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[Article]

Postrelease Performance of Acclimated and Directly Released Hatchery Summer Steelhead into Oregon Tributaries of the Snake River

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Abstract.—In a study using 14 paired-release groups over 10 release years, we compared the performance of hatchery summer steelhead *Oncorhynchus mykiss* that were acclimated as smolts (AC) for 16–57 d before release into ponds supplied with ambient stream water with that of fish trucked from the hatchery and directly released (DR) into Spring, Deer, and Little Sheep creeks in northeastern Oregon. After releasing the fish into streams, we monitored out-migration travel times and survival to Lower Granite Dam (LGD) on the Snake River using freeze brand marks or implanted passive integrated transponder tags in a subsample of each release group. Across all release groups, travel time was significantly slower for AC fish (34.7 d) than for DR fish (31.8 d), though there was no significant difference in survival probability to LGD. We used recoveries of coded wire tags to estimate smolt-to-adult survival (SAS) and a stray rate index (SRI) for the AC and DR strategies. Across all release groups, SAS was 33% higher and SRI 42% lower for AC steelhead. At each release site acclimation increased average SAS by at least 11% and decreased SRI by at least 16.5%. We found a significant, negative linear relationship between travel time to LGD and SAS; however, there was no significant relationship between survival to LGD and SAS, which implies that judgments about the success or failure of a novel rearing or release strategy should not be made based on out-migration survival. Acclimating juvenile steelhead produced significantly higher SAS and lower SRI in the hatchery program we evaluated; however, our results are not consistent with those of other steelhead acclimation studies.

In recent years, summer steelhead *Oncorhynchus mykiss* hatchery programs operating in the Columbia River basin have released over 10 million smolts annually into rivers and streams (Fish Passage Center 2007) at a total production cost per smolt that probably exceeds the US$0.18–0.62 range estimated by Radtke and Davis (2000) a decade ago. Given the substantial investment in steelhead hatchery programs, it is important that adult return goals be met. Often, though, hatchery steelhead programs have failed to meet their goals (Brannon et al. 1999), due in part to an overemphasis on producing large numbers of fish with less concern for their postrelease fate. Therefore, fishery managers will benefit from research to identify rearing and release strategies that maximize steelhead smolt-to-adult survival (SAS). However, successful hatchery programs do more than simply meet their production goals; among other things, they also minimize the impacts of hatchery fish on wild stocks (APRE 2004).

Low postrelease survival of hatchery-raised steelhead juveniles is one impediment to meeting adult production goals. To remedy this problem, biologists have, among other things, experimentally released fish at a larger size (Tipping 1997; Hume and Parkinson 1988); released them at different times, sites, and densities (Wagner 1968, 1969; Hume and Parkinson 1987; Slaney et al. 1993); provided a period of volitional release (Evenson and Ewing 1992; Gale et al. 2009); and released them after an acclimation period (Bjornn and Ringe 1984; Whitesel et al. 1994; Tipping 1998; Osborne and Rhine 1999; Kenaston et al. 2001). Regarding the latter strategy, many hatchery-reared fish are transported to release sites, and the crowding, handling, and confinement of transportation is known to be stressful (Schreck et al. 1989). Hence, an acclimation period may allow fish to recover from the stress of transportation, resulting in greater postrelease survival. However, of the five previously cited studies comparing the performance of hatchery steelhead juveniles acclimated in the waters of their release sites for 1–30 d (AC) with fish that were directly released (DR), acclimation failed to provide unambiguous postrelease survival benefits in four

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studies (Bjornn and Ringe 1984; Tipping 1998; Osborne and Rhine 1999; Kenaston et al. 2001).

Steelhead hatchery programs can impact wild stocks genetically and ecologically when mature adults spawn in streams other than those into which they were released. Schroeder et al. (2001) found that 4–26% of all sampled adult steelhead in 16 Oregon streams were strays from hatchery releases. Interbreeding between hatchery strays and wild fish may produce progeny that are less fit than wild conspecifics (Araki et al. 2007), and competition between hatchery and wild fish for spawning sites could pose significant risks to wild stocks (Fleming and Gross 1993).

Anadromous salmonids use olfactory imprinting during smoltification as one means of recognizing their home streams (Hasler et al. 1978). Therefore, acclimating juvenile hatchery steelhead at their release site may improve imprinting through greater exposure to olfactory cues and result in reduced adult straying rates. An acclimation period may also reduce the likelihood that juveniles will swim into another watershed before smolting and imprint on a nontarget stream. Yet when Kenaston et al. (2001) conducted a 3-year experiment with hatchery steelhead to evaluate whether a 30-d acclimation period in the waters of their release site would increase adult returns to the site, they found that acclimation provided only a 5% average increase in the number of returning adults, leading to the conclusion that acclimation is not helpful in achieving higher returns to release sites.

Funding and manpower availability often constrict experimental evaluations to a few years or less. However, natural annual variation in the survival and production of anadromous salmonids can be substantial and can hinder evaluations of short-term studies (Lichatowich 1997). The previously cited work comparing the survival or straying performance of AC and DR steelhead all relied on no more than three complete brood or release years of data. In contrast, this paper presents the results of a study over 10 release years and three release sites to compare the performance of yearling summer steelhead released after an acclimation period in raceways supplied with ambient stream water with that of fish released directly into the stream. In addition, our study is unique because we tracked the seaward migration of released smolts past Lower Granite Dam (LGD), the first dam encountered on the Snake River. Thus, in addition to comparing adult production and straying metrics between release strategies, we were also able to explore whether juvenile migration timing and survival to LGD could explain the observed SAS results.

