Comparative Dispersal Patterns for Recolonizing Cedar River Chinook Salmon above Landsburg Dam, Washington, and the Source Population below the Dam

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ARTICLE

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Abstract

Anadromous salmonid populations are particularly vulnerable to migration blockages, such as dams and culverts, because access to historic spawning and rearing habitats is prevented. The process of salmonid recolonization has not been well documented for river systems where anthropogenic migration barriers have been removed or where fish passage facilities have been constructed. In September 2003, Seattle Public Utilities completed construction of a fish passage facility that circumvented Landsburg Dam on the Cedar River, Washington. Chinook Salmon *Oncorhynchus tshawytscha* spawned in newly available main-stem habitats immediately after fish passage facility construction and in all subsequent years. Further dispersal into tributary habitats occurred 5 years after construction. Redds tended to be concentrated in the downstream third of the available habitat above the dam, although some fish did utilize suitable spawning sites throughout the main stem, even in the uppermost reaches of the newly available habitat. Median spawn timing for redds observed above the dam was not significantly different from spawn timing for the source population, indicating that migration delays through the fish passage facility were minimal. Male Chinook Salmon consistently outnumbered females, with annual sex ratios ranging from 1.3:1 to 4.7:1. Chinook Salmon spawning above the dam contributed between 2.7% and 14.7% of the total annual redd count (2003–2010) for Cedar River Chinook Salmon; upstream redds as a percentage of total redds increased over time, indicating that a new, naturally reproducing population above the dam was growing. The proportion of hatchery-origin fish spawning above the dam decreased over the duration of the study but was consistently higher than the hatchery component observed below the dam.

Migration barriers, such as dams, weirs, and culverts, have been identified as one of the major challenges in the restoration of river habitats and the recovery of freshwater fish communities (Langill and Zamora 2002; Pess et al. 2005). Anadromous fishes and other migratory fishes are particularly vulnerable to such blockages because access to historic spawning and rearing habitats is prevented at pivotal life stages. Severing access to spawning and rearing habitats inevitably causes a decline in the abundance of wild anadromous fishes and can result in population fragmentation (Richter et al. 1997; Rieman and Dunham 2000; Nilsson et al. 2005) or extinction (Kruse et al. 2001; Gustafson et al. 2007). Reconnection of isolated habitats using barrier removal or fish passage facility construction has become a primary river restoration technique (Hart and Poff 2002; Hart et al. 2002), especially in systems inhabited by salmonid populations that are listed under the U.S. Endangered Species Act. However, in rivers where migration barriers have been removed, very little research and monitoring have been conducted to determine the relative abundance, origin (hatchery or natural), or dispersal characteristics of salmonid colonizers and their source populations. We suggest that documenting dispersal into newly accessible habitats is important for determining the factors that promote colonization and for answering questions such as "Are colonizers a random subset of the source population or are there certain traits (e.g., sex, spawn timing, and origin) that influence the likelihood of dispersal into new habitats?"; "Do source populations donate more colonists in years of higher abundance?"; and "Do hatchery fish and wild fish have similar propensities to stray into the newly accessible habitats?"

Salmonid fishes typically exhibit philopatry (homing to natal waters) when they migrate to spawn, but some individuals stray to spawning habitats outside of their natal water body (Shapovalov and Taft 1954; Quinn 1993). Straying levels are typically low in wild populations (Quinn 1993), which is beneficial for local adaptation to natal habitats. However, some level of natural straying is important for the colonization of new habitats and the subsequent expansion of a species' range. Salmonids readily colonize newly accessible habitats, both naturally (McPhail and Lindsey 1986; Milner and Bailey 1989; Milner 2000; Shpigalskaya et al. 2008; McKeown et al. 2010) and through artificial introduction (Bakshtansky 1980; Kwain and Lawrie 1981; Kwain 1987; Quinn 1993; Quinn et al. 2001; Kinnison et al. 2002; Ciancio et al. 2005; Launey et al. 2010). However, salmon can take considerable time to take advantage of new passage opportunities (Gowans et al. 1999; Rivinoja 2005) or they may avoid those opportunities entirely (Solomon et al. 1999; Solomon and Sambrook 2004).

In September 2003, Seattle Public Utilities completed construction of a fish passage facility that circumvented Landsburg Diversion Dam (hereafter, "Landsburg Dam") on the Cedar River, Washington. Anadromous (hatchery and wild) and resident fishes were allowed to volitionally access approximately 33 km of main-stem and tributary habitats for the first time in over a century (Kiffney et al. 2009). This restored access

offered a unique opportunity to study recolonization of a threatened population of Chinook Salmon *Oncorhynchus tshawytscha* above a historic barrier in the context of an entire river basin.

To examine patterns of Chinook Salmon recolonization after the opening of Landsburg Dam fish passage on the Cedar River, our study had four primary objectives. First, we investigated annual abundance of colonizers and redds constructed upstream of the dam to determine whether fish passage operations and subsequent recolonization were successful. Second, we compared sex ratios for upstream migrants through the fish ladder to determine whether one sex (predicted to be males) would show a greater propensity to colonize. Third, we investigated the spatial and temporal distributions of redd construction by upstream and downstream Chinook Salmon populations to compare pre- and postpassage spawning activity as a function of river kilometer (rkm) locations, proximity to Landsburg Dam, and estimated spawn dates. Fourth, we investigated the origin (hatchery or wild) of the initial colonizers (2003–2005) and subsequent spawning cohorts upstream of the dam (2006–2010) and compared those data with data describing the source population below the dam. We hypothesized that (1) the proportion of hatchery fish among initial colonizers would closely reflect the hatchery proportion below Landsburg Dam and (2) subsequent Chinook Salmon spawning upstream of the dam would include fish that originated above the dam, causing the proportion of hatchery fish in the spawning population above the dam to decrease over time. The results of this study will help to support and inform future studies and management decisions related to barrier removal or circumvention in river systems that are inhabited by salmonid populations.

METHODS

Study site.—Originating at the crest of the Cascade Mountains in Seattle's Cedar River Municipal Watershed, Washington, the Cedar River passes through forested and urban environments before flowing into the southern end of Lake Washington (Figure 1). Anadromous fish migrate from salt water to freshwater through a ship canal into Lake Washington. The Cedar River is the largest tributary in the Cedar River–Sammamish River watershed, draining a catchment of approximately 487 km^2 (Williams et al. 1975). The National Oceanic and Atmospheric Administration designated the Cedar River as critical habitat for a wild population of threatened Chinook Salmon (NMFS 1999; WRIA-8 2005).

