INTRODUCTION

The objective of some anadromous salmon hatchery programmes is to provide fish for harvest, either in response to commercial or public demands for harvest fisheries or to mitigate for lost fisheries from an anthropogenic or natural activity that cannot be undone (Aprahamian, Smith, McGinnity, McKelvey & Taylor, 2003; Naish et al., 2008). In harvest programmes, importance is placed on matching the location and timing of adult returns with people's expected fishing effort to ensure a maximum harvest. Adults that escape the harvest often return directly to the hatchery, where they are collected for broodstock and spawned to make the next generation of hatchery fish. These hatchery stocks usually become more domesticated with each successive generation. As such, harvest hatchery programmes must minimise spawning interactions between hatchery and natural fish because domesticated hatchery fish can suppress the fitness of natural fish by introducing genes into the natural population that are adapted to a hatchery environment (Araki, Berejikian, Ford & Blouin, 2008; Araki, Cooper & Blouin, 2007; Chilcote, Goodson & Falcy, 2011). Maximising removal of hatchery fish through harvest management reduces unwanted spawning interactions, as will any efforts that improve the homing of hatchery fish back to where they were released, thereby reducing the number of fish that stray into other river basins.

Selective breeding of hatchery broodstock is one tool fisheries managers use to encourage desirable performance characteristics. The homeward migration timing of anadromous salmonids is a strongly heritable trait (Quinn, Unwin & Kinnison, 2000; Stewart, Smith & Youngson, 2002; O’ Malley, Camara & Banks, 2007), making this behaviour a potential candidate for selective breeding. Examples of altered migration timing through broodstock selection include a multi-generational
breeding programme designed to increase the proportion of coho salmon, *Oncorhynchus kisutch* (Walbaum), adults that returned to fresh water during the middle portion of the migration period (Tipping & Busack, 2004) and an effort to create temporal segregation in the migration timing of hatchery and natural origin anadromous steelhead, *O. mykiss* (Walbaum), by intentionally selecting the earliest returning adults for broodstock (Mackey, McLean & Quinn, 2001). However, rigorous evaluations of selective breeding efforts are a challenge because of difficulties associated with maintaining a selectively bred strain and an unaltered strain. When the intent of selective breeding is to maximise harvest, costly and time-consuming tagging, tag recovery and harvest monitoring of both the altered and unaltered strains may be required. In consequence, few published studies have assessed the efficacy of selective breeding efforts towards altering run timing for harvest purposes.

This study evaluates a selective breeding study in a steelhead hatchery programme to mitigate for lost harvest opportunities in the Grande Ronde River, a terminal fishery. The eight-month recreational fishery in this river system begins in September, and prior to the decline of this fishery, the autumn (September–November) period was important for harvesting fish (Flesher, Buckman, Carmichael, Messmer & Whitesel, 1994). Steelhead from this population is of a higher edible quality in autumn because adults undergo fasting after beginning their freshwater spawning migration (Penney & Moffitt, 2014); while in fresh water, lipids and proteins that have been stored within muscle tissue are metabolised by the fish for energy and these elements become depleted by springtime. Therefore, restoring the autumn fishery is important to anglers that harvest fish for consumption.

In this study, early arriving adults to the fishery were captured for broodstock and the homeward migration timing of their first-generation progeny was compared to that of an unaltered hatchery strain. The hypothesis was that earlier arrival timing to the river would result in greater harvest, particularly in autumn. An additional evaluation to address straying concerns was whether the early arriving strain exhibited the same homing behaviour to that of the unaltered strain. The paired-release study design employed called for progeny from the two strains to be reared similarly at the same hatchery. However, variability in the hatchery rearing experience may affect smolt release size and smolt seaward migration, two factors that influence the imprinting by smolts on their home waters and the subsequent homing behaviour of adults (Clarke, Flesher & Carmichael, 2014; Tipping, 1997; Wagner, Wallace & Campbell, 1963). Therefore, this study also reports on these juvenile metrics.