Methods

Paired-release experiments were conducted for release years 1987 through 1996 using summer steelhead raised at the Oregon Department of Fish and Wildlife's Irrigon Fish Hatchery (IFH) located near the town of Irrigon (45°90′07″N, 119°49′51″W) and released into Deer and Spring creeks (both tributaries to the Wallowa River in the Grande Ronde River basin) and Little Sheep Creek (a tributary to the Imnaha River) (Figure 1). The Grande Ronde and Imnaha rivers flow into the Snake River, which feeds the Columbia River. Broodstock for smolts produced at IFH come from marked (presumably hatchery origin) returns to the Wallowa Fish Hatchery (WFH) and associated Juvenile Acclimation Facility, located on Spring Creek approximately 1 river kilometer (rkm) upstream from the mouth, and from marked and unmarked adult returns to weirs located at the Little Sheep Creek Juvenile Acclimation Facility near rkm 8 on Little Sheep Creek. Low adult returns in some years have necessitated broodstock collection of marked WFH stock adult returns at a weir at the Big Canyon Juvenile Acclimation Facility located just upstream from the mouth of Deer Creek, and from marked WFH stock adults returning to an acclimation site on Cottonwood Creek on the lower Grande Ronde River. Water for IFH raceways comes from two wells and ranges in temperature from about 10.5°C to 13.9°C throughout the year.

Eggs from all locations were held at WFH to the eyed stage and then transferred to IFH for hatching and rearing, with Little Sheep Creek and WFH stocks maintained separately. Fry were initially reared in indoor tanks before being transferred to concrete outdoor raceways that were 30.5 m long × 6.0 m wide × 1.1 m deep in July, at which time automated pneumatic feeders provided BioMoist feed pellets (Bioproducts, Warrenton, Oregon). In midsummer steelhead were marked with an adipose fin clip, and in autumn approximately 50,000 fish from each release group received a left ventral fin clip and a unique coded wire tag (CWT; Table 1). We expected the AC groups to grow minimally during acclimation in stream waters ranging from 3°C to 16°C while the DR groups would continue to grow in the usually warmer waters at IFH. However, our goal was for both groups to be the same size at time of release. Therefore, in late summer fry were evenly apportioned into three size categories; large-sized fry (typically 55.15–65.93 fish/kg) were allocated to AC groups, medium-sized fry (66.15–88.20 fish/kg) were allocated to DR groups, and small-sized fry were excluded from the experiment because they could not be raised to a size equal to that of their

