

# Dispersal and productivity of Chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon colonizing newly accessible habitat

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**Abstract:** Following construction of a fish ladder at Landsburg Diversion Dam on the Cedar River, Washington, USA, in fall 2003, we used DNA-based parentage to identify second generation Chinook (*Oncorhynchus tshawytscha*) and coho (*Oncorhynchus kisutch*) salmon as recruits that were produced above the dam or “strays” dispersing into the new habitat that were produced elsewhere. For both species, strays colonized immediately but decreased as a proportion of the total run over time. Chinook salmon strays were more numerous in years when the species was more abundant below the dam and included a much larger proportion of hatchery origin salmon than did coho salmon. Productivity, calculated as the ratio of female recruits sampled at the dam to female spawners, exceeded replacement in all four coho salmon cohorts but only two of five Chinook salmon cohorts, leading to more rapid population expansion of coho salmon. However, estimates of fishing mortality and recruitment into the Cedar River below the dam substantially increased Chinook salmon productivity estimates. Our results demonstrate that Pacific salmon are capable of rapidly recolonizing habitat made accessible by restoration and emphasize the importance of demographic exchange with preexisting populations during the transition from recolonization to self-sustainability.

**Résumé :** Après la construction d'une passe à poissons au barrage de dérivation de Landsburg, sur la rivière Cedar (Washington, États-Unis), à l'automne 2003, nous avons utilisé l'ascendance basée sur l'ADN pour distinguer les saumons quinnats (*Oncorhynchus tshawytscha*) et coho (*Oncorhynchus kisutch*) de deuxième génération constituant des recrues produites en amont du barrage des individus « égarés » produits ailleurs qui s'étaient dispersés dans ce nouvel habitat. Pour les deux espèces, si les égarés ont immédiatement colonisé l'habitat, la proportion de la montaison totale qu'ils représentaient a diminué avec le temps. Les saumons quinnats égarés étaient plus nombreux les années où l'espèce était plus abondante en aval du barrage et comptaient une proportion beaucoup plus grande de saumons issus d'écloseries que les saumons cohos. La productivité, calculée comme étant le rapport du nombre de recrues femelles échantillonnées au barrage et du nombre de génitrices, dépassait le niveau de remplacement dans les quatre cohortes de saumons cohos, mais dans seulement deux cohortes de saumons quinnats sur cinq, entraînant une expansion plus rapide de la population de saumons cohos. Toutefois, les estimations de la mortalité par pêche et du recrutement dans la rivière Cedar en aval du barrage ont sensiblement accru les estimations de la productivité des saumons quinnats. Nos résultats démontrent que les saumons du Pacifique sont capables de recoloniser rapidement un habitat rendu accessible par la restauration et soulignent l'importance de l'échange démographique avec des populations préexistantes durant la transition d'une situation de recolonisation à une situation d'autosuffisance. [Traduit par la Rédaction]

## Introduction

Habitat loss from the construction of impassable dams poses a substantial threat to migratory fishes worldwide (Morita and Yamamoto 2002; Limburg and Waldman 2009; Dudgeon 2011). Dams are ubiquitous across the landscape of the United States (Graf 1999), and there is an increasing awareness that removal of ageing dams and provision of fish passage provide special opportunities to conserve migratory fishes (Burdick and Hightower 2006; Catalano et al. 2007; Hogg et al. 2013; Pess et al. 2014). In the US Pacific Northwest, dams and other structures have severely reduced the quantity and quality of spawning and rearing habitats accessible to Pacific salmon (*Oncorhynchus* spp.), contributing to lost biodiversity, local extinctions, and threatened or endangered conservation status within regions occupied by extant pop-

ulations (National Research Council 1996; Sheer and Steel 2006; Gustafson et al. 2007; McClure et al. 2008). Dam removal or circumvention projects intended to benefit Pacific salmon and steelhead (anadromous rainbow trout, *Oncorhynchus mykiss*) have increased markedly over the last decade, and research quantifying colonization patterns and processes is needed to provide a scientific foundation for management decisions confronting such projects (Anderson et al. 2014).

Simply increasing habitat connectivity does not guarantee success, however, and resource managers could adopt active or passive roles following barrier removal. Initially, the densities of a colonizing species are likely to be quite low, and a population may fail to become established unless it exceeds some critical abundance threshold (Deredec and Courchamp 2007). Active reintroduction strategies such as transplanting adults or releasing

Received 10 April 2014. Accepted 28 October 2014.

Paper handled by Associate Editor Paloma Morán.

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hatchery-produced juveniles offer ways of ensuring that adequate numbers of fish reach any unoccupied habitat, but may compromise long-term conservation goals by altering evolutionary and ecological processes (Anderson et al. 2014). Such risks could be avoided through passive reintroduction in which anadromous fishes are allowed to naturally recolonize habitat made accessible via barrier removal.

Although strict philopatry would preclude natural colonization, even in species famous for homing, a measurable proportion of salmonid populations does not return to the natal site (Quinn 1993; Keefer and Caudill 2014; Westley et al. 2013). Straying behavior plays an important role in the population biology of salmon because it permits the colonization of new habitat, including expansion of existing populations and founding new ones, processes that have occurred repeatedly following glacial recession in the Pacific Northwest (McPhail and Lindsey 1986; Milner et al. 2000). Strays might be defined at a variety of spatial scales; salmon dispersing even modest distances (hundreds of metres to a few kilometres) from natal sites may, in some circumstances, be ecologically and evolutionarily important (Keefer and Caudill 2014).

In the first generation following dam removal or circumvention, fish bypassing the former barrier must stray at least some distance from their natal sites. The number of strays or colonists entering a new habitat depends on the demographics and proximity of the source populations (Pess et al. 2012). To attain long-term sustainability, the initial colonists must produce enough offspring that survive and return to the new habitat to successfully reproduce. Precise homing by salmon recruiting back to natal sites above the former barrier will not only increase abundance within the new habitat, but over time will also provide the reproductive isolation necessary to maximize population fitness through natural selection and local adaptation (Quinn et al. 2001). In the generations following initial colonization, some straying into the newly accessible habitat may continue to occur, and some of the fish produced in that habitat may return to spawn elsewhere in the area (e.g., below the former site of the dam in the natal river or in other rivers nearby), complicating assessment of the project's success. Documenting the presence, or even estimating the abundance, of salmon occupying the newly accessible habitat is insufficient to demonstrate conservation success if the goal is a population that can not only replace itself but also support the level of fishing to which the region's salmon are exposed. Accounting for strays into and from the newly accessible habitat in the generations following colonization is therefore necessary to understand the success of initial colonists and the degree of interaction between the colonizing and source populations.

Here we use molecular genetics to measure the dispersal and productivity of Chinook (*Oncorhynchus tshawytscha*) and coho salmon (*Oncorhynchus kisutch*) recolonizing spawning and rearing habitat above Landsburg Diversion Dam on Cedar River, Washington, USA (Fig. 1). Following construction of a fish ladder, salmon were allowed volitional access to the new habitat without translocation or artificial supplementation. Therefore, this restoration action provided an ideal opportunity to test the efficacy of passive reintroduction and evaluate the capacity for preexisting source populations below the dam to colonize the newly accessible habitat. In this case, colonization proceeded through expansion of existing populations rather than founding new ones.

