 1996–1998 and 2000–2004, arranged by their detected locations on 1 January, for two sets of metapopulations: Deschutes and John Day rivers (top panel) and Clearwater, Salmon, and Snake rivers (bottom panel). The detection areas include the reaches above the following dams: Bonneville, The Dalles, John Day, McNary, Ice Harbor, Lower Monumental, Little Goose, and Lower Granite. The Snake River metapopulation is split into two stocks, a lower one (Umatilla and Walla Walla rivers; crosshatched bars) and an upper one (Tucannon, Snake, Grande Ronde, and Imnaha rivers; open bars).

increased significantly with migration date for the Deschutes ($\chi^2 = 5.51$, $P = 0.019$), Clearwater ($\chi^2 = 27.05$, $P < 0.001$), and Salmon River ($\chi^2 = 16.42$, $P < 0.001$) metapopulations but not for the John Day ($\chi^2 = 0.18$, $P = 0.675$) or Snake River ($\chi^2 = 3.04$, $P = 0.082$) metapopulations. After accounting for timing effects, origin and date × origin terms were not significant ($\chi^2 \leq 2.68$, $P > 0.10$) in any metapopulation model (logistic models were not run for the lower Columbia, Yakima, or mid-Columbia River metapopulations because of small [$n \leq 5$] overwintering samples).

Overwintering Locations

As might be expected, wintering locations differed among metapopulations. On 1 January, 10 of 14 (71%) overwintering Deschutes River steelhead were aggregated in the reach between The Dalles and John Day dams, whereas overwintering John Day River fish ($n = 25$) were distributed among reaches and tributaries both upstream and downstream from the John Day River (Figure 4). Overwintering Clearwater River steelhead were distributed throughout the FCRPS on 1 January; the largest concentration (53%) of these fish was observed in Lower Granite Reservoir, and about 25% were observed in lower Columbia River reaches. Steelhead from the Salmon River metapopulation were the most widely distributed: 41% were found in lower Columbia River reaches, 41% were detected in lower Snake River reaches, and 18% were observed in the Deschutes or John Day River. Fish from the Snake River metapopulation were distributed much like those from the Salmon River metapopulation, but relatively more were detected in the John Day and McNary reservoirs, reflecting the FCRPS wintering locations of Umatilla and Walla Walla River stocks (Figure 4). Overwintering steelhead from the other metapopulations (lower Columbia, Yakima, and upper Columbia rivers) mostly used lower Columbia River reaches near their home tributaries.

Many steelhead partially overwintered in tributaries other than their final locations (i.e., they were temporarily straying or staging). The percentage of overwintering fish detected in other tributaries was 14.0% on 1 November, 7.6% on 1 December, 7.6% on 1 January, 4.7% on 1 February, 5.8% on 1 March, and 1.7% on 1 April (percentages adjusted for the number of fish exiting the FCRPS into final tributaries, as in Figure 3). The most used nonnatal tributaries in winter were the Deschutes and John Day rivers, and most steelhead exhibiting this behavior were from the Snake River basin.

Overwintering locations for all metapopulations shifted through time, and the net movement was generally upstream. For example, the largest distribution changes from 1 January to 15 February were (1) the movement of many Clearwater River steelhead from Lower Granite Reservoir to the natal river and (2) reentry into The Dalles Reservoir by most Salmon River steelhead that used the Deschutes River.

Patterns of Mortality

In addition to examining the overwintering behavior of successful migrants, we analyzed associations between overwintering and three fate classes (successful migrant, main-stem harvest, and unknown) for two groups: fish that met our FCRPS overwintering criteria and those that did not. Across fate classes, steelhead that overwintered in the hydrosystem were more likely to complete migration (Table 2). About 82% of these FCRPS-overwintering fish were considered to be successful migrants, whereas 62% of the fish that did not overwinter were successful migrants. Some of the difference can be attributed to reduced harvest in the hydrosystem during winter: harvest rates were 3.8% (23) of the 608 steelhead in the FCRPS-overwintering group and 19.0% (885) of the 4,670 non-overwintering fish. However, the 1 January dam passage criterion probably resulted in underestimation of overwintering harvest rates. For example, of the 885 FCRPS-harvested fish that did not pass a dam after 1 January, 53 (6.0%) were nonetheless reported harvested between January and early May based on tag return data. If we consider these to be FCRPS-overwintering fish, then the winter harvest estimate increases from 3.8% to a maximum of about 11.5% (i.e., [23 + 53]/[608 + 53]). The 76 harvest events reported as occurring after 1 January were distributed throughout the FCRPS, and the largest numbers were reported in The Dalles (*n* = 19 fish; 25%), Little Goose (*n* = 12; 16%), Lower Granite (*n* = 11; 14%), and John Day (*n* = 9; 12%) reservoirs. However, there was little evidence that harvest of the overwintering group was as high as harvest of the population reaching tributaries before 1 January, which is consistent with the decline in fishing pressure in reservoirs during winter.

