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Via first class mail and email to willamettehatcheryEIS.wcr@noaa.gov

March 8, 2019

National Marine Fisheries Service
Upper Willamette River Basin Hatcheries FEIS
2900 N.W. Stewart Parkway
Roseburg, Oregon 97471

Dear Sir/Madam:

Thank you for the opportunity to comment on the final Environmental Impact Statement ("FEIS") prepared by the National Marine Fisheries Service ("NMFS") related to four proposed Hatchery and Genetic Management Plans ("HGMPs") for spring Chinook, and one each for summer steelhead and rainbow trout, in the upper Willamette River basin ("UWR") in Oregon.

These comments are submitted by McKenzie Flyfishers, The Conservation Angler, Willamette Riverkeeper, and the Native Fish Society.

1. Thank you for clarifying that NMFS is considering whether to approve the spring Chinook HGMPs under Limit 5 of the 4(d) rule, and it is considering whether to approve the summer steelhead and rainbow trout HGMPs generally pursuant to Section 7 of the ESA. FEIS at 1-2.

2. The FEIS repeats the legal error that "NMFS has a limited role (i.e., approve or deny) under Limit 5 of the 4(d) Rule" the proposed spring Chinook HGMPs. FEIS at 10. That position is inconsistent with the text of the rule, the procedures for exempting take under Section 9 of the ESA, the consultation process under Section 7 of the ESA, and the requirements of NEPA.

3. In our comments on the DEIS, we noted that the proposed alternative includes implementing, among other things, a "steelhead" HGMP, but that the DEIS states the "co-managers" are "updating the summer steelhead HGMP to reflect current management." DEIS at 2 n.2. We also noted that during the public comment period on the DEIS, there was no updated summer steelhead HGMP available for public review. In fact, the Corps of Engineers did not transmit to NMFS a final, updated summer steelhead HGMP until June 18, 2018 (attached as Ex. A), after the close of the comment period on the DEIS on May 29, 2018. In the FEIS, NMFS

responds by saying the public can "use the present commenting process under NEPA to express any concerns which would assist NMFS in its review" of the summer steelhead HGMP. FEIS, NMFS Resp. to Western Environmental Law Center ("WELC") Comments #5. We express concerns here, but note that the public, and entities such as the Environmental Protection Agency, which must be afforded the opportunity to comment on a draft EIS, could not meaningfully do so in the absence of a submitted and updated summer steelhead HGMP.

4. As NMFS is aware, the Corps of Engineers and other federal agencies have requested reinitation of consultation for the whole suite of federal actions that affect spring Chinook and winter steelhead in the UWR, including the hatchery programs. We assume that process will result in another Biological Opinion. It is improper for NMFS to single out solely the hatchery programs to consider for approval under NEPA and the ESA, without considering and disclosing the combined and cumulative effects of all of the federal actions that affect spring Chinook and winter steelhead in the UWR.

5. In our comments on the DEIS, we noted the findings of Johnson et al. (2013) and Prince, D.J., et. al., (2017) as to hybridization of winter steelhead and summer steelhead in the UWR. Certain of these findings have been amplified by Weigel et al. (2019) (attached as Ex. B). Johnson et al. (2013) found that 10-15% of the individuals sampled were winter x summer steelhead hybrids. Weigel et al. (2019) found that 25% of the individuals sampled were winter x summer steelhead hybrids. Differences in these estimates relate to the percentage of introgression (Q-value) and the number of populations (K=2 or 3) used to identify these hybrids. Weigel et al. (2019) uses the common standard of <90% native winter steelhead, while Johnson et al. (2013) uses a lower standard of <80% native winter steelhead. Weigel et al. (2019) shows how the bias in these parameters will result in under-estimating hybridization (incorrectly classifying hybrids as pure native winter steelhead) using a Q-value as low as 80%. The FEIS improperly fails to consider and disclose these findings and data.

6. The FEIS notes that Johnson et al (2013) "make recommendations on reducing the occurrence of summer steelhead on the spawning grounds [of winter steelhead]," FEIS at 122, but the FEIS fails to consider or disclose those recommendations, and the proposed alternative in the FEIS would approve the summer steelhead HGMP as submitted. The proposed alternative improperly fails to include specific, enforceable conditions to "ensure reproductive isolation between hatchery summer steelhead and natural-origin winter steelhead" in the Santiam River basin. Id.

7. The summer steelhead HGMP states that the estimated smolt to adult return ("SAR") ratio for summer steelhead is approximately 2.9%. StS HGMP at 13. NMFS proposes to authorize the release of 121,000 summer steelhead into the North Santiam River, and 161,500 summer steelhead into the South Santiam River. FEIS at 17. The SAR appears the best available scientific data upon which to estimate how

many adult summer steelhead will return to the North Santiam and South Santiam River basins based on these smolt release numbers. A release of 161,500 summer steelhead smolts should result in roughly 4,683 adult returns to the South Santiam River, and a release of 121,000 summer steelhead smolts should result in roughly 3,509 adult returns to the North Santiam River. The FEIS fails to consider or disclose that these return numbers will dwarf adult winter steelhead return numbers. And the FEIS fails to accurately consider or disclose the magnitude of resulting effects on winter steelhead, such as summer steelhead predation, competition, and residualization.

8. The FEIS discloses that the summer steelhead released into the UWR are not native to the basin, are released solely for fishing, and have "no conservation or recovery benefits for" winter steelhead. FEIS at 21. Historically, this non-native fishery never existed in the UWR. It was created by ODFW in the late 1960s because, as ODFW stated in its 2004 summer steelhead HGMP at 3, "[n]ative winter steelhead had not provided the angling opportunity desired by sportsmen and fisheries managers, since they spawned and were essentially gone from the system by late May. By the time dependable weather rolled around, the winter fish were gone. The creation of a healthy summer run was intended to expand the duration of the steelhead angling season through the summer and fall and, in fact, that has happened." The FEIS fails to consider and disclose current data as to the connected and cumulative effects of fishing for summer steelhead in habitat for winter steelhead. When we raised this issue in comments on the DEIS, NMFS referred us to sections 2.5, 5.4.4., and 5.5.3 in the FEIS. NMFS Resp. to WELC Comments #41. We've reviewed those sections, and have the following comments.

9. Section 2.5 states there are still "unused fishery impacts" on spring Chinook and winter steelhead "that are below the maximum authorized by the [Fishery Management and Evaluation Plans ("FMEPs")]." FEIS at 23. NMFS released its public evaluation under NEPA, and approved FMEPs for winter steelhead, 18 years ago. The data and assumptions in those evaluations are significantly outdated, especially, for example, assumptions about populations of winter steelhead. For example, NMFS approved an FMEP for winter steelhead based on population data from 1967-2000, the last year showing a run size of approximately 700 winter steelhead returning to the South Santiam River. By contrast, current best scientific data reveal winter steelhead run sizes that are a small fraction of previous estimates. For example, in 2018-2019, 19 winter steelhead returned to the North Santiam River. The FMEP evaluations are also outdated, for example, in relying on a 1987 study to presume merely 5% mortality of winter steelhead caught and released in the Santiam River basin. Currently, ODFW allows anglers to fish the North Santiam and South Santiam basins year-round, including when winter steelhead are present in the systems, and anglers may use baited, barbed hooks, including treble hooks. Even the FMEP evaluation and determination states, at attachment 1 at 8, that the "highest percentage (17.8%) of critical area hookings occur[] when using bait and treble hooks" in fisheries. The FEIS fails completely to consider or disclose the effects on winter steelhead of continued fishing for summer steelhead.

10. Section 5.4.4. states generally that "effects to natural-origin salmon and steelhead would be expected to decrease over time to the extent that fisheries management programs continued to reviewed and approved by NMFS." FEIS at 157. But the FEIS includes no information or data about any periodic review or approval of the fisheries by NMFS. Further, Section 5.5.3. states generalizations about ESA-listed fish in the UWR, but it does not respond to our comments about the effects on spring Chinook and winter steelhead of releasing hatchery fish into their habitats for the purpose of creating and maintaining a recreational fishery for hatchery fish.

11. Historically, ODFW has "recycled" a significant number of summer steelhead adults that return to the Foster Fish Facility in order to enhance fishing opportunities. For example, in 2013, for example, ODFW recycled 2,444 summer steelhead that returned to the facility. The FEIS fails to fully consider and disclose the significant effects of recycling. Erdman et al. (2018) (Ex. C) found that from 2012-2014, the majority of summer steelhead recycled in the Santiam River basin were not caught by anglers, and that a significant percentage of summer steelhead strayed after release. Indeed, the authors found that "[e]xpanded estimates indicate that the number of recycled summer steelhead remaining in the South Santiam River exceeded the winter-run steelhead spawning population size." NMFS notes that ODFW "may choose not to recycle," which appears to mean that NMFS believes ODFW has the discretion whether to do so or not. NMFS Resp. to WELC Comments #19. NMFS cannot prevent jeopardy to and ensure recovery of winter steelhead in the Santiam River basin unless it prohibits recycling of non-native summer steelhead.

12. Regarding recycling of summer steelhead in winter steelhead habitat to enhance fishing opportunities, NMFS notes that "there are management guidelines in the HGMPs that prohibit recycling after September 1st each year." NMFS Resp. to WELC Comments #19. That guideline appears to originate in the 2008 BiOp at RPA 6.1.7. The 2008 BiOp is out-of-date as to the best scientific data related to the effects of the summer steelhead program generally, and to the efficacy of the recycling guideline specifically.[1] Moreover, as noted above, reinitiation of consultation has begun on all federal actions that affect winter steelhead and spring Chinook in the UWR.

13. The summer steelhead HGMP states that for now, ODFW has chosen to "suspend the recycling programs in the Santiam Basin until there is evidence that the programs present little risk to winter steelhead (whether from introgression or from naturally produced summer steelhead)." StS HGMP at 15. There is ample evidence the summer steelhead program significantly harms winter steelhead in the

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[1] As just one example, the 2008 BiOp found an annual mean of 2,722 adult winter steelhead returning to the North Santiam River and 2,862 adult winter steelhead returning to the South Santiam River. BiOp at 3-21. Those figures are now dramatically out-of-date.

Santiam River basin. NMFS cannot prevent jeopardy to and ensure recovery of winter steelhead in the Santiam River basin unless it prohibits recycling of non-native summer steelhead in winter steelhead habitat.

Thank you again for the opportunity to comment.

References:

Erdman, C. S. et al. 2018. Release of hatchery adult Steelhead for angler opportunity increases potential for interactions with endemic Steelhead. Ecosphere, 9(10), e02448

Weigel D.E. et al. 2019. Introgressive hybridization between native and non-local steelhead (*Oncorhynchus mykiss*) of hatchery origin. Aquatic Conserv: Mar Freshw Ecosyst. 2019;29:292–302. https://doi.org/10.1002/aqc.3028

DEPARTMENT OF DEFENSE UNITED STATES OF AMERICA

DEPARTMENT OF THE ARMY
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JUN 13 2018

Planning, Programs and Project
Management Division

Ms. Allyson Purcell
Acting Anadromous Production and Inland Fisheries Branch Chief
National Marine Fisheries Service
1201 NE Lloyd Boulevard, Suite 1100
Portland, OR 97232

Dear Ms. Purcell:

Please find enclosed for your review the Summer Steelhead Hatchery Genetic Management Plan (HGMP) for the Upper Willamette River under the National Marine Fisheries Service's (NMFS) 4(d) rule for artificial propagation programs (65 Fed. Reg. 42,422; July 10, 2000). This is an update to the previous version submitted by the Oregon Department of Fish and Wildlife (ODFW) on 16 March 2018. The updates to the HGMP largely concern characterization of the purpose and authorization for the program. This final version is a collaborative effort between ODFW and the U.S. Army Corps of Engineers. It is submitted in accordance with, and in satisfaction of, Reasonable and Prudent Alternative Measures 6.1 and 6.2 of the 2008 Willamette River Basin Flood Control Project Biological Opinion.

It is our understanding that after review, NMFS will issue a sufficiency letter for the HGMP and continue its analysis of the proposed action pursuant to the Endangered Species Act. Upon completion of this process, it is our understanding that NMFS will issue a 4(d) authorization for the Upper Willamette River Summer Steelhead Program.

If you have any questions please contact Fish Biologist Ricardo Walker by email at ricardo.walker@usace.army.mil, or by phone at (503) 808-4709.

Sincerely,

Joyce E. Casey

Joyce E. Casey
Chief, Environmental Resources Branch

Enclosures

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RESEARCH ARTICLE

WILEY

Introgressive hybridization between native and non-local steelhead (*Oncorhynchus mykiss*) of hatchery origin

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Abstract

1. The artificial propagation and release of individuals from non-local populations is a widespread practice that can threaten the genetic integrity of native, locally adapted populations, because of domestication effects from the artificial rearing environments and inter-breeding with the local populations. Introgressive hybridization was examined in a threatened population of anadromous *Oncorhynchus mykiss* (Walbaum, 1792) (winter-run steelhead) in the Willamette Basin, Oregon. Non-local, hatchery-reared, summer-run steelhead are released annually into the basin as mitigation for the impact of numerous dams.
2. Sixteen microsatellite loci were used to detect introgression in adult steelhead of natural origin migrating into the basin before spawning during 2013 and 2014. Bayesian clustering analysis (STRUCTURE) was used to identify the level of admixture in the population and to assign individuals to clusters.
3. The Bayesian clustering analysis indicated that there are most likely two populations (or clusters) in the study area: a native, coastal, winter-run steelhead population and a non-local, summer-run steelhead population that was derived from artificial crosses between summer-run coastal and interior redband populations.
4. Introgressive hybridization was detected in 26.4% of the natural-origin adult steelhead. First-generation (F_1) hybrids were estimated as 4.9–10.1% of the natural-origin adult steelhead. Hybrids backcrossed to the native, coastal, winter-run steelhead were nine times more numerous than backcrosses to the hatchery, summer-run steelhead. The timing of upstream migration was significantly different between the native, winter steelhead and the F_1 hybrids.
5. Low numbers of summer steelhead and back-cross summer-run hybrids were identified in the natural-origin population, consistent with the reduced fitness of hatchery-reared summer steelhead in natural environments. Conservation actions that protect native populations from hatchery fish include altering stocking practices (such as integrated management or sterility), and protecting the remaining intact populations by designating genetic preserves and preventing the release of hatchery-origin or hybrid steelhead into these areas.

KEYWORDS

hatchery effects, hybridization, introgression, microsatellite, non-native species, *Oncorhynchus mykiss*, steelhead

1 | INTRODUCTION

The introduction of non-native species is a widespread management action implemented to support harvest in forestry, fisheries, and wildlife (Laikre, Schwartz, Waples, Ryman, & the GeM Working Group, 2010). The intentional introductions for the purposes of harvest programmes threaten native populations because of the high propagule pressure that is typical in these applications (Lockwood, Cassey, & Blackburn, 2005; Simberloff, 2009). Throughout the western USA, fisheries mitigation programmes largely developed in the early and mid-1900s rely heavily on artificial propagation to replace lost fisheries production (US House Document 531, 1949; Naish et al., 2007, and citations therein). Most of these programmes pre-date the US Endangered Species Act passed in 1973, and the subsequent listing of numerous salmonid species during the 1990s in the Pacific Northwestern USA. Fisheries management and mitigation programmes are challenged to balance these conflicting mandates, and may use non-local or non-native fish to satisfy harvest goals. Non-local and non-native salmonids cause significant impacts to the native populations, communities, and ecosystems (Buoro, Olden, & Cucherousset, 2016). Conflict between harvest or recreation management, and the conservation of native species (e.g. Shouse, 2003) can result in hatcheries having undefined or conflicting goals and objectives (Naish et al., 2007). Therefore, the evaluation of interactions between native and propagated populations is important to determine whether harvest and conservation programmes are in conflict, and to identify possible management strategies to reduce or eliminate any impacts to native species.

Non-local, domesticated, hatchery salmonids largely affect the native conspecifics through individual-based performance, such as physiological and fitness impacts (Buoro et al., 2016). Artificially reared non-native or non-local populations often have reduced fitness in the wild, because of domestication effects (Araki, Berejikian, Ford, & Blouin, 2008; Le Luyer et al., 2017). The demographic effect of continued introductions has been shown to cause the rapid extinction of native species, even with reduced fitness of the non-native or non-local population (Huxel, 1999; McGinnity et al., 2003). The reduced fitness of hatchery fish in the wild and the loss of production in the native population is identified in several commonly reared salmonid species, including *Oncorhynchus kisutch* (Walbaum, 1792) (coho salmon; Theriault, Moyer, Jackson, Blouin, & Banks, 2011), *Oncorhynchus mykiss* (Walbaum, 1792) (steelhead trout; Leider, Hulett, Loch, & Chilcote, 1990; Araki, Cooper, & Blouin, 2007; Berntson, Carmichael, Flesher, Ward, & Moran, 2011), *Salmo salar* (Linnaeus, 1758) (Atlantic salmon; Jonsson, Jonsson, & Hansen, 1991; McGinnity et al., 2003), and *Oncorhynchus tshawytscha* (Walbaum, 1792) (Chinook salmon; Chilcote, Goodson, & Falcy, 2011). Hatchery and wild crosses also have reduced fitness in the wild, with the poorest performance from non-local, hatchery sources (Araki et al., 2008).

Hatchery steelhead derived from an artificial mixture of non-local, summer-run subspecies are currently stocked in the Willamette Basin, a tributary of the lower Columbia River, USA, where the native winter-run steelhead population is protected under the Endangered Species Act. The stocking programme mitigates for impassable dams that block access for anadromous populations of steelhead and alters the remaining accessible habitats. The hatchery population of summer-run steelhead supports a local recreational fishery owing to the timing of return migration (from spring to autumn) and prolonged freshwater rearing before spawning (up to 12 months). The use of highly domesticated hatchery stocks, such as the Skamania stock used in the Willamette Basin (see below), is thought to limit the risk of colonization and hybridization resulting from low fitness in the wild (Naish et al., 2007). The objective of this study was to identify the extent of genetic interactions between the non-local, hatchery, summer-run steelhead and the native, natural-origin, winter-run steelhead by assessing the introgression and run timing of the hybrids. This study focused on the effects of introgression on run timing, which is the distinguishing phenotype between the summer- and winter-run steelhead; however, genetic impacts can occur in other phenotypes that were not measured, but can be meaningful to local adaptations and evolutionary potential.