This paper builds on previous work describing individual reproductive success (Anderson et al. 2010, 2013a) by adding new data and evaluating population-level metrics of dispersal and productivity. DNA-based parentage analysis identified salmon from the second generation of colonization as recruits if they were produced above the dam or strays dispersing into the new habitat if they were produced elsewhere. We use the term stray based on the rationale that fish dispersing even short distances from natal sites below the dam into the new habitat were ecologically important to colonization demographics, acknowledging that other

authors have defined strays at the coarser spatial scale of fish returning to non-natal rivers. First, we assess dispersal by quantifying the total number of strays and determine whether their abundance was correlated with that of proximate potential source populations. We then quantify productivity, testing the hypothesis that the adult salmon ascending the fish ladder in the second generation and beyond represent self-sustaining natural production from the initial colonists, against the alternative hypothesis that the newly accessible reach of the river continues to be populated by fish produced in the lower Cedar River or elsewhere.

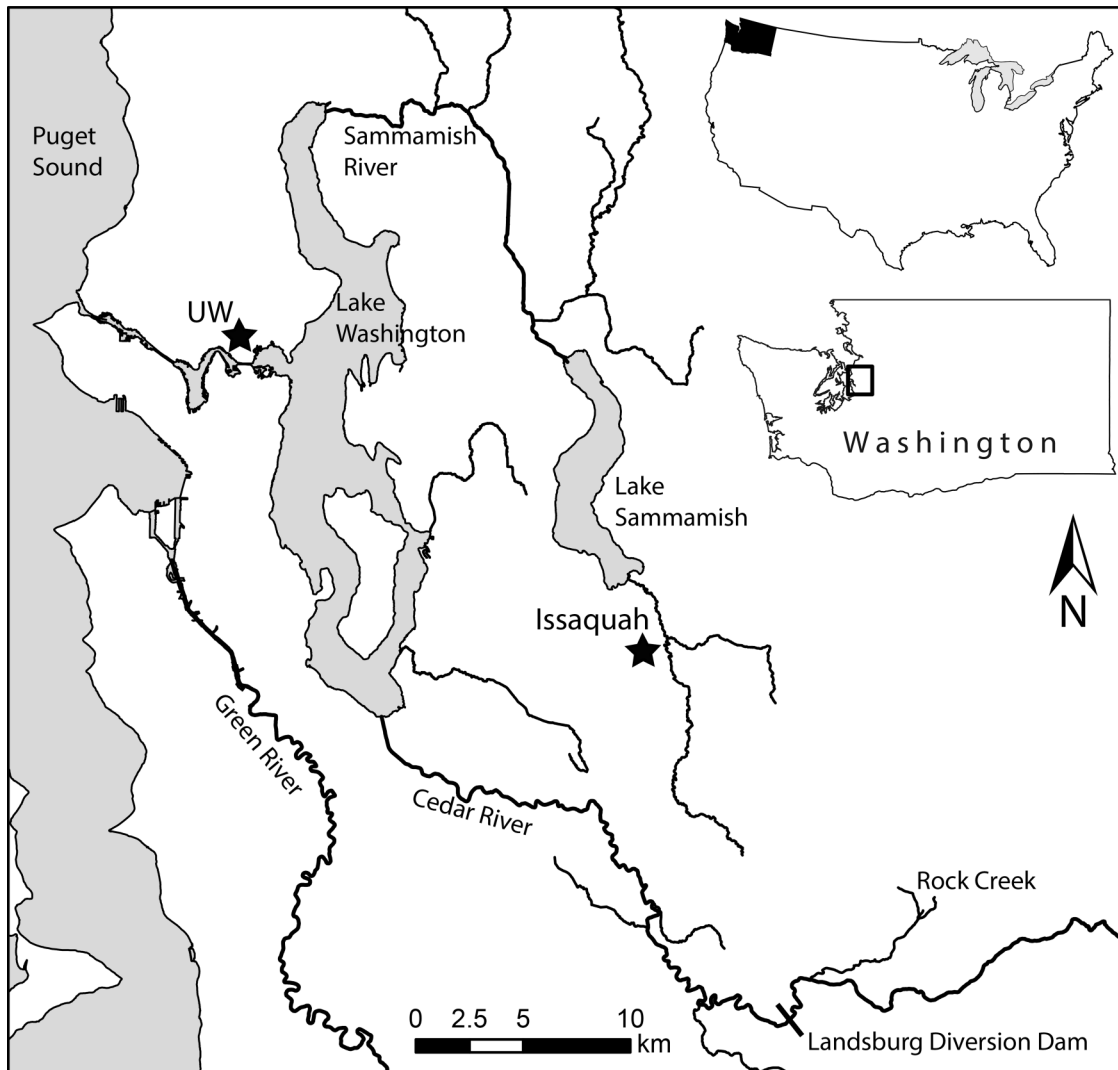
## Methods

The Cedar River flows west from the Cascade Range into the south end of Lake Washington, which is connected to Puget Sound via a man-made shipping canal through Seattle, Washington, USA (Fig. 1). Historically, the Cedar River was connected to Puget Sound via the Green River, but was diverted into Lake Washington in 1916 during construction of the navigational locks and shipping canal. Landsburg Diversion Dam, located at river kilometre (rkm) 35.1, blocked fish migration from 1901 to 2003. In fall 2003, fish passage structures added to the dam enabled salmon to volitionally recolonize approximately 33 km of habitat above the dam. The design of the passage structures allowed each fish to be counted and sampled prior to release upstream. The spawning and rearing habitat above the dam is generally high quality because the area is managed as a de facto reserve to protect Seattle's water supply. Approximately 20 km of habitat is available within the Cedar River from the dam upstream to Cedar Falls, a natural barrier to migration. Another 13 km of habitat are accessible within tributaries, primarily in Rock Creek, which enters the Cedar River 3.4 km upstream from the dam. Kiffney et al. (2009) provide a detailed description of the physical habitat and aquatic community.

Adult Chinook and coho salmon were counted and sampled as they ascended the fish ladder and bypassed the dam (Kiffney et al. 2009; Anderson et al. 2010, 2013a; Burton et al. 2013). Each sampled fish was identified by species and sex, and we took a small tissue sample for subsequent DNA analysis. Hatchery fish were identified by a missing adipose fin. For the vast majority of the migration period, the fish ladder was configured such that adult salmon could not bypass the dam without being handled by staff, providing us with a nearly complete census of all colonists. A few salmon migrated upriver before (Chinook salmon) or after (coho salmon) the ladder was configured in this fashion and so were not sampled, but an automatic camera system (described by Shardlow and Hyatt 2004) indicated that our sampling fraction was very high (mean: Chinook = 99.4%, coho = 93.8%; see Anderson et al. 2010 and 2013a for details). In either configuration, coho and Chinook salmon were rarely observed holding for an extended period below the entrance to the fish ladder, suggesting that it did not impede upstream passage. In 2010–2013, fish passage operations were changed and the ladder was opened to salmon without sampling during the middle of the coho salmon migration, but after the Chinook salmon run was complete. For these years, we estimated coho salmon abundance based on data from the camera system or the mean proportion from 2003 to 2009 that was trapped on or prior to the last date of sampling (if camera data were not available). We used spawning surveys by inflatable raft (Cedar River) and foot (tributaries) to quantify upstream dispersal distance from the dam by adult salmon (Burton et al. 2013).

We also obtained information on putative sources of colonizing salmon. Salmon of both species spawn in the Cedar River below the dam. Chinook salmon abundance below the dam was assessed by counts of spawning nests or "redds" in the Cedar River (Burton et al. 2013). We obtained scale and, in some cases, fin tissue samples from adult Chinook salmon carcasses from the lower river

**Fig. 1.** Map of the Cedar River and Lake Washington basin. The two hatcheries in the area producing Chinook and coho salmon are denoted by stars; UW, University of Washington (figure sources: Pess et al. 2011; Anderson et al. 2013a).



surveys in 2006–2009. Each of these adults was aged via scale analysis, and we only genotyped individuals that could have been produced above the dam (i.e., return year minus age  $\geq$  2003 and not hatchery-marked). No abundance data or samples were collected from coho salmon below the dam, in part because they spawn during the winter when turbidity and high flows make surveys difficult.