For over a century, anadromous salmonids did not have access to main-stem (20 km) and tributary habitats (13 km) above Landsburg Dam (rkm 37; Figure 1). In addition to the blockage by the dam, an aqueduct crossing the Cedar River approximately 0.5 km below Landsburg Dam also blocked upstream salmon migration. In 2002, fish passage was provided between the aqueduct and the dam; in 2003, a new fish passage facility was completed at the dam to meet mitigation conditions set forth in Seattle's Cedar River Watershed Habitat Conservation Plan
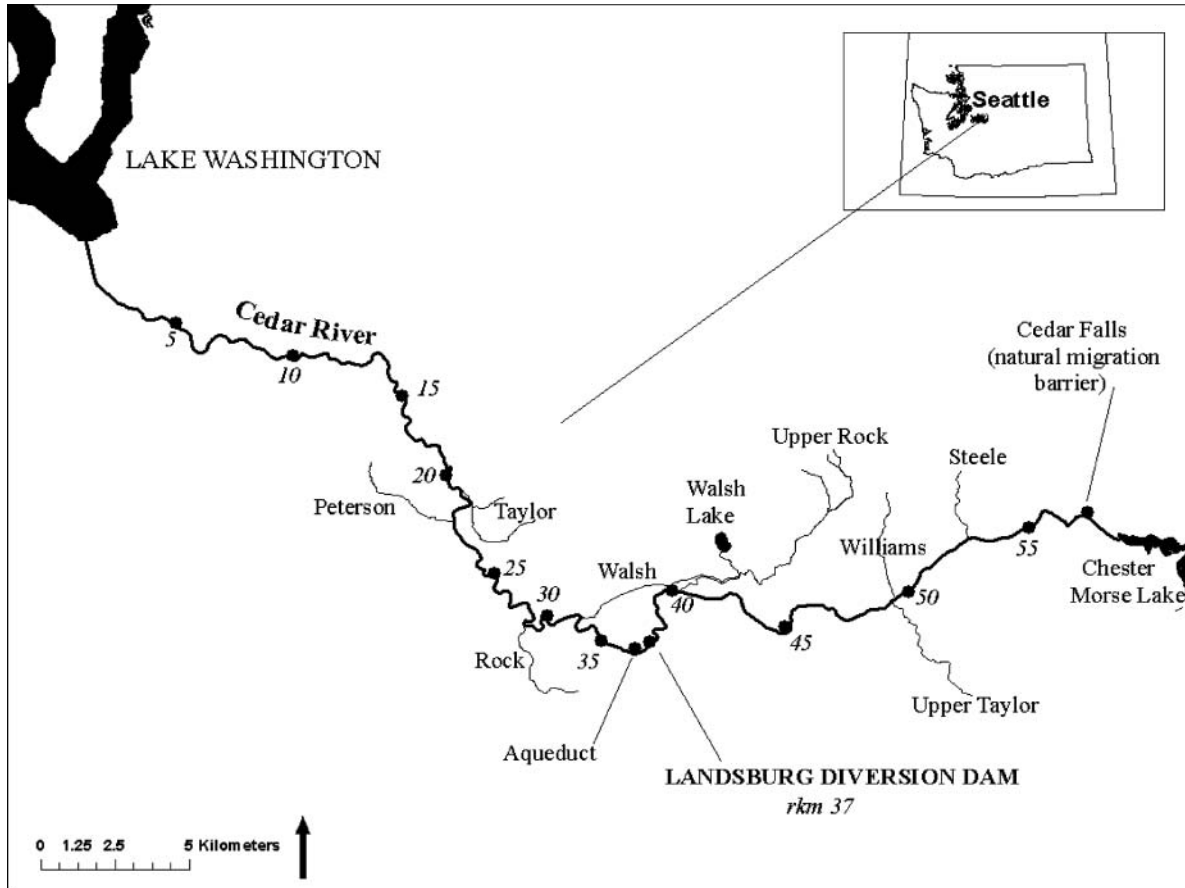
FIGURE 1.   Map of the Cedar River basin, Washington, from Chester Morse Lake to Lake Washington. Numbered points are river kilometers (rkm).

(City of Seattle 2000). The Cedar River basin above Landsburg Dam is managed by the City of Seattle as a municipal water source, where public access and any development of the forested landscape is severely limited. Between Landsburg Dam and Cedar Falls (a natural migration barrier upstream), there are four tributaries that are accessible to anadromous fish: Upper Rock, Upper Taylor, Williams, and Steele creeks (Figure 1). All tributaries except Upper Rock Creek have natural migration barriers within 0.5 km of their confluences with the Cedar River.

The Cedar River below Landsburg Dam has been substantially altered by anthropogenic activities, such as agriculture, residential and commercial development in the floodplain, bank hardening, and channel straightening. Although a portion of the lower river is naturally confined, the majority of the main stem is confined by levees, dikes, and revetments. The lower watershed has four primary tributaries, including Lower Rock, Lower Taylor, Walsh, and Peterson creeks. Lower Rock, Lower Taylor, and Walsh creeks have adequate flow for Chinook Salmon access, but Peterson Creek is often too shallow to permit access during the spawning season (Figure 1).

Beginning in 1964, the Washington Department of Fish and Wildlife conducted regular surveys to count fall-spawning adult salmon in the Cedar River. Historical Cedar River Chinook Salmon escapement index estimates (Figure 2) were derived from fish count surveys using the area-under-the-curve methodology (Perrin and Irvine 1990). The population was in decline during the 1990s and early 2000s but rebounded in subsequent years.

Currently, in the Lake Washington basin, large numbers of hatchery Chinook Salmon fingerlings are released annually from the Issaquah Creek and Portage Bay (University of Washington) hatcheries (Figure 3). However, none of these releases occur in the Cedar River. The Issaquah Creek Hatchery has released approximately 2 million Chinook Salmon parr annually, whereas the Portage Bay Hatchery releases approximately 200,000 parr. Since the late 1990s, nearly all (>90%) of the Chinook Salmon juveniles released from Washington hatcheries have been externally marked with an adipose fin clip, and since 2002 a small percentage of hatchery fish have been internally marked with a coded wire tag (CWT). Other proximal Chinook Salmon hatcheries include Soos Creek (Green River), Bernie Gobin (Tulalip Bay), Wallace River (Skykomish River basin), and Grovers Creek (Kitsap Peninsula; Figure 3).