1.1 | Steelhead taxonomy and the Willamette Basin

Oncorhynchus mykiss exhibits diverse life-history strategies. Variation is expressed within and among populations, and includes multiple return times for adults during spawning migrations, varying periods of freshwater and ocean residency, and the plasticity of life history between generations (Behnke, 1992; Busby et al., 1996). Two subspecies of *O. mykiss* are recognized in the Pacific Northwest: a coastal subspecies (*Oncorhynchus mykiss irideus*, also commonly called rainbow trout) and an interior subspecies (*Oncorhynchus mykiss gairdneri*, also commonly called redband trout) (Behnke, 1992). Life-history expression includes adult rearing in freshwater rivers (resident or fluvial) or in the ocean (anadromous) in both subspecies. Steelhead, the anadromous form of *O. mykiss*, exhibit different run timing and maturation phenotypes. The winter-run steelhead matures in the ocean and migrates upstream immediately before spawning. The summer-run steelhead matures in fresh water after returning from ocean rearing, resulting in a protracted period of freshwater rearing (Prince et al., 2017). Both phenotypes spawn in the late winter and spring months (from January to May; Van Doornik et al., 2015). The coastal subspecies largely expresses the winter-run maturation phenotype, but may also express an alternative summer-run phenotype in some locations, usually in upper-basin habitats. The interior, redband trout only expresses a summer-run, maturation phenotype (Behnke, 1992; Busby et al., 1996).

The native coastal steelhead in the upper portion of the Willamette Basin in western Oregon is a distinct population listed as threatened under the Endangered Species Act in 1999 (National Marine Fisheries Service, 2006). The native steelhead upstream from Willamette Falls had a unique migration timing that is later than other coastal steelhead populations and is thought to coincide with seasonal stream-flow conditions that allowed passage at Willamette Falls. Willamette Falls is a natural, 12-m high, horseshoe-shaped waterfall located at river km 42 that was altered with navigation locks in 1873 and hydropower facilities in 1889 (Oregon Historical Society, 2018; Portland General Electric (PGE), 2018). A fish ladder was installed in 1885 to assist the passage of salmon (PGE, 2018); before this ladder, only the later migrating native steelhead were able to ascend the falls.

The Willamette River Basin is 29 727 km^2, located in north-west Oregon, between the Cascade and the Coast Mountain ranges. The Willamette River is 301 km long and flows from south to north into the Columbia River. Most of the urban population in the state resides in the basin, including the cities of Portland, Salem, Corvallis, and Eugene (Figure 1). Hydropower and flood-control development in the basin occurred during the 1960s, and at present 13 high-head dams block access to 41% of native steelhead habitat (Sheer & Steele, 2006). The accessible, lower elevation areas of the basin are affected by habitat alteration, urbanization, and associated flood control, dam operations, and associated altered hydrology, climate trends, and landscape effects (see National Marine Fisheries Service, 2016 for more detail).

1.2 | Stocking history in the Willamette Basin

Stocking the non-local, summer-run (Skamania stock) steelhead began in 1966. Recently, the hatchery programme released an average of 572 411 juvenile steelhead annually between 2012 and 2017 at six sites in the study area (Oregon Department of Fish and Wildlife (ODFW) stocking records). Another non-native, hatchery-origin

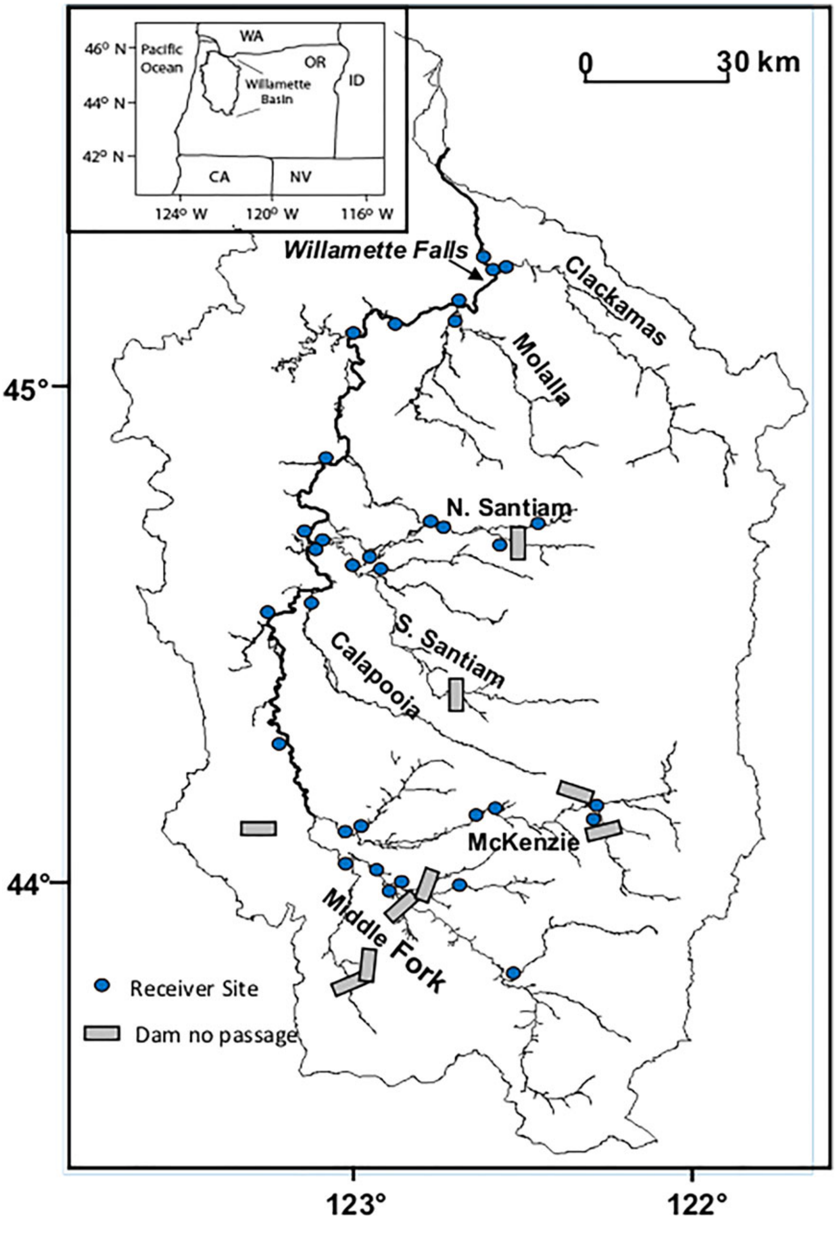

FIGURE 1 Map of study area and locations of the downstream-most impassable dams (grey rectangles) and stationary radio-telemetry receiver sites (blue circles) in the study area. Fish were captured and tagged at Willamette Falls fish ladder

coastal steelhead was artificially propagated and introduced in the basin upstream from Willamette Falls (commonly called 'early winter-run'), and naturalized populations are thought to migrate into the Willamette Basin during the autumn months, before spawning during the winter and early spring months (from October to February; Van Doornik et al., 2015). Introductions of this hatchery-reared, 'early winter' population (non-native coastal) were discontinued in the basin upstream of Willamette Falls during the 1990s, whereas introductions of the Skamania summer-run hatchery steelhead continue (Van Doornik et al., 2015).

Juvenile, hatchery-reared, summer steelhead are marked by removing the adipose fin, and these marked adults are collected for broodstock at hatchery facilities; adults with intact adipose fins are naturally produced steelhead, which can include the offspring of hatchery, summer-run steelhead that spawned in rivers, native winter steelhead, or hybrids. Hatchery-origin, adult, summer-run steelhead have outnumbered the natural-origin steelhead by 3 : 1 during the last 10 years (Figure 2). Overlap among the migration and spawning timing of these hatchery and native steelhead creates an opportunity for spatial and temporal overlap during spawning (Van Doornik et al., 2015).

2 | METHODS

Steelhead were collected to capture a representative sample of the natural-origin (with adipose fin present) steelhead population passing Willamette Falls. Some hatchery-origin, summer-run steelhead were analysed only to provide a reference for the population clustering, and provide an estimate of classification error from known (with adipose fin removed) individuals. Sampling of hatchery, summer steelhead ceased in late June because of high summertime water temperatures and compliance with sampling permits, and did not resume later in the run, after the summertime temperatures declined. Therefore, the hatchery, summer steelhead sample only captures the first half of the run during 2013.

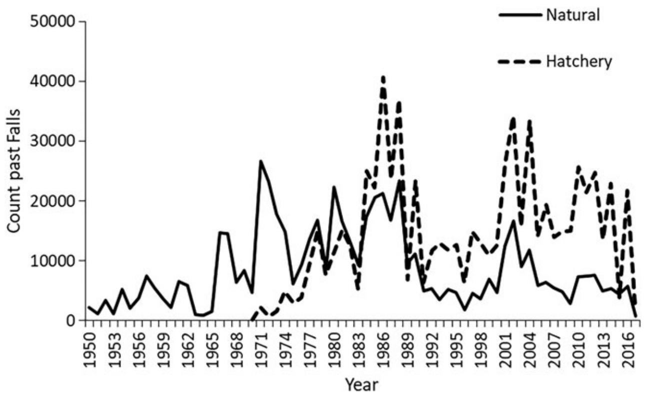

FIGURE 2 Counts of hatchery summer and native winter steelhead at Willamette Falls by year. Identification is based on adipose fin presence or absence. Data from Oregon Department of Fish and Wildlife (ODFW 2017)

2.1 | Fish collections

Upstream migrating adult steelhead were captured at the adult fish trap located at the Willamette Falls fish ladder from 22 January 2013 to 26 June 2013, and from 7 November 2013 to 4 June 2014. Steelhead were tagged and sampled in approximate proportion to the number passing the fish facility in each year. Sampled individuals represent an estimated 3.4% (2013) and 4.0% (2014) of the natural-origin steelhead (with adipose fin present) passing Willamette Falls.

Steelhead were anaesthetized with AQUI-S 20E (AquaTactics, Kirkland, WA) and a radio-tag implanted following the methods in Caudill et al. (2014). Total length and weight were measured, and the fish were checked for marks or tags, sex, and evidence of injuries or disease. Hatchery-origin, summer-run steelhead were identified by the removed adipose fin. Tissue was sampled as a caudal (tail) fin punch and dried on paper. Telemetry records from fixed-receiver sites (Figure 1) and mobile tracking were used to determine the upstream extent of migration and to infer spawning location using the methods described in parallel studies of Chinook salmon (Caudill et al., 2014; Keefer et al., 2017). In addition, radio tags provided information on the extent of upstream migration and potential spawning location, as well as the proportion of the individuals passing Willamette Falls that subsequently migrated downstream and out of the study area. All collection, handling, and tagging was performed using approved animal-care protocols and appropriate scientific collection permits.

2.2 | Laboratory methods

Sixteen microsatellite markers were used to genotype individuals. Thirteen of these markers were standardized across the Columbia River Basin, and are summarized by Stephenson et al. (2009). Additional primer sets analysed were *Omy*105, *Omy*2 (Heath, Pollard, & Herbinger, 2001), and *Omy*77 (Morris, Richard, & Wright, 1996). The DNA was isolated from fin clips using Qiagen DNEasy Blood and Tissue™ extraction kits (Qiagen, Inc., Germantown, MD), according to the manufacturer's protocols. Sixteen microsatellite loci were amplified by polymerase chain reaction (PCR) in three multiplex reactions using Qiagen Multiplex PCR Master Mix in 96-well plates on C1000 Touch and S1000 thermal cyclers (Bio-Rad, Hercules, CA). PCR details are provided in Appendix S1. The PCR products were run on an Applied Biosystems 3130xl Genetic Analyzer (Applied Biosystems, Foster City, CA). Forward primers were fluorescently labelled (6-FAM; Integrated DNA Technologies, Inc., Coralville, IA; VIC, PET, NED from Applied Biosystems). PCR product (1 μl) was added to 10 μl of formamide and 0.15 μl of LIZ500 size standard. Peaks were scored using GENEMAPPER 5 (Applied Biosystems). All samples were amplified two or three times to monitor for genotyping errors. Peaks were also visually checked for conformity with expected profiles. Laboratory error rates were estimated at 1%.

2.3 | Statistical analysis

The characterization of the natural-origin run is based on the genetic analysis of 'wild' (with adipose fin present) steelhead (*n* = 161 in

2013 and $n = 206$ in 2014). A sample of known hatchery-origin summer steelhead ($n = 89$) was included in the analysis during the 2013 spawning year to provide a genetic reference for this cluster (representing only the first half of this run). Data from the natural-origin run were first tested for allele frequency differences across spawning years for the natural-origin steelhead using GENEPOP 4.2 (Raymond & Rousset, 1995). All multiple comparisons were adjusted with a Bonferroni correction (Rice, 1989). No significant differences in allele frequency exact tests were identified, so data were grouped across years for the remainder of the analyses.

STRUCTURE 2.3.4 (Prichard, Stephens, & Donnelly, 2000) was used to identify the appropriate K value for the data set and to identify admixture among these populations in individual samples. STRUCTURE was run using the admixture model without location prior, with 10 000 iterations for burn-in followed by 100 000 iterations. Ten independent runs were performed for K values ranging from 1 to 8. The optimal number of populations (K) was chosen according to Prichard, Wen, and Falush (2010) and Evanno, Regnaut, and Goudet (2005). A K-means test was performed using GENODIVE (Meirmans, 2013) to confirm the number of clusters identified using STRUCTURE.

Individual admixture values (Q values) from the STRUCTURE output were averaged from the three runs with the lowest log likelihood, which indicates the best fit between the data set and the estimated parameters. Hybridized (admixed) individuals were identified from the averaged Q values at two levels of cluster membership (<0.8 and <0.9) to either parental cluster (native winter or hatchery summer), with hybrids assigned values between 0.2 and 0.8 or between 0.1 and 0.9, respectively. Individual steelhead were identified as native, hatchery, or hybrid fish based on the Q values and the most supported number of clusters. Fixation index (F_{ST}) and allele frequency exact tests were performed on the final population groups using GENEPOP 4.2 (Raymond & Rousset, 1995). The proportion of unmarked hatchery, summer steelhead was calculated as the number of hatchery steelhead out of the total number of the natural-origin steelhead. The hybridization rate was estimated as the proportion of the natural-origin first generation (F_1) hybrids in the sample. To account for a wide range of Q values documented for F_1 hybrids using STRUCTURE (Bohling, Adams, & Waits, 2012), a strict criterion (Q values from 0.4 to 0.6) and a relaxed criterion (Q values from 0.3 to 0.7) were evaluated to estimate hybridization in the sample. These Q values were selected based on STRUCTURE assignments compared with pedigree data that estimated individual F_1 hybrids with Q values from 0.23 to 0.73 (Bohling et al., 2012).

Simulated data were used to identify uncertainty in individual hybrid identifications, potential bias in the population-level estimate of introgression, and to inform error associated with misidentifications related to the different Q-value thresholds ($Q = 0.8$ versus 0.9). Error in the individual assignments was evaluated using HYBRIDLAB 1.1 (Nielsen, Bach, & Kotlicki, 2006) to simulate F_1 and backcross hybrids from the data set. The input data for the simulated hybrids were derived from 70 individuals from each subspecies collected during 2013 with Q values > 0.9 for native, winter steelhead and with Q values < 0.1 for hatchery, summer steelhead, with no missing data. Seventy F_1 hybrids and backcrosses to each parental species were simulated from the parental data. The input parental data and output hybrid data were run in STRUCTURE with $K = 2$, and all settings and procedures were similar to those described above. The assignments of the simulated individuals were compared with the true (known) genotypes.

A principal coordinate analysis on genetic distances was performed using GENALEX 6.5 (Peakall & Smouse, 2006, 2012) for individuals in the identified groups (native winter, hybrid, and hatchery summer, $Q = 0.9$). A chi-square test was used to test for differences from expected counts of native winter, hybrid, and hatchery, summer steelhead ($Q = 0.9$). Differences in the timing of upstream migration based on date of capture between the native winter and hatchery summer steelhead, and hybrids, were tested using a Kruskal–Wallis test in R 3.4.1 (R Core Team, 2017), followed by a Dunn test for multiple comparisons using FSA (Ogle, 2018). The date was converted to the number of days after 1 November when the fish was captured at the collection facility.

3 | RESULTS

STRUCTURE output identified the optimal number of clusters as two (Figure S1), and the K-means analysis supported two clusters in the data based on the maximum pseudo-F value (Meirmans, 2012, 2013). The genetic diversity measures (heterozygosity, allelic richness, etc.) between these two groups are summarized in Table S1. The potential for additional clusters in the data set were explored owing to previous research in the vicinity of the study area identifying three clusters in the study area (hatchery summer steelhead, and east side and west side tributaries; Van Doornik et al., 2015). The results considering three populations are included in Appendix S2. Briefly, the source of a third cluster is undefined, and only a small portion of the natural-origin adult steelhead collected at Willamette Falls (~7%, reduced to 5% after removing individuals that subsequently migrated downstream before spawning; Figure S2, Appendix S3). Steelhead in this cluster had an earlier timing of passage at Willamette Falls than the native (late) winter-run steelhead (Figure S3), and different F_{ST} and allele frequencies than the summer and winter groups in the data (Table S2); however, the principle coordinates analysis (PCoA) of genetic distances did not indicate clear clustering among the different genotypes (Figure S4). This additional cluster was not related to adult tributary migration (Figure S5) or life history. Hereafter, the results are presented for two steelhead populations, a native winter population and a hatchery summer population.