Both salmon species were also produced at two hatchery facilities in the basin: a large hatchery run by the Washington Department of Fish and Wildlife at Issaquah Creek and a smaller hatchery run by the University of Washington (UW) at Portage Bay (Fig. 1). The numbers of salmon returning to the Issaquah Creek hatchery were obtained from a Washington Department of Fish and Wildlife database, and the numbers of UW hatchery salmon were provided by the hatchery manager (J. Wittouck, UW, personal communication, 2011). Data queried from the Regional Mark Processing Center ([www.rmms.org](http://www.rmms.org)) indicated that both hatcheries adipose-marked a high proportion of released juveniles (median annual estimate: Chinook = 97%, coho = 95%) during the study period. Any unmarked 5-year-old Chinook salmon ascending the fish ladder in 2003 may have been hatchery fish because the Issaquah hatchery did not mass mark prior to brood year 1999, but we expect this number to be low based on the relative scarcity of 5-year-olds in the population (Anderson et al. 2013a).

We obtained genotypes at 10 microsatellite loci from Chinook and coho salmon using previously described protocols (Anderson et al. 2010, 2013a). Chinook salmon sampled at the dam in 2003–2011, Chinook salmon sampled below the dam in 2006–2009, and coho salmon sampled at the dam in 2003–2009 were genotyped. All samples that had been genotyped at seven or more loci were included in the parentage analysis, and the vast majority of these were genotyped at 9 or 10 loci (Chinook = 93.7%, coho = 89.9%). We were unable to genotype 11 Chinook and 12 coho salmon collected at the dam, and they were excluded from further analysis.

We used parentage analysis to classify natural origin salmon according to the location where they were spawned. We use the term “recruit” for fish that were offspring of parents who spawned above the dam. Conversely, we refer to individuals whose parents spawned in the Cedar River below the dam or elsewhere as “strays,” as inferred from the fact that their parents had not been sampled at the dam. All hatchery-produced salmon (identified by missing adipose fin) were classified as strays, as were all natural origin salmon in 2003–2004, because they returned too soon after dam modification to have been produced by parents that spawned above the dam.

Beginning in 2005, genotyped natural origin salmon were considered as offspring in a parentage analysis using FRANz (Riester et al. 2009). The pool of potential offspring was based on well-



known age at maturity patterns of each species (coho: age 2–3, Chinook: age 2–5; Quinn 2005), with the constraint that 2009 was the final year of DNA analysis for coho salmon and 2011 for Chinook salmon. For each parental cohort in year  $x$ , potential offspring were all natural origin salmon sampled in years  $x + 2$  and  $x + 3$  for coho salmon and years  $x + 2$ ,  $x + 3$ ,  $x + 4$ , and  $x + 5$  for Chinook salmon, but there were no expected or weighted probabilities of specific ages. Our assignments assumed a genotyping error rate of 1%. Within FRANz, we considered the unsampled lower Cedar River population as potential parents in estimating the fraction of sampled parents for each sex. For Chinook salmon, we used annual redd counts (Burton et al. 2013) and assumed a 50:50 sex ratio. For coho salmon, we conservatively assumed a very large lower Cedar River population of 5000 individuals of each sex.

Natural origin fish considered as offspring were classified as “recruits” if they assigned to a female that had bypassed the dam in a previous year. Salmon sampled at the dam that did not match any females sampled at the dam in previous years were classified as “strays.” We chose maternal parentage assignments for the recruit versus stray classification because female salmon determine the breeding site and typically spawn in a single location (Murdoch et al. 2009). In contrast, males often spawn at multiple locations, which in this case might have occurred both above and below the dam. The assumption that females sampled at the dam continued upstream to spawn above the dam is based on coho salmon radio telemetry (Anderson and Quinn 2007) and Chinook salmon redd surveys (Burton et al. 2013), though a small fraction of the females may have moved back downstream of the dam to spawn.

We used a simulation procedure to estimate the effects of parentage assignment uncertainty on the precision of our abundance estimates of recruits and strays. For each putative offspring, FRANz provides the posterior assignment probability of each potential parentage match. Thus, in some cases, a single offspring had multiple potential parentage matches, each with a unique posterior probability. For each putative offspring, we sampled one parentage assignment in proportion to the posterior probabilities of all possible assignments to that individual and classified the individual as recruit or stray based on this assignment. Within each simulation, we summed the total number of recruits and strays across all putative offspring. This sampling process was repeated 9999 times. We report the median number of recruits and strays from these 10 000 simulations as our estimate of the abundance of each category and provide the range across all simulations as an indication of the uncertainty due strictly to the statistics associated with the parentage assignments.

We used two different sets of samples, one positive control and one negative control, to assess the accuracy of the DNA-based parentage methods for classifying fish as either recruits or strays. First, as a positive control, we assigned parentage to  $N = 1412$  juvenile coho salmon samples collected from sites above the dam in the Cedar River and its tributary Rock Creek (see Anderson et al. 2013b for details). All of these juvenile coho salmon were produced by adults that bypassed the dam in 2003–2006, and therefore, in principle, 100% should have been assigned to parents. Second, as a negative control, we entered  $N = 45$  hatchery coho salmon and  $N = 267$  hatchery Chinook salmon sampled at the dam into our parentage assignment procedure. All of these salmon were produced in regional hatcheries, as indicated by a clipped adipose fin, and therefore none should have been classified as a recruit. The use of both positive and negative controls allowed us to validate the assumptions associated with our parentage-based approach to estimating the number of recruits and strays.

We calculated the productivity of the initial colonizing cohorts (Chinook: 2003–2007; coho: 2003–2006) as the total number of recruits divided by the number of spawners that produced them. We report two sets of productivity values: one based on females

only because this best represents the reproductive capacity of the population and one based on both males and females because this best represents the overall abundance of the population. For both sets of values, productivity  $\geq 1.0$  would indicate replacement, and multiple successive cohorts with productivity equaling or exceeding replacement would indicate a self-sustaining population. The samples collected from Chinook salmon below the dam were identified as originating from above the dam using the same criteria as that used for the samples collected at the dam. This generated a rate of assignment to above-dam parents; this rate was applied to redd counts from the lower river (Burton et al. 2013) to estimate the total number of Chinook salmon in the Cedar River below the dam that were produced above the dam. We assumed one female salmon and one male salmon per observed nest, and we excluded the estimated number of hatchery strays in the lower river for each sex based on the adipose mark rates reported by Burton et al. (2013). Finally, to allocate the estimated upper river recruits in a given return year to the parental brood year that produced them, we used the sex-specific age structure for each cohort and return year in the parentage assignments with posterior probabilities of assignment  $>0.95$ .

## Results

The numbers of Chinook and coho salmon that bypassed the dam tended to increase over the years (Table 1). Many Chinook salmon returned in 2007 but they were less numerous than coho salmon in 5 of 7 years in which the majority of the run for both species was sampled. In 2010–2013, when only a portion of the coho salmon population was handled and counted, estimates suggested a substantial increase in abundance (Table 1, see footnoted values). Chinook salmon had a much larger proportion of hatchery origin fish than coho salmon in all years (Table 1). Both species showed a surplus of males, but Chinook salmon had a greater fraction of males than did the coho salmon in 9 of 11 years (Table 1).