TABLE 2.—Estimated fate of Columbia–Snake River basis steelhead based on whether they were detected passing a dam after 1 January. Dam passage after 1 January was considered to indicate at least partial overwintering in the federal Columbia River power system. A priori removals (*n* = 598) and known-origin strays (*n* = 63) are not included.

	Dam passage after 1 Jan		
Estimated fate	Yes	No	Total
Successful migrants (*n*)	497	2,902	3,399
Percent of successful migrants	14.6	85.4	
Percent of column total	81.7	62.1	
Reported main-stem harvest (*n*)	23	885[a]	908
Percent of main-stem harvest	2.5	97.5	
Percent of column total	3.8	19.0	
Unknown (*n*)	88[b]	883[b]	971
Percent of unknown	9.1	90.9	
Percent of column total	14.5	18.9	
Total	608	4,670	5,278

[a] Includes 53 steelhead harvested after 1 January.

[b] Exact timing of presumed mortality is unknown.

Overall, 14.5% (88) of the 608 steelhead that met FCRPS overwintering criteria had unknown fates (presumed mortality) within FCRPS, whereas 18.9% (883) of the 4,670 fish that did not pass a dam after 1 January had unknown fates (Table 2). The final records for the 88 overwintering fish of unknown fate were distributed throughout the FCRPS, and the most last detections occurred in John Day (*n* = 17 fish; 19%), Lower Granite (*n* = 16; 18%), McNary (*n* = 12; 14%), and Lower Monumental (*n* = 12; 14%) reservoirs. As with harvest, the percentage of overwintering fish with unknown fates may represent an underestimate, since some individuals might have remained in the FCRPS past 1 January but died before detection; thus, the 14.5% presumed mortality estimate should be considered a minimum.

Discussion

Understanding the substantial behavioral variability of adult summer steelhead is critical for their management and conservation. This is especially true in the large, multistock Columbia River, where managers must balance protection of many threatened populations with the competing economic and cultural demands for fisheries and other ecosystem services. Our results indicate that adult steelhead migration complexity during winter rivals that reported for other seasons (e.g., Robards and Quinn 2002; High et al. 2006). As is typical for summer steelhead, we observed considerable variation in migration behavior among individuals and within and among stocks and metapopulations. During winter, radio-tagged steelhead moved upstream and downstream past dams, temporarily used nonnatal tributaries, held for widely varying lengths of time, and occurred in mixed-stock assemblages at locations throughout the monitored area. Despite this variability, some general patterns emerged, such as greater FCRPS overwintering by later migrants. Presumably, the observed behavioral diversity reflects underlying genetic differences among stocks, differences in juvenile experience and homing, and responses to environmental cues, both unaltered (e.g., photoperiod) and altered by damming (e.g., temperature and flow regimes). Below, we discuss (1) the potential underlying mechanisms influencing steelhead behavior during winter, (2) how the behavioral complexity of steelhead has interacted with hydrosystem development to affect steelhead at the population scale, and (3) some winter management implications.

Adult summer steelhead forego growth opportunities at sea by entering freshwater months before they are reproductively mature. This strategy presumably reflects past selection regimes that conferred fitness benefits in the unmodified (undammed) system by allowing fish to traverse seasonal barriers or ensuring timely arrival at interior spawning sites (Quinn 2005). Historic barriers in the Columbia River basin may have included large main-stem obstacles such as Celilo Falls (inundated by The Dalles Dam at rkm 323), seasonal obstacles closer to spawning grounds, and coldwater physiological barriers in winter and early spring prior to spawn times. Similarly, high-temperature thermal barriers may have blocked passage in summer and fall, a scenario supported by the extended use of coolwater refugia by present-day summer steelhead and fall Chinook salmon during warm seasons (Goniea et al. 2006; High et al. 2006). Seasonal return patterns to the lower Columbia River suggest that flow conditions at obstacles such as Celilo Falls influenced steelhead run timing but were not a primary limiting factor, because many adults return during periods of relatively high and low flow (Robards and Quinn 2002). Rather, nadirs in steelhead run timing historically corresponded with warm summer temperatures, implicating temperature as an important determinant of run timing for interior Columbia River basin steelhead.