Hatchery-origin, summer-run steelhead clustered together in the STRUCTURE analysis, mostly following the hatchery identification (with adipose fin removed; Figure 3). Three hatchery-origin steelhead could not be assigned to the hatchery steelhead cluster (3.4% misassignment rate) based on these known samples. One of these hatchery-origin steelhead had a Q value equal to 0.74, which would classify as hybrid based on the Q value but predominantly assigned to the correct cluster. One steelhead was assigned as a hybrid with equal admixture among the populations, and one steelhead was assigned to the native steelhead group with a population assignment of 0.94. Similarly, a small portion of natural-origin steelhead were assigned to the summer-run, hatchery group (3.5% at $Q = 0.9$ and

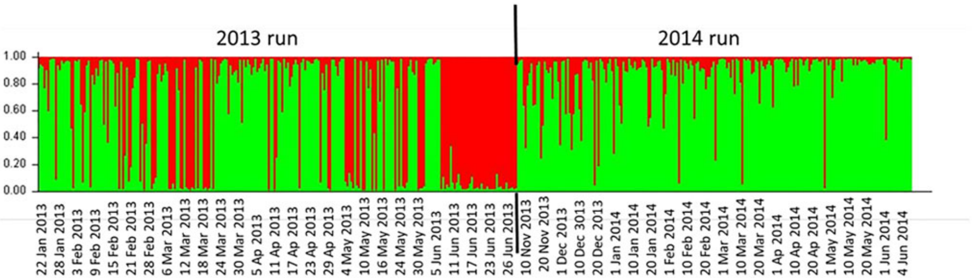

FIGURE 3 STRUCTURE plot with *K* = 2 for adult steelhead in the upper Willamette Basin. Individuals are represented by one bar in the plot and samples are ordered by date captured during the upstream migration (*x*-axis). The clusters group with native winter (green) and hatchery summer (red) steelhead. Hybridized individuals show contributions from both winter and summer steelhead, corresponding to the *Q* value shown on the *y*-axis

TABLE 1 Average *Q* value for individual assignments and standard deviation for hatchery and native steelhead and hybrids in the upper Willamette River Basin. Results for the two tested *Q* values (0.9 and 0.8) are presented

	Q = 0.90		Q = 0.80	
	Average	SD	Average	SD
Native, winter	0.96	0.00098	0.95	0.00132
Hatchery, summer	0.03	0.00069	0.04	0.00076
Hybrid	0.65	0.00375	0.56	0.00423

4% at *Q* = 0.8). Individual *Q* values were similar across the three independent runs examined (average standard deviation <0.005) with hybrids having higher average standard deviations than the parental populations (Table 1).

The estimate of introgressive hybridization ranged from 19 to 26.4% of the natural-origin steelhead at *Q* = 0.8 and 0.9, respectively. The hybridization rate, estimated as the number of F_1 hybrids, ranged from 4.9% (*Q* values of 0.4–0.6) to 10.1% (*Q* values of 0.3–0.7). The counts of individual native winter and natural-origin summer steelhead and hybrids were not significantly different across the two years ($P > 0.10$). Counts of the natural-origin (hatchery-lineage) summer, native winter, and hybrid steelhead were significantly different from the expected counts (χ^2 test, $P < 0.0001$), where native, winter steelhead were over-represented and hatchery summer steelhead were under-represented in the natural-origin steelhead (Figure S6). When the putative backcrossed individuals were examined (*Q* values 0.7–0.9 and 0.1–0.3 using the *Q* threshold of 0.9 for cluster assignment), there were nine times as many hybrids backcrossed to the native winter steelhead than the non-native hatchery summer steelhead in the sample.

The simulated data showed a wide range of individual *Q* values for each genetic assignment (native winter, hatchery summer, and hybrids), but the average values across the samples were close to the true genotypes (0.92 for native winter, 0.07 for hatchery summer, 0.49 for F_1 hybrids, 0.75 for F_1 × native winter and 0.22 for F_1 × hatchery summer) (Figures 4, S7). Individual misassignments between the native winter or hatchery summer steelhead and hybrid classifications generally ranged from 0 for F_1 hybrids using $Q = 0.9$ to 59% for backcrosses to hatchery summer steelhead using $Q = 0.8$ (Figure 5).

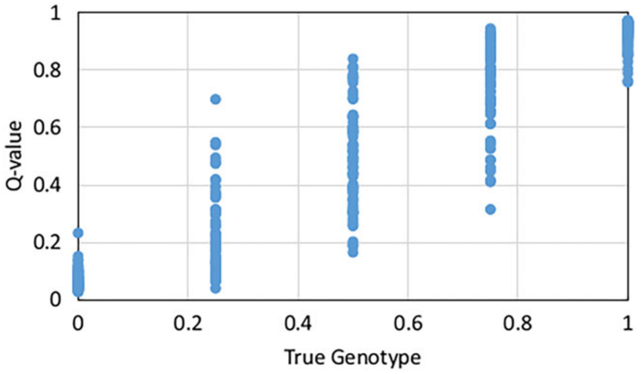

FIGURE 4 STRUCTURE output for individual simulated genotypes (*y*-axis) versus true genotypes (*x*-axis). The simulated hybrids are shown on the *x*-axis according to the proportion of native winter steelhead (0.5 for F_1 hybrids, 0.25 for F_1 × summer, and 0.75 for F_1 × winter)

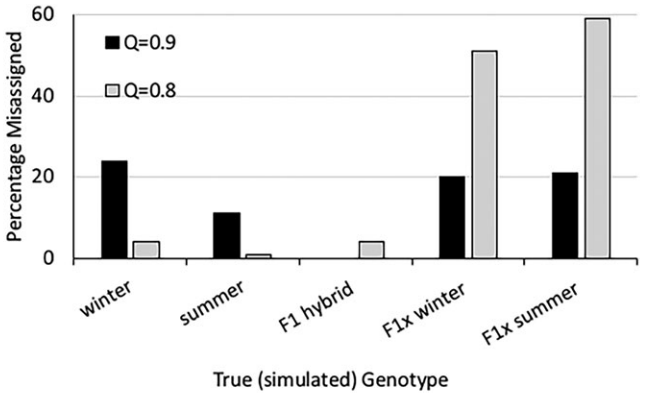

FIGURE 5 Percentage of individuals misassigned in each genotype category using a minimum *Q* value of 0.9 and 0.8 for cluster assignment. The misassignment rate is the proportion of true (simulated) individuals assigned as: known winter or summer assigned as hybrid; known F_1 or backcrossed hybrids assigned as winter or summer

TABLE 2 F_{ST} and allele frequency tests among clusters identified by STRUCTURE at *K* = 2. F_{ST} values using a *Q* value of 0.8 are shown above the diagonal and F_{ST} values using a Q value of 0.9 are shown below the diagonal. All pairwise comparisons had significantly different allele frequencies

	Native, winter	Hybrid	Hatchery, summer
Native, winter		0.015	0.057
Hybrid	0.013		0.022
Hatchery, summer	0.065	0.028	

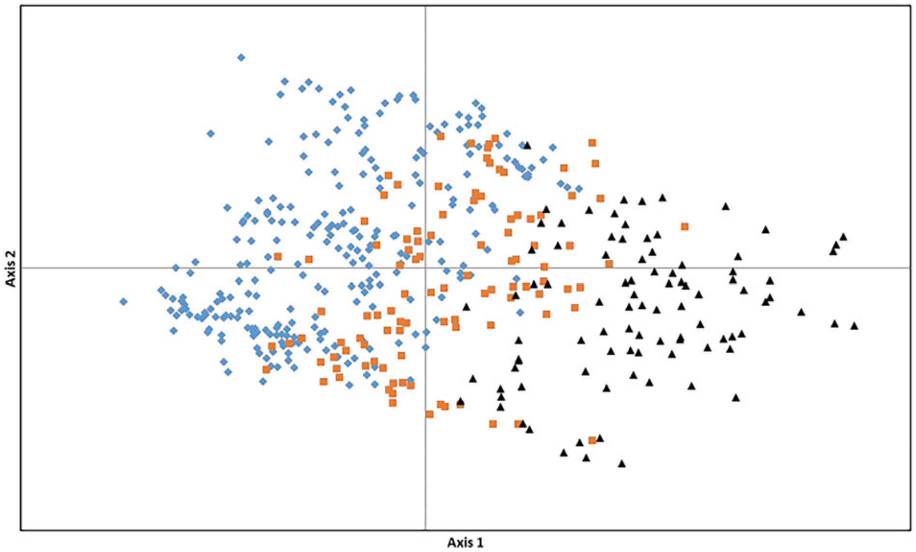

FIGURE 6 Principal coordinates analysis (PCoA) of individual genetic distances for steelhead in the upper Willamette Basin (Q = 0.9) for native winter (blue diamonds), hatchery summer (black triangles), and hybrids (orange squares) identified by STRUCTURE output

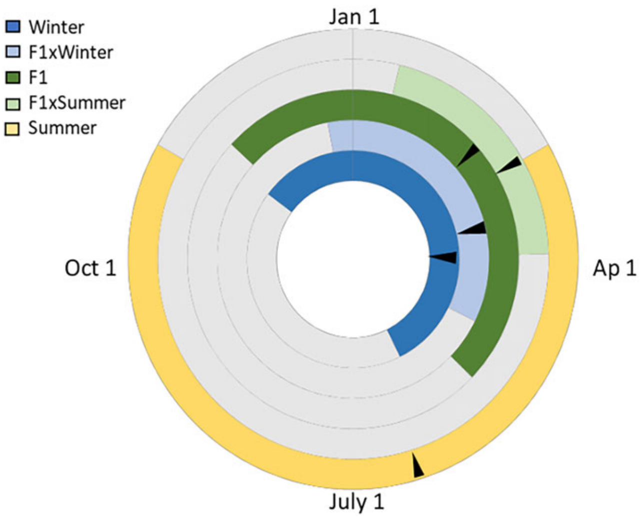

FIGURE 7 Migration timing (range and median) of natural-origin steelhead by genotype (native, winter steelhead, F_1, and backcrossed hybrids) and hatchery-origin summer steelhead at Willamette Falls. The native winter and hybrid run timing is based on the genotyped sample collected for this study. The hatchery summer steelhead run timing is based on the run counts at Willamette Falls for the adult returns for the 2014 spawning year (return date from 1 November 2013 to 31 October 2014) (ODFW, 2017)

The Q-value threshold of 0.9 generally provided lower error rates, and the incorrect identifications were nearly equal between the backcrossed hybrids identified as parental type and the parental (hatchery or native) groups identified as hybrids, providing the most accurate estimate of introgression overall. A Q-value threshold of 0.8 provided an unbalanced proportion of misassignments, with fewer parentals misassigned as hybrids, but with high proportions of backcrossed hybrids misassigned as parentals (>50%). In terms of our F_1 hybrid criteria (relaxed versus strict), the strict criterion only correctly identified 40% of the true F_1 hybrids and 11% of the backcrossed hybrids, whereas the relaxed criterion identified 73% of the true F_1 hybrids and 31% of the backcrossed hybrids. Neither the strict nor relaxed criterion identified a true parent as a hybrid.

Pairwise F_{ST} values were similar for the different Q values, but were slightly greater for the Q-value threshold of 0.9 (Table 2). Hybrids were more similar to the native group (F_{ST} 0.01 and 0.02) than to the hatchery summer group (F_{ST} 0.03). Only 9% of the variation of individual genetic distances was explained by the first and second principal coordinate axes; however, the data show a clear gradation of genetic distances among the groups, with hybridized individuals intermediate between the native and hatchery groups (Figure 6).

The date of upstream migration was significantly different among the native winter, hatchery summer, and hybrid groups ($P < 0.001$); however, pairwise tests identified that the F_1 hybrids and native winter steelhead were the only significantly different comparison ($P < 0.001$). The median migration date at Willamette Falls was earlier for all hybrid groups than the native winter-run steelhead (Figures 7, S8).

4 | DISCUSSION

The continued and frequent introduction of non-native or non-local populations results in high propagule pressure that artificially increases the abundance and density of the non-local, hatchery individuals (Lockwood et al., 2005; Simberloff, 2009), and counters the effects of reduced fitness of the hatchery fish in natural environments. In the upper Willamette Basin, the hatchery summer steelhead in the basin outnumber the native winter steelhead preceding reproduction (Erdman, Caudill, Naughton, & Jepson, 2018). Introgression was detected in 26.4%, and F_1 hybrids were detected in 4.9–10.1%, of the natural-origin samples. The simulation results support the estimated rates of introgression. Hatchery summer steelhead were significantly under-represented in the natural-origin steelhead samples, indicating a lack of fitness in the natural environment. Individual putative backcrossed hybrids to the native winter steelhead were nine times more numerous than hybrids backcrossed to the hatchery summer steelhead. Hybrid steelhead had an earlier median run timing than the native, winter-run steelhead. Although the original (pre-stocking) genetic differentiation between these populations is unknown, introgressive hybridization can alter the genetic integrity of the native population and lead to its replacement by the non-native population (Ford, 2002; Huxel, 1999). Local adaptations and genetic diversity lost in these processes may not be recoverable in time frames relevant to the management and preservation of natural resources (~100 years), which could reduce the evolutionary potential of the population (Prince et al., 2017; Waples & Lindley, 2018).

4.1 | Accuracy of hybridization and introgression estimates

A key question is whether admixture is under- or over-estimated at the population level using the STRUCTURE assignments. The estimation of introgression first depends on the ability to reliably detect the clusters in the analysis, the accuracy of which improves with greater genetic differences. Simulated data sets estimate that STRUCTURE is about 97% accurate when F_{ST} is 0.05 (Latch, Dharmarajan, Glaubitz, & Rhodes, 2006), a level of differentiation similar to the populations included in this study. Yet, at the individual level, hybrids have a wide range of admixture estimated by STRUCTURE, but the mean *Q* value of each type of hybrid was close to the expected value when tested with a known pedigree (also shown in Bohling et al., 2012). Furthermore, the user-defined *K*-value and *Q*-value thresholds will influence the amount of introgression estimated using these methods (for further discussion, see Appendix S5). In a simulated data set, using a *Q* value of 0.8 resulted in 42% of backcrosses being incorrectly assigned to the purebred group, whereas using a *Q* value of 0.9 reduced this error to 19% (Vaha & Primmer, 2006), similar to the simulation results. Certainly, at the individual level and with low genetic differentiation ($F_{ST} < 0.1$), there is error in the identification of individuals. Based on the findings in Vaha and Primmer (2006), at an F_{ST} value of 0.06 about 80% of the individuals in this sample would be correctly identified using 16 loci. The simulated hybrid data set confirms this 20% error in assignment between parental groups and backcrossed hybrids. Overall, these data and other studies suggest high rates of correct assignment for F_1 hybrids and unbiased population-level rates.

4.2 | Potential factors mediating introgression from hatchery steelhead

Hatchery summer steelhead have been stocked in the study area for about 10 generations, and two explanations are possible for the observed hybridization pattern in the natural-origin population. First, the genetic differentiation in the native winter and hatchery summer populations could be a result of genetic mixing that is reducing genetic differentiation over time and moving the populations towards a hybrid swarm; where the sample represents a ‘snapshot’ during a temporal process. Under this scenario, introgression is expanding towards an inevitable hybrid swarm, and delaying a management action will result in the extinction of the native genotype. An alternative hypothesis suggests that the level of introgression could be mediated by a loss in fitness of hatchery summer steelhead and hybrids – thereby resulting in a stable level of introgression (Chilcote et al., 2011). Epifanio and Philipp (2001) show that introgression will reach an asymptote at about 20% admixture in 10 generations, when the fitness of the hybrids is low. This scenario requires very low relative fitness of the hybrids at 0.15. In their model, even a slight increase of relative fitness to 0.20 resulted in complete introgressive hybridization within 11 generations. If introgression is stabilized at these levels, it is possible that discontinuing the release of artificially propagated summer-run steelhead, which have very low fitness in the natural environment, could result in eliminating the summer-run steelhead in the population. Under this scenario, the potential negative effects of introgression may be limited if selection can restore the phenotypic expressions of the native population. Although assortative mating could be a mechanism that maintains genetic differentiation, providing another alternative hypothesis, Epifanio and Philipp (2001) showed that strong pre-mating isolation alone is insufficient to prevent a complete hybrid swarm if the fitness of the hybrids is at least 0.20 of the fitness of the native species or population. Even considering a conservative estimate of F_1 hybridization, the spatial and temporal overlap between the native winter and hatchery summer steelhead is enough to cause introgression. In addition, the timing of spawning between the native winter and the hatchery summer steelhead overlaps (Van Doornik et al., 2015), minimizing the potential for segregation in the natural environment.

The timing of adult migration is a heritable trait in salmonids, and has substantial fitness consequences if not synchronized with local environmental conditions (Flagg, Waknitz, Maynard, Milner, & Mahnken, 1995; Hess, Zendt, Matala, & Narum, 2016; Jones et al., 2015; McLean, Bentzen, & Quinn, 2005; Quinn, Peterson, Gallucci, Hershberger, & Brannon, 2002). Few natural-origin summer steelhead were detected in the population, and lower numbers of putative hybrids were backcrossed to the hatchery summer steelhead, despite high abundances of hatchery summer steelhead in the population during reproduction. Jones et al. (2015) found similar proportions of hatchery, hybrid, and wild steelhead in a stream in south-west Washington (1% natural-origin, hatchery-lineage steelhead and 29% hybrids), and concluded that the earlier-spawning hatchery steelhead were emerging during unfavourable conditions; however, the later-emerging hatchery steelhead were more likely to encounter better environmental conditions for early rearing, resulting in selection for this later migration timing that is more similar to the native population.

Recent research indicates that modifications at the *GREB1L* gene are associated with premature migration, and that premature migration (expressed in summer steelhead) is not masked in the heterozygote (Prince et al., 2017). Yet, upstream migration after maturation is not a conduit for the premature migration allele, and data patterns indicate selection against the intermediate phenotypes (Prince et al., 2017). This interaction between run timing, maturation, and spawning timing is likely to be a complex expression of multiple gene complexes (Waples & Lindley, 2018, and citations therein). The earlier run timing expressed via the summer introgression in this data set suggests that the later-migrating hatchery summer steelhead (from August to October) may have a greater likelihood to hybridize with the native winter steelhead that spawn after the summer steelhead. An alternative explanation for the observed influence of the later-migrating hatchery summer steelhead in the hybridized individuals could be less opportunity for removal from the population through reduced fishing pressure or other mortality during freshwater maturation.

4.3 | Conservation and management

Options for harvest-focused hatchery programmes are to maintain programmes with complete segregation between the native wild and hatchery populations, or to fully integrate the two populations, with the hatchery programmes providing surplus production to meet harvest goals. Unfortunately, the efficacy of these approaches has not been tested over the long term (Naish et al., 2007). Complete segregation relies on the ability to collect all artificially propagated adults before spawning. Various other management strategies to support segregation have been attempted to address threats from hatchery fish, such as introducing sterile hatchery fish (Tiwary, Kurbagaran, & Ray, 2004), where the threat of introgression or inter-breeding is high (Cotter et al., 2000), and the designation of genetic preserves (also called gene banks) to protect and promote the recovery of native populations (Washington Department of Fish and Wildlife (WDFW), 2015). Integration is also commonly implemented, but the rapid epigenetic effects creates challenges to limit the transmission of genetic impacts on wild populations (Le Luyer et al., 2017).