Strong statistical confidence of assignment and our control samples both indicated that our parentage-based methods of classifying recruits and strays were robust. The majority of natural origin salmon entered into parentage analysis as potential offspring of above dam spawners yielded assignments with very high posterior probabilities (Table 2). This included salmon that did not match any potential parents, many of which had posterior probabilities  $\geq 0.95$  (Chinook: 80.5%, coho: 82.6%). Thus, for most salmon classified as strays, the parentage procedure did not assign parents because none in the potential pool matched genotypes, not because of failure to distinguish between two or more equally likely parents. Our control samples provided additional confirmation of the accuracy of our classification methods. The simulation procedure estimated that 97.5% of the positive control samples were correctly assigned (Table 3). Similarly, 95.6% of hatchery coho salmon and 97.0% of hatchery Chinook salmon were correctly classified as strays (Table 3).

For the samples of adult salmon collected at the dam, the two species showed different patterns of dispersal into the new habitat. Natural origin strays were more numerous in coho (mean  $\pm$  SD =  $99.4 \pm 58.3$ ) compared with Chinook salmon ( $67.0 \pm 64.3$ ) in all years except 2007 (Fig. 2), although this difference was not significant based on a Kolmogorov–Smirnov two-sample test (KS test,  $p > 0.10$ ). However, hatchery origin strays were significantly more numerous in Chinook salmon ( $50.4 \pm 26.8$  versus  $7.3 \pm 6.4$ ; Fig. 2; KS test,  $p = 0.0018$ ). The total numbers of strays (hatchery and natural origin combined) were similar between the species (Chinook:  $117.4 \pm 86.4$ ; coho:  $106.7 \pm 63.9$ ; KS test,  $p > 0.10$ ), but a much larger proportion of the Chinook salmon strays were from hatcheries (28%–68% versus 2%–9% for coho salmon). As a proportion of the total run, strays tended to decrease through time for both species (Fig. 2). This trend was apparent in each subsequent year for coho salmon and by comparing the first generation of

**Table 1.** Counts of adult Chinook and coho salmon sampled at Landsburg Diversion Dam on the Cedar River, Washington, USA.

Return year	Sampling period	Chinook salmon observed			Coho salmon observed		
		N	Male (%)	Hatchery (%)	N	Male (%)	Hatchery (%)
2003	Sept. 16–Dec. 22	79	79.7	69.6	47	55.3	8.5
2004	Sept. 7–Feb. 14	51	56.9	66.7	99	65.7	2.0
2005	Sept. 6–Jan. 25	69	75.4	42.0	170	61.2	3.5
2006	Sept. 5–Jan. 28	182	82.4	45.0	190	57.9	4.7
2007	Sept. 7–Feb. 28	397	75.1	23.4	142	62.7	0.7
2008	Sept. 2–Feb. 3	146	65.8	17.1	366	49.5	2.5
2009	Sept. 9–Feb. 1	138	78.3	29.7	679	58.0	2.9
2010	Sept. 7–Nov. 28	169	73.4	30.2	121 <sup>a</sup>	63.6	6.6
2011	Sept. 6–Nov. 14	211	78.2	36.5	115 <sup>b</sup>	78.3	0.9
2012	Sept. 4–Nov. 9	278	83.1	31.3	318 <sup>c</sup>	59.1	0.3
2013	Sept. 3–Nov. 6	262	67.9	23.7	414 <sup>d</sup>	55.1	0.2

<sup>a</sup>Truncated sampling period, extrapolated abundance estimate = 302 assuming 40.1% migration complete.

<sup>b</sup>Truncated sampling period, extrapolated abundance estimate = 412 assuming 27.9% migration complete.

<sup>c</sup>Truncated sampling period, total abundance estimate = 1085 based on data from camera system.

<sup>d</sup>Truncated sampling period, extrapolated abundance estimate = 2114 assuming 19.6% migration complete.

**Table 2.** The most likely posterior probability of assignment for natural origin adult salmon entered into parentage analysis.

Species	Return years	Assignment	Mismatching loci	N	Posterior probability	
					Median	Range
Chinook	2005–2011	Two parents	0	239	1.000	0.999–1.000
		Two parents	1	45	1.000	0.998–1.000
		Two parents	2	2	0.998	0.997–0.999
		Two parents	3	2	0.474	0.463–0.486
		Two parents	4	2	0.479	0.428–0.529
		One parent	0	100	1.000	0.808–1.000
		One parent	1	48	0.962	0.535–1.000
		One parent	2	35	0.725	0.503–1.000
		One parent	3	3	0.568	0.478–0.941
		No parents	—	641	1.000	0.411–1.000
Coho	2005–2009	Two parents	0	817	1.000	0.404–1.000
		Two parents	1	43	0.982	0.302–1.000
		Two parents	2	11	0.704	0.367–0.991
		One parent	0	122	0.968	0.302–1.000
		One parent	1	26	0.772	0.350–0.990
		One parent	2	3	0.540	0.380–0.696
		No parents	—	470	1.000	0.342–1.000

**Table 3.** Classification as either recruits or strays of control groups according to parentage-based methods.

Species	Control type	N	Recruits		Strays	
			Estimate	Range	Estimate	Range
Coho	Positive	1412	1377	1365–1385	35	27–47
Coho	Negative	45	2	1–2	43	43–44
Chinook	Negative	394	12	7–20	382	374–387

**Note:** The range represents uncertainty due to parentage assignments based on a simulation procedure (see Methods for details).

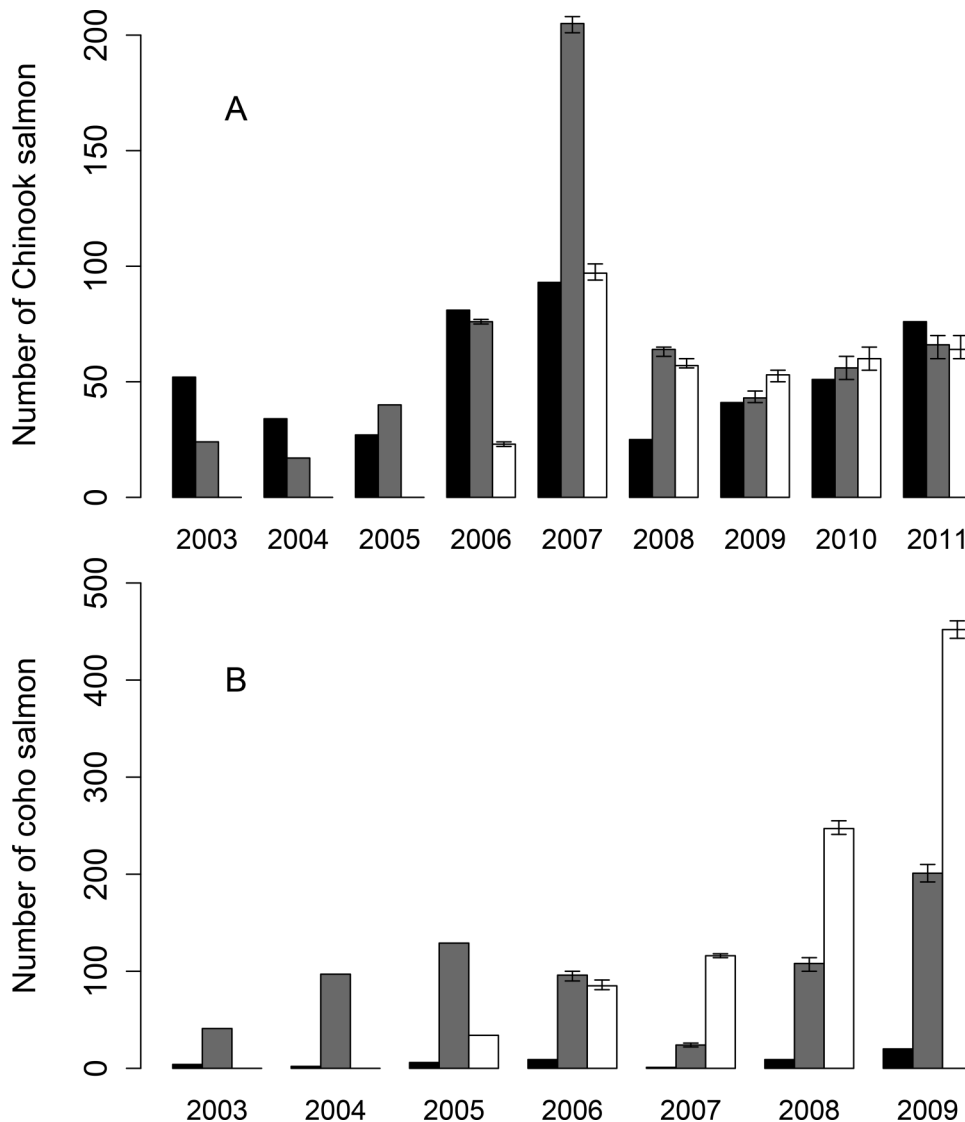
colonization (2003–2006) to the second generation (2007–2011) for Chinook salmon (Fig. 2).