Temperature appears to be a controlling factor for adult steelhead migration. Functional thermal barriers constrain migration at both high (i.e., 20–22°C; Baigun et al. 2000; Richter and Kolmes 2005) and low temperatures (i.e., 2–5°C; Lough 1980; Workman et al. 2002). Notably, both limits are encountered by many Columbia River migrants as they pass through the migration corridor. Steelhead moved at the highest- and lowest-recorded temperatures, but more than 97% of FCRPS-overwintering fish stopped upstream movement when main-stem temperatures fell to approximately 4°C. This is consistent with thresholds identified in radiotelemetry studies of steelhead in the Yakima River (~3°C: Hockersmith et al. 1995) and Lake Michigan tributaries (~4°C: Workman et al. 2002) and in an early study of Snake River steelhead (~3°C: Thompson et al. 1958). We also found that the majority of steelhead resumed upstream migration in March, when temperatures warmed from approximately 4–5°C to about 7°C. These movements occurred earlier and at warmer temperatures than were observed for British Columbia steelhead in the large Skeena River system, where springtime migration largely resumed in late April or early May at 2–5°C (Lough 1980). Differences among Skeena and Columbia River populations probably reflect adaptations to prevailing environmental conditions or differences in distances between overwintering locations and spawning sites. In all of these studies, upstream movement and egress into spawning tributaries increased as day length increased and as water temperatures rose (Lough 1980; Hockersmith et al. 1995; Workman et al. 2002).

Hydroelectric development of the Columbia and Snake rivers may therefore have had mixed effects on steelhead migration timing and overwintering behaviors. At low and moderate temperatures, impoundment has resulted in faster upstream migration rates by inundating migration obstacles and reducing water velocity (e.g., Keefer et al. 2004a; English et al. 2006). Rapid upstream migration through reservoirs would tend to reduce overwintering within the lower main-stem river. However, impoundment has also caused prolonged periods of high water temperature in the Columbia River system (Quinn and Adams 1996; Peery et al. 2003), prompting thermoregulatory behaviors that significantly delay some steelhead (Keefer et al. 2004a; High et al. 2006). Extended use of thermal refugia reinforces migration complexity and potentially increases overwintering in the lower basin because some migrants remain in refugia until late fall and (as our results show) even into winter. In a third scenario, the warmer thermal regime associated with damming could create a longer period of suitable migration temperatures in the fall and early winter, allowing late-season progression upstream. In any case, steelhead migration behaviors in the current system probably differ in complex ways from pre-hydrosystem conditions.

While water temperature is an important migration stimulus for many temperate fishes, photoperiod is generally considered the most influential proximate cue for maturation and the timing of reproduction (Bromage et al. 2001; Pankhurst and Porter 2003). Separating photoperiod and temperature effects in spring-spawning salmonids is difficult, however, because the two are often strongly correlated with each other and with seasonal discharge patterns. During March, for example, water temperatures at the studied Columbia and Snake River dams warmed rapidly (2–4°C overall or 0.06–0.13°C/d) and day length increased faster than during any other month (~100 min overall or ~3.2 min/d). At the same time, discharge increased in March during all years but 2001, an anomalously low-flow year. The reinitiation of migration by radio-tagged steelhead during this seasonal change was widespread, both geographically and across populations, despite the probable differences in temperature and flow conditions locally experienced by individual fish. The spatial synchrony of these movements and the observation that few fish responded to freshets during December–February generally support the hypothesis that photoperiod was the controlling cue for advancing steelhead migration in spring. Further, experimental manipulations of both temperature and photoperiod in hatchery rainbow trout have convincingly demonstrated that photoperiod largely determines the timing of both maturation and spawning, while temperature provides only a modulating effect (Davies and Bromage 2002). If the hypothesis that photoperiod triggers the cessation of migration in winter and the reinitiation of migration in spring is correct, then overwintering in the main-stem Columbia and lower Snake rivers may have occurred at similar rates prior to hydrosystem development. This could be tested by comparing overwintering rates in steelhead populations in other large rivers with fewer or no dams.