Reduced fitness and misidentification are a concern when stocking hatchery fish without complete segregation. Hybrids and natural-origin, hatchery individuals will be counted as native species during abundance estimates and population demographic analyses. At present, managers in the study area are transplanting wild and presumably native winter steelhead returning to the basin into inaccessible spawning areas upstream from dams, thereby introducing the hatchery-origin summer steelhead genes into these areas. Although the majority (~70%) of the natural-origin adults returning to the upper Willamette Basin are identified as native winter steelhead, the estimate of encounter rates based on the observed proportions of F_1 hybrids in the data set is a concern. This probably underestimates the effect of the hatchery summer steelhead, because of the low expected fitness in the wild. For example, at a hybridization rate of 5% and a relative fitness of 0.10, the hybrid encounter rates not expressed in the observed data could be as high as 50%. If the relative fitness is increased to 0.40, then hybrid encounter rates would be about 12%.

Future research should examine the fitness consequences to the hybridized individuals and identify the effects of the mitigation stocking programme on the population demographic. Fitness can be acquired from individual-based lifetime tagging studies and genotyping over time; however, spawning behaviour, hybridization attempts, and redd disturbance may be difficult to estimate because of the high stream flows, low water visibility, and large habitats where steelhead occur in the study area. Importantly, long-term studies are needed to best identify strategies for preventing impacts on the native, wild populations. Information on the migration and spawning behaviour of the later-migrating (passing Willamette Falls between 1 August and 31 October) hatchery summer-run steelhead is lacking, and information on whether these individuals are more likely to contribute to hybridization could assist in identifying potential management actions to reduce any effects in the basin. In addition, fisheries management in the local basin has included the practice of 're-cycling' hatchery, summer steelhead to maximize angler opportunity (trapping, transporting, and re-releasing adult hatchery steelhead downstream). However, although this programme boosts angler harvest by an estimated 15%, it is also likely to increase the reproductive interactions between hatchery and wild steelhead, by leaving many mature, hatchery steelhead in the river (Erdman et al., 2018).

Areas such as the Columbia River Basin, where existing harvest and conservation policies are in conflict, demonstrate that clear guidance on priorities and updated policies that ensure and encourage the conservation of native species and ecosystem functioning are needed to assist in the complex processes of implementing fishery programmes under these laws. Yet, defining common policies has proved challenging when management actions span multiple agencies with different underlying objectives. Even within agencies, different departments may have their own competing objectives and complex infrastructure. Areas currently developing new hydropower projects should strive to fully balance the conservation of native species with the replacement (or mitigation) for lost subsistence and commercial fisheries, and should create programmes and policies that can evolve with scientific advances and sociopolitical concerns. Areas where artificial propagation is planned or is continuing should implement genetic monitoring practices to ensure the preservation and evolutionary potential of native genotypes (Bohling, 2016; Schwartz, Luikart, & Waples, 2007), and should promote adaptive management based on scientific findings and the best available science.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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Supporting Information

Weigel et al. (2018) Aquatic Conservation

Introgressive Hybridization Between Native and Hatchery-origin Non-native Steelhead (*Oncorhynchus mykiss*)

S.1 Detailed PCR Methods

Multiplex 1 consisted of 0.04 µM of Ogo4, 0.06 µM of Ssa408, 0.10 µM of Omy2, 0.13 µM of Omy1001, 0.43 µM of Ots100, 1X Qiagen Multiplex PCR Kit Master Mix, 0.5X Q solution and 1 µl of DNA extract in a 7 µl total reaction volume. Multiplex 2 consisted of 0.03 µM of Ssa407, 0.04 µM of Oki23, 0.06 µM of Omy7, 0.71 µm of Omy105 and Oke4, 1X Qiagen Multiplex PCR Kit Master Mix, 0.5X Q solution and 1 µl of DNA extract in a 7 µl total reaction volume. Multiplex 3 consisted of 0.04 µM of Omy1011 and Ots4, 0.13 µM of One14, 0.21 µM of Omy77, 0.29 µM of Ssa289, 0.50 µM of Ots3, 1X Qiagen Multiplex PCR Kit Master Mix, 0.5X Q solution and 1 µl of DNA extract in a 7 µl total reaction volume. The thermocycler profile for Multiplexes 1 and 2 was an initial denaturation of 94 °C for 15 min followed by 15 cycles of 94 °C for 30 sec, touchdown 63 °C to 57 °C for 1.5 min and 72 °C for 1 min, followed by 15 cycles of 94 °C for 30 sec, 57 °C for 1.5 min and 72 °C for 1 min with a final elongation of 60 °C for 30 min. The thermocycler profile for Multiplex 3 was the same as above except a touchdown from 57 °C to 50 °C and a final annealing temperature of 50 °C.

S.2 Model Fit, Genetic Diversity and Analysis of Data Using K=3 in STRUCTURE

Another analysis of genetic data on the upper Willamette Basin steelhead indicate that there are three populations of steelhead: the hatchery summer run steelhead derived from the Skamania stock, and then two population divisions separating the eastern and western tributaries. The western portion of the basin is thought to maintain populations established from hatchery introductions of the non-native early winter steelhead, whereas the eastern portion of the basin is thought to maintain native, (late) winter-run steelhead (Van Doornik et al. 2015). The genotypic data from samples collected at Willamette Falls during this study indicate that two clusters of data is most supported, a native winter-run and a hatchery, summer-run. If a third population group is considered, potential populations would be non-native early winter hatchery steelhead or some population subdivision within the study area. Using K=3, the number of steelhead in this additional (3rd) cluster was small in our sample (~7% of the population, Fig. S2) and these fish returned only slightly earlier than the other natural-origin steelhead in our sample (Fig. S3). Additionally, examination of variation of individual genetic distances using PCoA also indicated that the identified clusters were not distinct from each other (Fig. S4).

Figure S1. STRUCTURE model output for lnP(K) with standard deviation bars and delta K. The number of clusters (K) is on the x-axis.

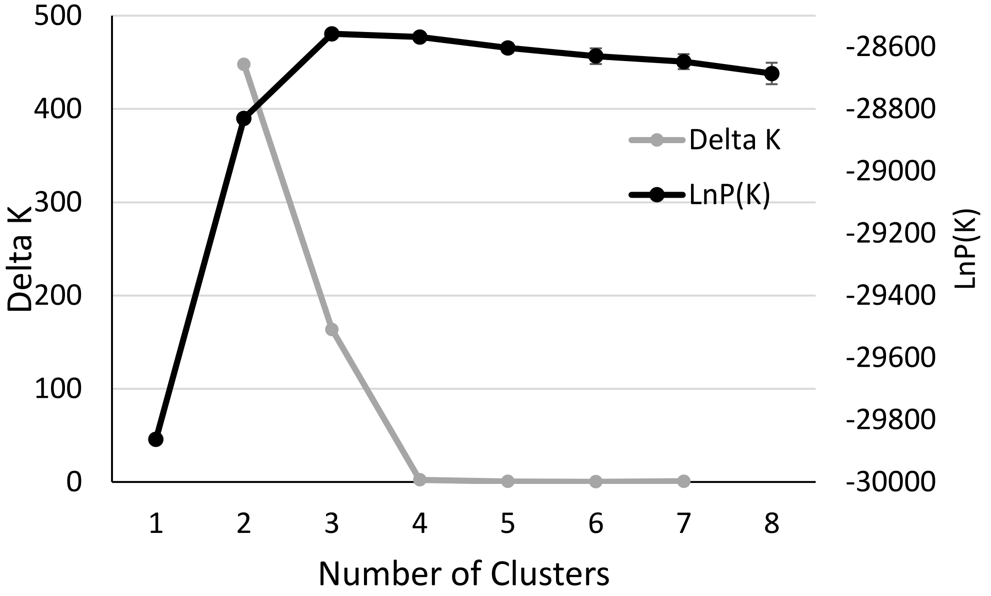


Table S1. Summary of sample size (n) and genetic diversity measures for native winter (natural-origin, adipose present, Q>0.9) and hatchery summer steelhead (adipose removed). Observed and expected heterozygosity and number of alleles were calculated using GENEPOP. Allelic richness and private alleles were calculated using HPRare (Kalinowski, 2005).

	native winter	hatchery summer
Sample size	258	89
	Observed	
Range of number of alleles per locus	5-38	5-24
Avg. over all loci	15.7	11.3
Range of Ho	0.43-0.91	0.56-0.95
Ho avg over all loci	0.71	0.78
	Adjusted for sample size	
Range of He	0.50-0.95	0.65-0.92
He over all loci	0.76	0.80
Allelic Richness	6.2	6.2
Private Alleles	3.4	3.4

Figure S2. STRUCTURE output for K=3 arranged in order of return date at Willamette Falls. Each bar represents one individual in the sample. Hatchery summer steelhead (non-local) are shown in blue, late migrant winter steelhead (native) are shown in red, and early-migrant winter steelhead (non-local) are shown in green. Known hatchery steelhead (adipose fin removed, n=89) were included in the 2013 run only.

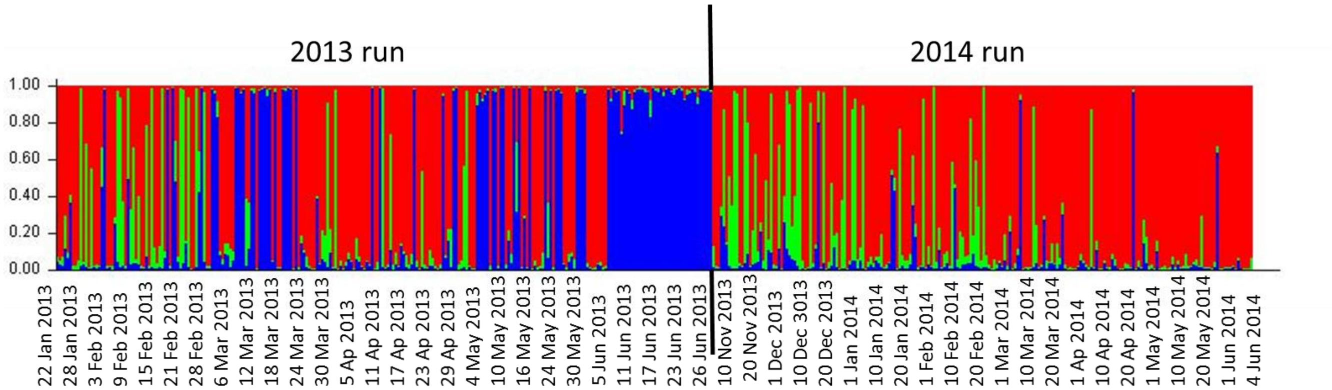


Figure S3. Migration timing for the (suspected) non-native early winter, native late winter and hybrid steelhead identified in the upper Willamette Basin. The Kruskal-Wallis test was significant ($p<0.001$).

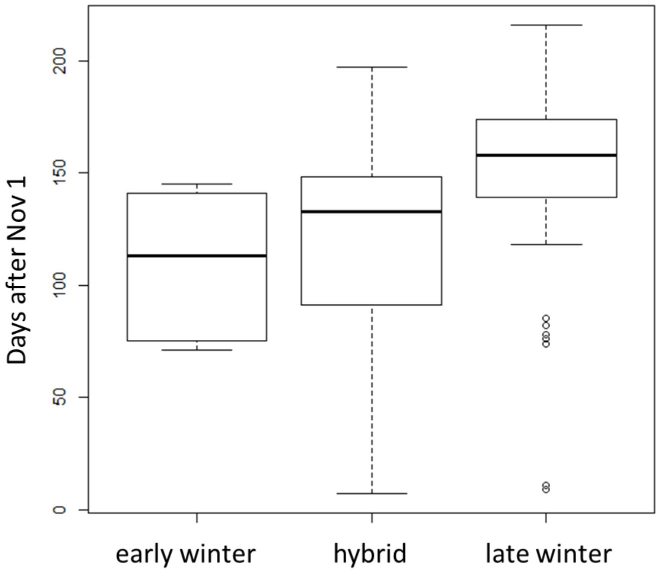
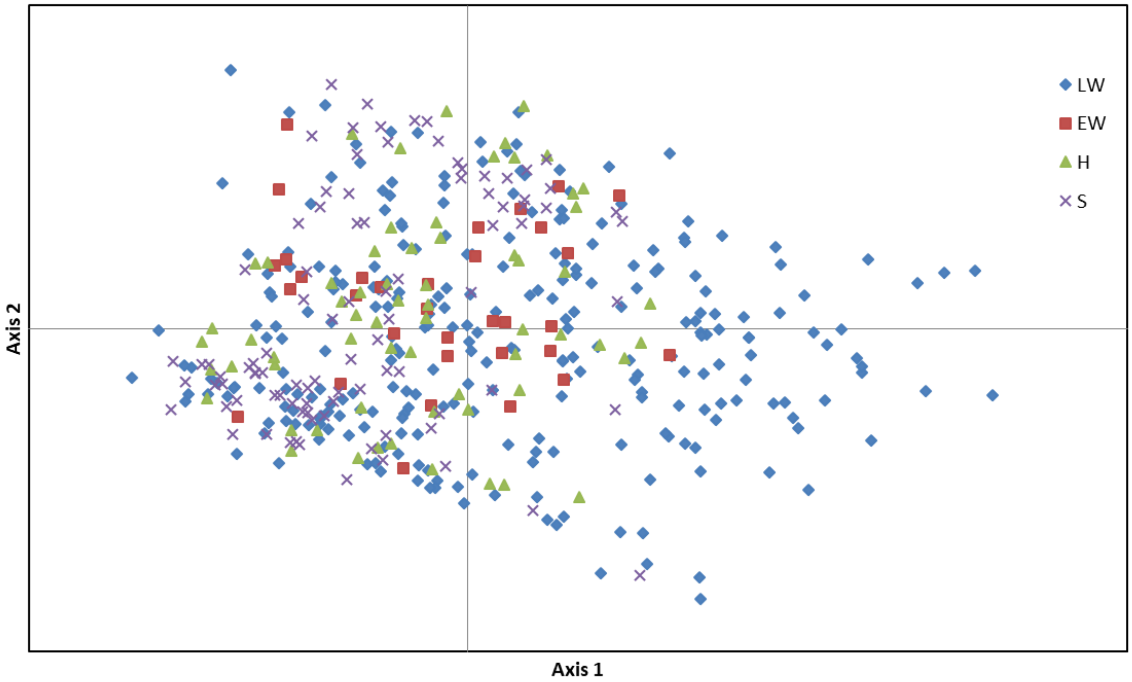


Table S2. F_{ST} and allele frequency tests among clusters identified by STRUCTURE at K=3 which included two winter (early and late migration timing) and one hatchery summer steelhead groups. F_{ST} values using a Q-value 0.8 are shown above the diagonal and Q-value 0.9 is shown below the diagonal. All pairwise comparisons had significantly different allele frequencies.

	winter early	hybrids	winter late	Hatchery summer
Winter Early		0.01	0.04	0.04
Hybrids	0.02		0.01	0.03
Winter Late	0.05	0.01		0.06
Summer	0.05	0.03	0.07	

Figure S4. Principal coordinates analysis of genetic distance performed in GENALEX version 6.5 for individuals based on the STRUCTURE identification with K=3. The clusters shown include the native, winter-run steelhead (LW), hybrids (H), hatchery, summer-run steelhead (S), and an earlier migrating winter-run steelhead (EW).



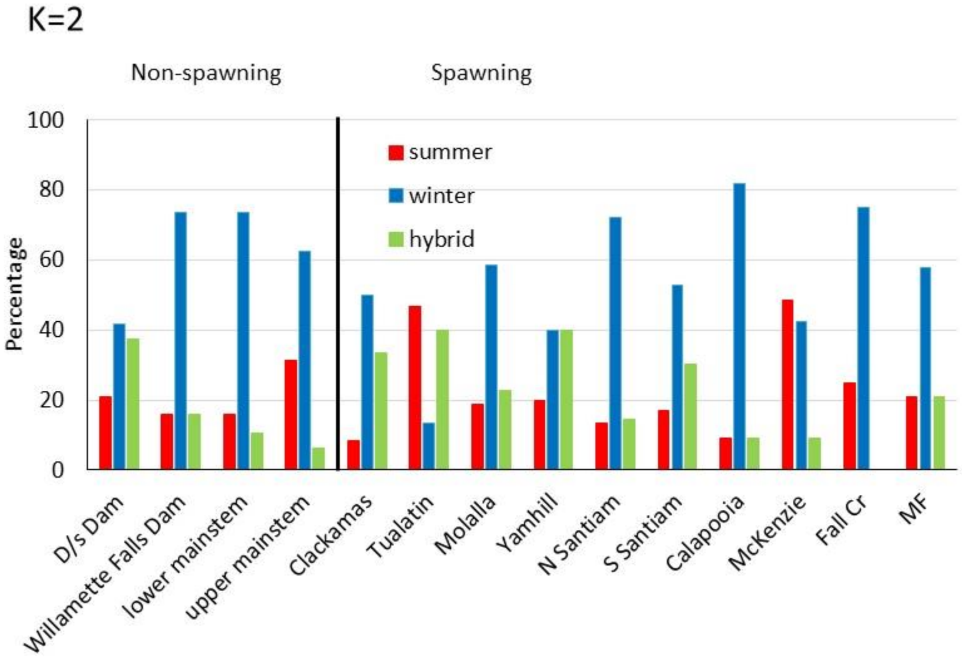
S.3 Upstream Migration and Spatial Distribution Based on Radio-tracking

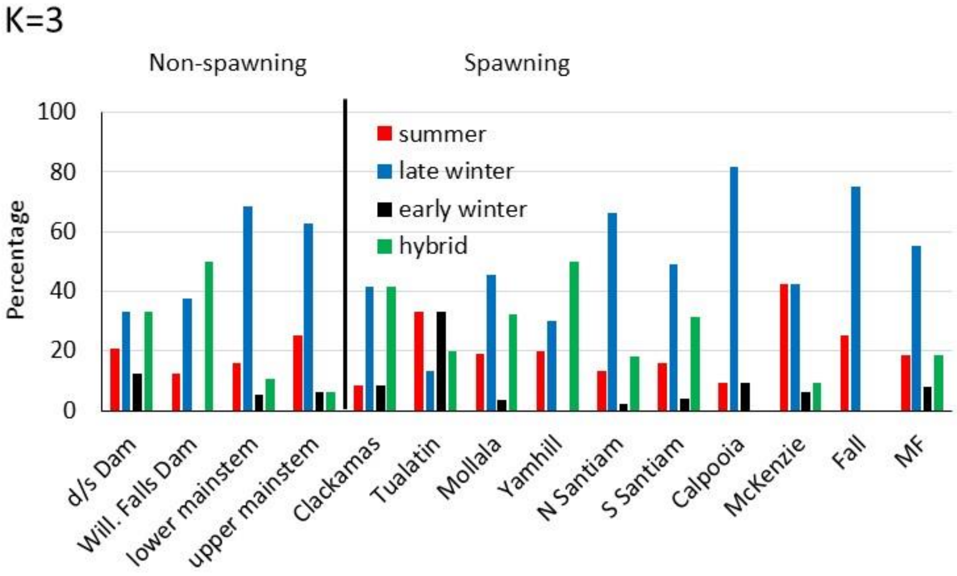
The proportions of native winter and hybrid steelhead migrating to various locations in the basin are representative of the total natural-origin population; however, the proportion of the hatchery summer steelhead under-represents the entire population because not all of the known hatchery summer steelhead were genotyped for this study, and some tag loss is expected due to the long instream residence time for this group (~12 months from tagging to spawning). The hatchery summer steelhead included in Fig. S5 represent individuals present during spawning after harvest and other potential instream mortality. The data presented here are based on individual genetic identifications and should be interpreted cautiously according to the data analysis from simulated crosses (*i.e.* about 20% error between parent (native winter or hatchery summer) and hybrid steelhead). Additionally, the percentages presented in Figure S5 are the proportion of the total number of steelhead (natural-origin plus hatchery-origin) that entered the tributary stream and are not the same as the percentages calculated for the natural-origin portion of the population in the main body of the published paper.