We also evaluated the relationship between the abundance of potential source populations and the number of salmon strays bypassing the dam. Chinook salmon strays (hatchery and natural origin fish combined) were more numerous in years when more redds were observed below the dam (Fig. 3A); a quasi-Poisson generalized linear model (QGLM) indicated this trend was significant ( $F_{1,7} = 7.84$ ,  $p = 0.027$ , 51.7% null deviance explained). In neither

species was the number of hatchery origin strays related to the number of hatchery fish returning to the Issaquah Creek hatchery, the UW hatchery, or their sum (Figs. 3B and 3C; QGLM:  $p > 0.10$ ). As a fraction of the total return to the two Lake Washington basin hatcheries in each year for 2003–2009, a consistently larger percentage of Chinook than coho salmon strayed into the newly accessible habitat above the dam (Fig. 4).

The two species began to differ in the composition of the colonizing population in 2005, the first year in which recruits produced by salmon spawning above the dam were expected to return. In each year from 2005 to 2009, recruits were more abundant in coho than Chinook salmon, both in numbers and as a proportion of the entire run (Fig. 2). The number of recruits increased in each subsequent year for coho salmon, but not for Chinook salmon (Fig. 2). Chinook salmon strays outnumbered recruits in each return year, whereas coho salmon recruits were more than twice as abundant as strays in 2007–2009 (Fig. 2). Chinook salmon recruits outnumbered hatchery strays in 2007–2010 but not in 2011. Coho salmon tended to disperse farther upstream from the dam than Chinook salmon, although there was consid-

**Fig. 2.** Counts of (A) Chinook salmon and (B) coho salmon categorized as hatchery origin strays (black), natural origin strays (gray), and natural origin recruits (white) during colonization of newly accessible habitat. The error bars are maximum and minimum estimates due to uncertainty from parentage assignments based on a simulation procedure (see Methods for details).



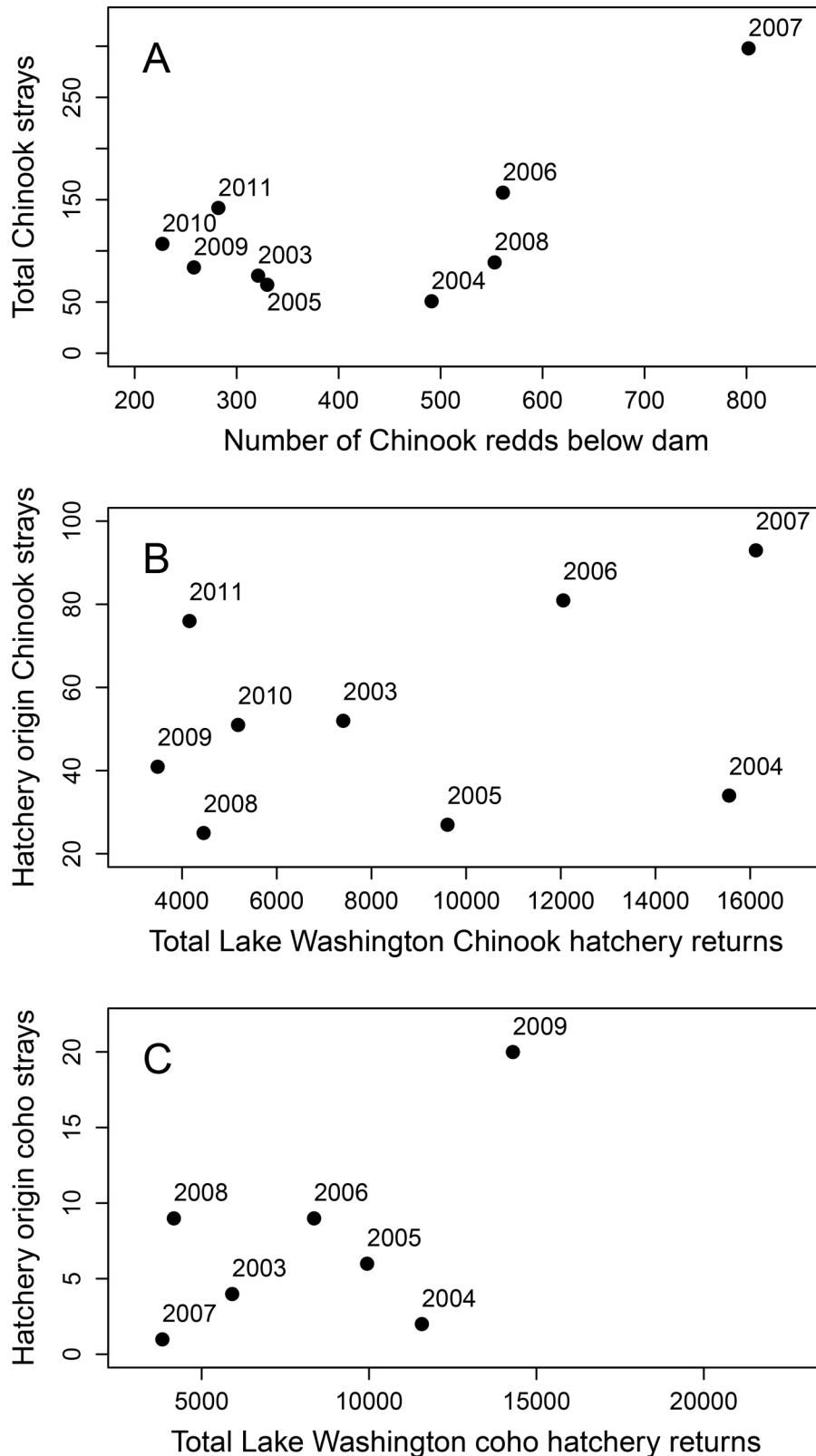
erable overlap in the spawning distributions of the two species (Fig. 5).

Some of the Chinook salmon sampled below the dam in 2006–2009 were produced by parents that spawned above the dam (Table 4). A binomial test of proportions indicated that the estimated fraction of fish produced above the dam was greater in the sample collected at the dam than in the sample collected below the dam from 2007 to 2009 (2007:  $p = 0.0014$ ; 2008:  $p < 0.0001$ ; 2009:  $p < 0.0001$ ) but not for 2006 ( $p > 0.10$ ). A binomial generalized linear model failed to detect an effect of return year on the proportion of the below dam samples originating above the dam ( $p > 0.10$ ), so samples were pooled across years to estimate the fraction of fish spawning below the dam whose parents had spawned above it in 2006–2009 ( $22/213 = 10.3\%$ ; Table 4). Although we did not collect samples from below the dam in 2010 or 2011, we assumed this same rate for these return years in estimating productivity.