### 2 | METHODS

#### 2.1 | Overview

Paired releases of the two steelhead strains were made in 2005 through 2008 using yearling smolts raised at Irrigon Hatchery, Oregon, USA (Fig. 1). Following rearing, smolts were trucked to acclimation ponds at Wallowa Hatchery, where they were acclimated for at least 4 weeks and then released into a tributary of the Grande Ronde River in the Grande Ronde River basin. The Wallowa Hatchery is located approximately 988 river kilometres (rkm) inland from the ocean in the Grande Ronde River basin. The Grande Ronde River is a tributary to the Snake River, itself the largest tributary to the Columbia River, which flows to the Pacific Ocean. Steelhead from the Grande Ronde River must navigate eight hydroelectric dams on the Snake and Columbia rivers during their journey to and from the ocean.

Once released from the hatchery to the river, downstream migrating smolts in this study travelled a 292-rkm section before reaching Lower Granite Dam on the Snake River, the first dam encountered during seaward migration. There a portion of smolts that arrived each day were collected, loaded onto barges and transported to below Bonneville Dam, located 234-rkm upstream from the ocean on the Columbia River. The remainder of smolts emigrated in the river.

Returning steelhead adults typically enter the Columbia River mouth in early summer, with adults passing Bonneville Dam from June through August (Keeler, Peery & High, 2009). This adult migration usually coincides with peak summer water temperatures that often exceed 20°C (Robards & Quinn, 2002). Two radio tracking studies have established that arrival timing of adults to the Grande Ronde River is protracted—occurring from about September through February—likely because some adults migrate directly up the Columbia and Snake River corridors while others seek refuge from the heat by holding in lower sections of cool tributary streams to the mid-Columbia River and still other adults overwinter in the Snake River before continuing their migration the following spring (Carmichael, Miller & Messmer, 1990; Keefler, Peery, Bjornn, Jepson & Stuehrenberg, 2004). A recreational steelhead fishery begins on the lower Grande Ronde River in September. Creel survey data dating back to the mid-1980s indicate that few Wallowa Hatchery adults are caught in September but the fishing improves in October as greater numbers of fish arrive to the river (Flesher, Carmichael & Clarke, 2012).

#### 2.2 | Broodstock collection

The Wallowa Hatchery programme typically releases adipose fin-clipped smolts so that returning hatchery adults can be differentiated from natural adults. During this study, hatchery broodstock consisted of adipose fin-clipped adult returns to the Wallowa Hatchery, and brood collection and spawning occurred throughout the early March to early May spawning run. Broodstock for the new strain were early arriving hatchery fish to the lower Grande Ronde River that were captured by hook and line angling in early October of return years 2003 through 2007. Between 77 and 115 angled adult fish were captured each year, and they were presumed to be Wallowa Hatchery stock because no other hatchery steelhead stock is released into the Grande Ronde River basin and only five stray steelhead from other hatchery programmes were captured in the fishery or at traps located throughout the basin in 10 years proceeding this study (data from annual project reports, available at https://www.fws.gov/federal/columbia/Reports/ODFWreports.html). Upon capture, fish were transported to a hatchery pond where they were held until spawning the following spring. These early arriving broodstock were spawned on the same schedule as the standard hatchery strain.
Embryos from the two strains were hatched and reared separately at the same hatchery facilities using the same protocols. Fry were initially reared in indoor circular tanks before transfer in July to concrete outdoor raceways. In late summer, approximately 100,000 juveniles from each early strain or standard strain release group were implanted with a coded-wire tag (CWT) that was uniquely coded to identify the release group. To indicate the presence of a tag, early arriving progeny were also right ventral fin clipped, whereas the standard strain received a left ventral clip. Maximum targeted raceway densities and loading for both strains were 11.0 kg·m$^{-3}$ and 0.9 kg·L$^{-1}$·min$^{-1}$.

To compare smolt downstream travel time and survival to Lower Granite Dam, a representative sample from each early strain or standard strain release group (3,600 and 6,900 fish respectively) were tagged with passive integrated transponder (PIT) tags. Fish from both strains were reared to a target release size of 113 g, a size that maximises post-release survival of Wallowa Hatchery steelhead (Clarke et al., 2014).

