Received: 8 April 2020 | Revised: 19 October 2020 | Accepted: 21 October 2020

DOI: 10.1002/rra.3748

RESEARCH ARTICLE

WILEY

Population effect of a large-scale stream restoration effort on Chinook salmon in the Pahsimeroi River, Idaho

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Funding information
Bonneville Power Administration

Abstract

Stream habitat restoration is an important tool for fisheries management in impaired lotic systems. Although small-scale benefits of stream habitat restoration are commonly investigated, it is difficult to demonstrate population effects. The Pahsimeroi River Chinook salmon *Oncorhynchus tshawytscha* population was previously restricted to the lower portion of the river by multiple irrigation structures. To address fish passage issues, a combination of restoration projects was initiated including barrier removals, instream flow enhancements and installation of fish screens on diversions. The largest barrier was removed in 2009, more than doubling the amount of accessible linear habitat. We hypothesized restoration efforts would expand the distribution of spawning salmon in the Pahsimeroi River watershed, leading to a broader distribution of juveniles. We also hypothesized a broader juvenile distribution would have population effects by reducing the prevalence of density-dependent growth and survival. Redds were documented in newly accessible habitat immediately following barrier removal and accounted for a median of 42% of all redds in the Pahsimeroi River watershed during 2009–2015. Snorkel surveys also documented juvenile rearing in newly accessible habitat. Juvenile productivity increased from a median of 64 smolts/female spawner for brood years 2002–2008 to 99 smolts/female spawner for brood years 2009–2014. Overall, results suggested increased habitat accessibility in the Pahsimeroi River broadened the distribution of spawning adult and rearing juvenile salmon and reduced the effects of density-dependent survival. Large-scale stream restoration efforts can have a population effect. Despite the large-scale effort and response, habitat restoration alone is likely not sufficient to restore this population.

KEYWORDS

barrier removal, population effect, restoration, salmon, stream habitat

1 | INTRODUCTION

Demonstrating the benefits of stream habitat restoration to fish populations has proven difficult. Several studies have questioned the benefits of habitat restoration measures (e.g., Bernhardt & Palmer, 2011) or found equivocal evidence (Roni, Hanson, & Beechie, 2008; Stewart, Bayliss, Showler, Sutherland, & Pullin, 2009). Not only are riverine environments physically and ecologically complex, but our knowledge of how fish interact with their physical habitat also remains uncertain. Rivers and fish populations are subject to multiple confounding factors such as varying environmental conditions, anthropogenic alterations and climate change. Anadromous salmonids have complex life histories crossing freshwater and oceanic habitats and have generation times that take several years to complete (Quinn, 2005; Webb, Verspoor, Aubin-Horth, Romakkaniemi, & Amiro, 2007). The combination of ecological variability with the scale at which management is focused (watershed or population) means that proper assessments are difficult and time-consuming.

Another potential problem is restoration tends to be incremental and at smaller scales than the degradation that occurred (Bernhardt & Palmer, 2011; Bond & Lake, 2003; Kondolf et al., 2008). At least 20% of a watershed needed to be restored in order to see a 25% increase in salmon smolt production (Roni, Pess, Beechie, & Morley, 2010). Restoration programmes should consider cumulative effects (Kondolf et al., 2008). Therefore, a large or coordinated group of projects are more likely to be successful than smaller ones (Lake, Bond, & Reich, 2007; Ogston, Gidora, Foy, & Rosenfeld, 2015). For example, Hood (2007) showed more benefit should be derived from restoring a single 100-ha channel in an estuary than 10 1-ha channels. Much of the foregoing work was conceptual and the conclusions need verification. In one case, extensive restoration of off-channel floodplain habitat ($\sim$157,000 m^2) contributed 27%–34% of the overall smolt production (Ogston et al., 2015). Self-sustaining pink salmon *Oncorhynchus gorbuscha* populations in the Fraser River developed within years of the Hell's Gate barrier removal (Pess, Hilborn, Kloehn, & Quinn, 2012). These examples show that larger-scale restoration should produce benefits that accrue to populations, not merely to individuals inhabiting a few reaches within a larger demographic unit.

Restoration at larger scales presents problems for monitoring and detecting a real response, even given sufficiently large restoration. The likelihood of confounding influences increases with scale, as do logistical costs of investigations (Hewitt, Thrush, Dayton, & Bonsdorff, 2007). Additionally, as scale increases it becomes harder to find valid reference systems to account for environmental effects confounded temporally with restoration treatments. Evaluations usually assume trajectories of control and reference systems would be parallel in the absence of intervention (Murtaugh, 2000; Stewart-Oaten & Bence, 2001); hence, increasing scale comes with the risk of confounding factors. The intensively monitored watershed approach addresses some of these issues (Bennett et al., 2016) but such intensive work is expensive and most intensively monitored watersheds do not encompass entire salmon populations.

The Pahsimeroi River in central Idaho is a good case study in which to test the benefits of restoration efforts, and understand the effect of restoration scale on an anadromous fish population. The Chinook salmon *O. tshawytscha* population inhabiting the river was confined to the lower portion of the main stem and is considered a key to the recovery of the Snake River spring/summer Chinook salmon Evolutionarily Significant Unit (National Marine Fisheries Service, 2017). The population shows signs of density-dependent effects on juvenile growth and survival (Walters, Copeland, & Venditti, 2013). Recent restoration projects greatly increased the length of river accessible to salmon. The presence of a robust monitoring programme near the downstream extent of spawning allows for examination of the effects of the restoration on the salmon population.

The goal of the Pahsimeroi River restoration effort is to increase production of juvenile salmon, in total and on a per capita basis, by relieving the density-dependent constraints observed in this population. We hypothesized the large increase in accessible stream length and increased instream flow in the Pahsimeroi River would elicit a detectable population effect. Furthermore, we hypothesized increasing salmon spawning and rearing distribution would alleviate density-dependent effects. The evaluation had two stages: (1) examination of salmon redd and juvenile distributions over the last 14 years to establish that newly accessible reaches were being used, and (2) comparison of abundance and productivity rate (juveniles per female spawner) of the salmon emigrating from the Pahsimeroi River before and after restoration with reference to selected nearby salmon populations.

