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[Article]

Migration Characteristics of Hatchery and Natural Spring Chinook Salmon Smolts from the Grande Ronde River Basin, Oregon, to Lower Granite Dam on the Snake River

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Abstract.—Smolts of spring Chinook salmon *Oncorhynchus tshawytscha* experience substantial mortality while migrating through free-flowing reaches of the Snake River basin before reaching Lower Granite Dam, the first dam encountered in the Columbia–Snake river hydrosystem. We investigated the patterns of travel time and survival of hatchery and natural smolts fitted with passive integrated transponder (PIT) tags through specific reaches of the migration corridor during the 2000–2006 migration years for two populations originating in the Grande Ronde River basin (Lostine River and Catherine Creek). For both populations, median travel times for natural smolts were significantly longer in the upper reaches of the migration corridor but shorter in the lower reaches than for their hatchery counterparts. Also, among both hatchery and natural smolts, smaller individuals spent more time in the upper reaches, presumably feeding to attain a larger size before continuing their migration. Within populations, both hatchery and natural smolts showed similar patterns of survival through the reaches of the migration corridor above Lower Granite Dam. Size-selective mortality was evident for hatchery and natural smolts from both populations, especially in the upper reaches, larger individuals experiencing higher survival. The Catherine Creek population experienced the majority of natural and hatchery smolt mortality (32.8–65.8%) in a relatively short (91-km), low-gradient reach immediately below the summer rearing habitat. In contrast, the Lostine River natural and hatchery smolts experienced lower mortality (3.6–46.1%) in a 174-km reach below the summer rearing habitat. The results of this study demonstrate the dynamic nature of survival and migration rate among spring Chinook salmon smolts during their initial seaward migration from tributaries.

Snake River spring–summer Chinook salmon *Oncorhynchus tshawytscha* populations, once the predominant run of stream-type Chinook salmon in the Columbia River basin, have dramatically declined and were listed as threatened in 1992 under the Endangered Species Act (NMFS 1992). The development of eight hydroelectric dams on the lower Snake and Columbia rivers, part of the Federal Columbia River Power System (hydrosystem), along with habitat degradation in the upper free-flowing portions of the Snake River basin, have been identified as major causes for the population decline (McConnaha et al. 2006; Stanford et al. 2006). Since the late 1980s, the National Marine Fisheries Service (now National Oceanic and Atmospheric Administration [NOAA] Fisheries), U.S. Fish and Wildlife Service, and Bonneville Power Administration have sponsored numerous tagging studies in the Snake River basin to assess success of actions designed to improve migration timing and survival of Chinook salmon smolts through the hydrosystem. The development of passive integrated transponder (PIT) tags that permit individual identification of marked fish along with tag-detection systems at dam sites (Prentice et al. 1990a) has greatly aided these studies. In addition, considerable efforts are underway to improve degraded habitats that exist in many of the Snake River tributaries. Despite these efforts, substantial smolt mortality occurs in the free-flowing portion of the migration corridor before reaching Lower Granite Dam, the first dam encountered in the hydrosystem (Giorgi 1991; Muir et al. 2001). Chinook salmon smolts migrate up to several hundred kilometers downstream through varying river environments before reaching Lower Granite Dam. Understanding the location, magnitude, and possible factors that affect smolt mortality en route to the hydrosystem is essential so that fisheries managers can apply limited resources to improve survival and

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develop effective recovery strategies for these listed populations.

Muir et al. (2001) noted that hatchery spring–summer Chinook salmon smolts released in the Snake River basin incur substantial mortality in the free-flowing reaches above Lower Granite Reservoir that was proportional to distance traveled and travel time. Fish size has also been identified as an important determinant in survival and migration rates of hatchery and wild smolts during out-migration, with larger fish experiencing greater survival (Zabel and Williams 2002; Zabel and Achord 2004). This greater survival is presumably because larger individuals within a population tend to have a faster migration rate (Zabel 2002) and arrive at the hydrosystem earlier than do smaller smolts (Achord et al. 2007), thereby experiencing less exposure to survival hazards. Travel time is also influenced by numerous factors such as river flows (Berggren and Filardo 1993; Smith et al. 2002) and level of smolt development (Zaugg et al. 1985; Muir et al. 1992).

Rearing history of smolts (hatchery or natural) can also influence smolt development and subsequent migration characteristics. A goal of conservation hatcheries, such as Lookingglass Fish Hatchery in the Grande Ronde basin, is to rear hatchery fish that exhibit similar life history characteristics as do wild fish to limit genetic and ecological risk to wild populations. However, high rearing densities and environmental conditions in hatcheries, such as an unchanging or artificial photoperiod, a constant temperature, or differing water chemistry, are not similar to those of the stream into which the smolts will be released and may impair the smoltification process and the resulting migration, imprinting, and survival of these salmon (Wedemeyer et al. 1980; Schreck et al. 1985; Hoffnagle and Fivizzani 1990, 1998; Dittman and Quinn 1996; Sundell et al. 1998). Fish reared in hatcheries under different environmental conditions than their natural counterparts may differ in the developmental timing of their parr–smolt transformation and subsequent migration timing. Additionally, hatchery smolts are generally reared to a larger size than that of their natural counterparts in an effort to increase their survival after release. How these factors affect survival and migration characteristics of hatchery smolts compared with natural smolts during their seaward migration is not well known.

In this investigation, we were able to take advantage of multiple years of tag–release studies and subsequent recapture information within a major Snake River subbasin (Grande Ronde River) to evaluate travel time and survival dynamics of hatchery and natural spring Chinook salmon smolts through specific reaches of the migration corridor above Lower Granite Dam. The PIT tagging of hatchery and natural juvenile spring Chinook salmon has been conducted within the basin to provide information on travel time, migration timing, and survival, and substantial mortality has been reported within the migration corridor (Jonasson et al. 2006; Monzyk et al. 2006; Cleary 2007). Our objectives in this study were to: (1) compare travel times to Lower Granite Dam between hatchery and natural Chinook salmon smolts within populations, (2) compare travel times to Lower Granite Dam between smolts of different size-groups within hatchery and natural origin groups, (3) estimate and compare survival probabilities to Lower Granite Dam for hatchery and natural smolts tagged and released along the migration corridor and use these estimates to calculate reach-specific survival within rearing groups, and (4) determine the influence of fish size on hatchery and natural smolt survival to Lower Granite Dam from release sites along the migration corridor.

Study Area

The Grande Ronde basin encompasses an area of about 10,000 km^2 in northeastern Oregon and southeastern Washington (Figure 1). The Grande Ronde River flows generally northeast 341 km from its origin to its confluence with the Snake River at river kilometer (rkm) 272, about 98 km upstream from Lower Granite Dam and 793 km from the mouth of the Columbia River. The basin is bounded by the Blue Mountains to the west and northwest and the Wallowa Mountains to the southeast. Elevations in the watershed range from 253 m at the confluence with the Snake River to nearly 3,000 m in the Wallowa Mountains. Numerous tributary streams support naturally spawning populations of spring Chinook salmon in the basin. Chinook salmon smolts originating from the basin can travel more than 350 km before reaching Lower Granite Dam. Depending upon the tributary from which smolts originate, the upper migration corridor can pass through varying habitat and land-use conditions.