In late February, smolts from both strains were trucked to an acclimation site and evenly stocked into two acclimation ponds measuring 91.4 m × 12.8 m × 1.1 m. They were held there until an early April release date. The number of smolts hauled to acclimation ponds was estimated from a bulk measurement of the total weight of fish divided by the average smolt weight, as determined on the day of fish liberation. A week before release from acclimation, 50 randomly selected fish from both strains (as recognised by the ventral clip) were sampled and individually weighed (g) and measured for fork length (mm), from which Fulton’s condition factor ($K = \text{weight}/\text{length}^3 \times 10^5$; Anderson & Neumann, 1996) was calculated.
2.4 | Tag recovery

Juvenile and adult PIT tag recaptures occurred passively by detectors located within Columbia and Snake Rivers dam sites. Cormack–Jolly–Seber (CJS) outmigration survival probabilities to Lower Granite Dam were calculated for each PIT-tagged group using recaptures in the juvenile bypass systems at the dam and at downstream dams on the lower Snake and Columbia rivers. Dam recapture data were downloaded from a centralised Columbia Basin PIT tag database maintained by the Pacific States Marine Fisheries Commission (available at www.PTAGIS.org). Release–recapture information was then entered into the PIT Pro 4.1 programme (Westhagen & Skalski, 2009) with a single release–recapture model (Skalski, Smith, Iwamoto, Williams & Hoffmann, 1998) for calculation of survival probabilities and confidence intervals. Juvenile migration timing from day of release to Lower Granite Dam was similarly calculated using recaptures at the dam.

Adults from this study returned to fresh water from 2006 through 2010 after spending 1 to 3 years in the ocean. Return timing was monitored using PIT tag recoveries in adult ladders at Bonneville Dam, McNary Dam at rkm 470 on the Columbia River and Lower Granite Dam at rkm 695 on the Snake River. Tag recoveries were summarised by week from mid-June through December, a time period that encompassed all recoveries for the study years. The mean date ± 1 SD that 50% of the runs reached each dam is reported to describe the distribution of recovery dates.

Coded-wire tag recoveries came from within the Grande Ronde River basin and from out-of-basin locations that included ocean fisheries and Columbia River basin fisheries and traps. Out-of-basin CWT recoveries were downloaded from the Regional Mark Information System database (available at www.rpmc.org), which summarises tag recoveries and sampling rates (total catch divided by sampled catch) throughout all fisheries, hatchery returns and spawning-ground carcass surveys in the Pacific region. Within the Grande Ronde River basin, CWT recoveries came mostly from adults trapped in fish ladders at hatchery facilities and angler harvest in the river fishery. At the traps, all hatchery adults were collected and fish from this study were recaptured using PIT tag recoveries in adult ladders at Bonneville Dam, McNary Dam at rkm 470, and Lower Granite Dam at rkm 695 on the Snake River. Tag recoveries were summarised by week from mid-June through December, a time period that encompassed all recoveries for the study years. The mean date ± 1 SD that 50% of the runs reached each dam is reported to describe the distribution of recovery dates.

2.5 | Data analysis

Annual steelhead stray rates for each strain were calculated using CWT recoveries from all locations. Straying was calculated as the number of adult steelhead tags recovered in a Columbia or Snake River tributary basin other than the Grande Ronde River basin into which they were released divided by the total number of tagged adults produced. Total number of adults produced from a release group was the summation of adults captured in all areas. This straying calculation is not a true stray rate because the intended ultimate destination of steelhead captured in out-of-basin tributaries is unknown; if not captured, some individuals may have returned to their release location at the Wallowa Hatchery.

The effect of brood strain on differences in smolt lengths, weights and condition factors within a release year was examined with the Mann–Whitney rank sum test because some data did not pass the Levene median test for equal variance. A paired t-test was used to test whether progeny from the two brood strains displayed significant differences in smolt travel time and survival to Lower Granite Dam, adult arrival timing at Bonneville Dam and straying over the 4 replicate release years. The paired t-test assumes that data have equal variances but does not assume a normal distribution (Zar, 1984); these PIT- and CWT-derived data passed tests for normality. Statistical significance of all tests was assumed at α = 0.05.