Estimates of productivity provided strong evidence that the colonizing coho salmon population was self-sustaining, but the results for Chinook salmon were less clear. Coho salmon productivity

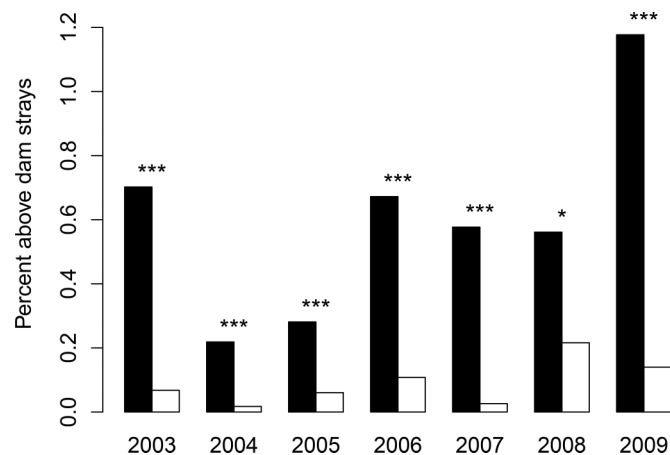
exceeded replacement in all four cohorts, and two cohorts (2003 and 2006) doubled from one generation to the next (Table 5). Coho salmon productivity exceeded Chinook salmon productivity in each year except 2004 (Table 5). Estimates of Chinook salmon productivity based on the samples collected at the dam exceeded replacement in only one (both sexes metric) or two (females only metric) of five cohorts (Table 5). However, expansion for the number of returning Chinook salmon produced above the dam that spawned below the dam substantially increased the estimated productivity and in some cases increased productivity above replacement (Table 5). Although the Chinook salmon produced above the dam but spawning below the dam were a small fraction ( $\sim 10.3\%$ ) of the total spawning below the dam, these samples expanded to a large above-dam recruit estimate because of the relatively large number of redds observed below the dam. Pooling the data from 5 brood years, inclusion of samples collected below the dam more than doubled the estimated numbers of recruits to the river as whole that had been produced above the dam (females only: 302 versus 108 sampled at the dam; males and females: 727 versus 328 sampled at the dam).

**Fig. 3.** Relationship between the estimated number of strays and the abundance of potential source populations. (A) Total Chinook salmon strays (both hatchery and natural origin) versus abundance of spawning nests (redds) in the lower Cedar River below the dam (quasi-Poisson generalized linear model:  $p = 0.027$ , 51.7% null deviance explained). (B) Hatchery origin Chinook salmon versus total Lake Washington basin hatchery returns (Issaquah Creek plus UW Portage Bay). (C) Hatchery origin coho salmon versus total Lake Washington basin hatchery returns.

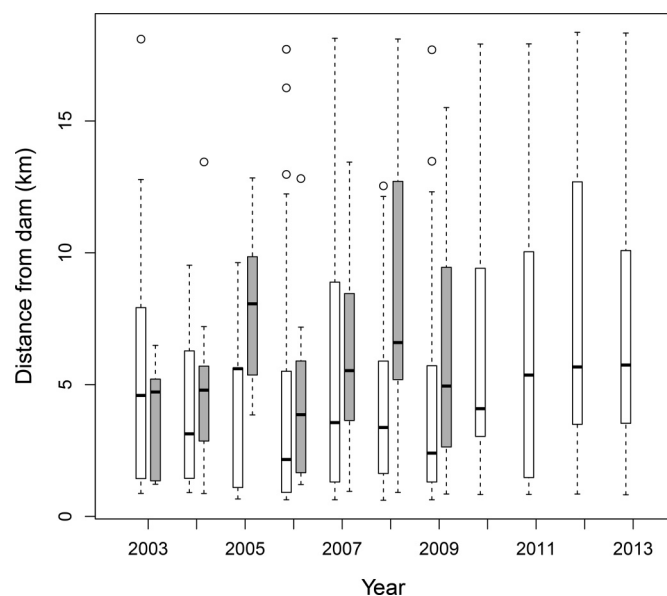




**Fig. 4.** Straying by hatchery Chinook salmon (black) and hatchery coho salmon (white), expressed as the ratio of hatchery salmon bypassing Landsburg Diversion Dam on the Cedar River to the total number returning to Lake Washington basin hatcheries (University of Washington plus Issaquah Creek). These numbers are an underestimate of the total hatchery stray rate because they do not include strays to other locations, but provide a robust comparison between species of colonization by hatchery fish. Asterisks denote  $p$  value from a binomial test of proportions: \*,  $p < 0.05$ ; \*\*\*,  $p < 0.001$ .



**Fig. 5.** Upstream dispersal distance (in river kilometres) of Chinook (white,  $N = 439$ ) and coho (gray,  $N = 252$ ) salmon spawning above Landsburg Diversion Dam in the Cedar River and tributaries based on redd surveys. Thick black lines represent the median, boxes are interquartile range, and remainder of data contained in whiskers and outlier circles. For both species, the majority of spawning sites were located in mainstem Cedar River (Chinook: 98%; coho: 89%) rather than tributaries (Chinook: 2%; coho: 11%). No systematic surveys were conducted for coho salmon in 2010–2013.



## Discussion

Despite the substantial expense of river restoration, such projects are rarely followed by population monitoring to evaluate their effectiveness in restoring the species of concern (Roni et al. 2008). Our study, therefore, provides unique documentation of the biological response following reconnection of isolated habitat, crucial information that will help inform future management

**Table 4.** Number of Chinook salmon samples collected below the dam and estimated number of these fish produced by parents that spawned above the dam.

Return year	No. sampled below dam	Produced above dam			
		Number		Percentage	
		Estimate	Range	Estimate	Range
2006	32	4	3–7	13%	9%–22%
2007	53	5	3–8	9%	6%–15%
2008	73	8	6–12	11%	8%–16%
2009	55	5	2–8	9%	4%–15%
Pooled	213	22	15–30	10%	7%–14%

**Note:** The range represents uncertainty due to parentage assignments based on a simulation procedure (see Methods for details).

of recolonizing populations. We report on two critical ecological processes during colonization, dispersal into the new habitat and productivity of initial colonizing cohorts, for sympatric coho and Chinook salmon populations. Our study design had two elements unique to recolonization studies. First, we had a count of adult colonists, data that would not be possible in many cases involving dam removal. Second, the DNA analysis distinguished strays from recruits produced above the dam during the second generation of colonization, providing precise estimates of productivity that are more informative than the typical time series of abundance.

In the Cedar River, coho and Chinook salmon dispersed into the newly accessible habitat under a passive management policy of natural recolonization. Strays were present in all years for both species and provided the basis for natural reproduction from the first generation onward. A key attribute of this study system was the naturally spawning populations of both species below the dam, the most likely source of the naturally spawned strays. The number of stray Chinook salmon was related to estimated abundance in the lower river, and this is the only breeding population of this species in the Cedar River watershed. Thus, in situations where a migration barrier is removed adjacent to a naturally reproducing, self-sustaining population of salmon, transplanting or hatchery supplementation does not appear necessary for population expansion. A primary goal for future research should be to determine how far colonizers will stray from their natal site in numbers sufficient to establish a new population and thus obviate the need for active reintroduction.

Demographic interaction between the population segment colonizing above the dam and its source below the dam continued beyond the initial years following barrier circumvention. Many salmon dispersed into the new habitat even during the second generation, when a portion of the run was produced above the dam. A much higher proportion of the Chinook than coho salmon ascending the fish ladder in 2006 and in subsequent years were strays rather than recruits (Fig. 2), indicating a higher recipient stray rate (sensu Keefer and Caudill 2014) for Chinook salmon. The number and dispersal distance of strays determines the spatial scale of genetic population structure (Neville et al. 2006), a prerequisite for local adaptation (Fraser et al. 2011). Although we had previously observed strong selection in both species (Anderson et al. 2010, 2013a), the evolution of traits adapted specifically to the environmental conditions above the dam will also depend on demographic independence.