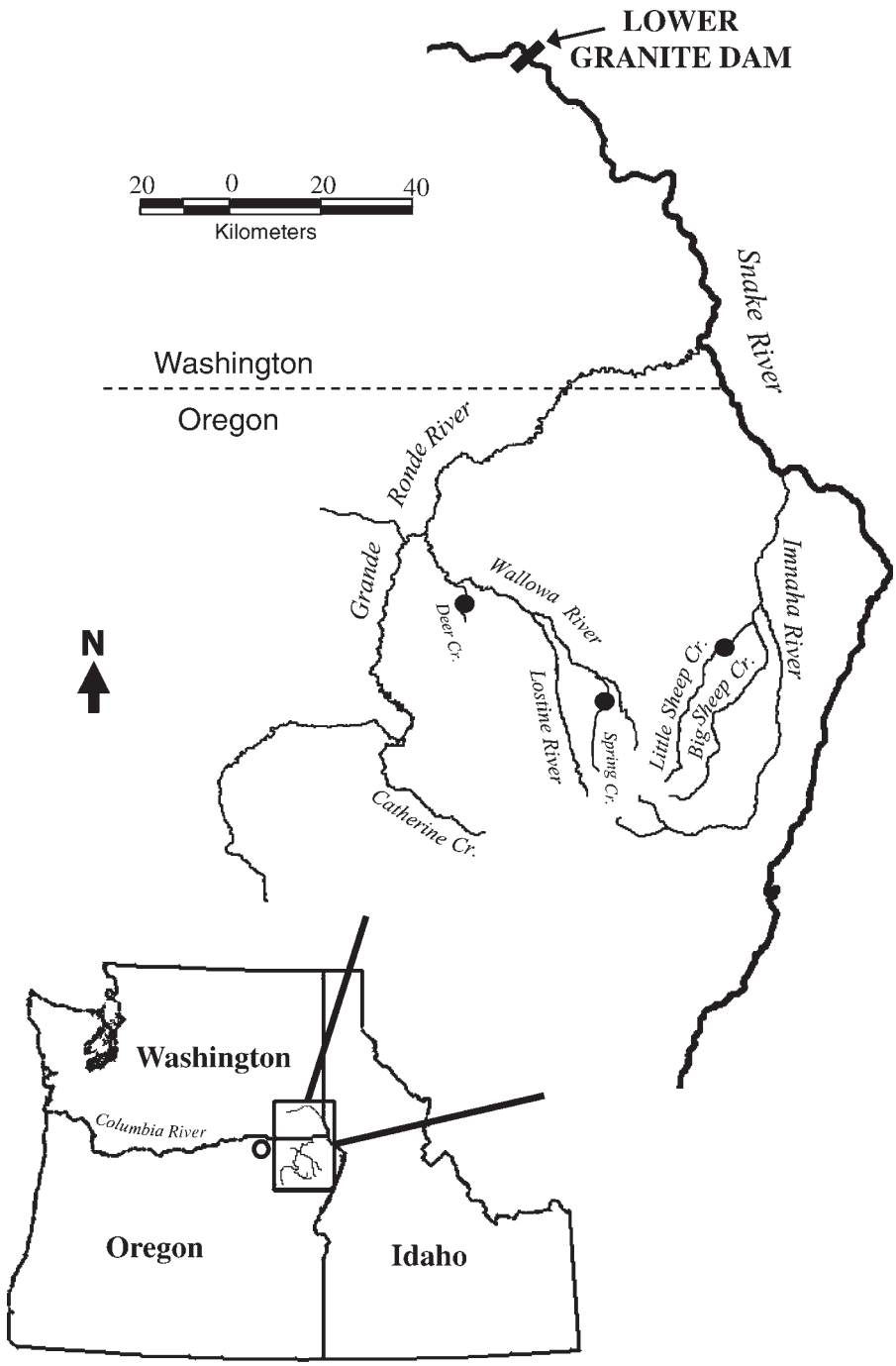

FIGURE 1.—Map showing the locations of steelhead acclimation sites (filled circles) on Deer and Spring creeks in the Grande Ronde River basin and Little Sheep Creek in the Imnaha River basin. The open circle in the inset marks the location of the Irrigon Fish Hatchery.

TABLE 1.—Average release size (fish/kg), condition factor (*K*), and number of tagged or branded summer steelhead smolts that were acclimated (AC) or directly released (DR) into Deer, Little Sheep, and Spring creeks, and the number of tags or brands that were subsequently detected or recovered at Lower Granite Dam. Abbreviations are as follows: CWT = coded wire tags, brands = freeze brands, and PIT = passive integrated transponder tags.

Release data					Number tagged or branded (thousands)			Number of tags or brands detected or recovered		
Year	Site	Strategy	Size	*K*	CWT	Brand	PIT	CWT	Brands	PIT
1987	Spring	AC	10.4	1.02	50.0			516		
		DR	9.7	1.01	50.3			306		
1988	Spring	AC	10.4	1.01	54.4	50.7		317	249	
		DR	10.6	1.09	50.8	50.5		255	349	
1989	Spring	AC	11.5	1.01	53.4	49.9		110	577	
		DR	11.6	1.01	50.5	51.0		86	610	
1990	Spring	AC	11.8	1.02	53.0	50.3		628	341	
		DR	11.3	1.10	52.2	48.8		514	358	
1991	Deer	AC	9.4	1.07	53.5	41.6		632	356	
		DR	11.7	1.05	51.4	41.0		503	254	
1992	Deer	AC	10.6	1.00	52.7	41.4		51	509	
		DR	11.5	1.05	52.1	41.0		40	481	
1993	Little Sheep	AC	12.1	1.07	49.1	40.3		122	207	
		DR	12.6	1.04	45.9	41.0		114	264	
	Deer	AC	11.5	1.07	51.1			193		
		DR	10.8	1.06	48.1			275		
1994	Little Sheep	AC	11.3	1.05	48.5	39.5		152	257	
		DR	11.3	1.11	47.0	37.7		73	113	
	Deer	AC	8.8	1.08	53.8		0.492	527		163
		DR	9.3	1.11	45.3		0.501	358		253
1995	Little Sheep	AC	11.0	1.10	53.6	40.7	0.987	160	634	492
		DR	12.5	1.14	54.9	20.3	0.497	321	26	172
	Deer	AC	8.6	1.10	54.2		0.469	424		243
		DR	9.9	1.11	50.5		0.475	359		290
1996	Little Sheep	AC	12.1	1.10	53.0	41.1	1.015	241	143	681
		DR	11.5	1.04	52.6	20.6	0.503	62	92	305
	Deer	AC	10.6	0.99	54.5		0.495	536		208
		DR	11.7	1.06	50.0		0.500	385		203

medium- or large-sized counterparts. Fish were reared to a target size of 11.0 fish/kg at targeted maximum raceway densities of 19.5 kg/m^3.

To estimate smolt survival and migration timing to LGD, between 20,000 and 51,000 smolts from the release groups were freeze branded each year in February or March using a silver-tipped brass branding rod cooled in a canister containing liquid nitrogen, with each group receiving a unique brand (Table 1). The 1987 Spring Creek DR group did not receive freeze brands, nor did the groups from the 1993 Deer Creek release; thus, no smolt survival and migration timing comparisons were made for these years. From 1994 through 1996 some release groups received implanted passive integrated transponder (PIT) tags in addition to or instead of freeze brands. PIT-tagging of 500–1,000 randomly selected fish per release group occurred in January.

Acclimated groups were transferred to concrete acclimation ponds at Deer, Little Sheep, and Spring creeks from 16 to 57 d before release. Deer and Spring creek ponds always received WFH stock smolts, and the Little Sheep Creek pond received Little Sheep Creek stock smolts. The two Deer Creek acclimation ponds each measure 45.7 × 9.1 × 1.1 m with a volume of 445.9 m^3 and a flow of 9,842 L/min. The measurements for the ponds at the other sites are as follows: Little Sheep Creek (one pond) = 59.4 × 15.2 × 1.1 m; 966.3 m^3; and 9,464 L/min; Spring Creek (two ponds) = 91.4 × 12.8 × 1.1 m; 1,248.7 m^3; and 18,927 L/min. Fish densities at Deer, Little Sheep, and Spring creeks averaged 25.8, 22.0, and 19.3 kg/m^3, respectively.