Two spawning tributaries of the Grande Ronde River, Catherine Creek and the Lostine River, have long time series of trapping and tagging information (1994–2006) and large numbers of PIT-tagged hatchery smolt releases. Reach boundaries in the migration corridor for these two populations were determined by trap locations within the basin (Figure 1). The 369-km migration corridor used by Catherine Creek smolts was divided into four reaches (Table 1). Hatchery smolts were evaluated from their release location at the Catherine Creek Acclimation Ponds (CCP) to a 1.5-m (5-ft) rotary screw trap located 16 km downstream on

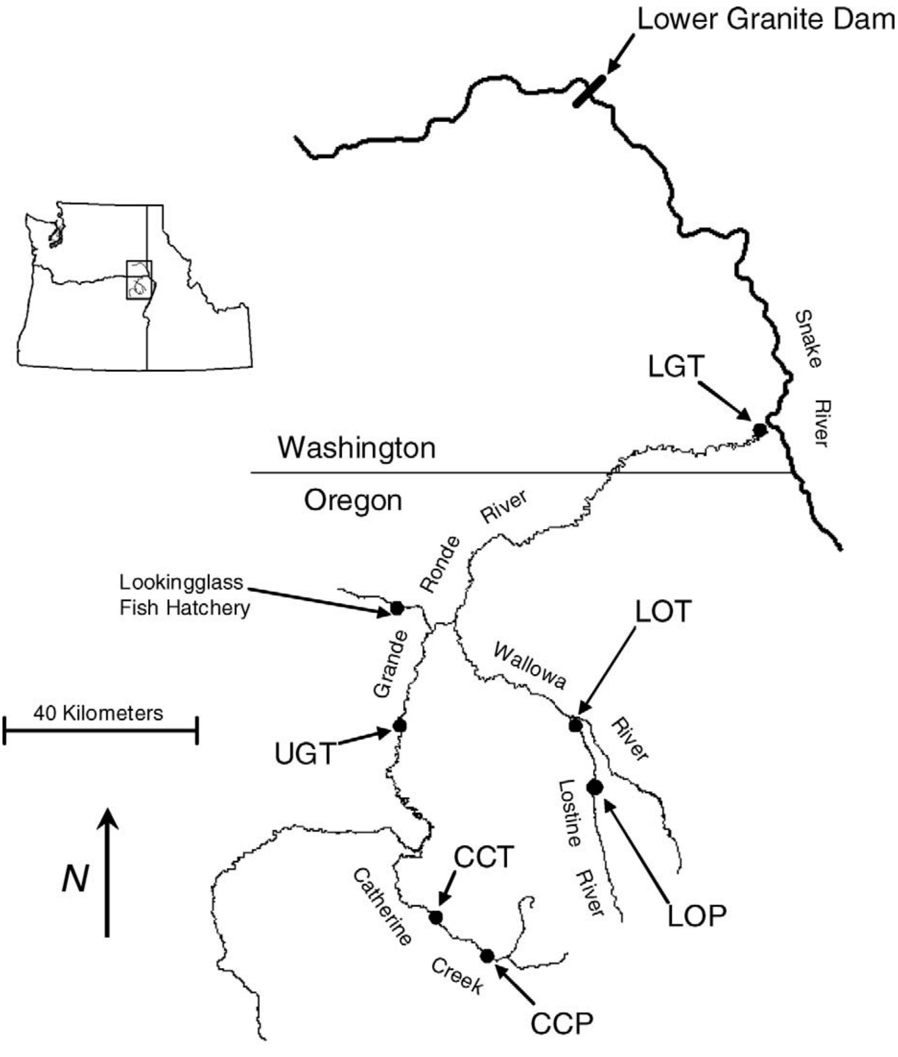

FIGURE 1.—Map of the study area showing the release locations for Chinook salmon smolts in the Grande Ronde River basin and at Lower Granite Dam. Only hatchery smolts were released at the Lostine River (LOP) and Catherine Creek acclimation ponds (CCP). Both natural and hatchery smolts were captured and released at the Catherine Creek trap (CCT), Lostine River trap (LOT), upper Grande Ronde River trap (UGT), and lower Grande Ronde River trap (LGT).

Catherine Creek (CCT). This reach (CCP–CCT), having a mean stream gradient of 8.0 m/km, comprises the majority of the spawning and summer rearing habitat for spring Chinook salmon in Catherine Creek. The Catherine Creek trap is the farthest upstream point where natural smolts are captured and tagged on Catherine Creek. An 2.4-m (8-ft) rotary screw trap, located 91 km downstream on the upper Grande Ronde River (UGT) marked the downstream endpoint of the next reach (CCT–UGT) where hatchery and natural smolts were evaluated. This reach meanders through the Grande Ronde Valley, where the gradient decreases to 0.35 m/km and stream velocity decreases. Beyond the valley reach, the gradient increases to approximately 3.5 m/km as the next reach flows 162 km to an incline plane trap located 2 km from the confluence with the Snake River (LGT). This reach (UGT–LGT) comprises the remainder of the Grande Ronde River main stem. The remaining 100 km of the migration corridor extends from the lower Grande Ronde River trap to Lower Granite Dam (LGT–Dam). In this Snake River reach, gradient decreases to approximately 0.29 m/km (depending on reservoir water surface elevation) and stream velocity again decreases as the free-flowing

TABLE 1.—Reach names and corresponding boundaries, lengths, and gradients for the Catherine Creek and Lostine River migration corridors. Release site boundary codes are as follows: CCP = Catherine Creek acclimation pond; CCT = Catherine Creek trap; UGT = upper Grande Ronde River trap; LGT = lower Grande Ronde River trap; LOP = Lostine River acclimation pond; LOT = Lostine River trap; and dam= Lower Granite Dam.

Reach name	Release site boundaries	Reach length (km)	Reach gradient (m/km)
Catherine Creek			
Catherine Creek summer rearing habitat	CCP–CCT	16	8.0
Grande Ronde Valley	CCT–UGT	91	0.35
Grande Ronde River main stem	UGT–LGT	162	3.5
Snake River	LGT–dam	100	0.29
Lostine River			
Lostine River summer rearing habitat	LOP–LOT	18	10.7
Wallowa–Grande Ronde River	LOT–LGT	174	5.0
Snake River	LGT–dam	100	0.29

river enters Lower Granite Reservoir, approximately 30 km below the confluence of the Grande Ronde and Snake rivers.

The 292-km migration corridor to Lower Granite Dam for Chinook salmon smolts emigrating from the Lostine River has a more uniform gradient. Trap locations divide this corridor into three reaches. Hatchery smolts were evaluated from their release from the Lostine River Acclimation Ponds (LOP) to a 1.5-m (5-ft) rotary screw trap located 3 km upstream from the mouth of the Lostine River (LOT). This 18-km reach (LOP–LOT) has a fairly constant gradient of 10.7 m/km and contains the majority of the summer rearing habitat for spring Chinook salmon in the Lostine River. The next 174-km reach (LOT–LGT) extends from the Lostine River trap, near the confluence with the Wallowa River, to the lower Grande Ronde River trap, near its confluence with the Snake River. The Wallowa River flows for 42 km to its confluence with the Grande Ronde River with an average gradient of 5.0 m/km. The migration corridor beyond the confluence with the Grande Ronde River is the same for both the Catherine Creek and Lostine River populations. Therefore, the last reach of this corridor (LGT–Dam) is the same Snake River reach previously described.

Methods

Data collection.—Natural populations of spring Chinook salmon in the Grande Ronde basin rear in freshwater for a full year before initiating seaward migration in the spring as yearling smolts. Some juveniles emigrate out of summer rearing areas in the fall to overwinter in downstream reaches. In this investigation, we were interested in the survival and travel time characteristics of juveniles that remained in upper rearing areas through the winter because these were more comparable to hatchery smolts released in these areas in the spring. Unless otherwise stated, we report only data from the 2000 to 2006 migration years because these years represent the time period of overlapping PIT tag data of natural and hatchery origin smolts. The Catherine Creek and upper Grande Ronde River traps have been in operation since 1994 and the Lostine River and lower Grande Ronde River traps since 1997.