Redd surveys, 1999–2010.—Redd surveys of main-stem and tributary habitats were used to estimate relative Chinook Salmon abundance (Gallagher and Gallagher 2005) and to compare
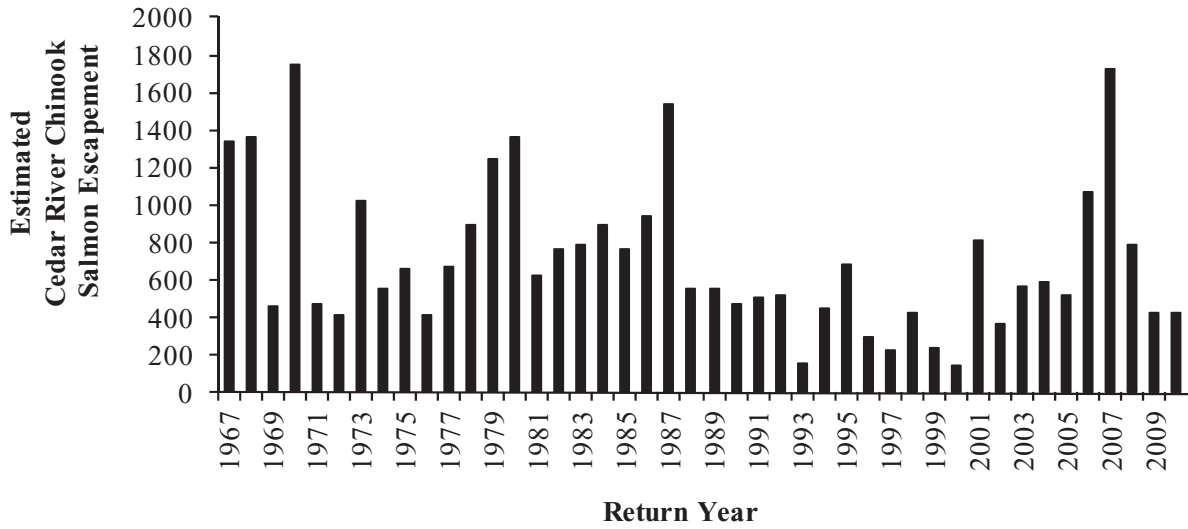
FIGURE 2. Historic escapement index for Cedar River Chinook Salmon based on fish counts and area-under-the-curve methodology, 1964–2010 (Washington Department of Fish and Wildlife, unpublished data).
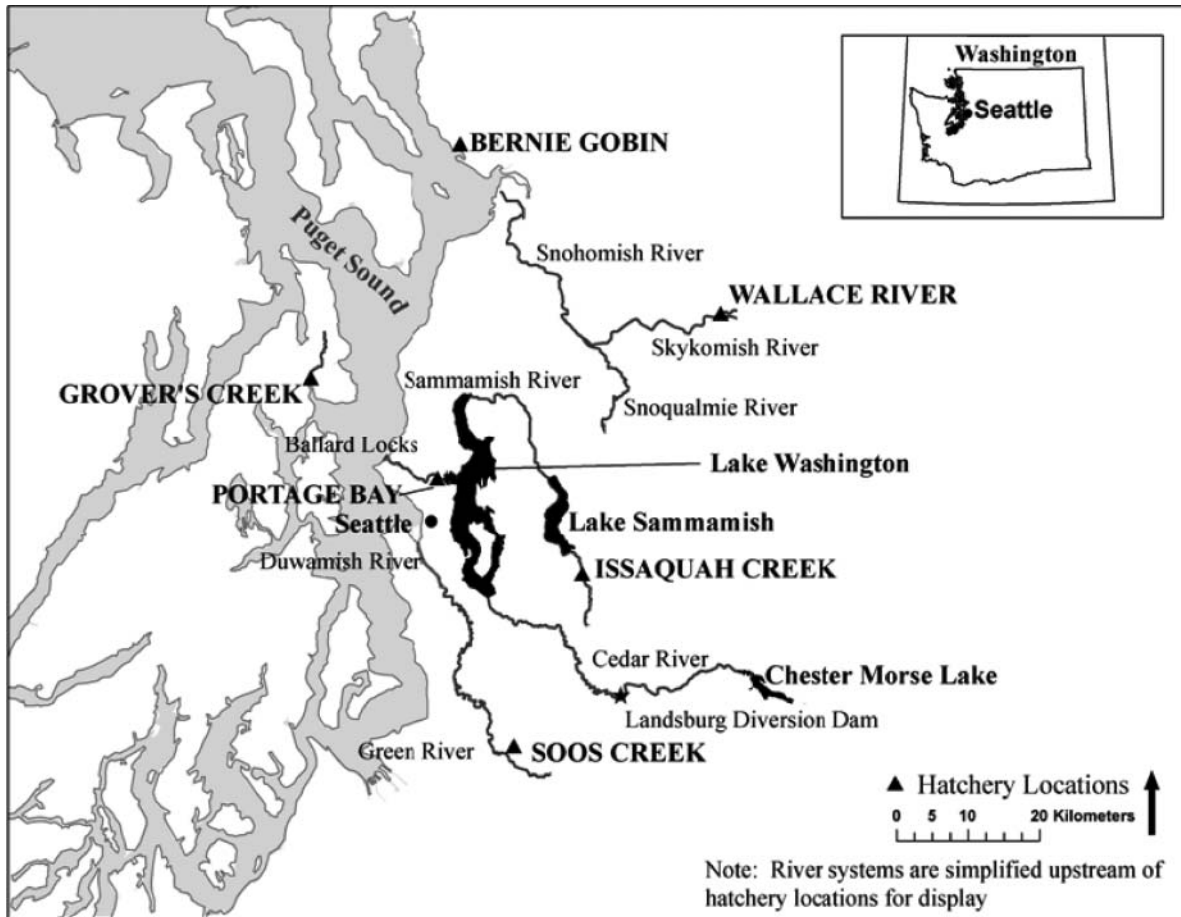

FIGURE 3. Hatchery locations and river basins near the Cedar River, Washington.

spatial and temporal spawning distributions above and below Landsburg Dam. Chinook Salmon redds in the Cedar River main stem were identified and enumerated from inflatable rafts, and side channels and tributaries were surveyed on foot. All identified Chinook Salmon redds were marked with flagging on the adjacent shoreline to enable relocation and to prevent double counting. Information recorded for each verified Chinook Salmon redd included the redd number, date of first observation, redd location, and number and sex of observed salmon. Female Chinook Salmon were assumed to spawn only one redd (Murdoch et al. 2009), and the proportion of redds without embryos was assumed to be negligible (Chapman et al. 1986) and equal between salmon spawning above and below the dam. Survey protocols required observed redds to be accompanied by at least one adult female Chinook Salmon in order to be classified as a Chinook Salmon redd. This strategy is particularly important in the Cedar River below Landsburg Dam, where the presence of sympatric populations of spawning Sockeye Salmon *O. nerka* and Coho Salmon *O. kisutch* can lead to misidentification of the parent species for redds that are not accompanied by spawning adults or guarding females.

For all redd surveys below Landsburg Dam, main-stem and side channel habitats were surveyed once per week in the last half of August and in November and two to three times per week throughout September and October, depending on Chinook Salmon abundance. Surveys were discontinued in November after two consecutive surveys produced no additional Chinook Salmon redd observations. Surveys of main-stem and side channel habitats above Landsburg Dam were performed weekly after the first female Chinook Salmon had passed above Landsburg Dam. Tributaries below Landsburg Dam (i.e., Peterson, Lower Taylor, Lower Rock, and Walsh creeks) were surveyed once per week during September–November (2000–2009), and accessible reaches in tributaries above Landsburg Dam (i.e., Upper Rock and Upper Taylor creeks) were surveyed once per week in 2007 and once per month in 2009. On rare occasions, surveys were not possible due to excessive turbidity and high river flows associated with rainstorms. Redd locations below Landsburg Dam were manually transcribed to digital aerial photos and digitized into ArcView (ESRI, Redlands, California) to assign rkm locations. Redd locations above Landsburg Dam were collected with a handheld GPS unit and consolidated into an ArcGIS database. River kilometer locations were computed by using the center of the low-flow channel as shown in LiDAR (light detection and ranging) imagery and orthorectified aerial photos taken in 2006, 2007, and 2009.