2 | METHODS

2.1 | Study area

The Pahsimeroi River is a tributary to the Salmon River, within the Snake River basin in central Idaho (Figure 1), and once supported a substantial Chinook salmon population (Good, Waples, & Adams, 2005; Parkhurst, 1950). The river lies in a dry intermontane sagebrush valley, with the mouth at approximately 1,500-m elevation. Perennial flow in the main stem formerly began approximately 60 river kilometres (rkm) upstream from the mouth (Meinzer, 1924). The earliest water rights date to the 1880s and over time extensive water withdrawals reduced salmon production (Parkhurst, 1950). Historically, irrigation diversions disconnected most tributaries and flow was often intermittent in upper parts of the basin. In some reaches, lack of flow led to simplification of riparian and instream habitats. A substantial portion of the diverted water returns to the river via large springs near the confluence with Patterson Creek, such that the lower Pahsimeroi River had substantial flow year-round (Williams, McNamara, & Whittier, 2006). In recent decades, Chinook salmon occupied only the lower portion of the Pahsimeroi River. Within this reach, the river is a low-gradient stream dominated by groundwater inputs, which moderates flow and temperature (Trapani, 2002). The channel is sinuous and well developed, with a large proportion of pools (Idaho Department of Fish and Game [IDFG], unpublished data). High water

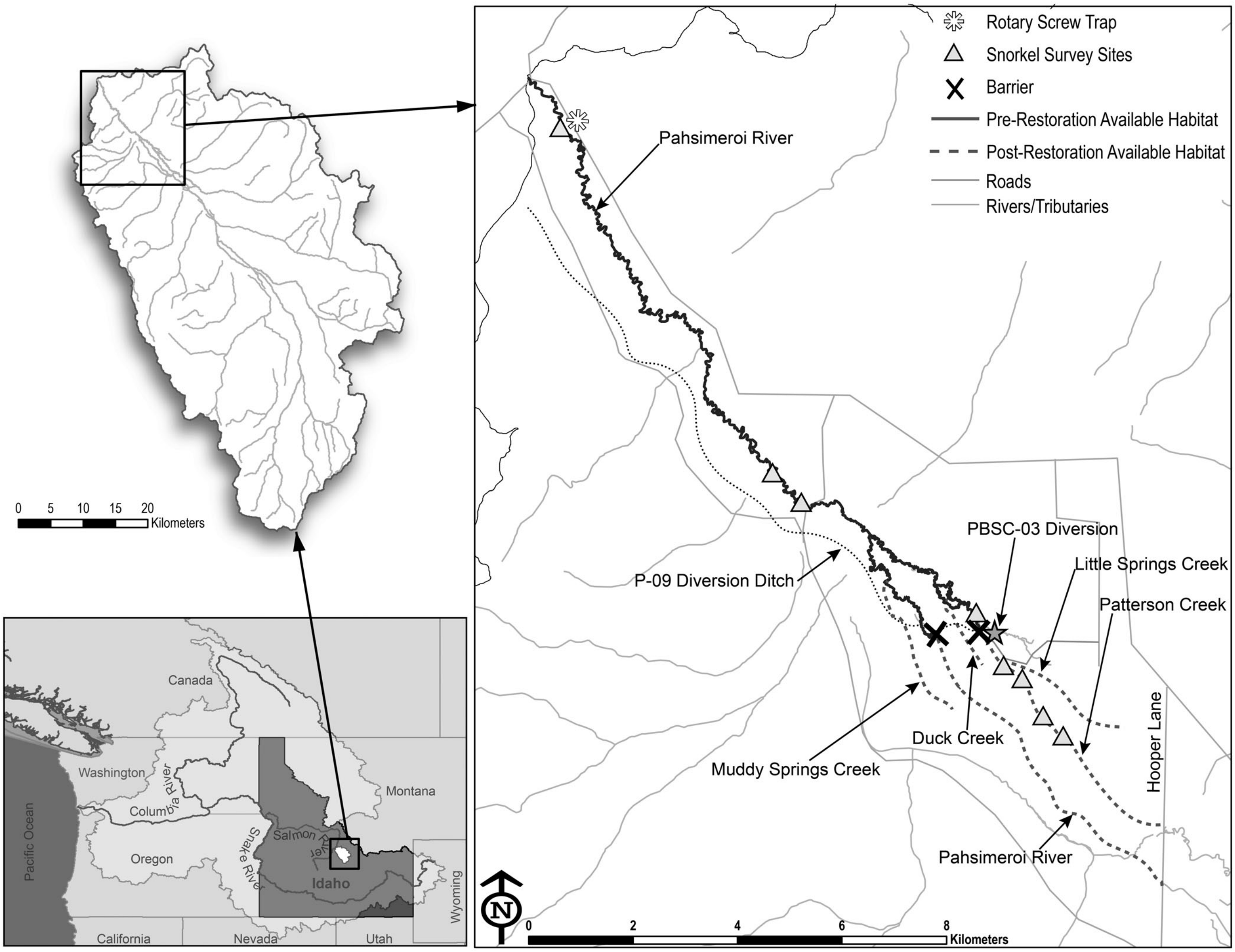

FIGURE 1 Map of the study area showing reaches accessible to salmon before and after restoration, locations of snorkel survey sites and the rotary screw trap. The insets show the location of the study area in the Pahsimeroi River drainage and in the Pacific Northwest U.S. Flow in the Pahsimeroi River is toward the northwest

clarity in this reach promotes growth of rooted macrophytes. Monthly mean discharge at the mouth ranged from 4 to 7 m^3/s.

The population of Chinook salmon spawning in the Pahsimeroi River is classified as summer-run, based on timing of adult entry into fresh water. Spawning occurs from mid to late September, after which the adults die. The population is part of the Snake River spring/summer Chinook salmon Evolutionarily Significant Unit, listed as Threatened under the Endangered Species Act (National Oceanic and Atmospheric Administration, 1992). All Snake River spring/summer Chinook salmon are considered to have an extended freshwater rearing phase and enter the ocean as yearlings (Good et al., 2005). After completing the freshwater phase, juvenile emigrants pass Lower Granite Dam, approximately 620 rkm from the mouth of the Pahsimeroi River, and another seven dams before reaching the Pacific Ocean, a journey of 1,314 rkm. The adults must navigate this course in reverse.

A hatchery operates on the Pahsimeroi River with a weir 1.5 km upstream from the mouth. All hatchery-produced juveniles were marked and excluded from this study. During the spawning run, marked adults were removed from the river at the weir, while unmarked fish were allowed to continue upstream. In some years, adult hatchery salmon were placed upstream of the weir intentionally for the purposes of supplementing the spawning population.