We also observed straying in the opposite direction; a small proportion of the Chinook salmon samples collected below the dam were produced by parents spawning above the dam. These fish were estimated to represent a substantial fraction of the returning fish that had been produced above the dam (Table 5), though this required a large expansion from a small subsample and was thus subject to various sources of inaccuracy. Nevertheless, Chinook salmon produced above the dam composed a con-



**Table 5.** Productivity of initial Chinook and coho salmon cohorts colonizing the Cedar River above Landsburg Diversion Dam, Washington, USA.

Species	Year	No. of spawners		Recruits group	Estimated no. of recruits (range)		Estimated productivity (range)	
		Females	Both sexes		Females	Both sexes	Females	Both sexes
Chinook	2003	16	76	Above dam	10 (10–10)	33 (33–34)	0.6 (0.6–0.6)	0.4 (0.4–0.4)
				Above + below dam	36	86	2.3	1.1
	2004	22	51	Above dam	33 (33–33)	114 (111–116)	1.5 (1.5–1.5)	2.2 (2.2–2.3)
				Above + below dam	130	295	5.9	5.8
	2005	16	67	Above dam	18 (18–19)	54 (52–58)	1.1 (1.1–1.2)	0.8 (0.8–0.9)
				Above + below dam	40	122	2.5	1.8
	2006	32	180	Above dam	19 (19–20)	52 (50–56)	0.6 (0.6–0.6)	0.3 (0.3–0.3)
				Above + below dam	34	86	1.1	0.5
2007	99	395	Above dam	28 (28–31)	75 (71–81)	0.3 (0.3–0.3)	0.2 (0.2–0.2)	
			Above + below dam	62	138	0.6	0.3	
Coho	2003	20	45	Above dam	47 (43–50)	110 (105–115)	2.4 (2.2–2.5)	2.4 (2.3–2.6)
	2004	34	99	Above dam	45 (44–48)	108 (105–112)	1.3 (1.3–1.4)	1.1 (1.1–1.1)
	2005	66	169	Above dam	132 (129–137)	256 (251–263)	2.0 (2.0–2.1)	1.5 (1.5–1.6)
	2006	80	190	Above dam	196 (190–202)	456 (447–465)	2.5 (2.4–2.5)	2.4 (2.4–2.4)

**Note:** Range represents uncertainty due to parentage assignments based on a simulation procedure (see Methods for details). No range is presented for recruits from “above + below” dam group because we were unable to estimate sampling error (i.e., small percentage of carcasses collected from lower river spawners).

siderably higher fraction of the naturally spawned fish sampled at the dam than those sampled below the dam in 2006–2009 (Fig. 2; Table 4; at dam: 230/618 = 37%; below dam: 22/213 = 10%). In these years, the number of naturally spawned strays observed at the dam was a small fraction of the total number of naturally spawned salmon estimated below the dam, the most likely source of the strays. On the other hand, based on the expansion of samples collected below the dam, a large percentage of the fish originating from redds above the dam stopped in the lower river below the dam as adults. These observations suggest greater within river straying from upstream natal sites to downstream spawning locations than the opposite direction, similar to the results of Wagner (1969) and Hamann and Kennedy (2012).

We also suggest a role for habitat in the selection of spawning sites. The spatial distribution of Chinook salmon redds above the dam was largely similar among years, even in consecutive years when fish could not be returning to their natal redd site, suggesting that fish sought certain habitat attributes (Burton et al. 2013). Furthermore, some Chinook salmon spawned >10 km upstream of the dam at the very onset of colonization, and surveyors consistently observed very few spawning sites in the few kilometres immediately below the dam (Burton et al. 2013). Thus, demographic exchange in both directions was not exclusively dependent on dispersal distance. Similarly, Dittman et al. (2010) examined the spatial scale of Chinook salmon homing within the Yakima River basin, providing evidence that habitat requirements and other factors may override precise homing.

Another important conclusion was that a large proportion of the Chinook salmon strays originated in hatcheries, despite the long swimming distance between the dam and both hatcheries in the Lake Washington basin, neither of which are on the Cedar River. Indeed, the proportion of hatchery origin Chinook salmon sampled at the dam was consistently higher than that observed in the Cedar River below the dam (Burton et al. 2013). In our study, the higher proportion of hatchery origin Chinook salmon compared with coho salmon was especially surprising because it did not correspond to the numbers of fish produced by the basin’s two hatcheries (Fig. 4). Westley et al. (2013) also reported higher straying rates by ocean-type Chinook salmon compared with coho salmon in a series of Columbia River basin hatchery populations, but it is not clear whether these differences can be generalized for the species.

The lack of a relationship between the number of hatchery salmon at the dam and returns to either Lake Washington basin

hatchery suggests that factors other than source population abundance influenced the number of hatchery strays. Chinook salmon migrate earlier in the year and therefore encounter warmer temperatures than later migrating coho salmon, and this could contribute to the higher rate of straying by hatchery-produced Chinook salmon. Portions of the migration route to the Issaquah Creek hatchery, particularly the ship canal below Lake Washington and Sammamish River above it, are prone to high temperatures during the Chinook salmon migration period in late summer and early fall. Indeed, the Sammamish River is considerably warmer (mean temperature 2002–2013: August = 22.3 °C, September = 19.4 °C, October = 14.5 °C; King County gage 51 m) than the Cedar River (August = 15.7 °C, September = 13.6 °C, October = 11.0 °C; United States Geological Survey gage 12119000). Hatchery Chinook salmon may stray to the Cedar River seeking thermal refuge, whereas hatchery coho salmon arriving later (fall or winter) face no thermal stress. Additionally, Burton et al. (2013) recovered some adult Chinook salmon in the Cedar River that had been released from hatcheries outside the Lake Washington basin, so some of the hatchery fish captured at the dam may have been long distance dispersers.

Coho salmon productivity above the dam exceeded replacement in all years, supporting the hypothesis that salmon ascending the fish ladder in the second generation and beyond ( $\geq 2006$ ) represented self-sustaining natural production from the initial colonists. This resulted in a rapidly growing coho salmon population. Despite low initial densities, mechanisms commonly cited for depensation did not preclude successful colonization. For example, reduced probability of fertilization success at low densities owing to difficulty in finding a mate can cause depensation (Liermann and Hilborn 2001), but the high mobility of males in this population (Anderson and Quinn 2007) likely prevented this problem. A large predator population could also cause depensation, but this apparently did not occur; juvenile coho salmon dispersed widely, and as the years progressed they quickly approached densities comparable to well-established populations elsewhere (Pess et al. 2011; Anderson et al. 2013b). In general, salmon populations are highly productive at low densities because they are released from competition for breeding sites and, in the case of coho and to a lesser extent ocean-type Chinook salmon, competition for rearing space in streams (Quinn 2005).

In contrast with coho salmon, estimates of Chinook productivity based on samples collected at the dam were considerably below replacement in three of five cohorts. Not only were coho

salmon more productive, but they also mature at younger ages than Chinook salmon (2–3 versus 2–5). As a result, in return years 2007–2009, the coho salmon population was dominated by recruits, whereas the Chinook salmon population was composed primarily of strays (natural plus hatchery). At least in this case, the rate of colonization was faster for coho than Chinook salmon.