Fish were fed while in the acclimation ponds. A week before release in mid to late April, 50 randomly selected fish from both release groups were weighed (g) and measured for fork length (mm), from which Fulton's condition factor (K = weight/length^3 × 10^5; Anderson and Neumann 1996) was calculated. On the release day, fish were forced out of the acclimation ponds. Direct release groups—held at IFH on well water until the release date—were transported to acclimation sites and released directly into the stream. Transportation distances from IFH to the acclimation sites ranged from 227 to 315 km, a 3.5–4.5 h trip.

Out-migrating juveniles at LGD were sampled

hourly from April to November, identified and enumerated by freeze brand mark using protocols described by the Fish Passage Center (1994), and measured for fork length (mm). Daily collections of branded smolts at the dam and estimated collection efficiencies were used to calculate the number of branded smolts that arrived at LGD (for details, see McKenzie et al. 1985) and juvenile survival of release groups to the dam was estimated by summing daily survival probabilities. Cormack–Jolly–Seber (CJS) survival probabilities to LGD were calculated for each PIT-tagged release group using recaptures of passively detected study fish recorded in the juvenile bypass systems at LGD and downstream at dams on the lower Snake and Columbia rivers. Release–recapture information was then entered into the SURPH 2.2 or PIT Pro 4.1 programs (Lady et al. 2001; Westhagen and Skalski 2007) with a single release–recapture model (Skalski et al. 1998) for calculation of survival probabilities and confidence intervals. Because studies suggest that a greater portion of PIT-tagged fish are recaptured at dams than freeze-branded individuals (Prentice et al. 1987), survival estimates from PIT tags should be more precise. Therefore, we used PIT-tag-generated survival estimates when release groups were both freeze branded and PIT-tagged. Juvenile migration timing from day of release to LGD was calculated using both freeze brand and PIT tag recaptures at the dam. Freeze brand recapture information was provided by the Fish Passage Center, whereas PIT tag data were downloaded from the PTAGIS database maintained by the Pacific States Marine Fisheries Commission.

We estimated annual steelhead SAS and a stray rate index (SRI) for each release group using CWT recoveries from in-basin and out-of-basin locations. Smolt-to-adult survival was calculated as the percentage of smolts estimated to have been captured as adults. The SRI is the estimated number of adult steelhead tags recovered in a river basin other than the Imnaha or Grande Ronde river basins into which fish were released divided by the estimated number of captured adults. The SRI is not a true straying rate because the intended ultimate destination of steelhead captured in out-of-basin fisheries is unknowable; if not captured, some individuals may have returned to their release location. In-basin CWT recoveries came mostly from adults trapped in fish ladders at the juvenile acclimation facilities at Deer, Little Sheep, and Spring creeks and fisheries in the Grande Ronde and Imnaha river basins. At Deer and Spring creek weirs all hatchery adults were collected, whereas at Little Sheep Creek a nonrandomized portion of hatchery fish from throughout the run were passed above the weir to spawn naturally; fish from our experiment were recognized by their left ventral fin clip and counted. Out-of-basin CWT recoveries were downloaded from the Regional Mark Information System database (Pacific States Marine Fisheries Commission), which summarizes expanded recoveries throughout all fisheries, hatchery returns, and spawning-ground carcass surveys.

Release strategy could influence the gender and age composition of returning adults if one strategy produced more residualized steelhead (i.e., individuals that fail to migrate to the ocean following release) because these fish are mostly male (Viola and Schuck 1995). Therefore, gender of adults trapped at the ladder was recorded, then the release group and release year were determined from the CWT.

A Levene median test of the SAS and SRI data indicated that the assumption of equal variances among release groups was not met; therefore, these data were $\log_e$ transformed. A Kolmogorov–Smirnov test indicated that the transformed SAS and SRI data met the normality assumption. We used paired *t*-tests on transformed data to assess whether AC steelhead had higher SAS and lower SRI than DR fish. Paired *t*-tests were also used to examine differences in smolt migration timing to LGD and changes in body length from the release date to when fish were sampled at LGD. Regression analysis was used to investigate relationships between untransformed SAS and migration timing or survival to LGD. Regressed data passed tests of equal variance and normality. In preliminary tests, the slopes of the regression lines for the AC and DR groups were not significantly different for either migration timing (analysis of covariance [ANCOVA]; $F = 0.42$; df = 1, 23; $P = 0.5238$) or survival data ($F = 0.04$; $P = 0.8491$); therefore, we report regressions on pooled data. Differences in the gender and age structure of returning adults were examined with a chi-square test. Statistical significance for all tests was assumed at the 0.05 error level.

Results

From 1987 through 1996, nearly 735,000 steelhead smolts were acclimated and released and nearly 702,000 were directly released (Table 1). Over the study, size at release differed by more than a 10% arbitrary standard for only two releases; DR groups were smaller than AC groups by about 20% and 13% for Deer Creek releases in 1991 and 1995, respectively. Condition factors at time of release averaged 1.05 for AC groups and 1.07 for DR groups. Between 26 and 634 freeze-branded fish from release groups were sampled annually at LGD, and between 172 and 681 PIT tags were recaptured annually. In this study, an