2.2 | Habitat restoration

Several irrigation structures constrained access for salmon to the upper parts of the Pahsimeroi River and its largest tributary, Patterson Creek (Figure 1). Patterson Creek flows into the Pahsimeroi River at rkm 19.6. Upstream access was blocked in the Pahsimeroi River at the P-09 diversion, 3.3 rkm upstream from the confluence with Patterson Creek, and in Patterson Creek by the PBSC-03 diversion 6.0 rkm upstream of its mouth. The two diversions were likely complete upstream barriers to juvenile salmonids. An irrigation ditch 0.5 rkm downstream of PBSC-03 also diverted water from Patterson Creek that flowed to the P-09 structure on the Pahsimeroi River and then on to distant fields (P-09 diversion ditch). Because the diversions diverted a significant proportion of water, they often created reaches of shallow water that greatly inhibited adult salmon from approaching and passing them. The P-09 diversion ditch also cut off three minor spring-fed tributaries (Duck Creek, Muddy Springs Creek and Little Springs Creek), taking their flow as well.

A group of local stakeholders developed a comprehensive restoration effort involving water rights transfers and barrier removals. The effort began in 1994 and was completed in 2009. In one case, water rights were transferred out of the P-09 diversion to the main stem of the Salmon River. In another, some irrigators converted strictly to sprinkler irrigation, resulting in water savings and the removal of four diversions. These projects were also the impetus for the removal of several additional instream barriers and improved instream flows upstream of the P-09 diversion (approximately 2.12 m^3/s). The final component of the project was removal of the P-09 diversion and reconfiguration of the PBSC-03 diversion to reconnect Patterson Creek during irrigation season and winter. This action created access for salmon in the Pahsimeroi River and Patterson Creek upstream to Hooper Lane beginning in 2009 (Figure 1). The P-09 diversion ditch conveyances across the three minor tributaries were also removed, adding flows and rearing habitat.

Habitat quality in the study area varied before restoration. The lower reach of Patterson Creek had flows driven by groundwater and complex pool habitats composed of macrophytes and willow clumps in the stream channel. Pahsimeroi River upstream of the barrier was intermittent, less influenced by groundwater and had less instream complexity. Habitat in the Pahsimeroi River downstream of the barrier was similar to Patterson Creek but with more flow and greater pool depths.

We measured accessible stream length (rkm) before and after the 2009 restoration. Our objective was to determine the change in distribution patterns; therefore, we used a linear measurement. We used National Agriculture Imagery Program aerial imagery in ESRI ArcMap software (version 10.3.1). Prior to restoration, salmon could access 22.9 rkm on the Pahsimeroi River (mouth upstream to the P-09 diversion), and 3.3 rkm on Patterson Creek (confluence with the Pahsimeroi River to irrigation diversion PBSC-03). After removal of the P-09 diversion ditch and remediation of the diversion structures, salmon could access 38.0 rkm on the Pahsimeroi River (mouth to Hooper Lane), 16.3 rkm on Patterson Creek (confluence with the Pahsimeroi River to Hooper Lane), as well as 10.2 rkm of potential rearing habitat in Duck, Muddy Springs and Little Springs creeks. Thus, the linear accessible rearing habitat increased by 246%.

2.3 | Data collection

Venditti et al. (2018) annually assessed spawning adult salmon with multiple-pass redd surveys. Redds are nests constructed in the stream gravel and are a surrogate for the number of eggs spawned. Trained observers walked the stream at least three times between early September and early October, scanning the stream substrate using polarized sunglasses. Because of the water clarity associated with groundwater flows, fresh redds were usually easy to identify. A short reach was closed to ground access; this reach was surveyed by helicopter near the end of spawning. Locations of redds were recorded using a global positioning system.

We used snorkel surveys at selected sites to index distribution and density of juvenile salmon (Apperson, Copeland, Flinders, Kennedy, & Roberts, 2015). The intent of the snorkel surveys was to track changes in fish density at selected sites. Three sites had been established within the connected reach in the 1990s for this purpose, were surveyed during this study, and we used those data. We established five sites within the restored reach in Patterson Creek and began annual surveys in 2008. Sites in the restored reach were selected systematically on accessible private property. The lower reach of Patterson Creek was chosen because it had enough flow prior to restoration to support fish. The first two sites were selected to bracket the PBSC-03 structure. Spacing varied as site locations were adjusted for access and to hydraulic controls, which act as the bounds for each site. Observers snorkelled slowly upstream, counting all juvenile salmonids observed. We used counts as minimum abundance estimates with no correction for probability of detection. However, snorkel surveys yield repeatable counts well correlated with other abundance estimates (Hankin & Reeves, 1988; Thurow, 1994). The high water clarity in the study reaches enhanced the ability to identify and count fish. Snorkel sites were approximately 100 m in length, and performed consistently every year between early- to mid-July. Because we consistently surveyed the same sites, at the same time of year, using crews trained to the same protocol, we could effectively track changes in fish density.

Emigrating juveniles were collected by a rotary screw trap located 1.5 rkm upstream from the river mouth (Figure 1). Over 99% of the spawning habitat in the drainage is upstream from the trap. The river is 12-m wide at the trap. The diameter of the rotating cone on the trap is 1.5 m. Depth at the trap varied from 0.6 to 1.2 m with flow but was consistently around 1.0 m. Technicians deployed the trap as early as possible in the spring, usually the last week of February or the first week of March, and operated it until the first week of December. They enumerated and processed captured fish at least once daily. All fish were measured for fork length (FL; mm), and scanned for a passive integrated transponder (PIT) tag. Fish ≥60 mm FL were tagged if they did not already have a tag (see tagging procedures below). After processing, all PIT-tagged fish were placed in a perforated container 0.4 km upstream from the trap and released at dusk. We calculated efficiency of the trap from recaptures of PIT-tagged fish. Technicians placed recaptured fish and any individuals not tagged in a second live box immediately below the trap and released them at dusk.

Tagging procedures followed recommendations of the PIT Tag Steering Committee (2014). Technicians injected tags into the fish's body cavity using a hypodermic needle. Needles and tags were sterilized in 70% ethanol for 10 min. All age-1 smolts were tagged (spring season only). All other groups were tagged at a rate determined by the expected number of emigrants and available tags. Technicians recorded tagging data into a computer file each day and uploaded it to the central repository for all PIT-tagging activities in the Columbia River basin (www.ptagis.org) within 48 h. Data entry and transcription errors were reduced by computerized data capture in the field using standardized routines (PIT Tag Steering Committee, 2014).