Analyses to characterize temporal redd distributions assumed that daily redd construction rates were equal over the period between surveys. Observed redds for each survey were therefore divided by the number of days over the previous survey interval to calculate the number of redds constructed per day over that interval. The results were pooled to compare temporal distributions between locations over the entire study period and to determine the median spawn date for each location.

Sampling of individual salmon.—Chinook Salmon were captured and sampled as they moved through the Landsburg Dam fish passage facility; the date of passage, body length, presence or absence of an adipose fin, and sex were recorded. The ladder was configured such that adult Chinook Salmon could not access the new habitat without being sampled. Live fish were not sampled for age information due to fish capture permit requirements that prohibited the sampling of scales. Each captured Chinook Salmon was fin clipped to provide an external mark, which was used to prevent recounting salmon that might drop back over the dam and re-ascend through the ladder. Fish passage sampling began in late August and continued daily throughout the Chinook Salmon spawning season (August–November) and into December. All sampled Chinook Salmon were released upstream of Landsburg Dam to continue their spawning migration. Carcasses were not sampled upstream of the dam due to a lack of available carcasses from the small number of fish, the relatively challenging viewing conditions (lots of whitewater), and the large number of scavengers. To estimate the proportion of precocious males (jacks) above the dam, we assumed that all of the males smaller than the largest 2-year-old male carcass collected below the dam (61 cm) were jacks.

Below the dam, Chinook Salmon carcasses were sampled concurrently during redd surveys, and tails were removed at the caudal peduncle to prevent resampling. All carcasses were examined for sex, TL, CWTs, and the presence or absence of an adipose fin, and scale samples were collected.

RESULTS

Upstream Migrants and Redd Abundance

Chinook Salmon abundance in the Cedar River basin, as indicated by Chinook Salmon redd counts, was highly variable, with a mean annual redd count of 395 redds (SE = 65; Table 1). Chinook Salmon used the Landsburg Dam fish passage facility (rkm 37) to colonize upstream habitats immediately after construction was completed in early September 2003. The number of Chinook Salmon moving upstream of Landsburg Dam was higher during survey years 2006–2010 than during the original years of colonization (2003–2005), when all Chinook Salmon passing the dam were strays (Table 1). In addition, annual redd abundance above the dam (as a percentage of total basin redds) exhibited a positive trend over time (Figure 4). Redd counts, which closely matched the female counts in all years but 2005, indicated that the majority of Chinook Salmon females that migrated upstream of the fish passage facility (minimum of 91%) spawned above the dam.

Redd Distribution

Redds observed upstream of Landsburg Dam were nearly all located in main-stem habitats. However, in 2007 and 2010, when Chinook Salmon redds above the dam reached the highest

TABLE 1.   Number of Cedar River basin Chinook Salmon redds by location (main stem or tributary) relative to Landsburg Dam (LD), 1999–2010.

		Main-stem redds		Tributary redds	
Survey year	Total basin redds	Upstream of LD	Downstream of LD	Upstream of LD	Downstream of LD
1999	180	0	180	0	0
2000	53	0	53	0	0
2001	398	0	390	0	8
2002	281	0	269	0	12
2003	336	15	303	0	18
2004	511	20	470	0	21
2005	339	9	322	0	8
2006	588	27	560	0	1
2007	899	91	762	6	40
2008	599	46	553	0	0
2009	285	27	258	0	0
2010	266	36	226	3	1
Mean (SE)	395 (65)	23 (8)	362 (56)	0.8 (0.5)	9 (4)

annual percentages of total basin redds to date (Figure 4), redds were also observed in Upper Rock Creek. Most of the redds that were found above Landsburg Dam were observed within 4 km upstream of the dam (Figure 5). In the majority of survey years, redds were located in the first available spawning gravels upstream of the dam pool. Although upstream redds were concentrated in areas proximal to the dam, some fish did spawn up to 18 km upstream of the dam. For redds upstream of the dam, the median distance to the dam ranged from 2.2 to 5.6 km and

was not significantly different (Kruskal–Wallis test: $P > 0.10$) across years.

The vast majority of Chinook Salmon redds that were observed downstream of Landsburg Dam consistently occurred in main-stem habitats, with relatively small numbers of tributary redds in some years. Chinook Salmon redds in the Cedar River main stem downstream of Landsburg Dam were spatially clustered, and annual redd superimposition rates ranged from 2% to 8%. Prior to fish passage construction, more than 75% of
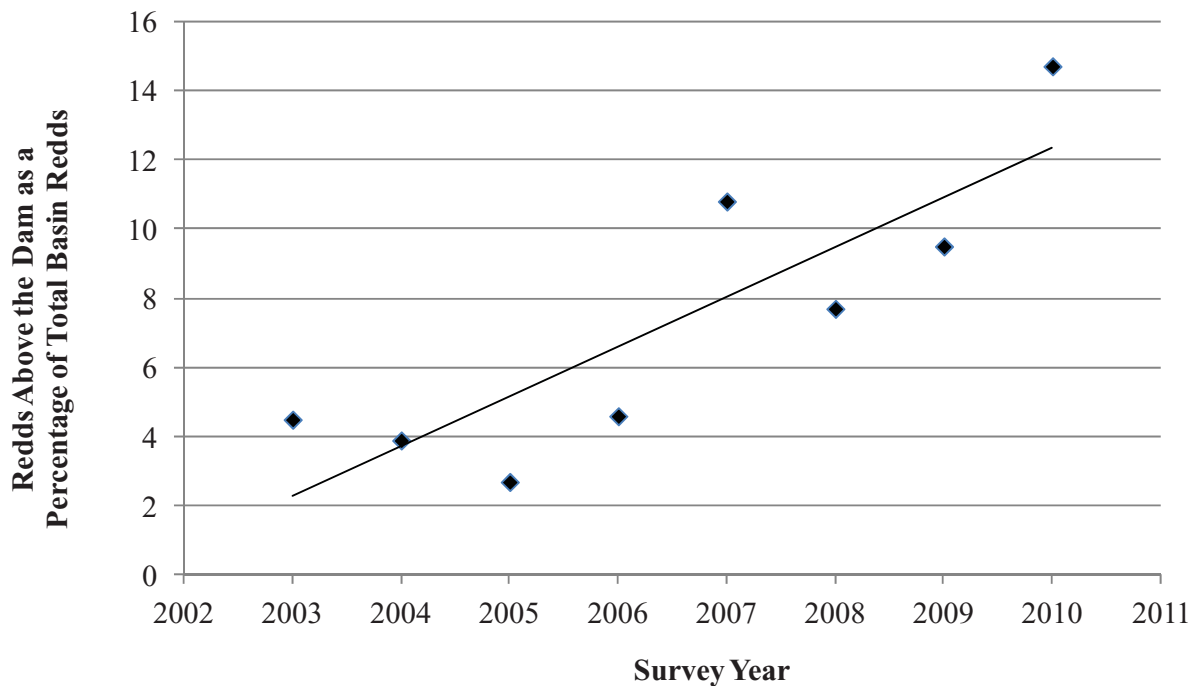