However, inclusion of the Chinook salmon samples collected below the dam resulted in productivity estimates that exceeded replacement for the 2003 and 2006 female cohorts (Table 5). Despite the aforementioned uncertainty with extrapolation, it was clear that salmon that spawned in the newly accessible habitat above the dam increased abundances below the dam. A recruitment “spillover effect” has been observed in other conservation contexts such as enhancement of fisheries adjacent to marine reserves (Gell and Roberts 2003).

We had no direct comparison of Chinook salmon productivity above versus below the dam using identical genetic methods. However, one might hypothesize greater freshwater productivity (i.e., smolts per spawner) of salmon spawning above the dam relative to below it based on large-scale differences in land use and hence habitat quality. The area above the dam is managed as de facto reserve, whereas the watershed below the dam is characterized by suburban development. Consistent with this idea, we note that within the entire river, the proportion of redds observed above the dam has increased through time (Burton et al. 2013).

What factors might account for the lower productivity, measured as recruitment back to the habitat above the dam, of Chinook salmon? We provide several plausible explanations, which are not mutually exclusive. Recent studies have demonstrated greater stray rates for Chinook salmon compared with coho salmon (Westley et al. 2013; Keefer and Caudill 2014; Fig. 4, this study). It is possible that finer scale homing fidelity by coho salmon increased the likelihood that recruits surviving to adulthood returned to the dam, where they would be sampled and included in our metric of productivity. In this case, homing to incubation sites above the dam rather than anywhere within the Cedar River would accelerate numerical growth within the newly accessible habitat. When interpreted in the context of metapopulation source–sink dynamics (Anderson et al. 2014), the above dam Chinook salmon productivities may simply indicate greater exchange with the population segment below the dam rather than recruitment failure.

Additional ecological and evolutionary factors may also have affected the relative productivity of Chinook salmon and coho salmon in this system. First, Chinook salmon may have suffered greater early life mortality because they were exposed to a large and diverse population of predators in Lake Washington and Puget Sound at a younger age, and hence a smaller size, than juvenile coho salmon. A large fraction of freshwater mortality occurred during seaward migration (Pess et al. 2011), and juvenile ocean-type Chinook typically migrate at age-0 compared with age-1 for coho salmon. Although Chinook and coho salmon spawned in largely similar reaches of the river above the dam (Fig. 5), we observed considerable dispersal by juvenile coho salmon during the period of freshwater residence (Anderson et al. 2013b). These movements may have increased growth opportunities for individual coho salmon and hence reduced vulnerability to size-selective predation. Tabor et al. (2007) found much higher levels of predation on subyearling salmonids compared with yearling salmonids, although they concluded that two predators, smallmouth bass (*Micropterus dolomieu*) and largemouth bass (*Micropterus salmoides*), have a relatively minor impact on the Lake Washington salmonid populations. In the marine environment, coho salmon typically survive at a higher rate than Chinook salmon (Quinn et al. 2005; Weitkamp et al. 2014). Another ecological mechanism might be differential vulnerability to redd scour (e.g., Montgomery et al. 1996); because of their earlier spawning timing, a much greater

fraction of Chinook salmon embryos are deposited prior to the November–December flood season compared with coho salmon.

Second, greater straying of hatchery Chinook relative to hatchery coho salmon (Table 1) may have contributed to their lower productivity. Hatchery breeding can reduce the fitness of salmonid populations for life in the wild (Araki et al. 2008; Williamson et al. 2010), and these effects can occur in a single generation via domestication selection (Christie et al. 2012). We previously found that hatchery male (but not female) Chinook salmon had consistently lower reproductive success than naturally spawned salmon, though this difference was not statistically significant (Anderson et al. 2013a). In addition, the small degree of genetic differentiation between hatchery and natural origin Chinook in this system suggests many of the unmarked “wild” fish had recent hatchery ancestry (Anderson et al. 2013a). Gene flow from the captive breeding environment into the wild, in both the past and present, may have created a Chinook salmon source population below the dam that is less fit for the natural conditions encountered above the dam than the coho salmon.

It is also important to emphasize that the estimates of productivity are very conservative because the salmon were sampled and counted after commercial, tribal, and recreational harvest. Recent estimates of Chinook salmon harvest were approximately 35%–45% (PSIT and WDFW 2010), and coho salmon harvest rates ranged from 32.0% to 61.1% for the relevant return years (M. Zimmerman, WDFW, personal communication, 2011). Thus, for both species, true biologically based productivity estimates would be substantially greater than those presented here. For Chinook salmon, when combined with the estimates of above to below dam demographic exchange, these observations provide a substantially more optimistic perspective on the success of the restoration project than considering the counts or samples from the dam in isolation.

For salmon in the Pacific Northwest, improving habitat connectivity is an increasingly common conservation strategy. In such cases, an important question is whether active reintroduction strategies such as hatchery supplementation should follow barrier removal or if fish should be allowed to colonize on their own volition. Our results demonstrated that salmon immediately took advantage of stream reaches made accessible by restoration. Under a passive management strategy of natural colonization, salmon entered the newly accessible habitat without direct human assistance. These initial colonists, especially the coho salmon, were remarkably successful, suggesting that removal or circumvention of barriers throughout the Pacific Northwest offer promising opportunities for conservation and recovery of anadromous salmonids. These results are also consistent with the rapid recolonization of the upper Fraser River system by pink salmon (*Oncorhynchus gorbuscha*) after passage facilities were established at Hell’s Gate (Pess et al. 2012). In that case, a large source population and highly suitable habitat above the former barrier seemed to be responsible for the success.

Allowing natural colonization maintains important ecological and evolutionary processes of population establishment that would be disrupted by more active strategies such as transplanting or hatchery releases. For example, hatchery releases may reduce the genetic fitness of wild salmon (Araki et al. 2008) or induce density-dependent ecological processes affecting naturally spawning fish (Kostow 2009). Although natural colonization may not be effective if the reintroduction site is isolated from potential sources, it minimizes risks that could have long-term consequences for colonizing populations (Anderson et al. 2014). On the Cedar River, there was some hatchery influence owing to straying by artificially propagated adult Chinook salmon. However, an active reintroduction strategy considered for this population, stocking of juvenile hatchery-produced Chinook salmon above the dam, would have increased the genetic and ecological risks to viability.

We therefore suggest a fundamentally different approach to reintroduction of anadromous fish than the strategies typically

employed for other species. Whereas most birds and mammals are actively relocated to the reintroduction site (Wolf et al. 1996; Fischer and Lindenmayer 2000), removing or circumventing movement barriers may be the only necessary action for migratory freshwater fish with high dispersal potential. Due in large part to impassable dams, anadromous fishes are in jeopardy in many areas around the globe (Limburg and Waldman 2009). The widespread movements of anadromous species such as striped bass (*Morone saxatilis*), shad (*Alosa* spp.), smelt (*Osmerus* spp.), lamprey (Petromyzontidae), and sturgeon (*Acipenser* spp.) demonstrate their capability of exploiting opportunities to recolonize spawning habitat (Burdick and Hightower 2006; Fernandes et al. 2010; Pess et al. 2014), similar to the salmon in our study.

## Acknowledgements

We thank J. McDowell for sampling and D. Chapin, D. Paige, H. Barnett, R. Little, and B. Bachen for their support of recolonization research on the Cedar River. M. Baird, I. Jimenez-Hidalgo, and L. Newton provided substantial help in the laboratory. This work was funded in part by a grant from Washington Sea Grant, University of Washington, pursuant to National Oceanic and Atmospheric Administration Award Nos. NA04OAR4170032 and NA07OAR4170007, Project Nos. R/F-148 and R/F-159, respectively. Additional funding was provided by Seattle Public Utilities, the H. Mason Keeler Endowment, and King Conservation District. K. Naish, J. Olden, P. Kiffney, J. Marzluff, and three anonymous reviewers gave helpful suggestions on earlier versions of the manuscript.

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