The Grande Ronde River basin harvest was estimated each month based on CWT recoveries in the creel survey. Differences in the percentage of all adult harvest that occurred in autumn and the total harvest over the fishing season were also assessed with paired t-tests on data that met the normality assumption. The monthly number of CWT recoveries in the harvest was highly variable, which would affect the power of statistical tests of these data. Therefore, the practical significance of differences in mean monthly harvest between the two strains was assessed using Cohen’s effect size d (Cohen, 1977), calculated as the mean difference in monthly harvest rates divided by the within groups standard deviation. Cohen suggests that a d value = 0.2 denotes a small effect size, d = 0.5 is a medium effect size and d > 0.8 is a large effect.

3 | RESULTS

Hatchery personnel successfully grew smolts from the two strains to a similar size (Table 1). Across all years, smolt fork length averaged 214 and 212 mm (SD = 21 for both) for the early arriving and standard strains, but in release year 2008, the 5-mm difference between the two strains was significant (U = 922.5, p = .010). Weight averaged 105 g for both strains and there were no significant differences in any release year. Condition factor averaged 1.04 (SD = 0.09) for the early arriving strain and 1.05 (SD = 0.09) for the standard strain, with the early strain release group being significantly leaner in release year 2007 (U = 764.0, p < .001).

Following release to the river, median smolt travel time to Lower Granite Dam ranged between 22 and 35 days (Fig. 2), but the difference in median travel time between the two strains was less than 3 days in each release year. Across all years, travel time was not significantly different (t = -1.057, df = 3, p = .260). Outmigration survival
The distribution of tag recovery dates was narrower for the early strain at Bonneville Dam (early strain = 15.6 days) compared to the standard strain (standard strain = 16 September, standard strain = 7 October). The distribution of tag recovery dates was narrower for the early strain at Bonneville Dam by 9 August, a median difference of 9 days earlier than their counterparts that was significant (t = -4.090, df = 4, p = .015). As the run moved upstream to McNary Dam, the difference in median return timing widened to 21 days (early strain = 3 September, standard strain = 24 September) and it remained at 21 days at Lower Granite Dam (early strain = 16 September, standard strain = 7 October). The distribution of tag recovery dates was narrower for the early strain at Bonneville Dam (SD = 15.6 days) compared to the standard strain (SD = 19.7 days), but the timing distribution of the standard strain was more truncated at upstream dams. PIT tag recoveries at Bonneville Dam ranged between 47 and 326 per group, but recoveries declined to as low as 26 per group as adults migrated upriver past Lower Granite Dam. A total of 6,653 CWTs were recovered for this study, 47% of which were from the Grande Ronde River basin. When these 6,653 recoveries were expanded for sampling rates, there was an estimated 14,693 adults that returned from this study. Coded-wire tag recoveries from the Grande Ronde River basin indicated a difference in the timing of harvest between the two strains (Fig. 4). Of all Grande Ronde River basin harvest, 49.1% (SE = 5.0) of the early arriving strain occurred in the autumn fishery compared to 21.9% (SE = 2.3) of the standard strain, a difference that was significant (t = -4.488, df = 4, p = .011). There were also seasonal differences in the monthly number of fish harvested (Fig. 5). Mean harvest of 172 early arriving strain steelhead in September was more than 400% higher than the standard strain (n = 37) and Cohen’s effect size (d) was 1.12, indicating a large difference in harvest between the two strains. There was a 51% mean harvest difference in October (early strain = 317, standard strain = 210), and Cohen’s effect size (d) was 0.64. Conversely, the standard strain had a greater harvest in 4 months during December through April. Total annual harvest over the entire fishing season averaged 937 fish for the early strain (SE = 31) compared to 799 fish (SE = 26) for the standard strain, but the 17% difference was not significant (t = 2.220, df = 3, p = .113). However, due to the low number of replicate years, the power of this test (0.282) was below a desired power of 0.80.