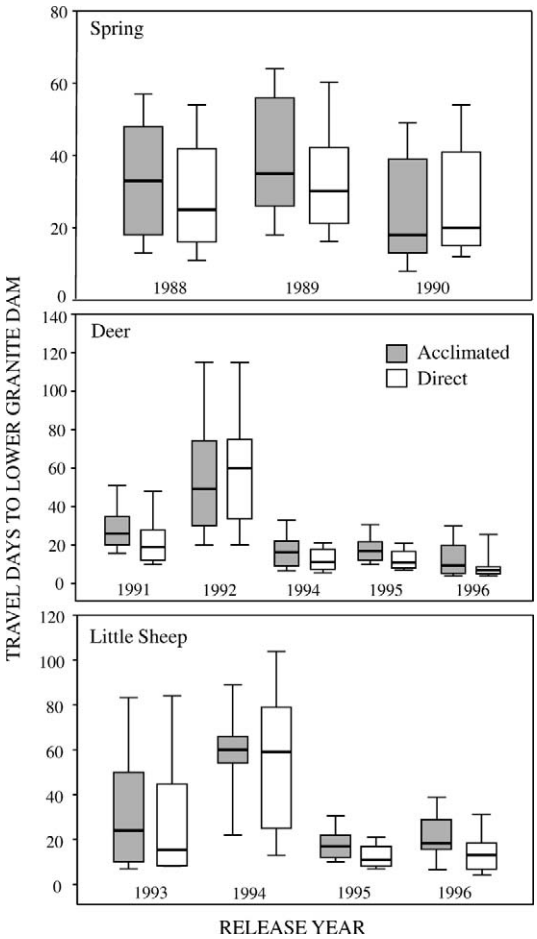

FIGURE 2.—Box plots of the number of travel days to Lower Granite Dam for paired groups of acclimated and direct-released steelhead smolts released into Spring, Deer, and Little Sheep creeks. The height of each box represents the interquartile range containing 50% of the values, with the horizontal line representing the median value. The vertical lines from each end of the box extend to the 10th and 90th percentiles; outliers are not shown.

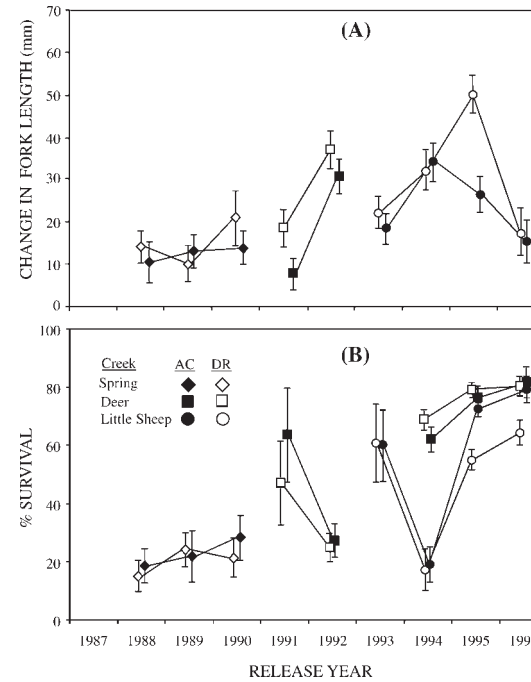

FIGURE 3.—**(A)** Average change in fork length of freeze-branded steelhead smolts from the date of release at the three acclimation sites to date of arrival at Lower Granite Dam and **(B)** percentage smolt survival to Lower Granite Dam. Survival estimates are based on PIT tag recaptures for release years 1994–1996 at Deer Creek and 1995–1996 at Little Sheep Creek; all other survival estimates are based on freeze brand recaptures. Data points are offset for clarity. Abbreviations are as follows: AC = acclimated, DR = direct release; The vertical lines represent the 95% confidence intervals.

estimated 8,260 CWTs were recovered for SAS and SRI calculation.

Upon stream release, juvenile steelhead from the two release strategies took between 11 and 60 d, on average, to reach LGD (Figure 2). Across all release groups, average travel time was about 11.5% slower for AC fish (31.7 d) than for DR fish (28.4 d), a difference that was not statistically significant ($t = 0.49$; df = 11; $P = 0.649$). All freeze brand release groups increased in average fork length between the time they were released and the time they were recaptured at LGD (Figure 3A), with DR groups having greater fork length increases in seven of nine release years, suggesting that size-dependent mortality was a more important factor for DR groups. Average increase in fork length was significant for both AC ($t = 1.85$; df = 8; $P < 0.001$) and DR groups ($t = 1.97$; $P < 0.001$). Survival probabilities to LGD were higher for AC groups in 8 of 12 releases (Figure 3B); however, average survival across all AC releases (45.7%) was only slightly higher than that across DR groups (44.0%), a difference that was not statistically significant ($t = 0.16$; df = 11; $P = 0.874$). Ninety-five percent confidence intervals on survival probabilities were always narrower for PIT-tag-generated estimates than for freeze-brand-generated estimates.

Percent SAS varied widely over the study years (AC range = 0.10–2.06, DR range = 0.08–1.21), but across all release years and sites average SAS was 33.3% higher for AC groups (0.72%) than for DR groups (0.54%), a difference that was statistically significant ($t = 2.86$; df = 13; $P = 0.013$). Fish that were acclimated prior to release had a higher SAS than DR groups in 12