We estimated abundance of emigrants leaving the Pahsimeroi River using mark-recapture methods developed by Steinhorst, Wu, Dennis, and Kline (2004). Data were partitioned primarily by developmental stage of juveniles at the trap, and secondarily by changes in flow, subject to the constraint that at least seven recaptures occurred during each time stratum. Stages are defined as spring young-of-year (through the end of June), summer (until September), fall (until trap removal) and spring yearlings. Cohorts overlap in time only during the spring and were easily separable by length. Secondary stratification was based on efficiency changes with flow as evidenced by a persistent change in the recapture rates. Flows were moderated by the groundwater-dominated hydrology and the irrigation system, so changes in trap efficiency were not frequent. Population abundance of all emigrants from a cohort was estimated using a summation of Bailey's modified estimator (Ricker, 1975). The estimator was computed using an iterative maximization of the log likelihood, assuming fish were captured independently and tagged fish mixed thoroughly with untagged fish. The estimating model produced estimates with standard errors for the cohort total and for individual strata.

We estimated emigrant survival from the detection of PIT-tagged individuals in the lower Snake and Columbia rivers. For this study, emigrants were considered successful if they passed Lower Granite Dam because we have no records indicating Pahsimeroi River salmon use reaches downstream from the dam for rearing. Daily detection records were obtained by querying the database (www.ptagis.org) for all observations of fish tagged at the Pahsimeroi River trap. We estimated survival and detection probability at the dam using a Cormack–Jolly–Seber model implemented with software by Lady, Westhagen, and Skalski (2013). We grouped fish for analysis by season of passage and length (subyearling smolts, summer parr, fall parr, yearling smolts; see definitions and explanations in Copeland & Venditti, 2009) because survival to Lower Granite Dam differed among these groups.

2.4 | Data analysis

Our analytical strategy was to assess the performance of seven cohorts of salmon prior to and seven cohorts after restoration. Pre-restoration cohorts were fish that were spawned during 2002–2008. These fish emerged the following year, were available to snorkel surveys that summer, and had completely emigrated from the study area by the end of their second spring (e.g., by spring 2010 for brood year [BY] 2008). The cohorts of fish influenced by restoration spanned an identical time frame: spawned during 2009–2015 and finished emigration by the end of spring 2017. We based inferences of restoration effects on equal groups of cohorts to maximize statistical power. Sample sizes were small, so we used non-parametric statistics to reduce the effects of extreme values (Zar, 1999). Number of statistical tests performed was kept low to control experiment-wise error.

The first question we addressed was, how had restoration affected spawning distribution? To visualize spawning distribution, we binned annual redd counts into 2-km segments starting at the mouth of the Pahsimeroi River. Distributions were standardized by dividing number in each bin by the total redd count for the year to compare years of differing abundance. We plotted median proportion in the pre-restoration and restoration periods by bin with the interquartile range to show inter-annual variability. We also summarized the proportion of redds upstream of the P-09 and PBSC-03 diversions. The median abundances of redds were compared between treatment phases with the Mann–Whitney test (Zar, 1999). We used a one-tailed test for the hypothesis that abundance should be higher following initiation of the restoration programme.

We also investigated changes in distribution and density of Chinook salmon juveniles. Pre-restoration surveys in treatment reaches occurred during the summers of 2008–2009. The restoration period encompassed surveys completed during 2010–2016. The three sites in the connected reach served as controls. However, none were surveyed in 2011 and only one in 2016 (21 observations). The treatment area was represented by the five sites in the reconnected reach in Patterson Creek. Densities were expressed as number of fish observed per 100 m^2. We summarized the data as median and interquartile range. We considered overlap of interquartile ranges between periods to indicate lack of a meaningful change. Because site locations did not change, water clarity was high and flows at the time of survey were consistent among years, observation bias was controlled. The effect of a non-systematic, varying observational efficiency would be to obscure real trends, so this analysis was conservative.

We used regression analysis to evaluate changes in the relationship between density and growth (Isley & Grabowski, 2007). Lengths were measured at the rotary screw trap, as described above. Mean length at a given life stage was treated as an index of growth and number of redds as an index of initial brood year density. We performed separate regressions for two life stages: fall parr and yearling smolt. The regression model had period (pre- and post-restoration) as a fixed effect and an interaction between female spawners (F) and period (p):

$$L = F + p + F * p.$$

The interaction term was the parameter of interest as it represented the effect of habitat restoration when controlling for initial density (see Smith, 2002).

The restoration goal is the production of more juvenile salmon from the spawning and rearing reaches in the Pahsimeroi River towards the Pacific Ocean, in total and on a per capita basis (i.e., productivity). We measured cohort abundance at the rotary screw trap and at Lower Granite Dam by brood year. Because of the widely varying spawning abundances during both periods, we examined productivity by dividing cohort abundance by the number of females passed over the weir to produce each cohort. Thus we examined abundance of juvenile emigrants at the rotary screw trap, smolts at Lower Granite Dam, as well as productivity expressed as emigrants/female and smolts/female. Each period was summarized using medians. We used the Mann–Whitney test to infer whether the distributions of values changed between treatment phases (Zar, 1999). We used a one-tailed test for the hypothesis that abundance and productivity should be higher following initiation of the restoration programme. The probability of seeing a higher value of the Mann–Whitney *U* statistic by random chance was determined by linear interpolation between critical values given by Zar (1999).

To evaluate the potential for spurious effects, we compared smolt productivity from the Pahsimeroi population to four other populations in the Salmon River basin. The Pahsimeroi population is subject to two different management tactics: habitat restoration and supplementation with hatchery fish. The population in the upper reaches of the Salmon River (upstream of Sawtooth Hatchery weir) and the South Fork Salmon River (upstream of the McCall Hatchery weir) have very similar supplementation histories (Venditti et al., 2018), so we used emigrant data and number of females passed from those populations. The neighbouring population in the Lemhi River has not been supplemented but is subject to a large habitat restoration programme, providing another perspective on the effects of restoration (Uthe et al., 2017). Lastly, we used the Marsh Creek population as a control because there are no hatchery releases or habitat restoration programmes there; Marsh Creek is managed as a wild fish refuge with downstream habitat in wilderness. Redd counts from Lemhi River and Marsh Creek are used as surrogates for number of females spawning because of the lack of weirs in those streams. The data sets are contemporaneous except that the data series for South Fork Salmon River and Marsh Creek ended with BY 2013. Given the differences among these areas in geology, elevation and hydrology (Servheen et al., 2004), we use these data in a weight-of-evidence approach rather than within a formal statistical framework.