All traps were designed to capture fish actively moving downstream and were equipped with live boxes that safely held hundreds of juvenile salmon trapped over 24–72-h periods. Field crews operated traps daily throughout the spring migration period. One exception was for the upper trap sites during the early and late parts of the migration period, when few fish were being captured. At these times, traps were checked every 48–72 h. At each trap site, hatchery smolts (identified by a clipped adipose fin) were examined for previously implanted PIT tags and natural smolts were PIT-tagged. Natural Chinook salmon were anesthetized with tricaine methanesulfonate (MS-222) at 40–60 mg/L, examined for previously implanted PIT tags and, if previously tagged, were measured for fork length (FL, mm). A portion of the untagged natural Chinook salmon collected each day received PIT tags and were measured for FL. Fish were tagged manually with a modified syringe equipped with a 12-gauge hypodermic needle following PIT tagging protocols described by Prentice et al. (1986, 1990b). We attempted to tag 500 natural Chinook salmon each year at each of the Catherine Creek and Lostine River traps during the spring migration period. At the upper Grande Ronde River trap, up to 400 natural Chinook salmon were tagged each spring from 2002 to 2006. As part of a smolt monitoring study, an additional 1,000–2,000 natural Chinook salmon were tagged each spring at the lower Grande Ronde River trap. All smolts were allowed to recover fully from the anesthesia before being released back into the stream. Further details of capture and tagging methods at trap sites can be found in Setter et al. (2005) and Jonasson et al. (2006).

Hatchery Chinook salmon in the Grande Ronde basin are reared at Lookingglass Fish Hatchery (Figure 1) and these native stocks are released into the streams from which their parents were collected as returning adults. Hatchery Chinook salmon were implanted with PIT tags 6 months before release. Fish were anesthetized in 60 mg/L MS-222 before tagging and their FLs were recorded (from every fish in the 2000–2003 release groups and from a representative sample of the 2004–2006 release groups). Further details of hatchery tagging methods are given by Jonasson et al. (2007).

In the spring, hatchery smolts were transferred to acclimation ponds on Catherine Creek and the Lostine River for 1–2 weeks of acclimation. Following acclimation, smolts were allowed to leave volitionally for 1–2 weeks, after which all remaining smolts were forced out, with the exception of the 2001 smolt release from the Lostine River acclimation ponds, which were forced out without an acclimation period. Acclimation ponds were equipped with PIT tag detection antenna arrays in most years to detect tagged individuals exiting during the volitional and forced releases. After release from acclimation ponds, a portion of the hatchery smolts were captured at downstream trap locations. During periods of low catch rates, fish were anesthetized with MS-222, examined for PIT tags, and, if a tag was detected, FL was recorded. The exception to this method was during times of high catch rates at the Lostine River, Catherine Creek, and upper Grande Ronde River traps, when hatchery fish were not anesthetized but only examined for PIT tags (no recapture FL recorded) and immediately released back into the stream to reduce overcrowding and stress. Also, at the upper Grande Ronde River trap, a flow-through system equipped with a PIT tag antenna was installed in the live box during times of expected high catch rates that allowed captured hatchery and natural fish to be passively examined for PIT tags as they exited the trap.

Through the examination of previously PIT-tagged hatchery smolts at acclimation sites and downstream trap sites, we developed yearly PIT tag-and-release groups from each site in the basin to evaluate population-specific travel time and survival. We used natural-origin smolts tagged at the trap sites to calculate survival probabilities and compare travel times to Lower Granite Dam. Natural smolts that comprised release groups from lower trap sites (traps from upper and lower Grande Ronde rivers) were from populations throughout the basin and may not represent survival and migration characteristics of specific populations from Catherine Creek or the Lostine River. However, a review of all available PIT tag recapture data at lower trap sites indicated that natural smolts tagged at the Catherine Creek and Lostine River trap sites in the spring generally began arriving at these traps later in the season than did smolts from other tributaries and later than those that began their downstream migration the previous fall. Therefore, we performed travel time and survival comparisons using the subset of the natural smolts tagged at these lower trap sites that best represented Catherine Creek and Lostine River smolts. At the upper Grande Ronde River trap, the earliest arrival of a Catherine Creek spring-tagged smolt occurred on day 99 (9 April). At the lower Grande Ronde River trap, the earliest arrival date was day 104 (14 April) for a Catherine Creek spring-tagged smolt and day 83 (24 March) for Lostine River spring-tagged smolts. Therefore, we used only the subset of natural PIT-tagged fish at the lower trap sites that were trapped on or after the earliest known detection date of spring-tagged smolts from the upper trap sites. Although the method of using only a subset of all possible tagging data had obvious limitations and assumptions, we felt that it better approximated survival and migration timing of our study groups.

The PIT tag data for each hatchery and natural smolt release group used in this study were downloaded from the Columbia Basin PIT Tag Information System (PTAGIS) database maintained by the Pacific States Marine Fisheries Commission (PSMFC 1996). In some years PIT tag data were not available or were insufficient at certain trap sites due to disruptions to normal trapping operations or by sampling protocols designed to limit the handling of hatchery smolts. Information on PIT-tagged hatchery smolts at the Lostine River trap in 2000 and 2004 and the Catherine Creek and upper Grande Ronde River traps in 2003 was insufficient to provide useful survival estimates. At the Catherine Creek trap in 2005, recaptured hatchery smolts were biased toward early release groups and not representative of the entire cohort, so we excluded this group from our analysis. Also, PIT tagging of natural smolts at the upper Grande Ronde River trap was not initiated until 2002.

Travel time.—The best measure of travel time through specific reaches within the migration corridor was based on the number of days between release date at an upstream release site and recapture date at the subsequent downstream trap site for individually PIT-tagged smolts. Because multiple recaptures of the same fish at two consecutive traps were rare, we used PIT tag information from all years that data were available to calculate these estimates. Small sample sizes prohibited us from directly comparing travel times between hatchery and natural smolts within reaches with this method. Therefore, to address the first objective (travel time comparisons between hatchery and natural smolts), we evaluated travel times to Lower Granite Dam using daily paired releases from each trap site for the 2000–2006 migration years. We used only those occasions when at least one PIT-tagged hatchery smolt and one tagged natural smolt were released from a trap site on the same day and subsequently detected at Lower Granite Dam. If more than one hatchery or natural smolt were released on a given day and later detected, the median travel time for that group was used in the comparison. Use of paired releases for comparisons accounted for potential seasonal trends in travel time. Similar methods were used to accomplish our second objective, that is, to compare travel times to Lower Granite Dam between smolts of different size-classes within hatchery and natural rearing histories. We classified a smolt as small if its FL was less than or equal to the 30th percentile of all lengths recorded throughout the spring migration period each year. A smolt was classified as large if its FL was larger than or equal to the 70th percentile of all lengths recorded for the cohort. However, for natural smolts at the Catherine Creek and Lostine River trap sites, there was a positive linear relationship between fish length and tagging day of the year. We were concerned that the above method of size classification would result in small fish being skewed toward the earlier part of the out-migration period. Therefore, at these sites (CCT and LOT), we also classified natural smolts into size-classes using an index of length adjusted for tagging day of the year. To remove the effect of time on fish size, we determined relative size of fish at the time of tagging by fitting FL to day of the year with the regression,

$$L_i = aD_i + e_i,$$

where L_i is the individual FL (mm), D_i is the day of year of tagging, and e_i is a normally distributed error term. Regressions were fitted for each year at our upper trap sites. The predicted length for each fish was determined by fitting its tagging day of the year to the regression and the residual calculated. The residuals represented an index of fish size relative to time of tagging and were used to group fish into size-classes similar to fish length. To compare travel times, we used only those occasions when at least one smolt from both the small and large size-classes were released from a trap site on the same day and subsequently detected at Lower Granite Dam. Differences in travel times between paired groups were compared with the Wilcoxon signed rank test with a significance level $\alpha = 0.05$.