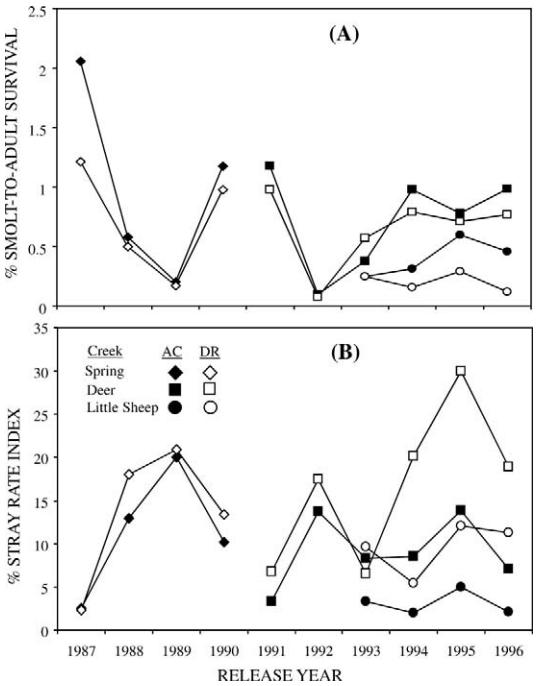

FIGURE 4.—**(A)** Average percentage smolt-to-adult survival and **(B)** percentage straying rate index for acclimated (AC) and directly released (DR) steelhead smolts.

of 14 releases (Figure 4A). Average SAS was higher for AC groups by 11% at Deer Creek, 49% at Little Sheep Creek, and 29% at Spring Creek. Release groups that took longer to travel to LGD had significantly lower SAS (Figure 5A); however, we found no significant relationship between SAS and survival to LGD (Figure 5B).

There were only 15 adult CWT recoveries at locations within the Snake River basin other than the basin into which fish were released, indicating that once adults from both release strategies returned to the Snake River basin they were unlikely to stray. We estimate that 845 CWTs were recovered from fish that did not reach the Snake River, of which 773 were recovered in the Deschutes River basin. The Deschutes River, located in north-central Oregon, joins the Columbia River approximately 194 rkm downstream from the mouth of the Snake River. Coded wire tag recoveries in the Deschutes River came from locations as far upstream as rkm 161 and from the lower Deschutes River sport and Native American tribal fisheries located from the river mouth to Sherars Falls (rkm 67.9). Fish that were acclimated prior to release had a lower SRI than DR groups in 12 of 14 releases (Figure 4B). Across all release years and sites the difference in overall SRI was large (AC = 8.05%, DR = 13.79%) and statistically significant ($t = 4.28$; df = 13; $P < 0.001$). Average SRI was lower for AC groups by 45.1% at Deer Creek, 68.2% at Little Sheep Creek, and 16.5% at Spring Creek.

Across all release years and sites, the gender of returning adults was similar (AC = 54.3% female, DR = 55.5% female). Though gender composition varied among release sites (Figure 6), there were only slight and nonsignificant differences in gender comparisons between release groups at a particular site ($P > 0.2000$ for all release sites). Similarly, we found a small and statistically insignificant difference in the age composition of returning adults ($P > 0.6000$ for all release sites); those originating from AC releases were composed of 71.6% age-3, 28.0% age-4, and 0.4% age-5 individuals, whereas the age composition for DR groups was 70.0, 29.7, and 0.3%, respectively (Figure 6).

Discussion

In the Pacific Northwest, acclimation of anadromous hatchery salmonids is a common practice, in part because off-site acclimation ponds provide operational flexibility that may allow for increased fish production by freeing up hatchery raceways. Moreover, advisory boards and independent scientists have recommended acclimation as one possible strategy to increase postrelease survival or reduce unwanted ecological interactions with wild fish (Hard et al. 1992; IHOT 1995; Kapuscinski 1997; HSRG 2004). However, the acclimation benefits for steelhead are poorly understood. In our study, AC juvenile steelhead survived to adulthood at higher rates than DR fish in most but not all paired releases, and we measured average SAS increases of at least 11% at each release site. In addition, acclimation was effective at reducing the overall percentage of adult steelhead that strayed. Most AC groups had a lower SRI than DR groups, and average SRI was reduced by at least 16.5% at each release site.

In an ideal experiment, AC and DR fish would be equal in every way except for release strategy. However, because steelhead smolt size at release correlates positively with postrelease survival (Ward and Slaney 1988; Slaney et al. 1993; Tipping 1997), and because we anticipated differential growth between release groups during the time that fish were being acclimated, we believed it necessary to allocate medium size grade juveniles to DR groups to achieve similar sizes at release. Yet the size grading, and the differential growth rates of release groups leading up to the release date, admittedly represent confounding factors that impart some uncertainty to our SAS results.