3 | RESULTS

Redd counts in the Pahsimeroi River were similar between periods (Figure 2). Median count during 2002–2008 was 124 redds, ranging from 47 redds to 355 redds. Median count during 2009–2016 was 101 redds, ranging from 68 redds to 265 redds. The median number of redds counted was not significantly different between periods (Mann–Whitney $U = 24$, $p < .10$). Spawning distribution expanded during the restoration period (Figure 3). During 2002–2008, redds were clustered near upper end of accessible reach. Following remediation of the P-09 diversion, fish immediately used the newly opened reach (see Figure 3, inset). Upstream expansion occurred in Patterson Creek and Pahsimeroi River, but most redds tended to be in Patterson Creek. Spawning was more evenly distributed during the restoration phase such that a median of 42% of the Chinook salmon redds in the population were in the reconnected reaches. Chinook salmon redd distribution post-restoration did not exhibit the strong peak downstream of the P-09 diversion observed pre-restoration (Figure 3).

Parr distribution changed between periods (Figure 4). During 2008–2009, four Chinook parr (two per year) were observed upstream of the PBSC-03 diversion but many were observed afterward restoration. However, densities in the newly opened reach (median of annual medians 2010–2016 = 7.2 fish/100 m^2) were about a third of those observed in the downstream sites. In the previously accessible reach, densities were high in both periods: medians were 29.8 and 22.8 fish/100 m^2, for pre-restoration and restoration periods, respectively. The interquartile ranges were very similar between periods at each downstream site. Densities in the newly opened reach are well-correlated with the number of redds found in that reach the previous year ($r = 0.56$); whereas, the opposite is true of densities in the previously accessible reach ($r = -0.28$) during the same years. We infer movement of redds upstream beginning with BY2009 did not decrease parr density in downstream habitats.

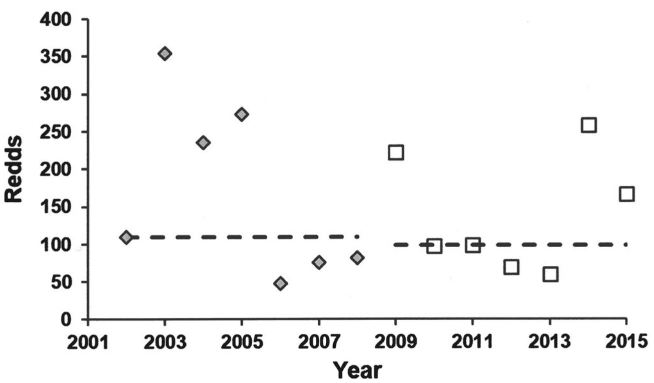

FIGURE 2 Numbers of Chinook salmon redds counted by year in the Pahsimeroi River drainage during the pre-restoration (grey symbols) and restoration phases (open symbols). Dashed lines show the medians for each phase. The difference in medians was not statistically significant ($p > .10$)

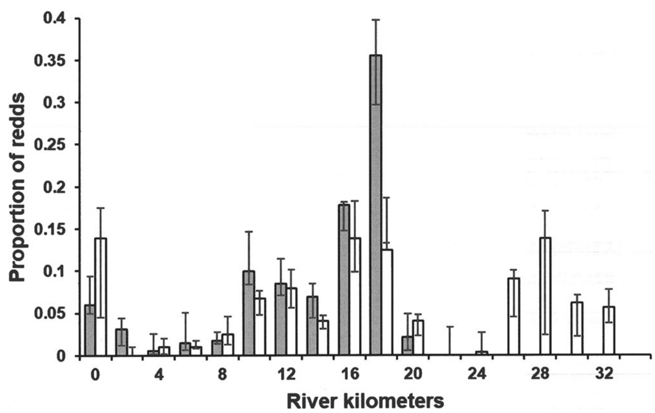

FIGURE 3 Median percentage of redds during the pre-restoration (grey bars) and restoration phases (open bars) by river kilometre upstream from the Pahsimeroi River mouth. Errors bars show the interquartile ranges. Approximate positions of the P-09 (Pahsimeroi River, dotted line) and PBSC-03 (Patterson Creek, dashed line) diversions are shown. Inset shows distribution in 2009

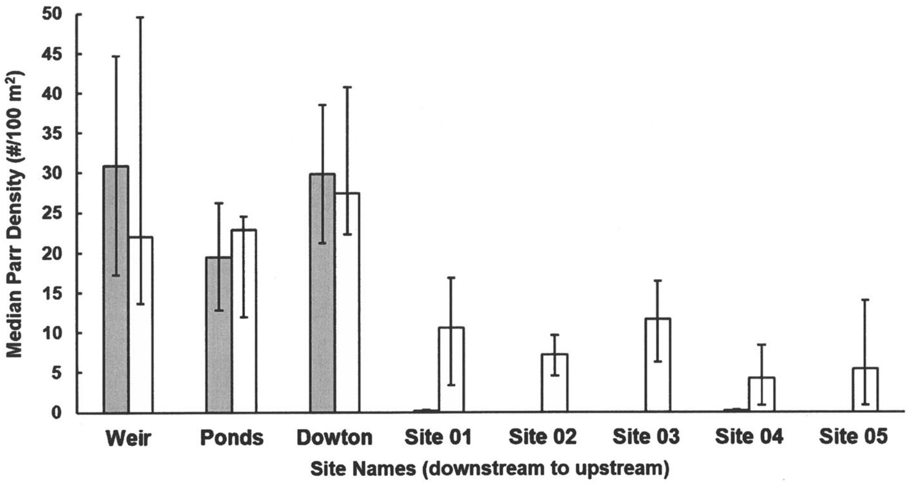

FIGURE 4 Median observed parr densities by site during the pre-restoration (grey bars) and restoration phases (open bars). Errors bars show the interquartile ranges. Relative position of the PBSC-03 diversion (dashed line) is shown