Survival.—Our third objective was to determine and compare survival probabilities to Lower Granite Dam and reach specific survival estimates for hatchery and natural smolts tagged and released at sites along the migration corridor. The PIT tag detection systems in the Columbia–Snake hydrosystem allowed us to develop release–recapture information to calculate Cormack–Jolly–Seber (CJS) survival probabilities to Lower Granite Dam for each release group using the SURPH 2.2 program (Lady et al. 2001) with a single release recapture model (Skalski et al. 1998). In the context of calculating survival probabilities, "recapture" refers to passive detection of PIT-tagged smolts at dam sites.

Once CJS survival probabilities to Lower Granite Dam were calculated for hatchery and natural smolts from each release site each year, we calculated reach-specific survival estimates between release sites each year as follows:

$$\hat{S}_j = S_{uj}/S_{lj}$$

where $\hat{S}_j$ is the survival estimate for release group j migrating between upper trap site u and lower trap site l, S_{uj} is the CJS survival probability to Lower Granite Dam calculated for release group j from upper release site u, and S_{lj} is the CJS survival probability to Lower Granite Dam for release group j from lower release site l.

Our fourth objective was to determine the influence of fish size on hatchery and natural smolt survival to Lower Granite Dam from release sites along the corridor. We determined the relationship between fish length and survival by comparing tag detection rates at dams of smolt size-classes in each release group. Size classifications used in this analysis were the same used to test difference in travel time for hatchery and natural smolts. We used tag detection rates at dams as an index of survival because sample sizes of size-class groups were too small for some groups to calculate CJS survival probabilities. We determined the number of smolts detected at any of the hydrosystem dams and compared detection rates between size-classes of hatchery and natural smolts for all years combined using the goodness-of-fit test (Sokal and Rohlf 1981) with $\alpha = 0.05$. Detection rates provide a measure of survival but do not account for fish that were undetected because they migrated past a dam via the spillway (spill) or through a turbine instead of the bypass system equipped with tag detectors. We assumed that fish size was independent of the route it took through the dam and both size-classes had equal probability of detection. This assumption was supported by Berggren et al. (2006), although Zabel et al.

(2005) reported that in some years there was negative relationship between Chinook salmon smolt size and detection probability. The percent spill around dams during the period that smolts entered the hydrosystem was fairly stable in most years. For those years where seasonal changes in percent spill were evident at some dams, the bias in detection rates was assumed to be minimal because we used detections at all possible dams in our calculations. Furthermore, because sample sizes for size-classes were roughly equal each year, we assumed that variation in percent spill around the detection system between years would not bias the results. Therefore, any differences in detection rates between size-classes would be due to differences in survival rates.

Results

During the 2000–2006 migration years, 129,010 PIT-tagged hatchery spring Chinook salmon were released from the Catherine Creek acclimation site and 91,202 were released from the Lostine River acclimation site, with a portion of the tagged fish recaptured and released from downstream traps in most years (Table 2). During the springs of 2000 through 2006, we PIT-tagged and released 2,797 natural Chinook salmon smolts from the Catherine Creek trap and 3,155 natural smolts from the Lostine River trap. Of the 1,539 natural smolts PIT-tagged at the upper Grande Ronde River trap, 1,331 were tagged on or after the earliest known arrival date of Catherine Creek spring migrants and were used for travel time and survival estimates. Of the 14,786 natural smolts PIT-tagged at the lower Grande Ronde River trap during the 2000 to 2006 migration years, 8,766 were tagged on or after the earliest known arrival date of a Catherine Creek spring migrant and 13,818 were tagged on or after the earliest known arrival date of a Lostine River spring migrant.

Hatchery smolts were typically larger than their natural counterparts (Tables 3, 4). Hatchery smolt FLs measured at the time of tagging approximately 6 months before release were highly correlated to lengths at recapture at the upper trap sites (Pearson correlation: $P < 0.001$), indicating the length at time of tagging served as a good predictor of actual size at release and could be used to classify fish into size-groups. Hatchery smolts from Catherine Creek grew an average of 12 mm and Lostine River smolts grew an average of 9 mm from time of tagging to release the following spring.

Travel Time

A seasonal trend in travel time was evident for both hatchery and natural Chinook salmon smolts traveling between trap sites and to Lower Granite Dam. Travel times for the earliest migrants were the longest and decreased as the season progressed. Although all release groups demonstrated a seasonal pattern in travel time, hatchery and natural smolts differed in overall magnitude of time spent traveling through specific reaches. The number of days between release and subsequent recapture of smolts between sites indicated that natural smolts took longer to migrate through the upper reaches compared with hatchery smolts but traveled faster through the lower reaches of the corridor (Table 5). For example, median travel time for natural Catherine Creek smolts through the Grande Ronde Valley reach (CCT–UGT) was 46.5 d (2.0 km/d) compared with 16.1 d (5.6 km/d) for hatchery smolts. Conversely, natural Catherine Creek smolts recaptured at the lower Grande Ronde trap and subsequently detected at Lower Granite Dam (Snake River reach) had a median travel time of 3.2 d compared with 10.8 d for Catherine Creek hatchery smolts.

Part of the difference in travel time between groups may be due to differences in median arrival date at a trap and the seasonal pattern in travel time. However, the same trend was evident when we compared travel times from trap sites to Lower Granite Dam for paired releases (released on the same day) of hatchery and natural smolts (Table 6). Natural smolts had significantly longer ($P < 0.001$) travel times compared with hatchery smolts when released from the Catherine Creek trap, but significantly shorter ($P < 0.001$) travel times when groups were released from the Lower Grande Ronde River trap, indicating that natural smolts initially traveled slower than their hatchery counterparts during their seaward migration but faster later in their migration. We could not detect differences in hatchery and natural smolt travel times from the Lostine River trap to Lower Granite Dam (Wallowa–Grande Ronde River reach and Snake River reach). However, when released from the lower Grande Ronde River trap (Snake River reach), natural smolts had significantly shorter ($P < 0.001$) travel times compared with Lostine River hatchery smolts, suggesting natural smolt travel time in the Wallowa–Grande Ronde River reach was longer.

A trend was evident in travel times of hatchery and natural smolts released from the lower Grande Ronde River trap and detected at Lower Granite Dam. Hatchery smolts in this reach exhibited longer travel times compared with natural smolts early in the season, but as the season progressed travel times became more similar. The trend was most evident with Lostine River hatchery smolts that reached the lower Grande Ronde River trap earlier in the season (Figure 2).

TABLE 2.—Number released and survival estimates to Lower Granite Dam for hatchery and natural Chinook salmon smolts PIT-tagged and released in the Grande Ronde River basin in the spring, 2000–2006.