Radio-tracking performed during our study found that 5% of the individuals captured and tagged at Willamette Falls immediately moved to downstream populations (Jepson et al., 2015) which included 15% of the early winter individuals. After removing the early winter individuals that migrated out of the study area (*i.e*. "fall back"), the 3rd cluster only represents 5% of the natural-origin run. It is possible that these individuals are remnants from stocking hatchery-reared, non-local, winter-run coastal steelhead in the basin (as proposed by Van Doornik et al., 2015); however, the spatial distribution of the upstream-most migration indicates that these individuals are not homing to a limited number of locations (such as the west side tributaries), but instead are dispersing throughout the study area, behavior more similar to strays (Fig. S5). Straying in coastal steelhead populations is about 14% (Schroeder et al., 2001), so the number of individuals in this cluster is smaller than the expected straying rates.

The upstream-most migration detected from radio-tags indicated no spatial patterns in the distribution of native winter, hybrids or hatchery summer steelhead in the upper Willamette Basin (Fig. S5). The Calpooia steelhead appear to remain a native, winter-run steelhead population; however, the radio-tags indicate that a small proportion of summer steelhead and hybrids successfully migrate into the tributary during spawning season, indicating that the habitat in the Calpooia may to some degree protect this population from introgression. The McKenzie is believed to be a naturalized population derived from returning hatchery, summer-run steelhead; however, the proportions of hatchery summer to native winter run steelhead are similar into this tributary, potentially indicating that this location is a demographic sink for some native winter steelhead returning to spawn. The Tualatin River also supports a larger proportion of hatchery, summer-run adult returns and hybrids (Fig. S5).

Figure S5. Upstream-most migration prior to spawning for radio-tagged steelhead in the upper Willamette Basin (Jepson et al., 2015) by genotype.





S.4 STRUCTURE Model Output and Analyses

Figure S6. Distribution of the percent native winter steelhead genotype (Q-value) in the natural-origin (adipose fin present) adult steelhead sampled at Willamette Falls. This figure shows more individuals in the natural-origin sample clustering with the native winter steelhead and higher numbers of individual F_1 x native winter hybrid backcrosses.

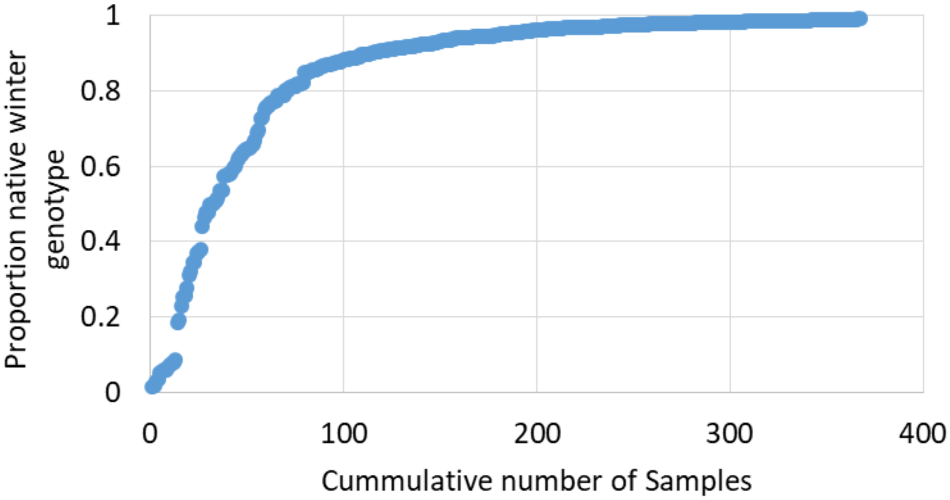


Figure S7. STRUCTURE output from simulated data used to estimate error rates for hybrid identification. The parental data (native winter and hatchery summer steelhead) were individuals with Q-values >0.9 from the samples collected between January and June 2013. The hybrid data were generated using HYBRIDLAB. Green indicates the native winter genotype and red indicates the non-local, mixed lineage hatchery summer genotype. The solid black lines represent the Q-value thresholds for the parental cluster assignments, and the dashed black lines represent the relaxed criterion for the identification of F_1 hybrids.

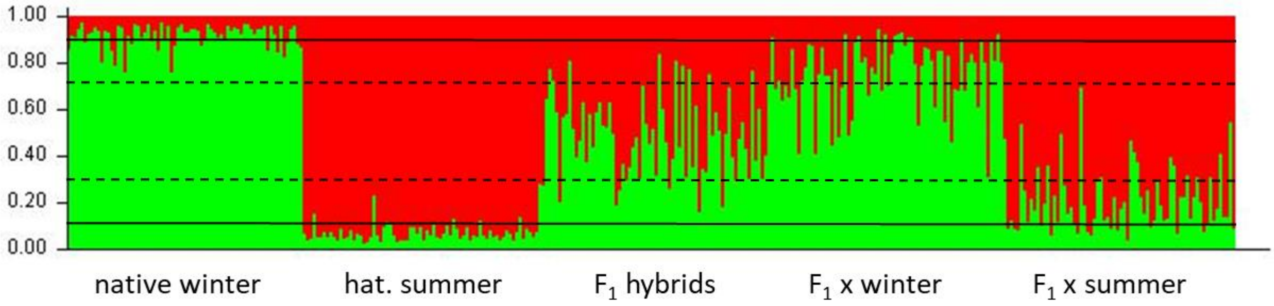
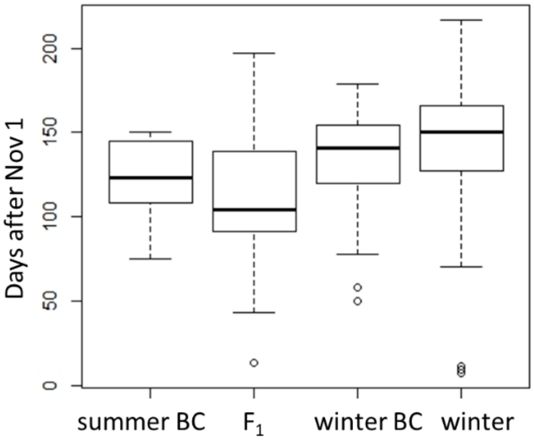


Figure S8. Run timing for hybrid (F_1 and back cross (BC)) and native winter genotypes.



S.5 Effect of K and Q on Estimating Introgression

The user-defined K-value and Q-value thresholds used with STRUCTURE input and output alters the identified proportions of individuals assigning to clusters or hybrid classifications. Therefore, the selection of these values coupled with an examination of classification accuracy is important. In this study, both STRUCTURE output and a K-means test supported the selection of K=2, over other possible K-values, and the simulation tests performed at K=2 supported more accurate sample-wide estimation using a Q-value threshold of 0.9 for cluster assignment. Yet, the selection of K-value and Q-value criterion can influence the estimate of introgression from the hatchery, summer-run steelhead in this data set. Figure S9 shows how these two values provide similar estimates when considering larger, population-wide estimation of cluster membership, and Fig. S10 shows how these two values interact when estimating introgression from hatchery, summer steelhead.

Simulated data sets estimate that STRUCTURE is about 97% accurate when F_{ST} is 0.05, and decreases with lower differentiation with F_{ST} value of 0.03 the limit of detection (Latch et al., 2006). When trying to also identify introgression, greater genetic differences (F_{ST}) and more loci are required (Vaha & Primmer, 2006). At an F_{ST} of 0.06, 48 loci would be needed to achieve accuracy of 95% (Vaha & Primmer, 2006). A Q-value of 0.9 has the highest number of correct identifications (Vaha & Primmer, 2006), and was more representative when assessing the extent of introgression in hatchery and wild Brown Trout (Sanz, Araguas, Fernandez, Vera, & Garcia-Marin, 2009). Although simulated data sets indicate that the difference between the performance of a Q-value of 0.9 and 0.8 may be as small as 6% (Vaha & Primmer, 2006), data from this study indicate that the difference is greater (~12%).

The estimate of F_1 hybrids provides an indication of current rates of inter-breeding between the hatchery and wild steelhead of 5 to 10%. However, the output of STRUCTURE cannot clearly distinguish later generation hybrids (such as F_2) from F_1 hybrids, because of similar Q-value ranges. Presuming that F_2 hybrids were not present in the population, then this estimate of F_1 hybrids would include 51% to 104% of the known F_1 hybrids present in the simulated data set using the strict and relaxed criteria, respectively. If F_2 hybrids were equal abundance, then the estimate of F_1 hybrids would include 91% to 170% of the known F_1 hybrids in the simulated data set using the strict and relaxed criteria, respectively. The presence of later generation hybrids relies on the relative proportions of spawners during reproduction, and subsequent fitness of progeny. Based on the proportions of hybridization identified in this study, assuming a 1:1 ratio of hatchery-origin to natural-origin adult steelhead (supported by Erdman et al., in press) and random mating, F_1 hybrids would have < 0.05 chance of encountering another F_1 hybrid to spawn. Significantly greater egg mortality (68% compared to wild) was detected in F_2 hybrids of hatchery and wild Atlantic salmon, and lower overall lifetime success, supporting lower abundances of later generation hybrids due to outbreeding depression (McGinnity et al., 2003). An introgression study on native sauger (*Sander canadensis*) provides an estimation of later generation hybridization using four diagnostic loci and 7 additional informative (microsatellite) loci, and supports low proportions of F_2 hybrids (5% of identified hybrids) in their study, even with high rates of stocking a non-native walleye (*Sander vitreus*) (Bingham, Leary, Painter, & Allendorf, 2012). Notably, most (78%) of the hybrids detected in Bingham et al. (2012) were back cross hybrids. Therefore, later generation hybrids are expected to have a low occurrence in the sample, and the range of hybridization rate estimated using the strict and relaxed criteria (5-10%) should accurately estimate F_1 hybrids.

Fig. S9. Percent of samples based on adipose fin presence classified using K=2 and 3 and Q-value cluster assignment thresholds of 0.8 and 0.9. At K=3, the maximum Q-value threshold needed to be reduced to 0.83 for individuals that did not meet the minimum hybrid Q-value of 0.1; therefore, this value is not reported. Hybrids include all hybrids identified among the K-clusters.

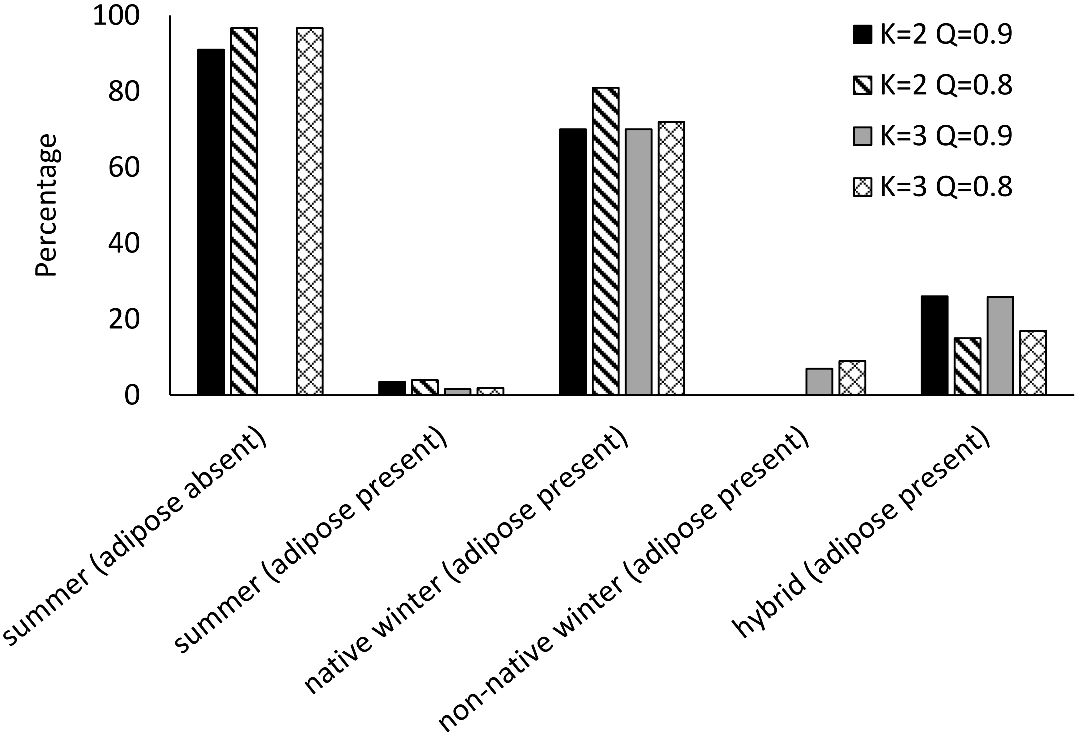
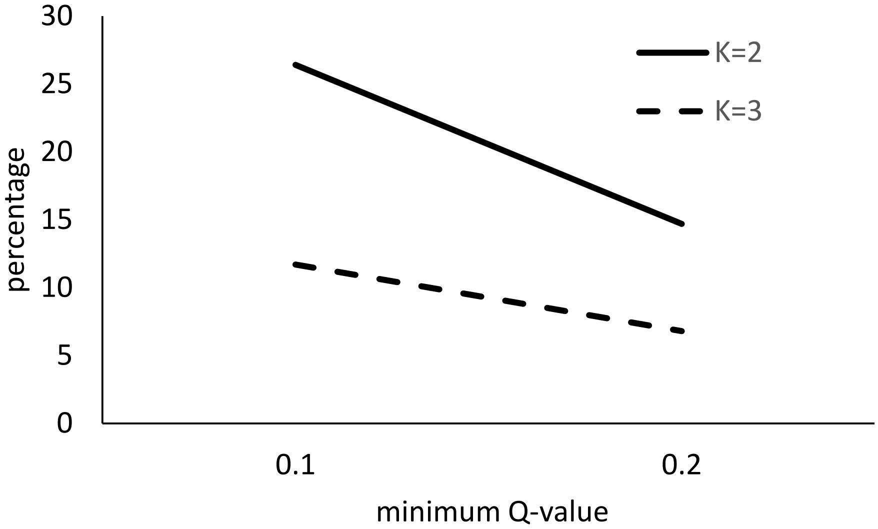


Figure S10. The estimates of introgression from hatchery, summer steelhead for K=2 and 3 and Q-value thresholds tested. The hybrids were identified with cluster memberships <0.9 or 0.8 with minimum Q-values of 0.1 or 0.2 for at least one other cluster, respectively. The estimate of introgression for K=3 includes summer x native winter and 3-way hybrids (summer x native winter x early winter). Note that the parental Q-value threshold was reduced to 0.83 for the K=3 with a minimum Q=0.1 when the minimum Q threshold was not met (*i.e*. Q-values were <0.9 but not >0.1).



Additional Citations

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Release of hatchery adult steelhead for angler opportunity increases potential for interactions with endemic steelhead

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Summary

Translocation is often used to increase local abundance of fish and wildlife populations for conservation or harvest purposes, and effects of releases on recipient populations are context dependent. Release of non-local animals intended for harvest can have negative demographic, genetic, and ecological risks to endemic populations when not harvested. In 2012-2014, we used radiotelemetry to monitor the fate and potential for interactions between non-local hatchery-origin adult summer-run steelhead *Oncorhynchus mykiss* (*n* = 423) and Endangered Species Act-listed native winter-run steelhead in two tributaries of the Willamette River, Oregon, USA. Summer steelhead were 'recycled'—collected, translocated downstream, and released—to provide additional angler opportunity as a part of a regional mitigation program. Overall, reported harvest rate of recycled steelhead was low (15%) and a majority of individuals (62%) were last recorded in the release tributary. Furthermore, 14% of radio-tagged recycled steelhead were last detected outside the release tributary (i.e., strayed after release). Expanded estimates indicate the number of recycled summer-run steelhead remaining in the South Santiam River exceeded the winter-run steelhead spawning population size. Low reported harvest and straying and demographic estimates indicate the recycling program may have negative effects on endemic winter-run steelhead. Translocation and hatchery supplementation are likely to remain important conservation and mitigation tools in the future, though these results highlight the importance of post-release monitoring and considering both the risks and benefits of translocations to endemic populations and communities.