TABLE 1 Output from regressions of fork length on number of female spawners

Parameter	Estimate	Standard error	*t* statistic	*p*-value
Fall parr				
Intercept	103.6	2.4	42.697	<.001
Females	−0.0111	0.0127	−0.876	.397
Period	−0.8287	2.9002	−0.285	.780
Interaction	−0.0028	0.0144	−0.195	.848
Yearling smolts				
Intercept	108.1	2.1	51.897	<.001
Females	−0.0092	0.0109	−0.847	.412
Period	0.6041	2.4931	0.242	.812
Interaction	0.0043	0.012	0.348	.734

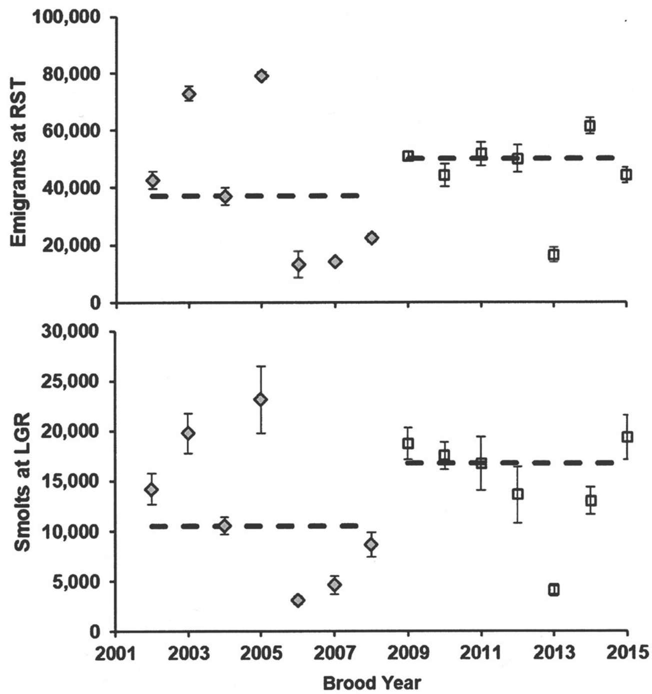

FIGURE 5 Estimated juvenile abundance from the Pahsimeroi River salmon population during the pre-restoration (grey symbols) and restoration phases (open symbols). Top panel shows emigrants past the rotary screw trap (RST). Bottom panel shows number of smolts past Lower Granite Dam (LGR). Error bars show standard errors. Dashed lines show the medians for each phase. Differences in medians were not statistically significant in either panel ($p > .10$)

Average lengths of fall parr and spring yearlings at the rotary screw trap did not fluctuate very much among brood years. Mean FL of fall parr averaged 101 mm across all brood years and varied from 96 to 106 mm. Mean FLs of yearling smolts averaged 107 mm and varied from 104 to 110 mm across brood years. We did not find a difference between periods in the relationship between number of female spawners and FL for either life stage (Table 1).

Abundance of juvenile emigrants from the Pahsimeroi River population overlapped broadly between periods (Figure 5). Emigrants for brood years 2002–2008 had a median abundance of 36,989 fish, ranging from 13,255 fish to 72,724 fish; whereas brood years 2009–2016 had a median abundance of 49,998 fish ranging from 18,063 fish to 61,447 fish. We concluded that the abundance of emigrants has not changed significantly since restoration was initiated (Mann–Whitney $U = 32$, $p < .10$). Smolts at Lower Granite Dam for brood years 2002–2008 had a median abundance of 10,495 fish, ranging from 3,074 fish to 23,113 fish; whereas brood years 2009–2016 had a median abundance of 16,705 fish ranging from 4,988 fish to 19,302 fish. Given the degree of overlap, we also concluded that abundance of smolts at Lower Granite Dam has not changed significantly since restoration was initiated (Mann–Whitney $U = 30$, $p < .10$). The overlap observed at both evaluation points was driven primarily by extreme fluctuations during the pre-restoration period.

Between periods, median productivity increased 26% for juveniles leaving the Pahsimeroi River and 54% for smolts at Lower Granite Dam (Figure 6). Juvenile emigrants per female for brood years 2002–2008 had a median of 196.3 fish/female, ranging from 141.0 to 244.3 fish/female; whereas brood years 2009–2016 had a median of 247.4 fish/female,

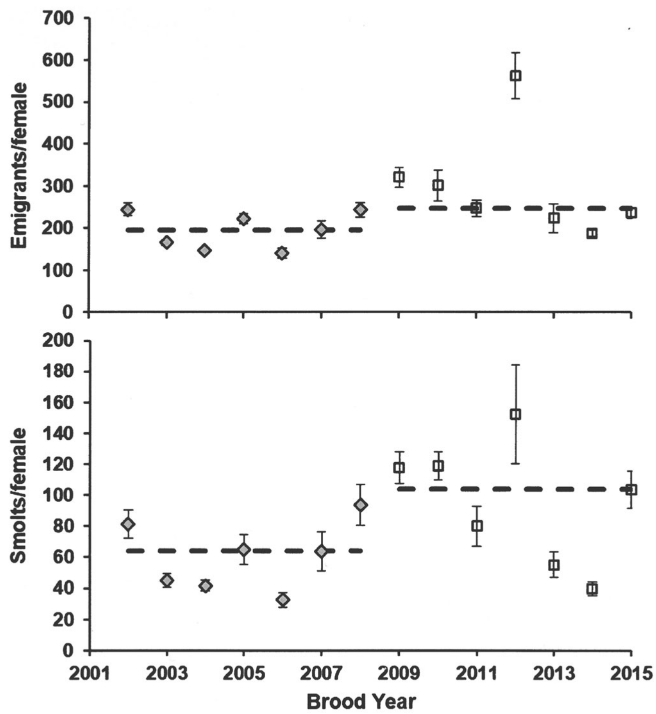

FIGURE 6 Estimated juvenile productivity (progeny per female) from the Pahsimeroi River salmon population during the pre-restoration (grey symbols) and restoration phases (open symbols). Top panel shows emigrants past the rotary screw trap (RST). Bottom panel shows number of smolts past Lower Granite Dam (LGR). Error bars show standard errors. Dashed lines show the medians for each phase. Differences in medians were statistically significant in the top panel (p = .0250) and bottom panel (p = .075)