Release site	Migration year	Hatchery smolts Number released	Hatchery smolts Survival (SE)	Natural smolts Number released	Natural smolts Survival (SE)
Catherine Creek					
Catherine Creek acclimation pond	2000	3,978	0.427 (0.014)		
	2001	20,913	0.540 (0.004)		
	2002	20,722	0.405 (0.008)		
	2003	20,611	0.349 (0.008)		
	2004	20,991	0.255 (0.003)		
	2005	20,833	0.233 (0.003)		
	2006	20,962	0.311 (0.007)		
Catherine Creek trap	2000	349	0.441 (0.046)	431	0.452 (0.058)
	2001	1,306	0.515 (0.017)	329	0.375 (0.028)
	2002	1,351	0.386 (0.028)	217	0.523 (0.076)
	2003			535	0.378 (0.030)
	2004	520	0.268 (0.023)	525	0.425 (0.022)
	2005			409	0.447 (0.046)
	2006	485	0.321 (0.043)	360	0.377 (0.049)
Upper Grande Ronde River trap	2000	162	0.654 (0.112)		
	2001	750	0.824 (0.019)		
	2002	159	0.874 (0.116)	166	0.781 (0.102)
	2003			250	0.770 (0.056)
	2004	297	0.784 (0.032)	467	0.732 (0.022)
	2005	270	0.656 (0.036)	115	0.659 (0.052)
	2006	100	0.790 (0.080)	333	0.748 (0.045)
Lower Grande Ronde River trap	2000	75	0.844 (0.127)	832	0.861 (0.034)
	2001	468	0.927 (0.020)	389	0.883 (0.018)
	2002	202	1.028 (0.147)	756	0.919 (0.056)
	2003	293	0.855 (0.083)	1,143	0.858 (0.036)
	2004	157	0.930 (0.048)	1,535	0.871 (0.011)
	2005	88	0.834 (0.078)	1,409	0.899 (0.013)
	2006	264	0.844 (0.054)	2,702	0.908 (0.017)
Lostine River					
Lostine River acclimation pond	2000	7,917	0.612 (0.013)		
	2001	7,887	0.479 (0.006)		
	2002	15,987	0.653 (0.009)		
	2003	15,896	0.559 (0.009)		
	2004	15,925	0.494 (0.005)		
	2005	13,339	0.403 (0.005)		
	2006	14,251	0.382 (0.007)		
Lostine River trap	2000			356	0.663 (0.068)
	2001	847	0.521 (0.019)	441	0.690 (0.024)
	2002	1,149	0.714 (0.041)	405	0.685 (0.057)
	2003	500	0.504 (0.039)	483	0.507 (0.041)
	2004			500	0.629 (0.024)
	2005	1,612	0.436 (0.013)	464	0.555 (0.025)
	2006	1,484	0.443 (0.023)	517	0.628 (0.039)
Lower Grande Ronde River trap	2000	190	1.028 (0.150)	1,380	0.913 (0.026)
	2001	201	0.753 (0.035)	720	0.895 (0.013)
	2002	222	0.741 (0.081)	1,336	0.929 (0.038)
	2003	348	0.739 (0.058)	2,110	0.898 (0.028)
	2004	32	0.804 (0.029)	2,832	0.868 (0.010)
	2005	114	0.758 (0.051)	1,857	0.890 (0.011)
	2006	252	0.822 (0.061)	3,583	0.915 (0.016)

Comparison of paired releases of small and large smolts within hatchery and natural smolt groups showed that smaller individuals took longer to travel through the upper reaches. For Catherine Creek hatchery smolts, smaller individuals released from the Catherine Creek acclimation ponds had a median travel time to Lower Granite Dam that was over 6 d longer than larger smolts (Table 7). The difference in travel time appeared to occur in the upper reaches because travel times to Lower Granite Dam were nearly identical between size-groups when released from the upper and lower Grande Ronde traps. Similarly, small Lostine River hatchery smolts released from acclimation ponds were over 4 d slower in traveling the 292 km to Lower Granite Dam than their larger counterparts. However, when released from the lower Grande

TABLE 3.—Median fork lengths at time of tagging of Catherine Creek and Lostine River hatchery Chinook salmon smolts approximately 6 months before release, with the 30th and 70th percentiles (in parentheses) used to designate length categories (small, large).

	Catherine Creek		Lostine River	
Migration year	*N*	Fork length (mm)	*N*	Fork length (mm)
2000	3,979	111 (106, 115)	7,922	112 (107, 116)
2001	20,889	117 (113, 121)	7,877	116 (111, 119)
2002	20,783	115 (111, 118)	15,962	116 (112, 119)
2003	20,610	123 (117, 136)	15,782	117 (112, 123)
2004	3,237	109 (105, 115)	2,713	105 (99, 108)
2005	3,204	106 (103, 108)	1,998	105 (99, 112)
2006	3,157	102 (97, 107)	2,156	106 (102, 111)

Ronde trap, the same groups differed by only 1 d in traveling the 100 km to the dam. Even when hatchery smolts from both populations were regrouped into size-classes based on recapture lengths at the lower Grande Ronde trap, travel times were not significantly different between size groups.

Natural smolts exhibited an even larger disparity in travel time between size-groups with the difference again manifested mainly in the upper reaches (Table 7). Small Catherine Creek natural smolts took nearly 20 d longer to reach Lower Granite Dam than did their larger counterparts in traveling the 353 km from the Catherine Creek trap. However, there was less than a 3-d difference between size-groups when released from the upper Grande Ronde trap, indicating that most of the delay occurred in the Grande Ronde Valley reach. Differences in travel time were consistent throughout the migration season (Figure 3). Similarly, size-classes of Lostine River natural smolts differed by nearly 17 d in their travel time to Lower Granite Dam when released from the Lostine River trap. Natural smolts released from the lower Grande Ronde trap differed by only 1 d between size groups. This pattern in travel time between size-groups of natural smolts was the same when size-classes were based on length adjusted for time of tagging.

Survival

Survival probabilities to Lower Granite Dam for natural smolts varied little between years at each release location (Table 2). However, there were significant differences in annual survival probabilities for hatchery smolts from the upper release sites to Lower Granite Dam for both the Lostine River and Catherine Creek populations (analysis of variance [ANOVA]: $P < 0.001$).

Both hatchery and natural smolts showed similar patterns in reach-specific survival (Figure 4). Survival was nearly 100% for Catherine Creek hatchery smolts through the summer rearing habitat reach of the migration corridor (CCP–CCT) and median travel times through this relatively short 16-km reach was about 1 d. The greatest mortality for both hatchery and natural smolts originating from Catherine Creek occurred in the next 91 km, through the Grande Ronde Valley reach (CCT–UGT). Mean hatchery smolt survival was estimated at 50% in this reach and ranged from 34% to 67% (Table 8). Natural smolts had a mean survival of 58% in this reach (range, 49–68%). Survival was high for the remainder of the migration corridor to Lower Granite Dam. Mean hatchery smolt survival was 85% (78–94%) in the remaining 162 km of the Grande Ronde River main-stem reach (UGT–LGT). Similarly, mean natural smolt survival was 84%

TABLE 4.—Median fork lengths (FLs) of natural Chinook salmon smolts measured at release sites, with the 30th and 70th percentiles (in parentheses) used to designate length categories (small, large).

	Catherine Creek		Lostine River		Upper Grande Ronde River		Lower Grande Ronde River	
Migration year	*N*	FL (mm)	*N*	FL (mm)	*N*	FL (mm)	*N*	FL (mm)
2000	431	90 (87, 95)	356	94 (90, 99)			1,380	118 (113, 123)
2001	326	87 (84, 91)	440	99 (94, 105)			719	123 (114, 126)
2002	214	89 (86, 94)	404	94 (88, 99)	167	105 (100, 114)	1,336	113 (108, 117)
2003	535	87 (83, 92)	480	89 (84, 94)	250	112 (107, 115)	2,666	110 (104, 115)
2004	524	84 (80, 88)	500	86 (82, 92)	486	109 (103, 114)	3,101	113 (107, 117)
2005	409	87 (83, 91)	464	90 (86, 95)	235	104 (99, 109)	1,975	113 (108, 119)
2006	360	88 (84, 91)	517	89 (85, 94)	400	102 (99, 108)	3,602	111 (107, 116)

TABLE 5.—Median (range) travel times of hatchery and natural Chinook salmon smolts through specific reaches in the Grande Ronde River basin. Reach codes are as follows: CCP–CCT = Catherine Creek summer rearing habitat; CCT–UGT = Grande Ronde Valley; UGT–LGT = Grande Ronde River main stem; LGT–dam = Snake River; LOP–LOT = Lostine River summer rearing habitat; and LOT–LGT = Wallowa–Grande Ronde River.