The steadily increasing likelihood of FCRPS overwintering for many steelhead stocks with advancing summer–fall passage date at Bonneville Dam probably reflects a mix of genetic and environmental factors. Genetically based timing differences among Columbia River steelhead populations almost certainly reflect local adaptations to migration distance and difficulty and to hydrologic and thermal characteristics of spawning sites and along the migration corridor (i.e., Beacham et al. 2000; Quinn et al. 2000; Hendry et al. 2002). Genetic differences are also evident in a major life history split related to migration timing. On average, so-called A-group steelhead spend one full year at sea and pass Bonneville Dam 4–8 weeks earlier than do B-group fish, which spend 2 years at sea (Busby et al. 1996; Robards and Quinn 2002). Most of the larger B-group fish return to the Clearwater or Salmon River, and relatively large proportions of these fish overwinter in the FCRPS. Migration rate data suggest that both A- and B-group fish initiate overwintering behaviors when water temperatures fall below about 8°C (Keefer et al. 2004a), coincident with rapidly decreasing photoperiod. However, it is unknown whether genetic effects on entry timing, ecological factors (e.g., migration distance), or proximate environmental cues (e.g., photoperiod and temperature) make the greatest contribution to overwintering differences among populations. It is certainly plausible that a combination of these factors generated the patterns we observed.

Wintering steelhead from all populations favored reservoirs near confluences with natal tributaries, although many used main-stem sites or nonnatal tributaries hundreds of kilometers downstream from their eventual spawning locations. The preference for deep, low-velocity habitats is not surprising, as such sites afford protection from predators and require limited energetic expenditures. Mixed stocks of overwintering steelhead similarly used low-velocity pools in the lower Yakima River (Hockersmith et al. 1995). On average, these fish overwintered about 75 km downstream from eventual spawning tributaries, and winter use of lower-river sites lasted for about 80 d (Hockersmith et al. 1995). A series of steelhead radiotelemetry studies in British Columbia rivers also found comparable habitat use patterns in which fish primarily overwintered in deep pools, at river confluences, and in lower main-stem habitats well downstream from eventual spawning tributaries (Lough 1980, 1983; Spence et al. 1990; Parken and Atagi 1998).

The considerable use of nonnatal tributaries by overwintering Snake and Salmon River steelhead appears to be more unusual. This behavior may be an artifact of thermal refugium use during summer and fall by these interior stocks, whereby some steelhead that move into colder tributaries like the Deschutes River remain well beyond the fall cooling phase that stimulates migration resumption for most delayed fish

(High et al. 2006). Other characteristics of these tributary sites, including favorable habitat conditions or aggregations of local overwintering steelhead, may also attract and hold fish from upriver populations.

Seasonally, the steelhead fate data indicated that mortality in the FCRPS due to harvest and other causes was lower during winter than during summer and fall. In part, this can be attributed to reduced fisheries effort in winter and perhaps to lower metabolic and activity rates. However, the minimum winter mortality estimate was about 18% (3.8% due to reported harvest, 14.5% to unknown loss in the FCRPS), and the estimates would have been higher had we been able to obtain a more precise determination of the final live record (i.e., instead of using the 1 January criterion). In addition to reported and unreported harvest, some winter mortality was probably attributable to natural attrition, and a portion may have been related to fallback at dams. About 21% of the successful overwintering fish fell back during winter, comparable to the 18–25% annual range reported for steelhead during the full migration (Boggs et al. 2004). In contrast, about half of the unsuccessful steelhead that at least partially overwintered in the FCRPS fell back during winter (our unpublished data). Multiple fallbacks for successful and unsuccessful fish were also more common in winter than during the rest of the year. Given clear links between fallback at dams and reduced escapement (Keefer et al. 2005a), further investigation of winter fallback may be warranted.

Regardless of whether winter fallback is related to dam operations, fish condition, overshoot behavior, or a natural proclivity for downstream winter movement, providing safer fallback routes at dams should improve overall adult steelhead survival. At most FCRPS dams, winter fallback routes are restricted to passage through power turbines—where injury and direct mortality risks are relatively high—or through navigation locks or debris sluiceways at some sites. Passage through locks is relatively safe, but monitoring of postspawn steelhead kelts suggests that downstream migrants are unlikely to locate and use locks (Wertheimer 2007). Injury and mortality risks for fish using debris sluiceways are currently unknown, as are rates of use. Provision of additional safer routes, perhaps including limited discharge over spillways (Wertheimer and Evans 2005) or bypass systems specifically designed for nonturbine passage (Wertheimer 2007), may help mitigate adult mortality. Mitigation efforts should also take into account configuration differences among dams and prioritize those projects where downstream winter movements by large numbers of fish are likely (i.e., The Dalles, John Day, and McNary dams).

The relatively high winter fallback rates also have implications for counting fish at the dams. There was a net upstream movement by radio-tagged overwintering fish in all months, suggesting that a portion of the annual run systematically goes uncounted during winter. Adjustments to steelhead run year counts for upstream winter passage and downstream fallback were beyond the scope of this summary, but the methodology established by Boggs et al. (2004) and other estimation techniques could be applied in future studies.