Key words: endemic, harvest, hatchery, non-local, recycling, steelhead, translocation

Introduction

The intentional release of animals (i.e., translocation) to increase abundance for conservation or harvest is a widely applied management strategy for fish and wildlife populations. Releases can buffer imperiled populations from extinction by creating self-sustaining populations (Griffith et al. 1989), reducing the effects of climate change through assisted colonization (Hoegh-Guldberg et al. 2008), and increasing genetic heterogeneity (Deredec & Courchamp 2007; DeMay et al. 2016). Programs may also be production-focused and enhance socially- and economically-important harvest opportunities (Allen 1956), which can both increase and decrease the risk of mortality to native populations. The release of animals outside their historic native range (i.e., introduction) or restocking of non-local conspecifics (i.e., genetically exotic populations; Armstrong & Seddon 2008; Champagnon et al. 2012) can have direct and indirect adverse effects on endemic biodiversity (Allendorf & Waples 1996; Gebhardt 1996; Westemeier et al. 1998; Christian & Wilson 1999; Sih 2010). Given the potential consequences associated with the release of non-local animals, the risk to locally-adapted populations can be substantial. Therefore, it is critical to understand the movement and fate of animals after intentional release.

Harvest of some managed species relies on augmentation through the continued intentional release of alien or non-local animals including birds, mammals, and fishes (Laikre et al. 2010) and often these animals are captive-bred or artificially propagated (hereafter hatchery-produced; Champagnon et al. 2012). A central implicit or explicit tenet is that the majority of released individuals are harvested, perish due to unsuitable environmental conditions or maladaptation due to domestication (Bereijikian & Ford 2004), or otherwise have minimum effects on recipient systems. In some cases, deliberate segregation from endemic populations is desired or required when non-local conspecifics are introduced (Mobrand et al. 2005; Naish et al. 2008) because individuals that escape harvest are expected to negatively affect local adaptations and population structure (Utter 2004). For example, Iberian populations of the red-legged partridge *Alectoris rufa* experience widespread hybridization with captive-reared birds released to increase hunting activity (Blanco-Aguiar et al. 2008) and segregation between wild and farm-raised individuals is necessary to minimize admixing and protect the genetic integrity of endemic partridge populations. Thus, the relative benefits of augmentation with artificially produced fish and wildlife versus risks posed by intentionally-released animals that avoid harvest depend on the ecological, conservation, and social context.

Salmon and steelhead have been artificially propagated to enhance harvest since the 1870s and propagation programs have frequently transferred broodstock across basins (Naish et al. 2008). Because salmon and steelhead populations display extensive life history diversity (Moore et al. 2014), adaptations to local freshwater environments (Taylor 1991), and genetic structuring at small spatial scales (Waples et al. 2001), the release of non-local, hatchery-produced genotypes can be detrimental to endemic populations (Araki et al. 2007). Hatchery-produced summer-run steelhead *Oncorhynchus mykiss* (anadromous form of Rainbow Trout; SRS) have been widely stocked to non-native watersheds with endemic ecotypes. Beginning in 1956, hatchery SRS derived from two lower Columbia populations (Washougal and Klickitat rivers) were artificially cultivated at the Skamania Hatchery, Washington and released throughout Oregon, Washington, and California to provide recreational opportunity (Crawford 1979). Introductions occurred into areas with native winter-run steelhead (WRS), areas previously lacking SRS, and areas with indigenous summer-run populations. Segregation is often a requirement since listing of endemic populations under the U.S. Endangered Species Act (ESA; NMFS 2008) and because of potential negative effects to endemic populations (Chilcote et al. 1986; Leider et al. 1990; Kostow 2003). Thus, there is considerable interest in determining to what degree SRS management actions result in increased mixing between endemic and propagated non-local SRS populations.

Anadromous salmonid hatchery programs rely on the homing mechanism of salmon and steelhead (Hendry et al. 2004; Quinn 2005) whereby adults return to their hatchery of origin or a juvenile release site (i.e., acclimation site). Returns can exceed broodstock requirements, allowing managers to allocate surplus fish to other goals (ODFW 2004). One management action is recycling, where collected adults are released back to fisheries for additional angling opportunity (Lindsay et al. 2001; Kock et al. 2016). The implicit or explicit assumption is adults will home again and be recollected at a hatchery if not harvested. However, any SRS not harvested or recollected could increase competition for mates on spawning grounds, spawn with other hatchery-produced fish, or hybridize with endemic conspecifics locally or after straying to other basins (Araki et al. 2007; Berntson et al. 2011). The net effects of a recycling program could be detrimental in basins with endemic populations, depending on the degree to which recycled SRS avoid harvest and their distribution and behavior during spawning. Recycling protocols may influence the fate and distribution of recycled fish. For example, we expected earlier release and release further downstream from the collection site would result in higher harvest rates through greater additional exposure to fisheries. Therefore some recycling protocols could increase the harvested proportion of recycled fish and decrease potential interactions with endemic conspecifics. Finally, comparison of the relative size of recycled and endemic populations during the spawning period is important because the potential effects on recipient populations is expected to increase as the ratio of released animals to endemics increases.

In this study, we: (i) used radiotelemetry to evaluate post-release fates of non-local SRS recycled in the Willamette River, Oregon, USA, (ii) altered the timing, location, and sex ratios of releases to explore whether varying these might be used to increase harvest of recycled SRS, and (iii) evaluated the potential demographic effects of recycling on endemic populations downstream of the collection site. Analyses were used to test two specific hypotheses. First, we tested the assumption that recycled steelhead return to their acclimation site a second time if not harvested. Second, we hypothesized that increasing the distance of releases from an acclimation site and earlier releases would result in increased exposure to harvest and higher capture rates. Finally, we compared expanded estimates of recycled steelhead that avoid harvest to the estimated spawning population size of endemic steelhead populations.

Methods

Study Area.— Historically, late-run WRS were the only ecotype of steelhead present in the Willamette River upstream of Willamette Falls (205 river kilometers [rkm] from the Pacific Ocean; Fig. 1; Myers et al. 2006; Van Doornik et al. 2015) because the Falls restricted passage except during winter and spring high flows (Clemens 2015). Construction of a fish ladder at the falls in 1885 (Kostow 1995) later allowed for the introduction and subsequent colonization of SRS in the upper Willamette River (UWR; Keefer & Caudill 2010; ODFW & NMFS 2011). Summer steelhead were introduced to the UWR in 1966 by the Oregon Department of Fish and Wildlife (ODFW) to mitigate loss of WRS spawning and rearing habitat after construction of Willamette Valley Project dams (ODFW 2004). Released SRS smolts (approximately 570,000 annually) are adipose clipped and assumed to migrate rapidly through their release rivers (ODFW 2004). Since 1990, the average annual count of SRS passing Willamette Falls has been four times higher than WRS (ODFW 2015a). The UWR WRS distinct population segment was listed as threatened under the ESA in 1999 (NMFS 1999) and minimizing interactions between WRS and SRS has been identified as a conservation and management priority (NMFS 2008; ODFW & NMFS 2011). In the Willamette River basin, recycling of SRS has occurred in South Santiam River since at least 1974 (ODFW 1975) and continues today in the North Santiam, South Santiam River, Middle Fork Willamette, and McKenzie rivers (Fig. 1). Recycling generally occurred from June through mid-October in the McKenzie and Middle Fork Willamette rivers and June through August in the South Santiam River (ODFW 2004); however, beginning in 2013, ODFW restricted releases to only June and July in the South Santiam River. During these periods, an individual SRS can be recycled more than once.

Fish tagging.—SRS were trapped at Dexter Fish Collection Facility (Dexter; rkm 491.2) on the Middle Fork Willamette and Foster Fish Collection Facility (Foster; rkm 418.2) on the South Santiam River during June-August in 2012-2014 (Fig. 1). Adult fish traps at both collection facilities were operated by ODFW personnel and all trapped SRS were initially anesthetized (CO_2: Dexter and Foster 2012, 2013;

AQUI-S 20E [active ingredient: 10% eugenol; AquaTactics Fish Health and Vaccines, Kirkland, Washington]: Foster 2014) and tagged dorsally with colored T-bar tags (Floy Tag Inc., Seattle) to indicate that they were to be recycled. A subsample was randomly selected, immediately placed in a 90- or 265-L plastic holding tank containing hatchery water and 5-10 mg/L AQUI-S 20E. University of Idaho personnel recorded sex based on morphology (only in 2013 and 2014) and fork length (FL; cm), and intragastrically inserted a uniquely-coded radio transmitter (model MCFT-3A; Lotek Wireless, Newmarket, Ontario; 6-s burst rate; 16 × 46 mm; 16 g in air; 455 day battery; Keefer et al. 2004). A 1-cm diameter ring of silicone tubing was used to increase transmitter retention (Keefer et al. 2004). Immediately after tagging, individual fish were either placed in a recovery tank for a minimum of 5 min (Dexter), loaded into ODFW hatchery trucks (Foster 2012, 2013) or sent down sorting pipes to holding ponds (Foster 2014) prior to release.

A US$25 reward was offered in exchange for return of the radio tag and the corresponding harvest information (e.g., date and location of capture) in 2013 and 2014. Reward tags were not used in 2012 due to concerns that rewards would increase angling pressure (Pollock et al. 2001; Pine et al. 2003; Kerns et al. 2016). All fish handling methods were approved by the University of Idaho Institutional Animal Care and Use Committee and permitted by the State of Oregon and the U.S. National Marine Fisheries Service.

Fish releases.—Releases generally occurred immediately after tagging. In the Middle Fork Willamette, 140 steelhead were radio tagged over three years and released to the Dexter Dam tailrace, the river reach immediately downstream of the dam. At Foster Dam, 283 fish were radio tagged and recycled to one of four sites in the South Santiam River over three years. Fish collected at Foster were released at the Waterloo County Park in Waterloo, Oregon (Waterloo; rkm 395.6) and the Pleasant Valley Boat Ramp in Sweet Home, Oregon (Pleasant Valley; rkm 411.7) in all three study years. In 2013, SRS were also released into Wiley Creek (rkm 417). In 2014, fish were also released to the Foster Dam tailrace (rkm 418.1). Releases in the Middle Fork Willamette and South Santiam River occurred in June, July, and

August. The total radio-tagged samples in the South Santiam River were 2.7% of all SRS recycled by ODFW below Foster across the three years.

Monitoring movement.—Steelhead movements were monitored using a combination of fixed receiver sites and mobile tracking, as detailed in Keefer et al. (2015). Briefly, a minimum of 44 fixed-site radio receivers were distributed throughout the Willamette River basin each year (Fig. 1; Keefer et al. 2015). Receivers provided time-stamped detections that were assembled into a telemetry database annually. Fixed-site detections were supplemented with mobile tracking data collected by UI and ODFW crews using antennas mounted to vehicles. Mobile tracking occurred in the Middle Fork Willamette from Dexter Dam to the confluence of the upper Willamette River (rkm 465.2) and in the South Santiam River from Foster Dam to Waterloo, Oregon (rkm 395.6). Tracking occurred weekly during the summer when steelhead were released and the following late-winter/spring during spawning periods. Transmitter returns from fisheries, hatcheries, and traps were used to refine fish distribution and fate.

Fate assignments.—Fate classes differed between releases in the South Santiam River and Middle Fork Willamette basins due to differences in SRS management between the basins. Adults were classified to three fates in the South Santiam River: (a) reported as harvested, (b) remained in a river, or (c) recaptured and removed at Foster. In the Middle Fork Willamette classes (a) and (b) were used; (c) did not occur at Dexter Dam because all recaptured SRS were rereleased in the tailrace. We assumed that individuals last detected by a fixed-site or during mobile tracking had remained in the river. Thus this category included fish that remained in the river and spawned, died prior to spawning, were unreported harvest by anglers, or moved to another river without detection. Consequently, reported estimates may underestimate harvest and straying. Twelve (4.5%) individuals tagged at Foster and 9 (6.0%) at Dexter were assigned an unknown fate and censored from all analyses because these individuals had no detections after release, their tag was recovered on the riverbank without the fish, or recapture data were not consistent with fixed-site detection data (e.g., no fixed-site detections in tributary where recapture was reported). A fish was classified as being recycled more than once in 2014 if it was detected a second time at radiotelemetry receivers at the entrance of fish ladders at Foster and Dexter or if personnel from ODFW or University of Idaho handled a previously-tagged SRS during fish processing at the two facilities. Enumerating the number of recycled fish that re-entered the Dexter Dam fishway in 2012 and 2013 was not possible because a radiotelemetry receiver was not positioned at the entrance of the Dexter Dam fish ladder, and fish-processing personnel at the hatchery did not check SRS for the presence of a radio tag during these two years. Regardless, SRS that were recycled more than once were monitored in all study years in the South Santiam River.

Straying behavior is defined as adult migration to and attempted reproduction at non-natal sites (Quinn 1993; Keefer and Caudill 2014). Because we were unable to directly quantify reproduction, a radio-tagged recycled steelhead was classified as a stray if it was last detected in-river but outside of the release tributary. Estimates of straying behavior of radio-tagged recycled steelhead were not corrected for detection efficiencies at the furthest-downstream telemetry receiver sites in the South Santiam River and the Middle Fork Willamette. Therefore, straying estimates are likely conservative.

Analyses.—The association between fate class and recycling-related management actions (e.g., release location) in each basin was evaluated using logistic regression (Hosmer et al. 2013). A binomial logistic regression model for the Middle Fork Willamette included covariates for sex, release day (i.e., day fish was first recycled after being radio tagged), and year. We used a multinomial logistic regression model of fate in the South Santiam River in relation to sex, release day and location, and year. Release day was measured as days since 1 June, the typical start of recycling each year. Logistic regression analyses only included data from releases in 2013 and 2014 because sex was not estimated and reward tags were not used in 2012. Likelihood-ratio tests were used to assess the significance of model covariates in influencing the fate of SRS recycled in each basin. We used chi-square tests of independence to evaluate whether straying rates were higher for males than females and ANOVAs to test for differences in distance traveled and time elapsed between release and last detection for fish classified as strays.

The effects of sex could not be disentangled from size because males were significantly larger than females (Dexter: males: 71.34 ± 3.24 cm (mean ± standard deviation); females: 68.27 ± 3.17 cm; $t = 4.67$, df = 92.84, $P < 0.001$; Foster: males: 70.67 ± 4.30 cm; females: 67.17 ± 3.10 cm; $t = 5.74$, df = 92.35, $P < 0.001$). We conducted an exploratory analysis to determine whether sex or length was more strongly associated with fate of recycled steelhead. When sex was replaced with FL in each of the models, FL was not significant in predicting the fate of recycled steelhead in both the Middle Fork Willamette and South Santiam (Middle Fork Willamette: $\chi^2 = 0.45$, df =1, $P = 0.50$; South Santiam: $\chi^2 = 0.45$, df = 2, $P = 0.07$). We note it was unlikely males were larger because they were older because little variability exists in the total age of adult SRS when they return to freshwater (Buchanan 1977, Buchanan et. al 1979, Wade and Buchanan 1983). SRS from a particular brood year are released at the same age and little variability exists in the length of ocean residence. For example, as part of a different project, scales were used to estimate freshwater age, ocean age, and total age of 567 SRS collected at Willamette Falls in 2012-2014 (Jepson et al. 2015). Five hundred and twenty-six (92.8%) fish spent 1 year in freshwater and 2 years in the ocean. The percent of males and females that spent 1 year in freshwater and 2 years in the ocean was 95.0 and 91.4, respectively. Consequently, we report models with sex rather than FL, in part because sex ratio in release populations is frequently manipulated, but note both factors may have had causal influence.

We compared estimates of population size for recycled SRS remaining in the South Santiam River below Foster Dam to estimates of WRS population size for the same river reach (confluence of South and main Santiam rivers to Foster Dam). Annual numbers of recycled SRS by fate class were estimated by expanding observed proportions for each fate class in the radio-tagged samples by the total number recycled by ODFW. The total number of fish recycled annually by ODFW was corrected to account for double counting of SRS recycled more than one time (17.7%). To assess the 95% confidence limits for the estimates, a non-parametric bootstrap percentile method (Efron 1987) was used after the data were re-sampled 1,000 times. Annual values for WRS escapement were provided by a larger radio-telemetry study of WRS migration in the Willamette River during the same study period (Jepson et al. 2015). The population size comparison was conducted only for the South Santiam River basin because the Middle Fork Willamette is outside the ESA-listed range of WRS, though recent evidence suggests WRS also spawn there (Jepson et al. 2015). All analyses were conducted using the R statistical computing language (R Development Core Team 2009).

Results

Middle Fork Willamette.—The majority (77.1%; *n* = 108) of radio-tagged SRS recycled below Dexter Dam in the Middle Fork Willamette remained in a river and proportions did not differ among years (χ^2 = 1.7, df = 2, *P* = 0.44; Fig. 2). Approximately one in five adults strayed from the Middle Fork Willamette into the main stem Willamette River or a tributary outside the Middle Fork Willamette (*n* = 31; 22.1% of all Dexter-released radio-tagged fish; Fig. 3). Females tended to stray more frequently than males, though this trend was not significant (χ^2 = 2.55, df = 1, *P* = 0.11; Table 2). The median distance traveled between release at Dexter and last detection by fish classified as strays was 102.3 ± 213.5 rkm (median ± interquartile range [IQR]; Table 1), and there were no significant differences in distance traveled across years (*F* = 0.36, df = 2, *P* = 0.72). The median number of days elapsed between release and last detection of strays was 91.0 ± 82.0 days (median ± IQR; Table 1), and there were no significant differences across the three study years (*F* = 1.6, df = 2, *P* = 0.23). Approximately half of the fish that remained in the Middle Fork Willamette were concentrated in the 5 km below Dexter Dam, and a third were last detected in the Dexter Dam tailrace. Only three (2.1%) individuals displayed behavior consistent with post-spawn downstream movement (i.e., kelt behavior; detected at Willamette Falls moving downstream in January, February, and April), and at least five fish in 2014 (10.4% of fish recycled in 2014) were recycled for a second time after their initial recycling events.

Reported harvest rates were similar to straying rates, with slightly more than one in five radio-tagged steelhead recycled in the Middle Fork Willamette reported as harvested during the study (*n* = 32; 22.9%; Fig. 2). Annual harvest varied from 19.2% in 2013 to 29.2% in 2014, and reported harvest rate did not increase with the addition of tag rewards beginning in 2013 ($\chi^2 = 1.02$, df = 2, $P = 0.60$). The spatial distribution of reported harvest was concentrated in the Dexter Dam tailrace (*n* = 21; 65.6% of reported harvest). Five steelhead (15.6% of reported harvest) were captured in the main stem Willamette River between the confluence of the Santiam River (rkm 338.7) upstream to the Middle Fork Willamette, and one fish (3.1% of reported harvest) was harvested in the Willamette River downstream of the confluence with the Santiam River. Males were harvested more frequently (Table 2) and the odds of being reported as harvested was 2.72 times higher for males recycled below Dexter Dam than females ($\chi^2 = 3.95$, df = 1, $P = 0.047$; Table 3). Neither release day nor year were significantly associated with fate (release day: $\chi^2 = 1.80$, df = 1, $P = 0.18$; year: $\chi^2 = 0.25$, df =1, $P = 0.62$; Table 3), although there was an expected negative relationship between the probability of being harvested and release date.