	Hatchery smolts			Natural smolts		
Reach	*N*	Median travel time (d)	Median release date	*N*	Median travel time (d)	Median release date
Catherine Creek						
CCP–CCT	2,600	0.9 (0.4–70.7)	10 Apr			
CCT–UGT	69	16.1 (4.1–48.8)	17 Apr	40	46.5 (7.0–71.9)	30 Mar
UGT–LGT	55	2.8 (1.6–38.9)	23 Apr	37	2.9 (0.9–34.9)	4 May
LGT–dam	699	10.8 (1.5–35.4)	28 Apr	11	3.2 (2.3–7.0)	8 May
Lostine River						
LOP–LOT	4,461	1.3 (0.3–62.8)	20 Mar			
LOT–LGT	123	4.4 (1.1–63.8)	31 Mar	53	19.9 (2.4–76.0)	11 Apr
LGT–dam	584	22.5 (2.0–67.2)	10 Apr	27	5.7 (2.5–27.2)	4 May

and ranged from 78% to 91%. In the Snake River reach (LGT–Dam), survival to Lower Granite Dam averaged 89% (83–100%) for Catherine Creek hatchery smolts. Survival was also 89% (86–92%) for natural smolts that were tagged during the time when natural Catherine Creek spring migrants were expected to enter this reach. Survival in this reach was substantially greater than through the Grande Ronde Valley reach, despite similar gradients and reach lengths.

Hatchery and natural smolts from the Lostine River did not experience a reach with relatively low survival, as did smolts from Catherine Creek. Lostine River hatchery smolts had a high mean survival of 95% (range, 86–100%) through the initial 18-km summer rearing habitat reach (LOP–LOT) below the acclimation release site (Table 8). Mean survival was 69% for both hatchery and natural smolts in the 174-km Wallowa–Grande Ronde River reach (LOT–LGT). Mean survival through the 100-km Snake River reach (LGT–Dam) was 81% (74–100%) for Lostine River hatchery smolts and 90% (87–93%) for natural smolts tagged in the reach during the time when Lostine River natural smolts were expected to be migrating.

Although the pattern of reach-specific survival was similar between hatchery and natural smolts, when median travel time and reach-specific survival of tag groups are viewed together to provide a mortality rate per day, a different pattern emerges. Hatchery fish showed a greater mortality rate in the upper reaches compared with natural smolts, but the reverse was true in the lowest reach. For instance, the daily mortality rate for Catherine Creek hatchery smolts in the Grande Ronde Valley reach was 3.1% compared with 0.9% for natural smolts. However, in the Snake River reach, daily mortality rate for Catherine Creek hatchery and natural smolts was 1.0% and 3.6%, respectively.

Size influenced survival for hatchery smolts released at the acclimation sites (CCP and LOP) and the upper traps (CCT and LOT), but not for the upper and lower Grande Ronde River traps (UGT and LGT). Comparison of detection rates at dams of small and large size-classes of hatchery fish showed that larger fish survived at a higher rate (Table 9). For example, small hatchery smolts released from the Catherine Creek acclimation pond had a mean detection rate of 29%, which was significantly lower ($P \leq 0.001$) than the

TABLE 6.—Comparison of travel times to Lower Granite Dam for paired releases of hatchery and natural Chinook salmon smolts, with Wilcoxon signed rank test results.

		Median travel time to Lower Granite Dam (d)			
Release site	Distance to Lower Granite Dam (km)	Hatchery	Natural	*N*	*P*
Catherine Creek					
Catherine Creek trap	353	32.2	55.9	55	≤0.001
Upper Grande Ronde River trap	262	10.5	11.0	58	0.157
Lower Grande Ronde River trap	100	10.6	8.1	136	≤0.001
Lostine River					
Lostine River trap	274	31.5	30.6	102	0.735
Lower Grande Ronde River trap	100	15.6	8.7	159	≤0.001

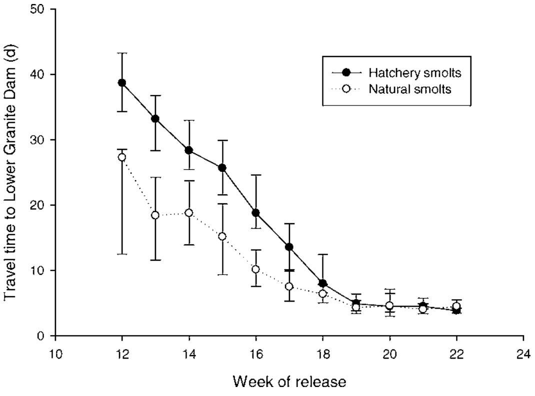

FIGURE 2.—Median travel times to Lower Granite Dam from the lower Grande Ronde River trap for Lostine River hatchery and natural Chinook salmon smolts by release week during the 2000–2006 migration years. The error bars indicate the 25th and 75th percentiles. Natural smolts did not necessarily originate from the Lostine River but were captured during the migration period of known Lostine River natural smolts.

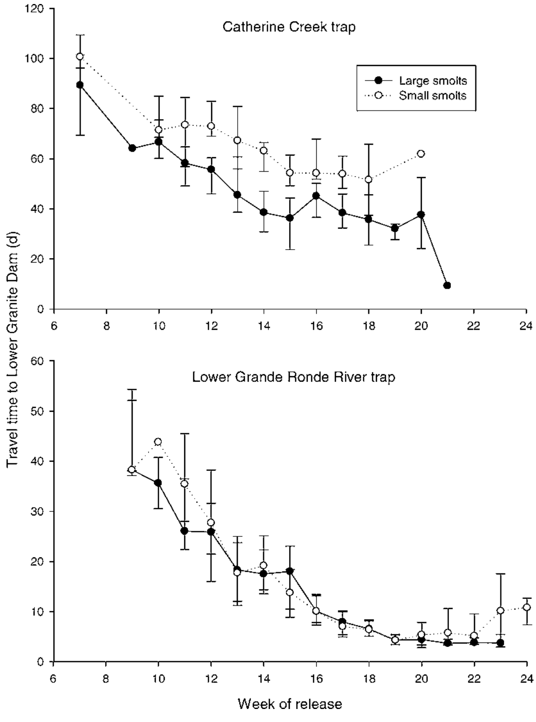

FIGURE 3.—Median travel times to Lower Granite Dam from the Catherine Creek and lower Grande Ronde River traps for large and small size-classes of natural Chinook salmon smolts by release week during the 2000–2006 migration years. The error bars indicate the 25th and 75th percentiles. The Catherine Creek trap is located 353 km from Lower Granite Dam and the lower Grande Ronde River trap 100 km from the dam.

mean detection rate of 39% for the large size-class. However, the mean detection rate of small Catherine Creek hatchery smolts released at the lower Grande Ronde trap (78%) was not significantly different from the mean detection rate of large smolts released from this trap (76%). For the Lostine River population, the small size-class of hatchery smolts released from acclimation ponds had a significantly lower mean detection rate (41%) compared with the large size-class (46%, $P \leq 0.001$), but there was no significant difference in detection rates for these size-classes released from the lower Grande Ronde trap (61% for both size-classes).

The pattern of size-selective mortality was similar for natural smolts. Smolts from the small size-class released from the upper trap sites had lower mean detection rates than those from the large size-class, indicating lower survival (Table 9). Similar results occurred when we performed the analysis using fish length adjusted for time of tagging at our upper trap

TABLE 7.—Comparison of median travel times to Lower Granite Dam for paired releases of small and large hatchery and natural Chinook salmon smolts, with Wilcoxon signed rank test results. See Table 1 for release site codes.