Winter fisheries probably affected steelhead from all metapopulations, but migration timing and long migration distances may have increased the harvest vulnerability of Snake, Salmon, and Clearwater River fish. For instance, concentrated fishing effort in The Dalles and John Day reservoirs targeted mixed-stock overwintering groups that included many fish from upriver metapopulations. Considerable winter harvest also occurred in Little Goose and Lower Granite reservoirs, which are extensively used by wintering Clearwater River steelhead and to a lesser extent by other Snake River populations. This spatial distribution differs from full-year FCRPS harvest patterns for steelhead, in which the greatest harvest is typically concentrated in Bonneville Reservoir in the lower Columbia River followed by more moderate rates in upstream reservoirs (Keefer et al. 2005a). In general, ESA-listed wild summer steelhead will be protected in winter fisheries because release is required for fish with adipose fins. Nonetheless, some catch-and-release handling mortality is probable (e.g., Bendock and Alexandersdottir 1993; Dempson et al. 2002; Nelson et al. 2005), and illegal winter harvest rates are unknown.

The majority of Columbia River steelhead are either hatchery derived or hatchery influenced (Busby et al. 1996), which presents a significant challenge for identifying and isolating hatchery effects on behaviors like overwintering. Given the tendency for hatcheries to select for traits that favor early reproductive timing (e.g., Leider et al. 1984; Mackey et al. 2001; McLean et al. 2005), we expect that some of the reported overwintering patterns reflect hatchery influences at a broad scale. Relatively early exit from FCRPS by many overwintering Clearwater River fish, for example, may reflect past selection of early migrants at the various hatcheries on the Clearwater River and throughout the Snake River system (e.g., Busby et al. 1996). The considerable overwintering variability we observed within and among populations may also be partly attributable to historical hatchery activities (e.g., interbasin transfers) that inadvertently or deliberately introduced shifts in migration timing.

In summary, the diverse set of steelhead overwintering behaviors described here reveals a remarkably flexible and adaptive set of strategies for long-distance migration. The wide variation in winter distributions and behaviors, even among successful migrants within populations, suggests past selection for behavioral plasticity in response to environmental variability. Such flexibility will be important in future years, as climate change and water management decisions continue to alter the migration environment encountered by interior summer steelhead. Given near-term forecasts for reduced winter snowpack and increased temperatures in the Columbia River basin (Hamlet and Lettenmaier 1999; Barnett et al. 2005), we expect that summertime migration conditions will become less favorable for steelhead. Thermal migration barriers will probably increase in frequency, distribution, and duration, potentially constricting the number of suitable migration days. Steelhead use of coolwater refugia will probably become an increasingly important migration feature characterized by growing concentrations of upriver steelhead staging in cooler lower-river tributaries. In response, overwintering distributions may shift downstream and prespawn spring migrations will consequently be longer and more demanding for some fish. Importantly, these costs will vary among populations and may be partially offset by milder winters, earlier spring warming, or shifts toward later fall migration. Managers working to protect Columbia River summer steelhead should consider population-specific behaviors and distributions by, for example, closing winter fisheries at sites with concentrations of listed stocks. In addition, ensuring safe passage routes upstream and downstream past dams will reduce fish injury and mortality and improve habitat connectivity, benefiting migrants from all populations.

Acknowledgments

Many people provided time and assistance during this study. We especially thank the many collaborating agency personnel at the National Marine Fisheries Service (National Oceanic and Atmospheric Administration–Fisheries). B. Burke, M. Moser, A. Matter, S. McCarthy, K. Frick, and T. Bohn provided valuable reviews or helped manage the telemetry database; many others allowed radio-tagging of the PIT-tagged fish in our samples. U.S. Army Corps of Engineers personnel, especially J. Harmon and T. Mackey, assisted with operations at the dams. We also thank T. Bjornn and L. Stuehrenberg for their early management of the adult radiotelemetry project. At the University of Idaho, R. Ringe, K. Tolotti, M. Jepson, S. Lee, T. Reischel, G. Naughton, W. Daigle, M. Heinrich, D. Queampts, M. Morasch, T. Dick, D. Joosten, C. Morat, C. Nauman, and C. Williams helped with field operations and telemetry data collection and processing. The U.S. Army Corps of Engineers provided funding for this study; we thank D. Clugston, M. Shutters, R. Dach, M. Langeslay, and K. Zelch for their support.

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