South Santiam River.—Overall patterns in fate of recycled steelhead were similar to the Middle Fork Willamette, but harvest and straying rates were lower in the South Santiam River, perhaps because steelhead were also removed at the hatchery (Fig. 2). Most were last detected in a river during our study (*n* = 154; 54.4%; Fig. 2), followed by recaptured and removed at Foster Dam (*n* = 97; 34.3%) and reported as harvested (*n* = 32; 11.3%). Reported harvest rate was not associated with the addition of tag rewards beginning in 2013 ($\chi^2 = 0.89$, df = 2, $P = 0.64$), though harvest was lowest in 2012 (8.8%) when reward tags were not used. Individuals last detected in a river were generally concentrated in the South Santiam River (*n* = 128; 82.5%; Fig. 3). Approximately 10% of all recycled steelhead strayed outside the South Santiam River (*n* = 26; 9.2%; Fig. 2). One (0.4%) fish was last detected in Wiley Creek, a spawning tributary for upper Willamette River WRS emptying to the Foster Dam tailrace (Fig. 3). The point estimate of straying rate for steelhead released at Wiley Creek (15.0%) was higher than rates for the other three release sites, but differences were not significant (χ^2 = 3.63, df = 3, P = 0.30). Median distance traveled by steelhead released at Wiley Creek and classified as strays was lowest for fish released at Waterloo (Table 1), but differences were not significant (F = 1.96, df = 3, P = 0.15). The median number of days elapsed between release and last detection of strays was lowest for SRS recycled at Pleasant Valley (Table 1), and there were no significant differences across the release sites (F = 2.76, df = 3, P = 0.07). Point estimates of straying were higher in males than females, though this difference was not significant (χ^2 = 3.42, df = 1, P = 0.06; Table 2). Fifty (17.7%) individuals were recycled more than once, including three fish that were recycled four times.

Fate of steelhead released to the South Santiam River differed between males and females in a complex manner (Table 2). Overall, sex was associated with fate (χ^2 = 6.78, df = 2, P = 0.03; Table 4). Males (n = 16, 25.8%) were recaptured and removed less frequently than females (n = 59; 45.4%), most likely reflecting broodstock collection practices. The model illustrated that the odds of removal at Foster compared to remaining in a river was 60% lower for males (Table 4). Reported harvest of males (16.1%) was not significantly higher than females (10.8%; χ^2 = 0.48, df = 1, P = 0.49). Other management actions were not associated with the fate of steelhead recycled in the South Santiam River. Specifically, neither release timing (χ^2 = 0.0003, df = 2, P = 0.99; Table 4) nor release distance from Foster Dam (χ^2 = 7.15, df = 6, P = 0.31; Table 4) were associated with fate or harvest rate.

Recycled SRS remaining at large.—The number of SRS recycled annually by ODFW in the South Santiam River varied based upon annual hatchery returns to Foster. Oregon Department of Fish and Wildlife recycled 3,901 ± 2,651 SRS annually during the study. Annual population estimates of fish recycled in the South Santiam River that remained at large were greater than WRS escapement point estimates during 2012 and 2013 and similar in 2014 (Table 5). The greatest difference occurred in 2012 when the estimated population of SRS remaining in a river (4,647 [3,961 – 5,256; 95% CI]) was approximately six times higher than the estimated WRS escapement (811 [579 – 1,119; 95% CI]; Table 5).

Discussion

Our findings have direct application to managing programs that release animals to increase harvest opportunities in systems with species of conservation concern. We observed that most recycled SRS in the Middle Fork Willamette and South Santiam River avoided angler harvest and removal at Foster and remained in the release tributary or main stem Willamette River. Substantial numbers also moved out of the recipient streams prior to spawning. Reported harvest rates were generally low. Contrary to expectations, the effects of release day and location on fate were weak or not significant, but sex was important in predicting fate in both basins. Expansion of radio-tagged recycled SRS fates suggests the number remaining in a river after recycling by ODFW was greater than the number of adult endemic WRS returning to spawn in the South Santiam River. In the sections that follow we interpret our results with respect to potential bias in our fate estimates, address the effects of management actions, discuss potential demographic and genetic effects on WRS populations, and present a conceptual framework for assessing the potential costs and benefits of non-local translocations with respect to the donor population and recipient community.

Potential Biases:

The exploitation of wild animals and plants often relies on releases of translocated individuals, and accurately quantifying harvest is therefore important. Harvest estimates in this study were almost certainly biased low because harvest rates are commonly underreported in many salmonid studies (Meyer et al. 2012a). Self-reported harvest data can be sensitive to self-reporting bias, including deliberate misreporting bias and nonresponse (Pollock et al. 1994; McCormick et al. 2015). Anglers could misreport harvest as an attempt to influence season length (McCormick et al. 2013); however, this is an unlikely in the UWR because the SRS angling season is long (ODFW 2015b). Reward tags can be used to reduce bias associated with self-reporting and Nichols et al. (1991) found that approximately US$100 was needed to generate reporting rates approaching 100%. Thus our reward rate ($25) may have contributed to underreporting. However, the absence of an observable change in reported harvest rate between 2012 (no reward tags) and later years implies that self-reporting bias was relatively small. Application of corrections based on other studies may inform how a bias might impact our study conclusions. Specifically, weighted mean reporting rates were 69.7% for $10 tags and 91.7% for $50 tags in a reward-recovery study in Idaho (Meyer et al. 2012a). Extrapolating to an expected reporting rate of 78% for the $25 rewards used in this study, an adjusted harvest rate of recycled steelhead increases from 22.9% to 33.6% in the Middle Fork Willamette and from 11.3% to 16.3% in the South Santiam River. Finally, the observed harvest estimates were similar to the minimum estimate of recycled steelhead harvest in the Clackamas River (10.3%; Schemmel et al. 2011) and the Cowlitz River (19.2%; Kock et al. 2016) and to estimated harvest of Atlantic Salmon *Salmo salar* and upper Columbia River steelhead radio tagged with tags of similar reward value (Smith et al. 1998; Keefer et al. 2005). However, estimates of harvest in the South Santiam River were over 50% lower than an initial estimate of recycled steelhead harvest in the same basin from 2003 creel data (39.2%; confidence interval not reported; ODFW 2004) but similar to an estimate from 2013 (12%; ODFW unpublished data). Collectively, our data and rates reported from other systems suggest that the degree of non-reporting was likely not more than ~20-25% and true harvest rates were 40% or less. Therefore, adjustment for bias would not likely alter the conclusion that a minority of recycled steelhead are harvested and most remain in a river.

Tag retention and tag-related mortality are concerns for any tagging study (Ramstad & Woody 2003). Our results rely on the assumptions that tag retention and tag-related mortality were sufficiently high and low, respectively, to meet the study objectives (Pine et al. 2012). While we were unable to directly evaluate these assumptions, past studies on tag regurgitation rates for steelhead radio tagged in the Columbia River using similar tags and methods (6.7%; Keefer et al. 2004) and tag-related mortality among adult Sockeye salmon *Oncorhynchus nerka* (2.0%; Ramstad & Woody 2003) suggest these potential biases were also unlikely to alter the qualitative conclusions of the study.

Management Actions:

Translocation supplementation protocols are expected to affect the fate of released animals depending on the timing, location, and habitat conditions upon release. Contrary to our expectations for SRS, additional exposure to fisheries from greater release distance and earlier release date did not measurably increase the probability of harvest. In fact, although it was not statistically significant, point estimates of harvest rates were higher for adults released within ~1 km of Foster Dam and were similar to harvest rates in the Middle Fork Willamette where all fish were recycled into the dam tailrace. The higher harvest rates near juvenile release sites (i.e., the dam tailraces in these basins where philopatric adults return) were associated with a concentration of anglers who perceive higher potential catch rates at juvenile release sites (Wagner 1969; Slaney et al. 1993; Quinn 2005). A single tailrace release site could increase the removal of steelhead recycled in South Santiam River, but multiple release sites decreases angler density and could increase the quality of the fishing experience. The trade-off between harvest probability and quality of experience, both metrics of the quality of a fishery, are important for managers to consider (McCormick et al. 2014). Although reported harvest was low, recreational anglers could be releasing a large proportion of recycled fish, indicating that the program may be successful at providing a robust fishery with suitable catch rates. Mandatory removal of all captured animals could be implemented to further improve segregation between released animals and endemic populations. Additionally, managers could limit the number of times an individual is recycled. Sex, and therefore length, was important in predicting fate probabilities for recycled steelhead in both basins. Limiting recycling in the Middle Fork Willamette to only male steelhead (i.e., longer fish) would potentially increase harvest and therefore decrease the proportion that remains at large, but could also affect interactions on the spawning ground by, for example, biasing sex ratios. Historically, releases of genetically distinct populations of species that already exist naturally in the release area were rarely monitored for possible effects on endemic populations (Laikre et al. 2010). Specific release strategies can increase survival of released animals to improve harvest opportunities or to aid in the conservation of imperiled populations (Brennan et al. 2006; Burner et al. 2011), generally demonstrating the importance of understanding how release strategies interact with spatial patterns of harvest to influence the fate of released animals. These results highlight that intuitive assumptions about the effects of management protocols may not manifest as expected.

Potential Demographic and Genetic Effects:

The release of non-local animals that remain at-large can affect animals in recipient systems through behavioral, demographic, or genetic effects. Quantifying these effects was beyond the scope of the study, but effects were likely given that the estimate of recycled SRS remaining in-river in the South Santiam River in all study years exceeded the number of WRS, even when accounting for strays leaving the South Santiam River. Evidence for spatial and, to a lesser degree, temporal overlap in spawning exists between the two ecotypes in the Willamette River basin (Jepson et al. 2015). Releases of non-local organisms can negatively affect locally adapted populations through decreased effective population size (Wang & Ryman 2001; Chilcote 2003; Chilcote et al. 2011), decreased fitness (McGinnity et al. 2003; Araki et al. 2007), changes in life history traits (Fast et al. 2015) and gene expression (Christie et al. 2016), and reduced survival (Peterson et al. 2004). Work is underway to determine the amount of gene flow needed to cause these negative impacts on local adaptation in WRS steelhead in the UWR. Offspring of SRS generally emerge earlier than WRS potentially placing WRS at a disadvantage for occupying prime juvenile rearing habitats (Kostow et al. 2003). Large numbers of SRS spawners could decrease spawning success of WRS through demographic processes such as density-dependent feedback (Stewart et al. 2005; Putaala & Hissa 1998). Hybridization can cause direct and indirect genetic effects, including introgression, outbreeding depression, or altered selection regimes (Waples 1991; Araki et al. 2008), and studies have documented gene flow from genetically alien populations released into native, conspecific populations (Mamuris et al. 2001; Barilani et al. 2005). The continued outnumbering of WRS in the South Santiam River by SRS could lead to a hybrid sink effect (Allendorf et al. 2013). Unlike salmon, steelhead are iteroparous which could exasperate these potential issue; however, few radio-tagged SRS in the UWR make multiple return trips to freshwater to spawn (2%, n = 4, in 2012; <1%, n = 2 in 2013; Jepson et al. 2015). Although recent genetic analyses by Van Doornik et al. (2015) showed low effective rates of introgression into adult populations, higher rates of introgression were observed in preliminary samples of naturally produced juveniles collected at Willamette Falls (Johnson et al. 2014). Regardless, under the ESA, the SRS hatchery program must be monitored and managed to maximize segregation and minimize genetic and fitness-related effects of SRS on WRS populations (NMFS 2008). Releases of non-local animals can provide important harvest opportunities, but consequences of such releases are expected if released animals avoid harvest, indicating that future research should focus on quantifying the ecological and genetic effects of such releases.

Movement by translocated individuals outside of target management areas after release may have important ecological and socioeconomic implications that are challenging to quantify. Straying of recycled fish to WRS spawning tributaries is a concern because WRS populations are depressed and strays can have considerable effects when the recipient population is small (Keefer & Caudill 2014). Keefer & Caudill (2014) reported typical straying rates of 3-10% for SRS, suggesting that straying rates of steelhead recycled in the Middle Fork Willamette were high, though we note that straying rate depends in-part on the scale of observation and most estimates in Keefer & Caudill (2014) were at larger scales. Minimizing the movement of animals outside the release area is critical because release strategies that promote widespread straying can result in homogenized populations (Lindley et al. 2009). If the specific goal of a release program is to increase abundance in the release area, then dispersal of introduced organisms outside the release area is problematic, both ecologically and socioeconomically (Skjelseth et al. 2007). For example, straying of recycled fish reduces angling opportunities in the targeted release rivers. However, dispersal of released organisms to habitats outside the release area may be necessary in order to find suitable mates, favorable foraging opportunities, or distribute novel alleles, which could be beneficial for rescuing populations or species suffering from lower population sizes (Ebenhard 1995). The probability of released animals moving into adjacent habitats depends on the behavioral, physiological, and ecological characteristics of the released species (Westley et al. 2013) and the habitat to which animals are released. These results demonstrate released animals can frequently move out of the respective release area.

Harvest and Non-local Translocation:

Intentional releases of non-local animals are generally used to increase population abundance for either conservation or harvest purposes. The management strategies for release should explicitly consider the origin of released animals and the goals of the program (Fig. 4). For example, if releases are intended to buffer the recipient population from extinction, then integration between the non-local and endemic animals is expected and desired (Griffith et al. 1989; DeMay et al. 2016), and therefore, harvest of the non-local animals would be detrimental to management objectives. However, if releases are for harvest enhancement, either segregation- or integration-based management strategies could be warranted. If segregation is required by the ESA, for example, harvest or removal of all released non-local animals is essential because individuals that avoid harvest conflict with conservation goals mandated by the ESA. In the Willamette River basin, harvest or removal of all released SRS fulfills ESA requirements to minimize opportunities that lead to interactions. Recycling of anadromous fishes remains a practical method to increase angling opportunity by using a surplus of hatchery-produced fish that have returned to a hatchery. However, recycling of non-local genotypes could increase risk to endemic populations and actions should be taken to minimize this risk. Continued separation between these populations will help ensure that vulnerable endemic populations are better able to persist in the face of future environmental and anthropogenic challenges. This case study highlights the multiple, frequently conflicting, management goals for populations affected by translocation or augmentation. Similar frameworks should assist in structuring risk-to-benefit analyses considering ecological and genetic effects.

Whether the objective of intentionally releasing non-local organisms is to conserve imperiled populations or improve harvest opportunities, identifying post-release fates are important. Post-release fate may affect native conspecifics, similar species within the same guild or assemblage (i.e., other cold-water fishes), community dynamics via food web effects, or energy and nutrient flows within the recipient ecosystem. To assess how programs balance providing harvest options of non-local animals through intentional releases, such as put-and-take fisheries (Johnson et al. 1995; Meyer et al. 2012b), big game hunting preserves (Adams et al. 2016), and upland bird introductions (Blanco-Aguiar et al. 2008), with conservation of endemic populations, quantification of the proportion of released individuals that avoid harvest or removal is the first step to quantifying these potential effects. Quantifying post-release fate provides insight on how to carry out releases in a way that does not unnecessarily reduce biological diversity.

Post-release fitness is also important to consider because a naturalized population of translocated animals has more potential long-term impact compared to true put-and-take animals. There could be cause for ecological and genetic concern if the population size of non-local releases is greater than the endemic recipient population (e.g., demographic or genetic swamping). The necessity of understanding demographic effects of translocations, regardless of the specific objectives, becomes even more critical in the face of climate change, as many populations will not be able to migrate sufficiently (Loarie et al. 2009), anthropogenic pressures on endemic populations may become more intense, and assisted migration is considered as a management strategy. There is also a need to address issues in a more interdisciplinary action (Champagnon et al. 2012). Hunting and angling are important components of natural resource management and strategies for increasing interest in these resources and opportunities should be provided; however, it is critical to test assumptions about programs where releases are used to increase harvest in systems with native populations of conservation concern.

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Authors' Contributions

CE, CC, GN, and MJ conceived the idea and designed methodology; CE and GN collected the data; MJ and CE coded the data; CE analyzed the data; CE and CC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Table 1. The distance traveled and time elapsed between release and last detection and number of detections for non-local summer-run steelhead that strayed after being recycled in the Middle Fork Willamette River and South Santiam River, Oregon. A recycled fish was classified as a stray if it was last detected in a river outside of its release tributary. PLV = Pleasant Valley; WTL = Waterloo; WLC = Wiley Creek; FST = Foster Dam tailrace; DXD = Dexter; rkm = river kilometer; IQR = interquartile range.

Year	Release Site	N (Percent)	Distance traveled	Time Elapsed	Number of detections
			Median rkm (IQR)	Median days (IQR)	Median (IQR)
2012	PLV	9 (13.4)	106.8 (50.1)	19 (25)	6 (18)
2012	WTL	4 (16.7)	26.5 (138.0)	260 (111)	8 (6)
2012	DXD	12 (26.7)	95.0 (128.9)	84 (84)	8 (12)
2013	PLV	4 (10.8)	66.1 (21.1)	286 (70)	5 (5)
2013	WTL	2 (5.3)	93.7 (106.1)	272 (14)	58.5 (59)
2013	WLC	3 (15.0)	78.0 (52.8)	100 (116)	14 (27)
2013	DXD	12 (25.5)	93.1 (217.4)	97.5 (78)	9 (18)
2014	PLV	3 (9.4)	67.8 (19.5)	19 (2)	10 (9)
2014	WTL	0 (0.0)	-	-	-
2014	FST	1 (2.9)	71.1 (0)	263 (0)	32 (0)
2014	DXD	7 (14.6)	116.8 (222.0)	21 (100)	7 (102)

Table 2. The number, size, fate, and straying rate of non-local male and female radio-tagged recycled summer-run steelhead in the (A) Middle Fork Willamette River and (B) South Santiam River, Oregon, 2012-2014. Sex was not estimated in 2012 (i.e., unknown). Sex assignment was conducted during tagging. The number and percent of fish remaining in a river other then their release tributary are included the group classified as remaining in river.