FIGURE 4.   Annual Chinook Salmon redd abundance above Landsburg Dam on the Cedar River as a percentage of total basinwide redd counts, 2003–2010. [Figure available online in color.]
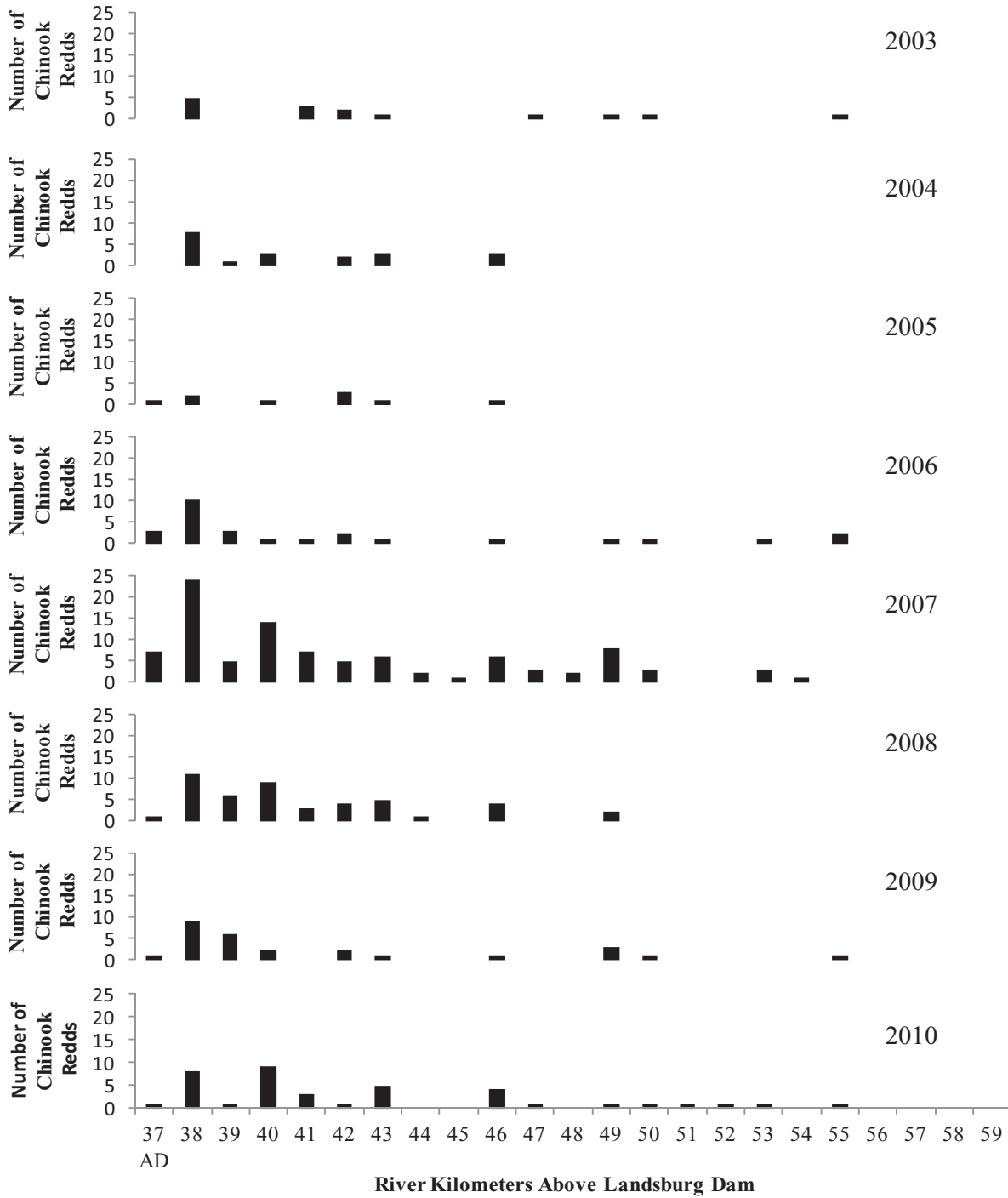
FIGURE 5. Number of Chinook Salmon redds on the Cedar River at river kilometer locations upstream of Landsburg Dam (AD = above dam), 2003–2010 (river kilometer 0 = mouth of the Cedar River).

observed redds were concentrated upstream of rkm 14 (Figure 6). The lower 5 rkm of main-stem habitat were rarely used for spawning. After fish passage was re-established (survey years 2003–2010), the distribution of redds constructed below Landsburg Dam was very similar to that observed prior to 2003.

Spawn Timing

Chinook Salmon redds downstream of the dam were constructed between early September and mid-November, with peak spawning typically occurring in the first week of October (Figure 7). Above the dam, spawning typically began in
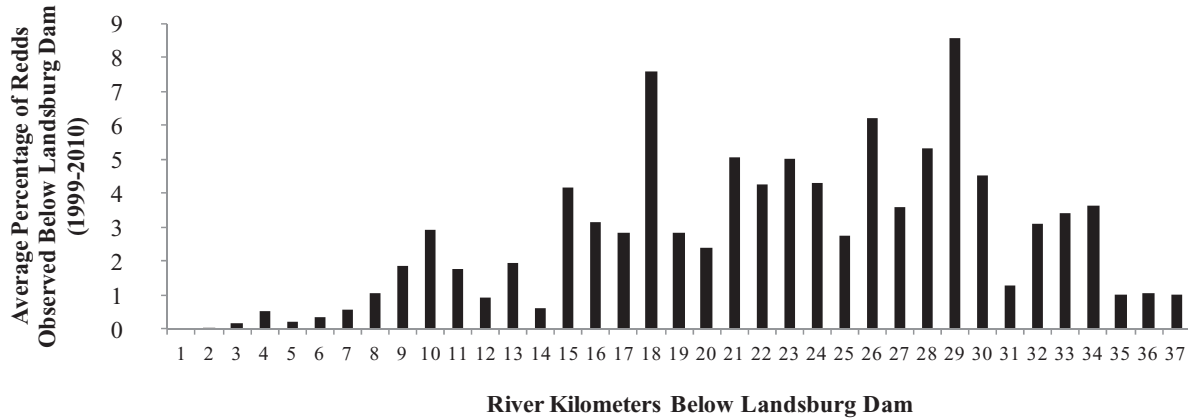
FIGURE 6.   Relative Chinook Salmon redd abundance by river kilometer (1999–2010 pooled).

mid- to late September and was usually complete by the end of October. For pooled survey years 2003–2010, the median spawn date below the dam (October 14) was not significantly different (paired-sample *t*-test: $P > 0.05$) from the median spawn date above the dam (October 16).