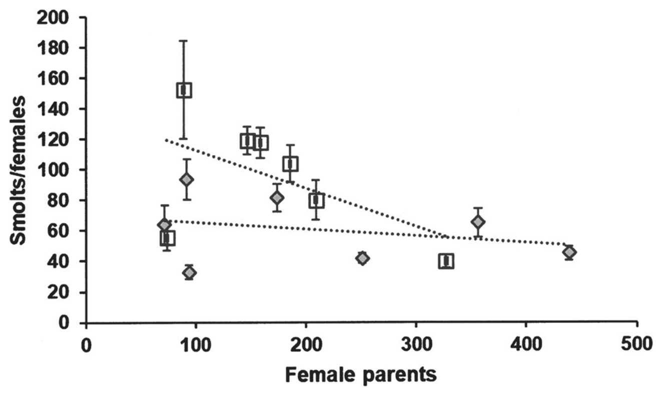

FIGURE 7 Trends in juvenile productivity (smolts per female) with numbers of female spawners during the pre-restoration (grey symbols) and restoration phases (open symbols). Error bars show standard errors. Dotted lines show the linear trends for the two phases

ranging from 187.9 to 561.8 fish/female. We concluded that the median productivity after restoration has significantly increased (Mann–Whitney U = 42, p = .025). Smolts at Lower Granite Dam for brood years 2002–2008 had a median of 63.9 fish/female, ranging from 32.7 fish to 93.6 fish/female; whereas brood years 2009–2015 had a median

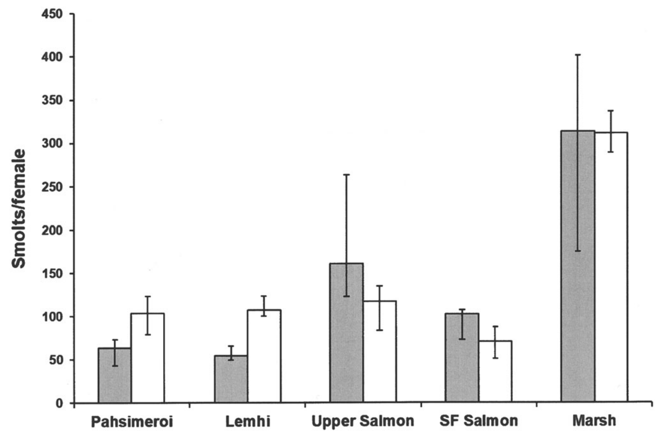

FIGURE 8 Median juvenile productivity (smolts per female) from selected Chinook salmon populations in the Salmon River basin for brood years corresponding to the pre-restoration (grey bars) and restoration phases (open bars) in the Pahsimeroi River watershed. Errors bars show the interquartile ranges

abundance of 103.8 fish/female ranging from 39.8 to 152.4 fish/female. Although annual variability was greater in smolt productivity, the restoration median had significantly increased (Mann–Whitney U = 39, p = .075). The trend in the estimates in the pre-restoration phase increased as numbers of spawning females decreased, whereas it was relatively constant before restoration (Figure 7).

Productivity of nearby populations, in terms of smolts/female had changed in different ways during BYs 2009–2015 relative to BYs 2002–2008 (Figure 8). Median productivity had increased in populations with large habitat restoration programmes (Pahsimeroi and Lemhi rivers, 97% increase in the latter) but had decreased in other supplemented populations (upper Salmon and South Fork Salmon rivers, decreases of 27% and 31%, respectively). Median productivity had not changed in Marsh Creek (<1% decrease) and was about three times greater than elsewhere.

4 | DISCUSSION

In this study, we used spawning distribution and the abundance and productivity rate of juvenile Chinook salmon to assess the population-level effects of a large-scale restoration effort. The restoration efforts increased accessible habitat 246% and had an immediate, detectable effect on spawning adults and juvenile productivity. While the abundance of redds did not increase within our study period, we observed a spawning distribution expansion, with a median of 42% of the redds within the newly reconnected reaches. We also observed parr above the PBSC-03 diversion in subsequent sampling surveys, though densities were still relatively low compared to the higher-density reaches downstream. Importantly, the trend in smolts per female with spawning abundance in the post-restoration phase had shifted upwards. The large increase in accessible stream length appeared to reduce density-dependent effects on juvenile survival. We concluded the population is now more efficient and resilient, producing more juveniles per female at low densities since initiation of restoration.

Opening blocked areas can have relatively quick benefits, by either creating more opportunities for fish to move from high density to low density areas or by allowing access to more suitable habitat for spawning or rearing (Birnie-Gauvin et al., 2018; Roni et al., 2008; Uthe et al., 2017). One benefit of our restoration effort was it addressed a clear impediment, and thus increased the amount of viable instream habitat (e.g., Ogston et al., 2015). There are other important benefits to barrier removal for anadromous fishes, including increasing abundance, expanding spatial distribution, or creating a self-sustaining population (Anderson et al., 2014; Pess, Quinn, Gephard, & Saunders, 2014). Increasing abundance and sustaining a population can mitigate extinction risk, increase genetic diversity and decrease density-dependent processes (Anderson et al., 2014). In this study, we observed the population responded immediately, and we observed redds and parr upstream of the former barriers the following year. Studies documented rapid recolonization of reconnected habitats by anadromous salmonids (Anderson & Quinn, 2007; Bryant, Frenette, & McCurdy, 1999). Where rapid recolonization occurred following removal of passage barriers, spawning distribution was a function of distance from the source population, with highest redd densities occurring in the nearest suitable spawning habitat above the circumnavigated barrier (Kiffney et al., 2009). Previously, most spawning in the Pahsimeroi River was near the upper end of accessible habitat. After the PBSC-03 and P-09 diversion remediation, the salmon immediately colonized the opened reaches within Patterson Creek and the Pahsimeroi River.

Restoration efforts that remove barriers expand spatial distribution and increase the likelihood of production (Koed, Birnie-Gauvin, Sivebk, & Aarestrup, 2020; Nieland, Sheehan, & Saunders, 2015). We observed that opening additional habitat also increased productivity of the Pahsimeroi population. The increased productivity was readily apparent when we compared results with those from four nearby populations: the Lemhi, upper Salmon, South Fork Salmon and Marsh Creek populations. Redd counts for Chinook salmon in central Idaho became strongly synchronous in recent decades (Isaak, Thurow, Rieman, & Dunham, 2003). In other words, high- and low-spawning abundances tend to happen in the same years for all populations; hence, the trend in the primary driver of juvenile production (i.e., number of eggs) is similar among populations. Management of these populations varies from a combined habitat restoration and supplementation effort (Pahsimeroi), habitat restoration only (Lemhi), supplementation only (upper Salmon and South Fork Salmon) and in the case of Marsh Creek, neither habitat restoration nor hatchery supplementation. The Pahsimeroi and Lemhi populations have been subject to similar and concurrent restoration efforts, and the Lemhi River population increased (Uthe et al., 2017) in a similar manner to the supplemented Pahsimeroi population. Productivity of the other supplemented populations, upper Salmon and South Fork Salmon, decreased such that their median productivities are very similar to those of the Pahsimeroi and Lemhi following restoration; however, note how low pre-restoration productivity was in the Lemhi and Pahsimeroi populations compared to the others (Figure 8). Other hatchery-supplemented populations in Idaho have seen natural productivity decrease with supplementation (Venditti et al., 2018), but the Pahsimeroi population has not followed this trend. Productivity from Marsh Creek did not change between periods, and remains much higher than in the others, an example of the potential of a stock not influenced by domestication or habitat degradation. We concluded large restoration efforts in the Pahsimeroi River and Lemhi River watersheds increased population productivity.