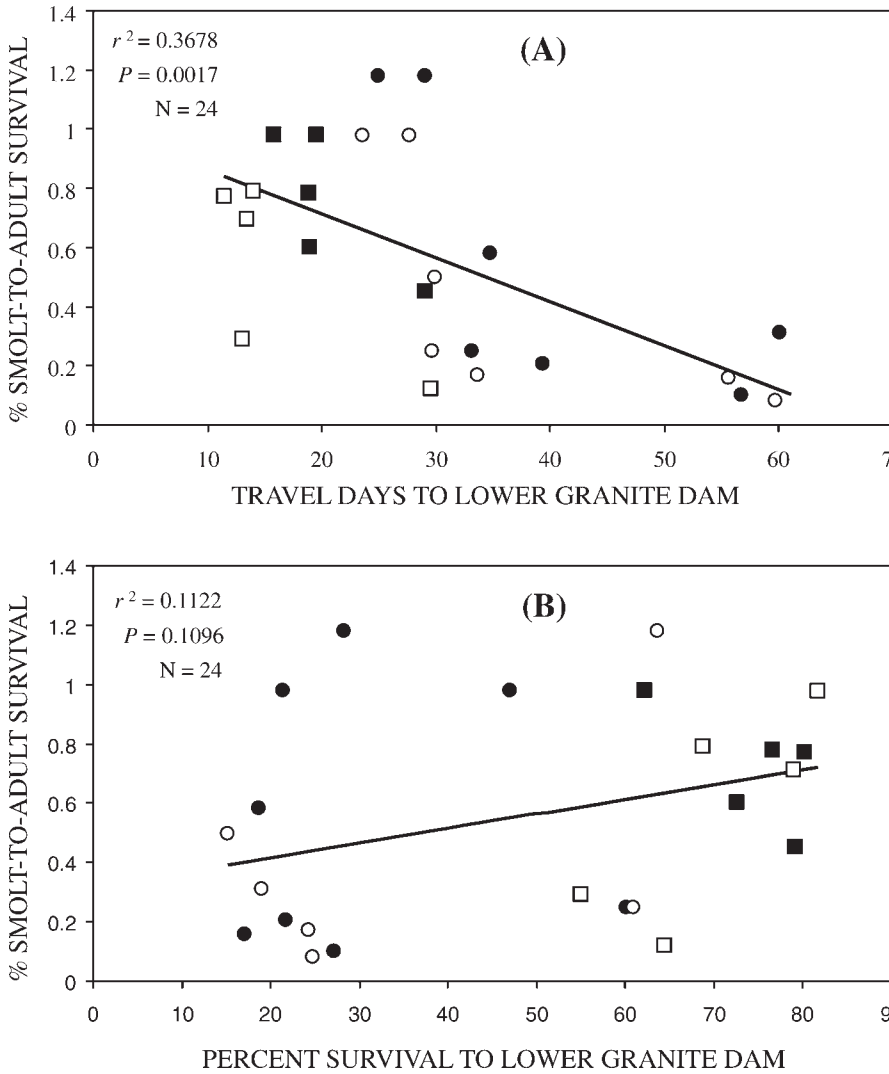

FIGURE 5.—Relationships between average percentage smolt-to-adult survival and **(A)** average travel days to Lower Granite Dam and **(B)** percentage survival to Lower Granite Dam for all acclimated (solid symbols) and directly released (open symbols) steelhead smolt groups. Estimates from freeze brand recaptures are shown as circles, whereas those from PIT tags are shown as squares.

Ultimately, we do not know whether the size grading procedure biased our results; we could find little information in the literature to directly address this question. Several lines of evidence reinforce our belief in the utility of acclimation as a management tool for improving hatchery steelhead SAS. First, the overall average size-at-release difference between AC and DR groups was small, with AC groups being just 3.9% larger. While size is known to affect hatchery steelhead smolt survival, evidence suggests that a small size difference should not produce the large survival inequality that we measured (Slaney et al. 1993; Tipping 1997). Second, a fast springtime growth rate may improve postrelease survival compared with a slow or no-growth rate, which would have advantaged DR fish in this study. For example, Beckman et al. (1999) observed that growth rates of spring Chinook salmon *O. tshawytscha* from February through April (prior to April releases) were positively correlated with SAS. Further, in experimental paired releases Beckman et al. (1998) found that spring Chinook salmon that were manipulated to have high spring growth rates

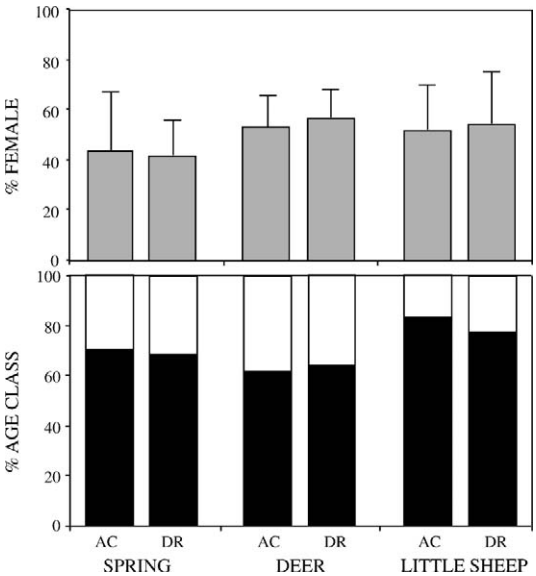

FIGURE 6.—Gender (top panel) and age composition (bottom panel) of adult steelhead originating from acclimated (AC) and directly released (DR) groups at Spring, Deer, and Little Sheep Creek acclimation facilities. In the top panel, the vertical lines represent 2 SEs. In the bottom panel, the dark portions of the bars are the percentages of age-3 adults, the light portions those of age-4 adults (age-5 adults were always $\leq$1% of the returns and are not shown in the graph).

migrated faster and had better survival to a weir than release groups having slow spring growth, even when the faster-growing fish were significantly smaller at release. Thus, even though the DR groups in this study may have been advantaged by higher prerelease growth rates, they still exhibited lower postrelease survival. Finally, investigations into the physiological stress responses of our AC and DR smolts during the early years of this study provide a plausible explanation for the survival differences we observed. Reporting on those investigations, Whitesel et al. (1994) found higher plasma chloride levels in smolts at the end of 27–39-d acclimation periods than in DR fish just prior to transportation from the hatchery and that AC and DR release groups exhibited different plasma cortisol and chloride responses to stress challenges administered to a sample of fish on the release date (following transportation of DR fish). Lower plasma chloride and higher plasma cortisol levels are generally recognized as indicators of stress in fish (Wendelaar Bonga 1997), although the physiological stress response of hatchery salmonids is variable and may not be represented by any single biochemical indicator (Barton 2000). However, based on their evaluation, Whitesel et al. (1994) hypothesized that acclimation may ameliorate the cumulative stress effects associated with transport and DR.