In all survey years, migrating and staging Chinook Salmon were observed in main-stem Cedar River habitats downstream of Landsburg Dam prior to the initial observation of Chinook Salmon at the fish passage facility. Initial observation of Chinook Salmon redds below the dam consistently occurred before Chinook Salmon had initiated spawning above the dam and, in most years, occurred before the first Chinook Salmon had passed upstream of the dam. Annual spawn timing distributions observed downstream of the dam after fish passage facility construction did not change appreciably from pre-passage distributions. In most survey years, Chinook Salmon continued to

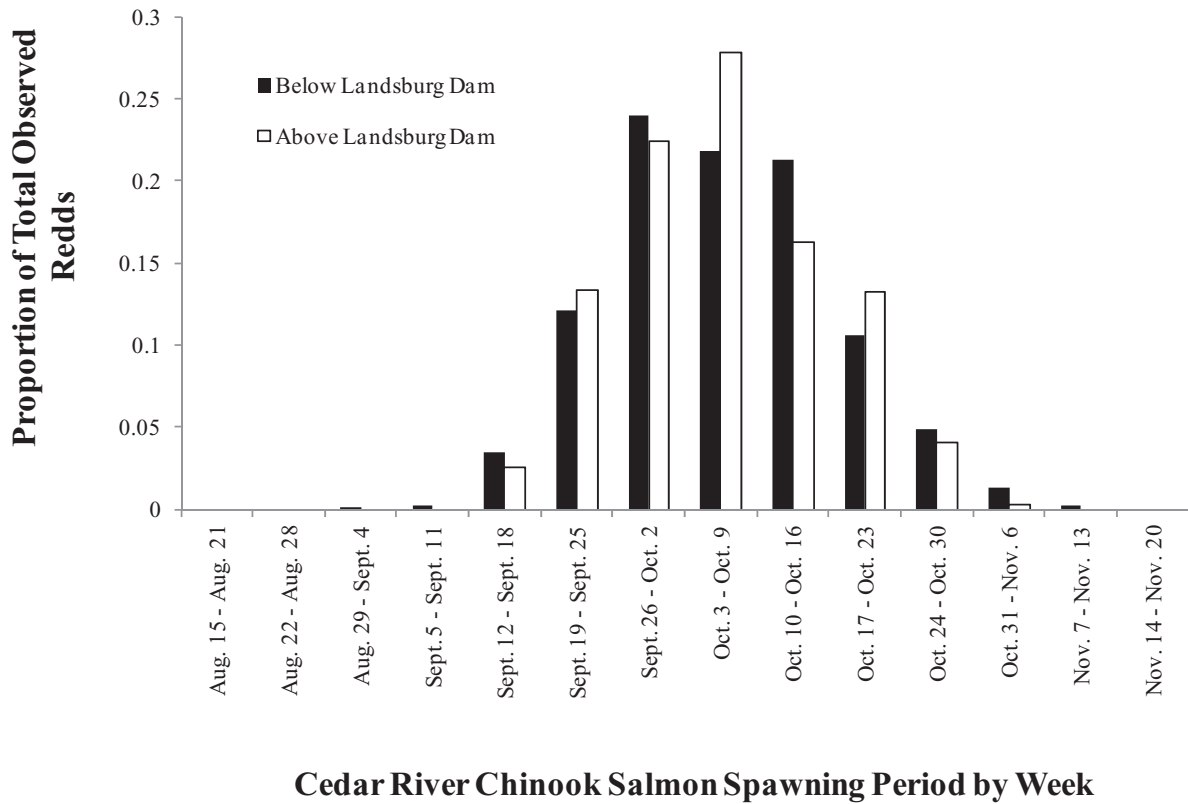**Cedar River Chinook Salmon Spawning Period by Week**

FIGURE 7.   Weekly spawn timing of Chinook Salmon in the Cedar River above and below Landsburg Dam, 2003–2010.

TABLE 2.   Sex and origin (hatchery [adipose fin clipped] or wild [unclipped]) of live Chinook Salmon and carcasses sampled on the Cedar River above and below Landsburg Dam (LD), 2003–2010.

Survey area	Total fish sampled	Percent unclipped	Percent adipose clipped	Males, unclipped	Males with adipose clips	Females, unclipped	Females with adipose clips
2003							
Above LD	79	30	70	18	45	6	10
Below LD	288	78	22	125	35	99	29
Tributaries below LD	41	30	70	10	23	3	5
2004							
Above LD	51	33	67	10	19	7	15
Below LD	373	70	30	113	49	148	63
Tributaries below LD	26	96	4	1	10	0	15
2005							
Above LD	69	58	42	28	24	12	5
Below LD	259	71	29	110	32	73	44
Tributaries below LD	20	60	40	8	7	0	5
2006							
Above LD	182	55	45	80	70	20	12
Below LD	472	80	20	198	37	180	57
Tributaries below LD	4	0	100	0	2	0	2
2007							
Above LD	397	77	23	225	73	73	20
Below LD	607	89	11	274	34	269	30
Tributaries below LD	58	53	47	24	10	6	18
2008							
Above LD	147	83	17	83	14	39	11
Below LD	304	90	10	93	9	175	21
Tributaries below LD	0	0	0	0	0	0	0
2009							
Above LD	138	70	30	73	35	24	6
Below LD	170	81	19	70	20	69	11
Tributaries below LD	0	0	0	0	0	0	0
2010							
Above LD	169	70	30	85	39	33	12
Below LD	131	85	15	57	8	55	11
Tributaries below LD	1	0	0	0	1	0	0

spawn below the dam for 1–2 weeks after spawning had concluded above the dam.

Chinook Salmon Abundance by Sex and Origin (Hatchery versus Wild)

Fish counts at the dam indicated that male Chinook Salmon consistently outnumbered females, with a mean sex ratio of 3.1:1 for survey years 2003–2010 (range = 1.3:1–4.7:1; Table 2). Jacks were estimated to contribute between 5.0% and 42.7% of the annual total number of males above the dam; the mean jack percentage was 15.8% (SE = 4.2%). In the first 2 years after fish access was restored, the proportion of hatchery-origin colonizers outnumbered wild Chinook Salmon by more