Straying of adult progeny from smolts released in 2005 was 16.4% and 10.8% for early strain and standard strain, respectively, but groups released in 2006–2008 strayed at no higher than a 6.1% rate (Table 1). Across all years, early strain straying was 7.7%, whereas the standard strain had a lower rate of 5.0% that was not significantly different (t = .629, df = 3, p = .539). There were also seasonal differences in the harvest of early strain steelhead in September with a 140% higher harvest for the early strain compared to the standard strain (SE = 37) and Cohen’s effect size (d) was 1.33. Conversely, the standard strain had a greater harvest in 4 months during December through April. Total annual harvest over the entire fishing season averaged 937 fish for the early strain (SE = 31) compared to 799 fish (SE = 26) for the standard strain, but the 17% difference was not significant (t = 2.220, df = 3, p = .113). However, due to the low number of replicate years, the power of this test (0.282) was below a desired power of 0.80.
DISCUSSION

While mostly circumstantial evidence has shown that hatchery practices may artificially change the run timing of anadromous salmonids over time (e.g. Hoffnagle, Carmichael, Frenya & Keniry, 2008), results from this experiment provide a clear example of how only one generation of broodstock selection for steelhead run timing can affect this behavioural trait in first-generation progeny. The authors know of only one other study with a salmon population, conducted by Smoker, Gharrett and Stekoll (1998) with pink salmon, *O. gorbuscha* (Walbaum), which demonstrated that a single generation of artificial selection for run timing can affect this trait in first-generation progeny. Selective breeding of fish to enhance desirable performance traits has often been carried out over many generations (e.g. Quinn, Peterson, Gallucci, Hershberger & Brannon, 2002) because the heritability of the trait is either unknown or suspected to be under weak genetic control. Carlson and Seamons (2008) and Gjedrem (2000) reviewed the heritability of certain traits in salmonids and concluded that morphological traits are more readily heritable than behavioural or life history traits such as the timing when migration begins.

The early arriving strain successfully shifted the harvest timing to earlier in the fishing season. However, the comparison of total annual harvest between the two strains was not statistically significant and, therefore, the null hypothesis of no significant harvest differences cannot be rejected. Yet, Cohen’s *d* statistic indicated a substantially greater harvest of the early strain in autumn. Because *p*-value results are a function of both the size of treatment effects and the number.
of replicates in an experiment, and this study could only be replicated for 4 release years, the practical significance of the differences in autumn harvest should not be overlooked. This study demonstrated that manipulating the timing of steelhead arrival to the fishery may be a useful tool for accomplishing the original objective of improving the early autumn harvest fishery.

This study also provides a good illustration of the trade-offs that may occur when broodstock selection is used to accomplish a management objective. The greater straying of the early arriving strain increased the possibility of introgression of hatchery genes into natural steelhead populations in the Deschutes River if the domesticated Wallowa stock adults are successfully spawning there. Cool flows of the Deschutes River seem especially attractive to hatchery steelhead stocks originating from Snake River basin hatcheries (including the Wallowa stock) because these fish migrate the Columbia River in summer when peak water temperatures usually exceed 18°C (Keefer et al., 2009). Therefore, steelhead use the Deschutes River as refuge from the warm migration corridor (High, Peery & Bennett, 2006). Although it may seem contradictory, further broodstock selection for an even earlier return timing could lessen the straying behaviour as a radio tracking study of adult steelhead migrants through the Columbia River corridor showed that steelhead stocks with a July median passage date at Bonneville Dam strayed at lower rates than stocks that passed in August (Keefer et al., 2009). The median passage of the early arriving strain was 9 August.

Smolts that are barged downriver from Lower Granite Dam have a greater propensity to stray compared with those that migrate in-river (Keefer, Caudill, Peery & Lee, 2008). The proportion of smolts that is collected for barging on a daily basis is a function of environmental conditions (e.g. flow and dam spill rates) and established collection protocols (Hurson et al., 1999). Interpretation of straying results in this study assumed that the downstream migration pathway (i.e. barged or in-river migration) was similar between the two strains. The small and statistically insignificant difference in smolt travel days to Lower Granite Dam provides supporting evidence that barging rates were similar between the two strains and that this variable would not affect the interpretation of straying results.