The magnitude of restoration in the Pahsimeroi River was substantial. More than 20% of a watershed must be restored to generate a measurable population effect and that effect needs to be greater than 25%–30% to be detected by a rigorous monitoring programme (Roni et al., 2010). In this study, the restoration effort increased accessible habitat by 246%. For the Pahsimeroi River population, we observed increases in median juvenile abundance (35% and 59%) and productivity (26% and 54%) following our restoration efforts. Though changes in abundance were not statistically significant, those in productivity were because that metric was less volatile. We bolstered our results by contrast to populations under similar and different management programmes, ensuring our conclusions were not spurious.

Parr densities in opened reaches were about half of those in downstream reaches. We surmised many parr spawned in opened reaches migrated downstream to better habitat as fish grew and required more space and food (self-thinning; Elliott, 1993). The result should be increased competition in downstream reaches through the growing season. Mean length of emigrating fall parr and spring smolts did not change. Improving habitat quality upstream should reduce competition, given similar levels of reproduction. However, if escapement levels were much higher, capacity in the newly accessible reaches likely would be attained quickly, given current habitat quality.

Restoration continues in the Pahsimeroi River watershed. Restoring access and flow was the first step. More work is needed to improve habitat quality in newly accessible reaches. Habitat in the reconnected reaches has moderate to high levels of sinuosity and is primarily pool-riffle morphology, but riparian vegetation is discontinuous and has been cleared in some portions of the floodplain (IDFG, unpublished data; Idaho OSC Integrated Rehabilitation Assessment Team, 2019). Since 2014, stakeholders removed barriers and improved flow in an additional 10 rkm on the Pahsimeroi River and 9 rkm on Patterson Creek. Other projects are focusing on habitat quality by increasing floodplain access, installation of woody structure, riparian plantings and grazing management. This work is the result of large-scale vision and long-term partnerships between willing landowners and government agencies. Continued restoration efforts and monitoring programmes are greatly dependent on maintaining these relationships.

We demonstrated a means to detect restoration effects at the population level and at a large scale. A true population effect requires a significant restoration effort at the intended scale, as done in this case. Detecting this effect also requires information at that scale to tease out variation among populations. Thus, this evaluation depends on population-scale juvenile monitoring (the rotary screw trap) with confirmatory surveys in the affected reaches (spawning ground and snorkel surveys). True replication is impossible at this scale; therefore, contrasting populations with a range of management types/effects is useful as we demonstrated here. This observation implies two things for detecting a population response. Because of the lack of control, the grain of inference is likely to be coarse. Second, a collaborative monitoring network is necessary for this approach. We used a logical sequence of cause-and-effect relationships based on several data sources, each with weaknesses, to evaluate our hypotheses. We contemplated a stock-recruit analysis with a period effect but lacked sufficient years to parameterize it reliably. The snorkel surveys were quite limited and not calibrated to a true estimate of abundance, making quantitative estimation of change in parr density difficult. However, it is important to provide managers with reliable information on a timely basis. Given the necessarily small sample sizes, we applied a conservative weight-of-evidence framework using multiple types of data to show the effect is real and not spurious.

In conclusion, we have shown large-scale stream restoration efforts can have a population effect, as postulated by Lake et al. (2007) and Roni et al. (2010). Despite the response observed in our results, restored habitat is likely not sufficient to increase the spawning population. Many factors limit stages of the anadromous salmonid life cycle downstream, including warming ocean conditions, hydroelectric development and changes to the natural flow regime. Variations in the conditions encountered by emigrating smolts in rivers and the ocean confound the effects of management programmes in spawning and rearing habitats in terms of returning adults (Nieland et al., 2015; Venditti et al., 2018). Increased productivity at low densities should reduce probability of extirpation; but, ultimately, a sufficient number of spawning fish must return to realize the full benefits of the habitat restoration. Regardless, our study illustrates that restoration efforts focused on increasing habitat connectivity and flow will allow redistribution of both spawning adults and juveniles, improving egg-to-smolt survival. In an era of habitat fragmentation and alteration, this study documents the importance of expanding access to diverse habitats, which has the potential to build future resilience for anadromous salmonid populations.

ACKNOWLEDGEMENTS

The Idaho Department of Fish and Game, Natural Resource Conservation Service, Custer Soil and Water Conservation Service and local landowners formed the initial stakeholder group. Funding from the Bonneville Power Administration brought the project to where other partners joined the effort. Additional partners include the U.S. Fish and Wildlife Service (Partner Funds), NOAA Fisheries (Pacific Coast Salmon Recovery Funds and Mitchell Act Funds), Idaho Department of Water Resources, Columbia Basin Water Transaction Program, Bureau of Reclamation and The Nature Conservancy. Landowner cooperation and willingness to modify their irrigation systems was the key to success throughout the entire project. Operation of the weir was funded by Idaho Power. Redd surveys were funded by grants from the Pacific Salmon Commission and Bonneville Power Administration. Operation of the rotary screw trap was funded by Bonneville Power Administration (project 1989-098-00). Mike Biggs and Chuck Warren set up additional snorkel surveys and initial data compilation. Bruce Barnett and Evan Brown completed data queries. The manuscript was greatly improved by suggestions from George Pess and two anonymous reviewers.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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How to cite this article: Copeland T, Blythe D, Schoby W, Felts E, Murphy P. Population effect of a large-scale stream restoration effort on Chinook salmon in the Pahsimeroi River, Idaho. *River Res Applic*. 2021;37:100–110. https://doi.org/10.1002/rra.3748