than a factor of 2 (Table 2). However, wild fish outnumbered hatchery fish after 2004, and the hatchery component for males and females above and below the dam generally decreased from 2003 to 2010, although the decrease was more pronounced for upstream fish (Figure 8). The mean percentage of hatchery-origin fish among Chinook Salmon that passed upstream of Landsburg Dam (2003–2010) significantly exceeded (paired t-test: $P > 0.05$) the mean percentage of hatchery-origin fish among carcasses that were collected below the dam. Above the dam, males (including jacks) outnumbered females, irrespective of origin. Downstream of the dam, carcasses of wild males and wild females were more abundant than those of their respective hatchery counterparts (Table 2).
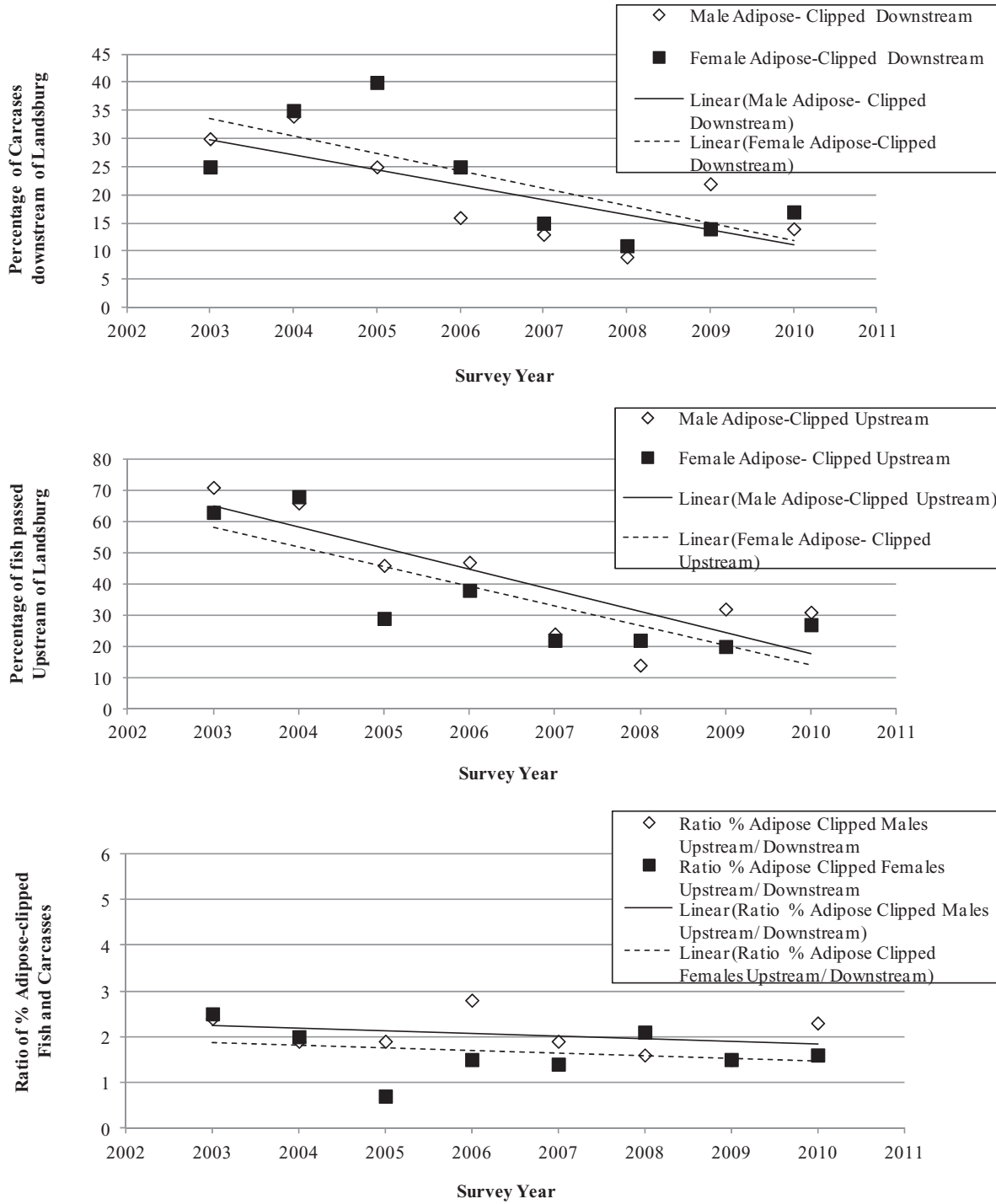
FIGURE 8. Percentage of hatchery-origin (adipose fin-clipped) males and females among Chinook Salmon carcasses that were observed downstream of Landsburg Dam on the Cedar River, 2003–2010 (upper panel); percentage of hatchery-origin individuals among males and females that passed upstream of the dam (middle panel); and the upstream : downstream ratio of the percentage of hatchery fish within each sex (lower panel).

Since 2003, 47 carcasses with CWTs have been collected below Landsburg Dam (<2% of all sampled carcasses). Fourteen (30%) of the carcasses with CWTs were from Issaquah Creek Hatchery, and 22 (47%) were from Portage Bay Hatchery

(University of Washington); both of these hatcheries are located within the Lake Washington–Lake Sammamish watershed. The remaining 11 fish originated from outside the watershed: nine were from Grovers Creek Hatchery on the Kitsap Peninsula,

one was from Bernie Gobin Hatchery (Tulalip Bay, north of the Lake Washington basin in central Puget Sound), and one was from the Cowlitz River Hatchery in the Columbia River basin.

DISCUSSION

Restoration of fish passage via barrier removal or circumvention has had positive results for many species and populations. Burdick and Hightower (2006) reported that Striped Bass *Morone saxatilis*, American Shad *Alosa sapidissima*, and Hickory Shad *A. mediocris* used newly accessible spawning habitat after the removal of a low-head dam on the Neuse River in North Carolina. Farlinger and Beamish (1984) documented upstream range expansion and lacustrine habitat utilization by Pacific Lampreys *Entosphenus tridentatus* (formerly *Lampetra tridentata*) after the removal of a rock slide barrier on the Babine River, British Columbia. In the Cedar River, Anderson et al. (2008) documented recolonization of newly accessible habitats by Coho Salmon in the same reaches as were examined during this study. These examples, combined with our study, demonstrate that barrier removal or circumvention is a highly effective way to re-establish connectivity in lotic habitats and provide benefits for numerous species.

Cedar River Chinook Salmon took immediate advantage of reconnected habitats when passage was provided around the aqueduct in 2002 and then around Landsburg Dam in 2003. Even though redd abundance was low in the first year after passage was re-established, Chinook Salmon did migrate to and spawn in the upper 20% of the main-stem habitat above the dam. After the initial year of passage, Chinook Salmon have continued to spawn above both barriers in each subsequent year. Until 2005, virtually all Chinook Salmon passing above Landsburg Dam were strays, as few Cedar River Chinook Salmon return prior to age 3 (Burton et al. 2009). These colonists were either naturally produced Cedar River Chinook Salmon or out-of-basin hatchery strays. We assumed that the straying of naturally produced fish from other basins was rare. Beginning in 2006, however, a portion of the natural-origin adults migrating upstream of the dam could have been fish that were homing to their natal spawning location. The number of fish migrating above the dam and the abundance of redds above the dam have trended upward since access was restored, indicating that fish passage operations and subsequent recolonization by Chinook Salmon have been successful. In addition, the percentage of upstream redds relative to total redds (upstream + downstream) has also trended upward, suggesting that the total population has grown in response to the increased amount of available habitat.

Similar to Chinook Salmon redd observations in other rivers of the Pacific Northwest, Chinook Salmon redds in the main-stem Cedar River below the dam were often clustered (Geist 2000; Geist et al. 2000; Isaak and Thurow 2006). The use of tributaries was not common above or below the dam. However, the existence of small numbers of Chinook Salmon redds in upstream tributaries and at rkm locations high in the system indicates that colonizing Chinook Salmon will disperse and spawn throughout the available habitat, although in the initial years of colonization the abundance of redds may decrease with increasing distance from the circumvented barrier.