(A)

	Radio-tagged	Fork Length (cm)	Reported as harvested		Remained in river		Remained in river: outside release tributary	
Sex	N	Mean (SD)	N	%	N	%	N	%
				2012				
Unknown	45	69.9 (3.1)	9	20.0	36	80.0	12	26.7
				2013				
Male	25	71.2 (3.2)	5	20.0	20	80.0	4	16.0
Female	22	68.5 (2.6)	4	18.2	18	81.8	8	36.4
				2014				
Male	22	71.6 (3.4)	10	45.5	12	54.5	1	4.5
Female	26	68.1 (3.7)	4	15.4	22	84.6	6	23.1

(B)

	Radio-tagged	Fork Length (cm)	Reported as harvested		Remained in river		Removed at Foster		Remained in river: outside release tributary	
Sex	N	Mean (SD)	N	%	N	%	N	%	N	%
					2012					
Unknown	91	69.5 (8.2)	8	8.8	61	67.0	22	24.2	13	14.3
					2013					
Male	39	70.8 (4.0)	8	20.5	22	56.4	9	23.1	6	15.4

Female	56	67.8 (3.2)	5	8.9	20	35.7	31	55.4	3	5.4
				2014						
Male	23	70.5 (4.9)	2	8.7	14	60.9	7	30.4	2	8.7
Female	74	66.7 (3.0)	9	12.2	37	50.0	28	37.8	2	2.7

Table 3. Parameter estimates and 95% confidence intervals for the binomial logistic regression model that predicted the fate of non-local summer-run steelhead recycled below Dexter Dam in the Middle Fork Willamette River, Oregon. Estimates expressed as odds of being harvested. Parameter estimates shown in bold have 95% confidence intervals that do not include 1.

		Confidence interval	
Variable	Estimate	Lower	Upper
Intercept	1.17	0.04	31.86
Sex (male)	**2.77**	**1.01**	**7.85**
Release day	0.97	0.92	1.02
Year (2014)	0.61	0.08	4.20

Table 4. Estimated odds ratios and 95% confidence intervals for the multinomial logistic regression model of fate (angled, recaptured at hatchery, remained in river) including sex, release location (release rkm), year, and release day covariates for non-local summer-run steelhead recycled below Foster Dam in the South Santiam River, Oregon. Parameter estimates shown in bold have 95% confidence intervals that do not include 1. PLV = Pleasant Valley; WLC = Wiley Creek; WTL = Waterloo.

		Confidence interval	
Variable	Estimate	Lower	Upper
Reported as harvested			
Intercept	0.68	0.12	3.87
Sex (male)	0.94	0.36	2.44
Release site (PLV)	0.68	0.16	2.92
Release site (WLC)	0.54	0.05	5.90
Release site (WTL)	0.23	0.04	1.24
Year (2014)	0.49	0.12	2.01
Release day	1.00	0.96	1.05
Removed at hatchery			
Intercept	1.28	0.39	4.21
Sex (male)	**0.40**	**0.20**	**0.83**
Release site (PLV)	1.31	0.45	3.78
Release site (WLC)	0.56	0.10	3.27
Release site (WTL)	1.16	0.40	3.35
Year (2014)	0.56	0.24	1.32
Release day	1.00	0.97	1.03

Coefficients are expressed as odds ratios relative to fate probability of remaining in a river (i.e., remaining in a river was the reference category).

Table 5. Annual estimates of the number of recycled non-local summer-run steelhead harvested and remaining in a river based on the fates of radio-tagged steelhead recycled below Foster Dam, South Santiam River, Oregon and annual estimated escapement of winter-run to the South Santiam River. Winter-run escapement from Jepson et al. 2015. 95% confidence interval in parentheses. Estimates are not corrected for reporting biases, tag retention rate, or tag-related mortality.

Year	Number of fish recycled by ODFW	Percent radio-tagged	Estimate of fish recycled once by ODFW	Percent radio-tagged reported as harvested	Percent radio-tagged remaining in river	Harvest estimate of recycled fish	Estimate of recycled fish remaining in river	Estimated winter steelhead escapement
2012	8423	1.08	6932	8.79	67.03	609 (229 – 1067)	4647 (3961 – 5256)	811 (579 – 1119)
2013	3355	2.83	2761	13.38	44.21	369 (203 – 581)	1227 (959 – 1511)	833 (627 – 1083)
2014	2444	3.97	2011	11.34	52.58	228 (104 – 352)	1057 (850 – 1265)	1085 (848 – 1364)

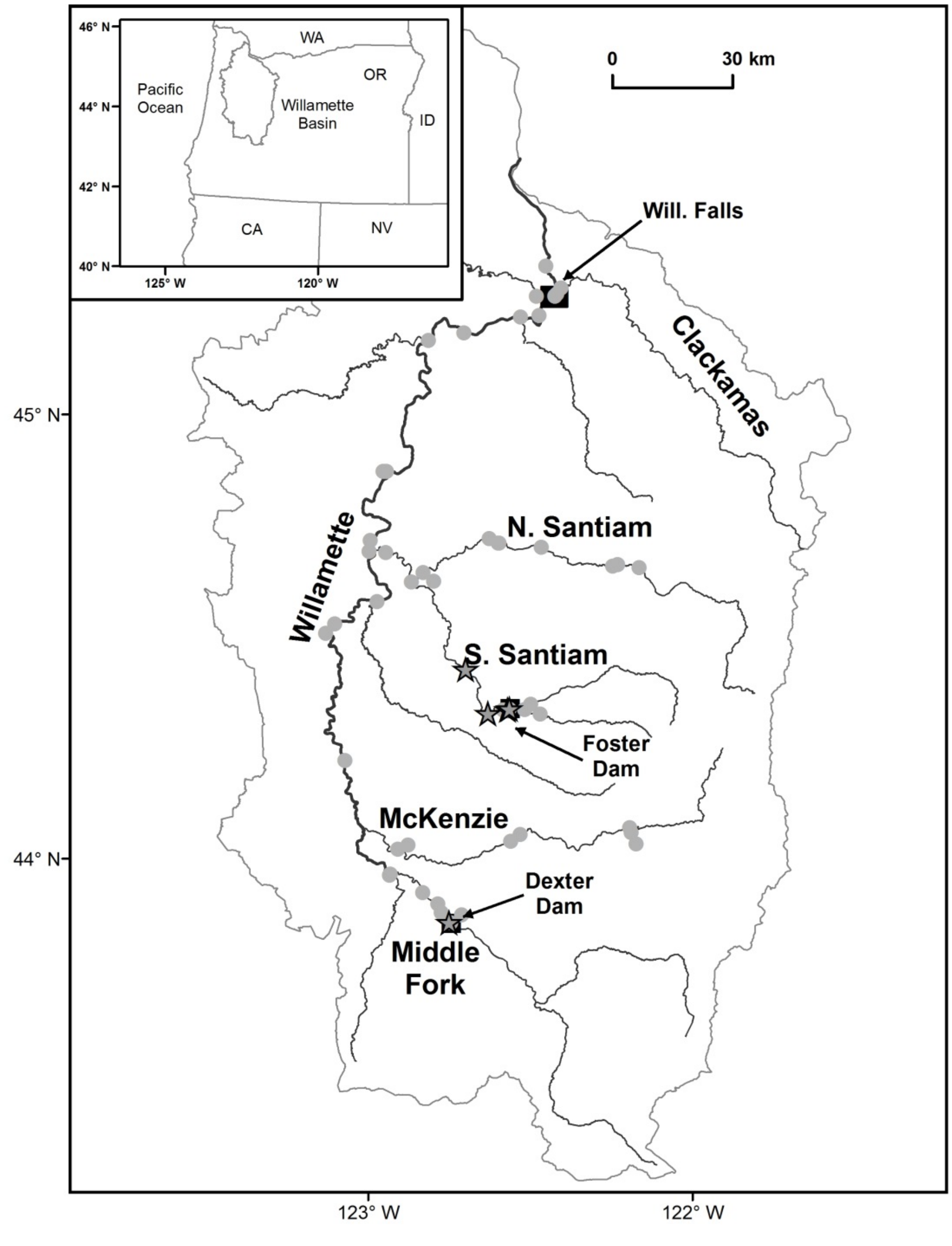

Fig. 1. Map of Willamette River basin, Oregon showing release sites (stars) and locations of fixed radiotelemetry receivers (circles).

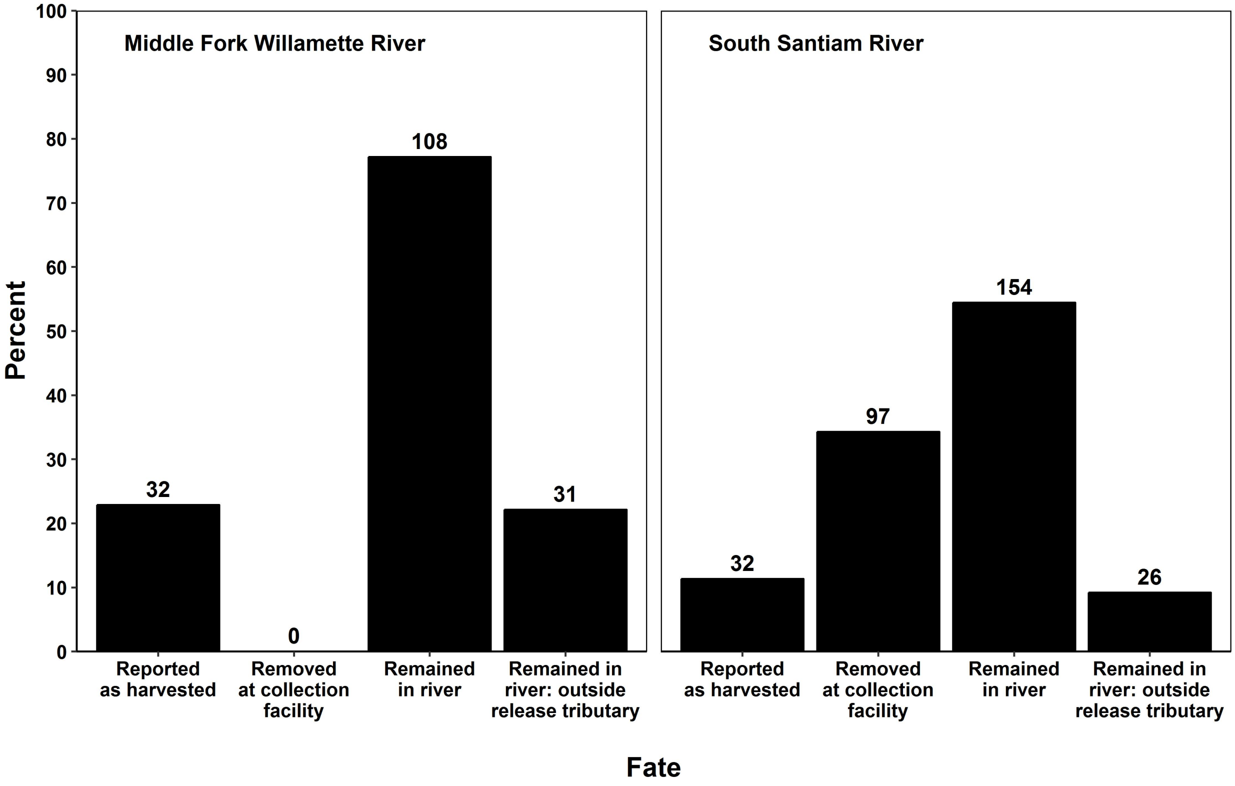

Fig. 2. Fate of non-local radio-tagged summer-run steelhead recycled in the Middle Fork Willamette River (left) and South Santiam River (right), Oregon 2012-2014. Sample size of each fate category is above each bar. The percent of fish remaining in a river other than their release tributary are included the group classified as remaining in river.

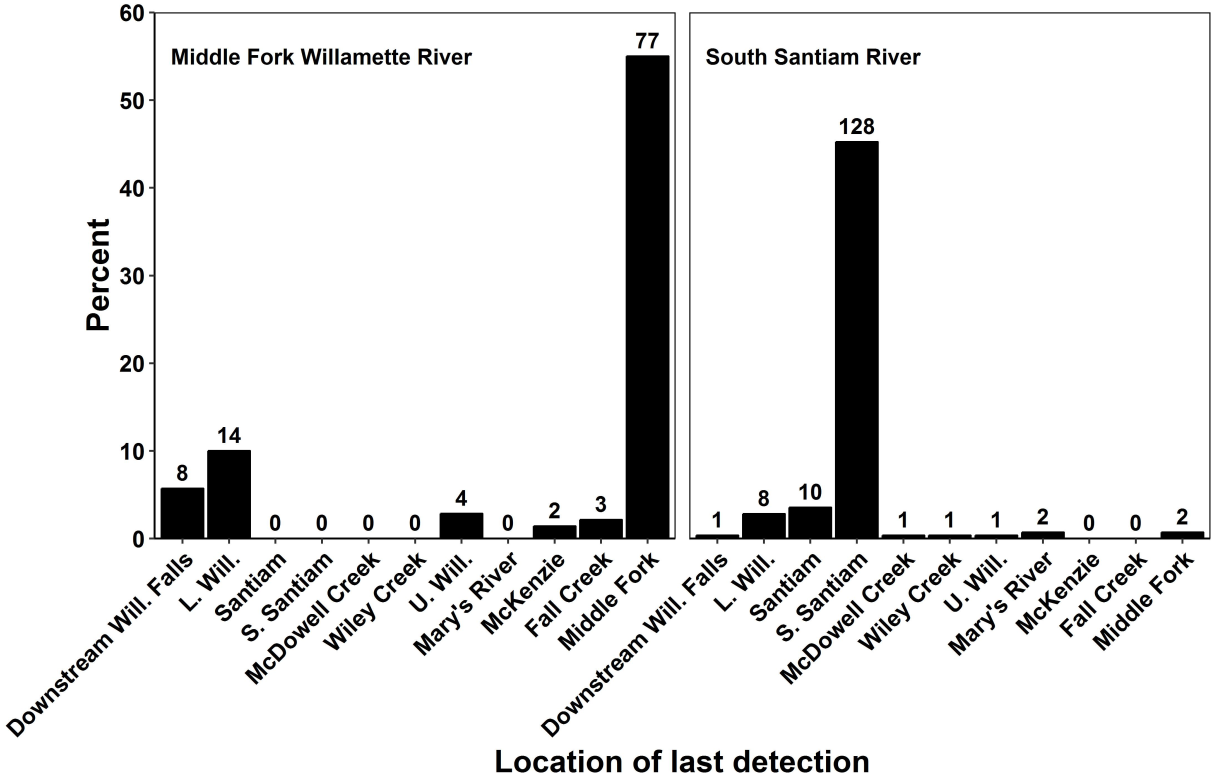

Fig. 3. Locations of last detections for 108 and 154 non-local radio-tagged summer-run steelhead recycled in the Middle Fork Willamette River (left) and South Santiam River (right), Oregon, respectively, that were assigned a fate of remaining in a river. Sample sizes for individual locations are above the bars.

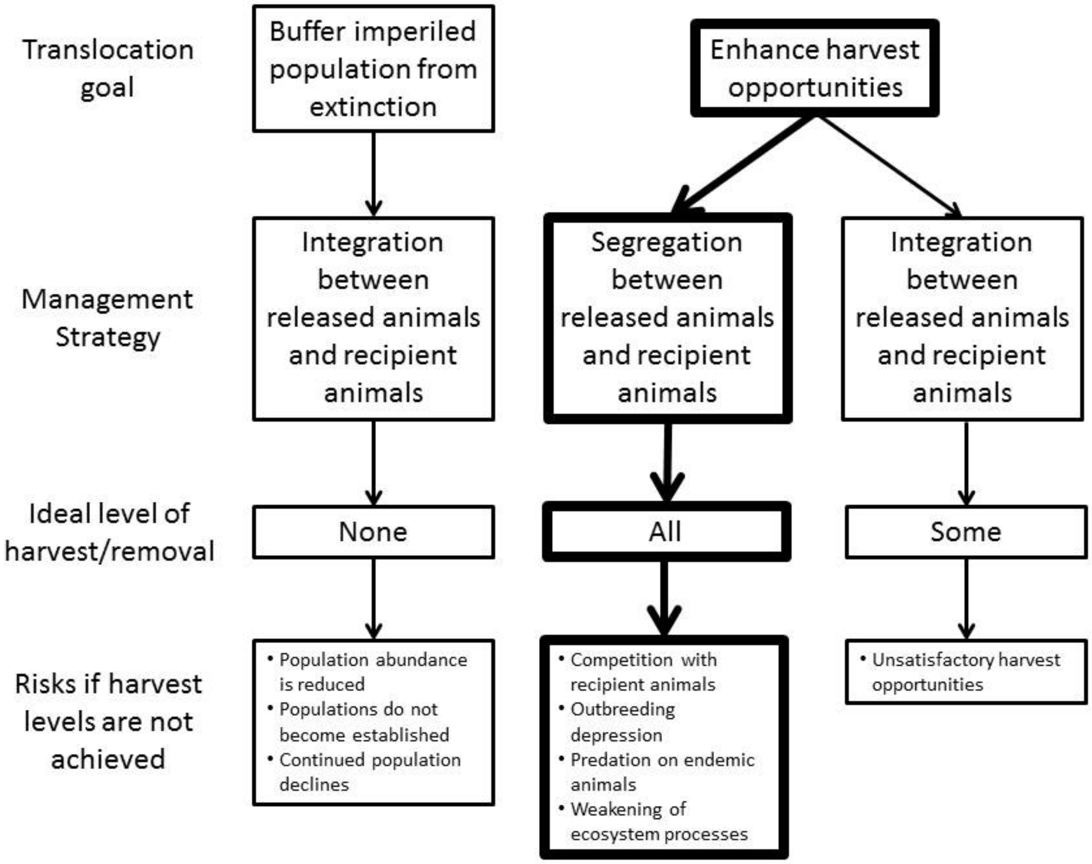

Fig. 4. Diagram illustrating acceptable harvest levels of non-local animals intentionally released and the associated ecological and social costs and benefits. Thicker boxes indicate scenario in Willamette River basin, Oregon where non-local summer-run steelhead are released and recycled to increase harvest opportunities.