Following their arrival at the Grande Ronde River, adults from Wallowa Hatchery releases have historically shown strong homing back to the Wallowa Hatchery. Trapping data from five adult fish traps in operation on tributary streams in the Grande Ronde basin during the steelhead migration helps to illustrate this point. For example, in the 5 years preceding this study, only 19 hatchery adult steelhead of potential Wallowa Hatchery origin (origin of release could not be determined for some individuals) were recovered at those traps from over 17,000 total adult hatchery and natural steelhead that were captured (L. Clarke, unpublished data). Similarly, during this study, both strains displayed the same strong homing fidelity to the Wallowa Hatchery with only one early arriving adult and no standard strain adults captured at the five traps.

Given that vulnerability to angling is a heritable trait (Philipp et al., 2009), and broodstock for the early arriving strain were collected by angling, it is tempting to ask whether the new strain yielded a greater angler harvest because their parents responded aggressively to an angler’s lure. However, adults from the early arriving strain encountered water temperature and flow conditions in the Grande Ronde River in autumn that were different than those experienced by the later returning strain, and other factors such as seasonal differences in gear types used by anglers might have influenced each strain’s vulnerability to angling. These factors would confound any attempt to understand whether the genes inherited by the early arriving strain caused them to be more likely to strike a lure or bait. Selective breeding to increase vulnerability to angling using hatchery broodstock captured by angling has been attempted but with mixed results (e.g. Kozfkay & Megargele, 2002; McIntyre & Johnson, 1977; Philipp et al., 2009).

Due to the appreciable and mounting cost of operating salmonid hatchery programmes (Radtke & Davis, 2000), fishery managers who wish to improve harvest can no longer rely on increasing hatchery smolt production. More efficacious methods must be found. To increase autumn harvest in a terminal fishery, this study took advantage of the natural variation in adult migration timing of an anadromous steelhead stock to selectively create a strain that returned earlier and could be fished upon throughout more of the fishing season. Selective breeding to better match adult return timing with the timing of fishing effort may be an expedient approach for improving harvest fisheries. However, managers contemplating this strategy should also be mindful of several factors. First, selectively bred hatchery fish have an altered and potentially less genetically diverse profile; therefore, if these hatchery fish spawn in nature they may pose additional risks to natural populations (e.g. Bourret, O’Reilly, Carr, Berg & Bernatchez, 2011). For this reason, selective breeding would certainly not be appropriate for hatchery programmes whose objectives include supplementing the number of natural fish spawning in nature through additions of hatchery fish or programmes that cannot exclude hatchery fish from natural spawning areas by harvest or by employing traps and weirs. Second, adults with an altered migration timing may experience a different set of environmental conditions (e.g. temperature and flow) along their migratory route that
could influence their behaviour in unknown ways, and salmon stocks with a longer migratory journey might swim through a greater variety of habitats. Related to this point are observations that salmon migrations are not always directly to their natal streams (Silla, Erkinaro & Jounela, 2009; Thorstad, Økland, Aarestrup & Heggberget, 2008). Hence, run timing manipulation may produce more uncertain outcomes when migrations are complex. In addition, selective breeding simply does not always produce the expected results (Cooke, Suski, Ostrand, Wahl & Phillip, 2007; Houde, 1994; Quinn et al., 2002); other factors that vary through time, such as habitat conditions, could confound attempts to match return timing with harvest timing. And finally, altering run timing to boost harvest in one location could reduce harvest in other locations, potentially reducing the overall harvest. Proper consideration, planning and scientific evaluation of these factors using a paired-release design will help avoid undesirable results. Following completion of this study, managers opted to continue hatchery production of both the early arriving and standard strains, and they continued selective breeding of early arrivals to encourage an earlier adult migration timing that could further enhance the mitigation fishery and reduce straying.

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