With restoration of access to higher-quality habitat, first- and second-generation colonists may have higher productivity than their noncolonizing downstream cohorts. In addition, lower redd densities and juvenile densities (Anderson et al. 2008; Einum et al. 2008) are likely to produce higher survival rates for fish that are spawned upstream of the dam (Ward and Slaney 1988; Hendry et al. 2001; Isaak and Thurow 2006). This appears to be the case in the Cedar River, as an increasing proportion of the total number of Chinook Salmon redds has been constructed above Landsburg Dam beginning in 2007, when female progeny of the original colonizers returned as mature 4-year-olds (Figure 4). Anderson (2011) used microsatellite markers to estimate that 20.3% of Chinook Salmon passing upstream of the dam between 2006 and 2010 were from parents that had spawned above the dam. These results, combined with the increasing proportion of total basin redds located above the dam, support the hypotheses that (1) salmon use fine-scale homing to locate and spawn in areas where their parents spawned and (2) the increasing proportion of Chinook Salmon redds above the dam is a result of homing to natal habitats (Bentzen et al. 2001; Neville et al. 2006; Quinn et al. 2006) above the dam and improved survival of the progeny of first-generation colonists rather than being a result of continued natural straying alone.

Above Landsburg Dam, Chinook Salmon redds are concentrated in main-stem riffle habitats near the dam (Figure 6). These spawning sites feature a low gradient, an abundance of gravel and cobble substrates, relatively low levels of fine sediment, and local upwelling (Kiffney et al. 2009). In all years of this study, Chinook Salmon redd densities diminished with increasing distance upstream of the dam. Since the abundance of colonists and the competition for spawning sites above the dam have been low, it is probable that initial female colonists simply selected the first area they encountered with suitable spawning site characteristics upstream of the dam. Higher productivity for the relatively pristine habitats above the dam, along with the fine-scale homing behavior displayed by fish originating above the dam, should increase the abundance of Chinook Salmon in areas upstream of the dam over time. Although further study is needed, an increasing number of redds has been constructed further upstream as escapement and competition for spawning sites have increased (Figure 4). However, for upstream redds, the median distance to the dam was not significantly different among years because the annual proportion of redds located near the dam was similar. We expect that redd abundance and upstream dispersal will continue to increase over time until the spawning and rearing habitats are more fully utilized.

In the Cedar River, spawn timing above and below Landsburg Dam corresponded closely to previous Chinook Salmon spawn timing predictions (based on latitude) presented by Healey (1991). The close similarity of spawn timing for upstream and

downstream Chinook Salmon redds suggests that spawning site fidelity to areas below the dam does not significantly delay migration and spawn timing for naturally produced colonizers. In addition, migrating and spawning hatchery colonizers do not appear to be significantly delayed by the lack of olfactory cues from their natal system. Close similarity of spawn timing between upstream and downstream subpopulations also indicates that the new fish passage facility does not substantially delay migration or spawning.

Among Chinook Salmon that passed upstream of the dam, males (including jacks) outnumbered females in all eight spawning seasons after passage facilities became operational, indicating that male Chinook Salmon have a higher propensity to colonize new habitats than females. Male salmon have been shown to migrate longer distances (both upstream and downstream) before spawning than their female counterparts (Keefer et al. 2006; Anderson et al. 2008), thus increasing the probability that males would account for a greater proportion of the fish that volitionally enter the upstream Cedar River habitats. Alternatively, male Chinook Salmon may be more abundant than females within a spawning cohort. This pattern has been seen in other salmonid populations, including Coho Salmon (Holtby and Healey 1990; Spidle et al. 1998; Anderson et al. 2008) and Chinook Salmon (Olsen et al. 2006), and is typically attributed to a gender bias in marine survival. Higher ratios of males to females above the dam likely increased the probability that females would find a mate, and this may have influenced the observed propensity for females that passed the dam to remain upstream to spawn.

For both sexes, the component of upstream-migrating fish was disproportionately made up of hatchery-origin individuals in comparison with the hatchery contributions downstream, suggesting that hatchery fish stray into newly available habitats at a higher rate than their wild counterparts. These results did not support our hypothesis that the proportion of hatchery fish among initial colonizers would closely reflect the hatchery proportion below the dam. An increased tendency for straying has been observed among several hatchery stocks (Keefer et al. 2006; Quinn 1993), and in the Cedar River this behavior contributed substantially to initial colonization. Since salmon tend to home to their natal streams (Hasler and Scholz 1983), hatchery fish in a nonnatal system may move longer distances while searching for homing stimuli. Keefer et al. (2006) observed this tendency for spring Chinook Salmon in the Columbia River, where hatchery-origin fish wandered greater distances before spawning than did their wild counterparts. As hatchery fish arriving in the lower Cedar River had already demonstrated an inclination to stray, it is not surprising that these fish would wander into the upstream reach at a higher rate than natural-origin Cedar River fish homing to their natal downstream spawning reaches. This is important because hatcheries have been implicated as contributing to the declines of natural-origin salmonids through genetic impacts (Reisenbichler 1997; Myers et al. 1998; McElhany et al. 2000; Utter 2004) and delete-

rious demographic interactions with sympatric, wild-spawning fish (NRC 1996; Levin et al. 2001; Chilcote 2003; Puget Sound Technical Recovery Team 2003; Goodman 2005; McGinnity et al. 2009); furthermore, hatcheries have been widely used as a tool to supplement wild salmonid stocks as mitigation for losses caused by anthropogenic barriers to spawning grounds (Lichatowich 1999; Blumm 2002). However, the proportion of upstream escapement represented by hatchery strays in the Cedar River has progressively decreased over the years—no doubt in response to an increasing number of natural-origin fish homing to their upstream natal reaches. Further, we observed a downward trend in the upstream : downstream ratio of percent adipose fin-clipped fish within sexes, supporting the expectation that the new growing population above Landsburg Dam is not the product of increased upstream straying but rather is a result of natural-origin offspring migrating back to their natal habitats and establishing a natural population above the dam. As time progresses and as spawning densities upstream of the dam approach those observed downstream, we expect the natural : hatchery ratio observed upstream to converge with the ratio downstream.

The CWT recoveries indicate that the majority of hatchery Chinook Salmon in the Cedar River were from the Issaquah Creek and Portage Bay hatcheries, the most proximal hatcheries to the Cedar River. Portage Bay Hatchery strays may have been more numerous than Issaquah Creek Hatchery fish because Portage Bay Hatchery uses water from the City of Seattle, and the city's water originates from the Cedar River. These hatchery populations originated from the Green River, the most proximal river basin south of the Cedar River. This ancestral geographic proximity of hatchery fish in the Cedar River likely increases the probability that local adaptation to geology, climate, and flow would allow successful reproduction in the wild (Salmenkova 2002). All of the recovered CWTs except one were from hatcheries in the central Puget Sound region, suggesting that strays from hatcheries tend to migrate to nearby river systems. Given our results and the potential impacts of hatchery fish on wild fish populations, we suggest that monitoring of the abundance of hatchery fish straying into newly accessible habitats is important because survival rates for salmon originating from these habitats will reflect the fitness of their colonist parents (Araki et al. 2008).

In river systems with depressed or Endangered Species Act–listed fish populations and artificial migration barriers, the rationale for future fish passage construction or barrier removal is bolstered by the results of this study. Successful colonization of newly accessible, high-quality habitats by Chinook Salmon in the Cedar River should provide insight into potential fish passage projects that have been recently proposed or implemented in the Pacific Northwest (e.g., on the Elwha River, Washington). The results of this study confirm that circumvention of fish migration barriers is an effective restoration approach to increase the availability of productive salmon spawning and rearing habitats in rivers.

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