Release site	Distance to Lower Granite Dam (km)	Hatchery smolts: Travel time (d) Large	Hatchery smolts: Travel time (d) Small	Hatchery smolts: *N*	Hatchery smolts: *P*	Natural smolts: Travel time (d) Large	Natural smolts: Travel time (d) Small	Natural smolts: *N*	Natural smolts: *P*
Catherine Creek									
CCP	369	28.9	35.3	71	≤0.001				
CCT	353	27.2	33.4	27	0.009	47.3	67.0	46	≤0.001
UGT	262	13.5	13.6	21	0.044	7.8	10.3	32	0.012
LGT	100	11.6	11.9	36	0.114	5.4	6.5	167	≤0.001
Lostine River									
LOP	292	31.4	35.9	60	≤0.001				
LOT	274	31.4	36.3	36	0.003	21.1	38.0	77	≤0.001
LGT	100	23.6	24.6	27	0.990	7.4	8.4	249	≤0.001

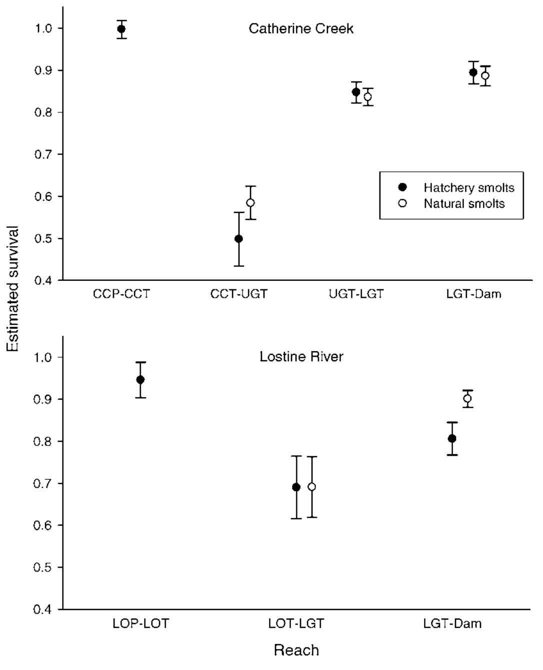

FIGURE 4.—Mean ± SE survival estimates for hatchery and natural Chinook salmon smolts from Catherine Creek and the Lostine River through specific reaches of the migration corridor during the 2000–2006 migration years. For smolts originating from Catherine Creek, the estimates were from the Catherine Creek acclimation pond (CCP) to the Catherine Creek trap (CCT), from CCT to the upper Grande Ronde River trap (UGT), from UGT to the lower Grande Ronde River Trap (LGT), and from LGT to the Lower Granite Dam tailrace (dam). For Lostine River smolts, the estimates were from the Lostine River acclimation pond (LOP) to the Lostine River trap (LOT), from LOT to LGT, and from LGT to the dam.

sites. At the lower trap sites, there was no significant difference in detection rates between size-groups.

Discussion

Smaller Chinook salmon smolts took longer to migrate through all reaches compared with larger smolts, with the difference being most pronounced in the upper reaches. Similar results were noted by Zabel (2002) in which migration rate varied with fish length for smolts released in the Salmon River, but not for smolts tagged downstream at Lower Granite Dam. Although it may be expected that smaller smolts would have slower migration rates due to their smaller physical size, in this study the delay in travel times appeared to be related to smaller fish feeding in the upper reaches to attain a larger size before continuing their migration because growth was positively related to the amount of time spent in the upper reaches for natural smolts (Figure 5). Salmonids feed during their downstream migration (Muir and Emmett 1988; Muir and Coley 1996) and larger fish migrate sooner than smaller fish (Ewing et al. 1984; Beckman et al. 1998). Achord et al. (2007) suggested that initiation of Chinook salmon smolt migration is determined by a balance between migrating as soon as possible and attaining adequate size to maximize survival. Our results do not conflict with these observations, but because fish traps in this study only captured fish actively moving downstream, our results suggest that migration rate may also be determined by this trade-off. Smaller smolts may initiate their downstream migration at the same time as larger smolts, but their propensity to continue migrating downstream may be balanced by a need for further growth to attain an adequate size. Although information on hatchery smolt growth is limited due to the infrequency of multiple recaptures of individual smolts where length was recorded, it appears they also experience growth during migration to Lower Granite Dam.

Not only did size of smolts affect travel time, but rearing history also appeared to have an influence. Hatchery smolts of both populations took less time than their natural counterparts to migrate through the upper reaches, but took longer to travel to Lower Granite Dam once they entered the Snake River reach. The slower travel times of hatchery smolts in the lower reaches occurred despite hatchery smolts maintaining a size advantage compared with natural smolts throughout their migration. The larger size of hatchery smolts may explain their faster travel time through the upper reaches but not their slower travel times in the Snake River reach. Behavioral differences associated with natural smolts being tagged as they entered the Snake River reach while hatchery smolts were tagged before release does not appear to the cause of the travel-time differences because Setter et al. (2005) also reported hatchery smolts with slower migration rates compared with natural smolts when both groups were tagged during the same week at the lower Grande Ronde River trap. The natural smolts tagged at lower trap sites in this study were an aggregate of all natural populations in the basin and, therefore, may not represent travel times of smolts originating from Catherine Creek or the Lostine River. However, recapture information at the lower Grande Ronde River trap of natural smolts tagged in Catherine Creek, from all years for which data were available, indicated that their travel times to Lower Granite Dam were actually faster than the aggregate of natural smolts tagged at this site (Wilcoxon signed rank test: $P = 0.022$). This suggests that travel time differences between natural and hatchery smolts from Catherine Creek were actually greater than reported here. Similar analysis showed no

TABLE 8.—Reach-specific survival estimates for hatchery and natural Chinook salmon smolts in the Grande Ronde River basin. See Table 5 for reach codes.

Migration year	Catherine Creek				Lostine River		
	CCP–CCT	CCT–UGT	UGT–LGT	LGT–dam	LOP–LOT	LOT–LGT	LGT–dam
				Hatchery smolts			
2000	0.968	0.674	0.775	0.844			1.028
2001	1.048	0.624	0.889	0.927	0.919	0.692	0.753
2002	1.048	0.442	0.850	1.028	0.915	0.964	0.741
2003				0.855	1.109	0.682	0.739
2004	0.949	0.342	0.843	0.930			0.804
2005			0.786	0.834	0.924	0.575	0.758
2006	0.969	0.406	0.937	0.844	0.863	0.539	0.822
Mean (SE)	0.997 (0.021)	0.498 (0.064)	0.847 (0.025)	0.894 (0.027)	0.946 (0.042)	0.690 (0.074)	0.806 (0.034)
				Natural smolts			
2000				0.861		0.726	0.913
2001				0.883		0.771	0.895
2002		0.670	0.844	0.919		0.737	0.929
2003		0.490	0.905	0.858		0.565	0.898
2004		0.580	0.829	0.871		0.724	0.868
2005		0.678	0.777	0.899		0.624	0.890
2006		0.504	0.824	0.908		0.686	0.915
Mean (SE)		0.584 (0.040)	0.836 (0.021)	0.886 (0.009)		0.691 (0.027)	0.901 (0.008)

significant difference in travel time between paired releases of Lostine River natural smolts recaptured at the lower Grande Ronde River trap and the aggregate of natural smolts tagged at this site (Wilcoxon signed rank test: $P = 0.728$). Therefore, the slower travel times of hatchery smolts in the Snake River reach indicate possible behavioral or physiological differences compared with natural smolts (Wedemeyer et al. 1980).