Our conclusion that SAS was enhanced by an acclimation period does not accord with the conclusions from three similar acclimation experiments performed with steelhead (Bjornn and Ringe 1984; Tipping 1998; Kenaston et al. 2001). Given that we measured highly variable SAS between our 14 releases and the acclimation benefit did not manifest itself in all releases or release years, we think it is possible that the aforementioned studies had too few replicate releases (i.e., $\leq$3 release years) to identify a significant SAS advantage from acclimation. Indeed, Bjornn and Ringe (1984) and Tipping (1998) each reported higher SAS for AC fish in one of their two study years, and Kenaston et al. (2001) reported higher SAS for AC fish in two of three years, but their average acclimation benefit was only about 5% and not statistically significant. Variations in experimental protocols, including intrinsic differences among hatchery and acclimation facilities, could have accounted for the observed performance differences. For example, Tipping (1998) acclimated steelhead smolts for just 24 h following transport, but studies have demonstrated measurable physiological and behavioral stress responses of *O. mykiss* (including rainbow trout) from 3 to 7 d following transport (Barton et al. 1980; Barton 2000; Chandroo et al. 2005). In addition, hatchery and release site water temperatures may have been an important factor. Fish released by Kenaston et al. (2001) and Tipping (1998) were reared in hatcheries supplied by river water; hence, their DR groups experienced little or no temperature variation upon stream release. By comparison, when our fish were moved from hatchery waters of about 10–11°C into prechilled water of 7–8°C inside transport trucks, they probably received a "cold shock" that is known to induce increased plasma cortisol levels in rainbow trout exposed to chilled water just 1°C below ambient temperatures (Barton and Peter 1982). Moreover, Deer and Spring creek stream temperatures were often at least 2°C warmer or colder than the transport water, which may have resulted in an additional layer of temperature-induced stress. Finally, transport distances to acclimation sites also differed among studies, with our fish experiencing transport times that were about two to five times longer than those reported in Kenaston et al. (2001) and Tipping (1998); transport times or distances were not reported in Bjornn and Ringe (1984). Fish collection and loading onto transport trucks is a known stressor for juvenile *O. mykiss*, and the physiological effects of this process can persist over the next 4 h of transport (Barton and Peter 1982).

Juvenile out-migration survival to LGD did not correlate as well with SAS, as did travel times. River velocities are generally believed to influence steelhead smolt migration times (Berggren and Filardo 1993), and there appears to be a viable positive relationship between flow and smolt survival in the Columbia River basin (Cada et al. 1997). Flow—and other correlated environmental factors that produced the observed travel times to LGD—may also influence out-migration timing and survival of nonbarged smolts through the rest of the Columbia River corridor, so that smolts that experience faster travel times and higher survival to LGD probably also experience greater survival to the ocean. Survival estimates based on freeze brand data should be interpreted cautiously, in recognition of collection uncertainties at LGD that typically produced larger error variances than PIT tag technology (Prentice et al. 1987; Smith et al. 1993). However, following this study, a portion of most steelhead groups released from our acclimation ponds were PIT-tagged, and out-migration survival of those groups also did not correlate significantly with SAS (L. Clarke, unpublished data). The lack of correspondence between juvenile out-migration survival and SAS implies that judgments about the success or failure of novel rearing and release strategies should be made only after adult returns are counted.

Studies show that a portion of Snake River basin steelhead that enter the Deschutes River in summer and become vulnerable to fisheries capture will ultimately exit to resume their migration up the Columbia River (High et al. 2002). Since over 90% of our out-of-basin tag recoveries came from the Deschutes River, our conclusion that straying was less in AC releases might be incorrect if DR fish are more likely to enter the Deschutes River or are more vulnerable to fisheries capture upon entry. We do not believe that one release strategy produced adults that were more vulnerable than the other. Moreover, a spatial and temporal examination of Deschutes River tag recoveries supports our conclusion that acclimation reduced straying. To illustrate, of the 290 tags recovered from August through October in the lower river sport and tribal fisheries (below rkm 67.9), 54% were from AC groups, suggesting that both the AC and DR groups were likely to enter the lower river in summer. However, of the 463 tags recovered above the lower river fisheries, 59% came from DR groups, and of the 203 tags that were recovered after 1 February (when adults start to arrive at Deer, Little Sheep, and Spring creek acclimation sites), 56% came from DR groups. Thus, DR groups were more likely to migrate further up the Deschutes River and to remain there during the steelhead spawning season.

Acclimation of steelhead in our study significantly improved SAS and decreased straying. Although our conclusions are not consistent with those of other steelhead acclimation studies, hatchery trout are known to survive better when held in waters of their release site following transport (Ayles et al. 1976; Cresswell and Williams 1983; Jonssonn et al. 1999), as are anadromous salmon (Ísaksson et al. 1978; Schreck et al. 1989; Johnson et al. 1990; Finstad et al. 2003; but see Appleby et al. 2002). Other than this study and the study by Kenaston et al. (2001), we know of no others that compare straying between paired AC and DR groups of anadromous salmonids. However, more than one study has demonstrated improved site fidelity by acclimating salmonids (Jonssonn et al. 1999; Garcia et al. 2004). The acclimation benefits to survival appear to be associated with amelioration of a variety of stressors associated with transport (e.g., loading, length of transport, and the conditions into which fish are released). Therefore, when considering initiation of an acclimation program, fisheries managers should take into account the extent to which cumulative stress events imposed on their hatchery steelhead during transport and release might influence postrelease performance. Managers may also want to test the benefits of acclimation using temporary holding ponds before constructing permanent acclimation facilities.

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