The difference between hatchery and natural smolt travel times may be the result of differences in their developmental stage in the parr–smolt transformation. The greatest difference between hatchery and natural travel time occurred early in the season and diminished later in the season. Many hatchery smolts, especially those released in March, may have been released into the streams before they were physiologically ready to migrate downstream (Wedemeyer et al. 1980). Hatchery fish may have passively moved downstream and travel-time differences observed in the Snake River reach may be related to the physiological readiness of smolts to migrate. Later in the season, as the smoltification process progresses, travel times between hatchery and natural smolts become more similar. The seasonal trend in decreasing travel time to Lower Granite Dam evident from all groups at all release sites was also probably the result of an increasing level of smoltification and river discharge as the season progressed (Beeman et al. 1990).

Despite different rearing histories, hatchery and natural smolts from the Grande Ronde basin demon-

TABLE 9.—Dam detection rates (%) for large and small hatchery and natural Chinook salmon smolts from different release sites in the Grande Ronde River basin.

Release site	Distance to Lower Granite Dam (km)	Size-group		*P*
		Large	Small	
	Hatchery smolts			
Catherine Creek acclimation pond	369	38.8	29.4	≤0.001
Catherine Creek trap	353	38.8	33.4	0.009
Upper Grande Ronde River trap	262	68.7	67.1	0.627
Lower Grande Ronde River trap	100	76.3	78.0	0.604
Lostine River acclimation pond	292	46.4	40.7	≤0.001
Lostine River trap	274	47.0	43.3	0.073
Lower Grande Ronde River trap	100	60.7	61.3	0.874
	Natural smolts			
Catherine Creek trap	353	40.7	29.5	≤0.001
Upper Grande Ronde River trap	262	65.7	65.7	0.997
Lower Grande Ronde River trap	100	78.2	77.1	0.168
Lostine River trap	274	60.3	47.3	≤0.001

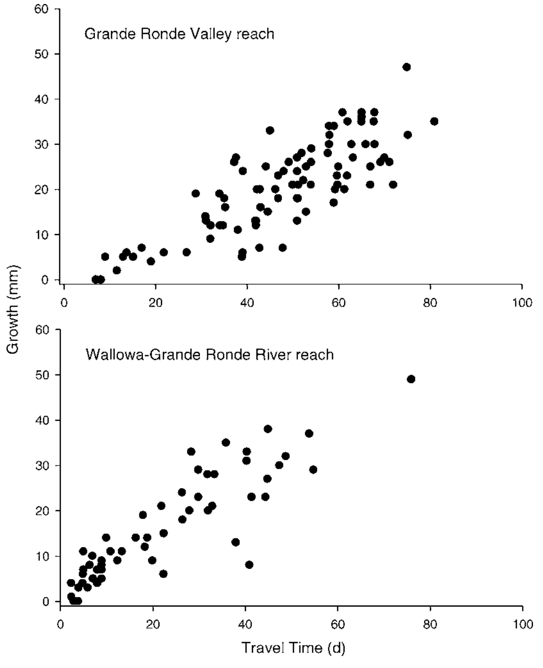

FIGURE 5.—Growth of individual natural Chinook salmon smolts between Catherine Creek trap and the upper Grande Ronde River trap (upper panel) and between the Lostine River trap and the lower Grande Ronde River trap (lower panel) in relation to travel time between trap sites for all years for which information was available (1996–2006).

strated similar patterns in survival through the various reaches from natal streams to the Lower Granite Dam tailrace. Survival for both Catherine Creek and Lostine River smolts was high in the main-stem Snake River reach, which consists mainly of the Lower Granite Reservoir. Muir et al. (2001) reported similar high survival of Chinook salmon smolts through the same reservoir. However, substantial mortality occurred before smolts reached the Snake River and that mortality was most pronounced in specific reaches of the migration corridor. The majority of Catherine Creek smolt mortality occurred in the first 91 km below their summer rearing habitat (Grande Ronde Valley reach). This is in contrast to the survival of Lostine River smolts in the Wallowa–Grande Ronde River reach. Both reaches were immediately below summer rearing areas, but survival of Catherine Creek smolts through the Grande Ronde Valley reach was much poorer in comparison. Mortality for hatchery and natural smolts in this low-gradient 91-km reach was 50% and 42%, respectively. In contrast, mortality for Lostine River smolts was only 31% for both hatchery and natural smolts in the Wallowa–Grande Ronde River reach, which was nearly twice as long but had higher gradient. The lower gradient and subsequent longer travel times of smolts migrating through the Grande Ronde Valley reach may have increased their exposure to survival hazards in this reach. Furthermore, survival of smolts in both reaches was size-selective.

The mechanism for the high mortality of Catherine Creek smolts observed in the Grande Ronde Valley reach requires further investigation. One possibility for natural smolts, which experienced much longer travel times than hatchery smolts, is that the longer duration spent in the Grande Ronde Valley reach may increase their exposure to survival hazards from predation and extreme environmental conditions. This would be especially true for the smaller individuals of natural smolts. Northern pikeminnow *Ptychocheilus oregonensis* and introduced smallmouth bass *Micropterus dolomieu* along with numerous avian and mammalian predators occur in the Grande Ronde Valley reach. In addition, water temperatures in this reach increase rapidly through the season and can reach 20°C by early June. Smolts that remain in the reach in late spring may experience increased mortality due to a combination of greater susceptibility to predation, disease, and unsuitable environmental conditions.

Hatchery smolts would seem to be less susceptible to this proposed mortality mechanism, given their larger size and shorter duration in the reach compared with natural smolts. Muir et al. (2001) suggest that a culling of poor-quality hatchery fish occurs soon after release in the Snake River basin. It seems likely that this low-gradient meandering valley reach is more energetically taxing for Catherine Creek smolts compared with the higher gradient corridor through which Lostine River smolts migrate. This may cause higher mortality for poor-quality smolts and may also partially explain why Catherine Creek hatchery smolts have higher survival farther downstream in the Snake River compared with Lostine River hatchery smolts, which are simply culled out later.

Another possibility for the high mortality in the Grande Ronde Valley reach may be due to smolts becoming stranded in the numerous oxbow lakes located along the reach that are used as storage reservoirs for irrigation. Some of these lakes are connected to the stream with unscreened diversion structures that could allow smolts to enter and become trapped when the structures are closed or stream levels recede. Smaller smolts that spend greater time foraging in the reach may be more likely to enter such lakes and become stranded.

Larger smolts from both hatchery and natural tag groups released at upper trap sites were detected at downstream dams at a higher rate than smaller smolts, but we could not detect size-selective mortality for smolts released at the lower Grande Ronde River trap. We suspect that size-selective mortality occurs to some extent throughout the migration corridor for both hatchery and natural smolts, at least for the Lostine River population, but limited sample sizes prohibited us from being able to detect it at all trap sites. For instance, when we increased sample size of Lostine River hatchery smolt size-classes at the lower Grande Ronde River trap by using fish length at time of recapture instead of length at time of tagging, there was a significant difference in detection rates at the dam ($P = 0.023$). When we used the same approach with Catherine Creek hatchery smolts, we still were unable to detected differences between size-classes ($P = 0.859$).

This study showed that Snake River Chinook salmon smolts demonstrate a complex pattern of survival and migration characteristics during their seaward migration from tributaries. The mechanisms that cause the observed differences are probably equally as complex. A recent biological opinion by the National Marine Fisheries Service calls for efforts to increase survival for these threatened populations in areas outside the hydrosystem (NMFS 2000). Smolt survival to Lower Granite Dam can be highly variable between tributaries in the Snake River basin (Venditti et al. 2007). Part of this variability is probably due to the unique set of geomorphologic features and land-use practices in each tributary that could influence survival rates. A better understanding of the migration dynamics at the reach scale would enable managers to address factors that currently limit smolt survival and hinder recovery efforts. As PIT tag detection technologies continue to advance, opportunities may arise to perform reach-specific survival analyses in other tributaries within the basins above the hydrosystem to determine and address the threats and limiting factors that result in high mortality.

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