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

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Abstract. 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 (ESA)-listed native winter-run steelhead (WRS) 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 WRS spawning population size. Low reported harvest and straying and demographic estimates indicate the recycling program may have negative effects on endemic WRS. 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.

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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 and 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 and Seddon 2008, Champagnon et al. 2012) can have direct and indirect adverse effects on endemic biodiversity (Allendorf and Waples 1996, Gebhardt 1996, Westemeier et al. 1998, Christian and Wilson

1999, Sih et al. 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 and 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 vs. 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 (SRS) *Oncorhynchus mykiss* (anadromous form of rainbow trout) 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 (NMFS 2008) and because of potential negative effects to endemic populations (Chilcote et al. 1986, Leider et al. 1990, Kostow and Zhou 2006). 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 are expected to increase as the ratio of released animals to endemics increases.

In this study, we (1) used radiotelemetry to evaluate post-release fates of non-local SRS recycled in the Willamette River, Oregon, USA, (2) altered the timing, location, and sex ratios of releases to explore whether varying these might be used to increase harvest of recycled SRS, and (3) 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 and Caudill 2010, ODFW and 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 2015*a*). 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 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, USA]: Foster 2014) and tagged dorsally with colored T-bar tags (Floy Tag, Seattle, Washington, USA) 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, Canada; 6-s burst rate; 16×46 mm; 16 g in air; 455-d 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),

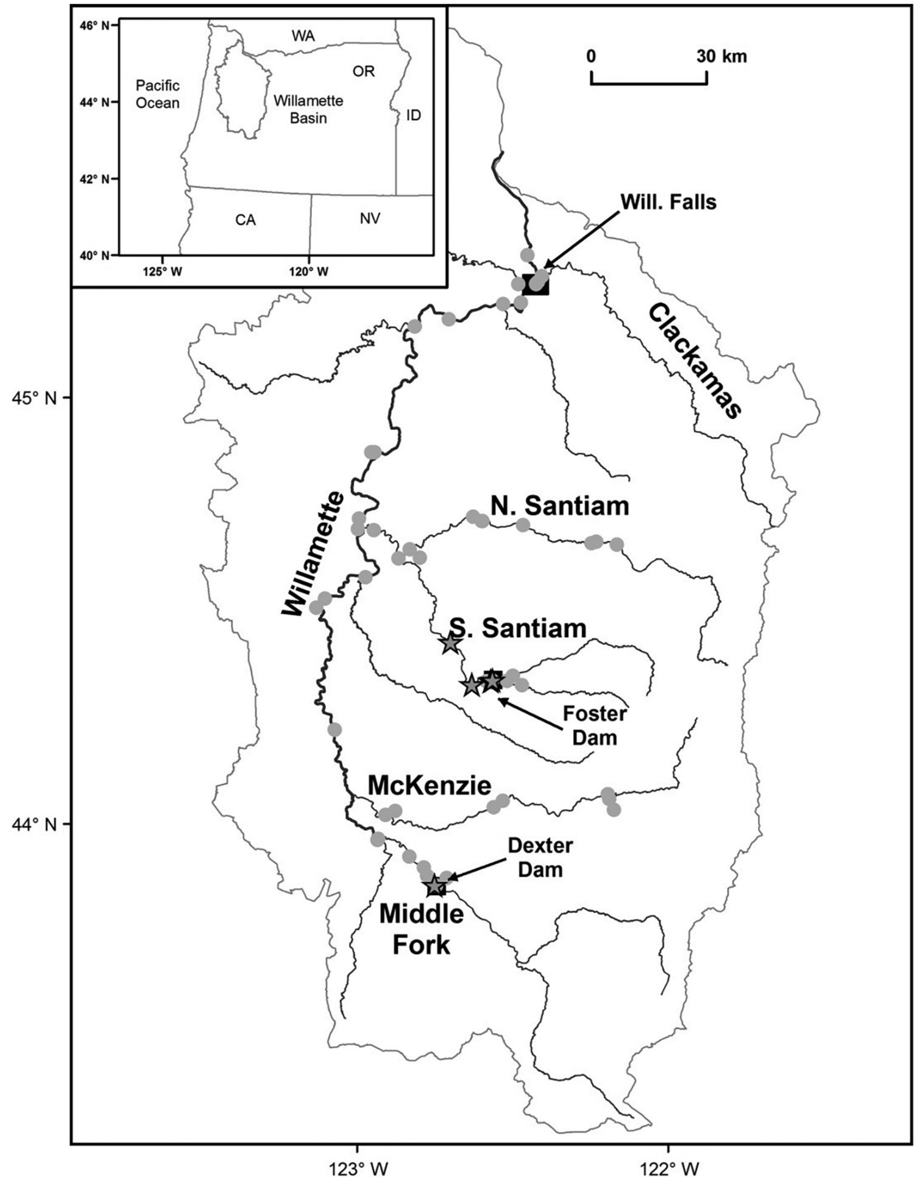

Fig. 1. Map of Willamette River basin, Oregon, showing release sites (stars) and locations of fixed radiotelemetry receivers (circles).

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 UWR (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 into three fates in the South Santiam River: (1) reported as harvested, (2) remained in a river, or (3) recaptured and removed at Foster. In the Middle Fork Willamette, classes (1) and (2) were used; (3) 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 yr in freshwater and 2 yr in the ocean. The percent of males and females that spent 1 yr in freshwater and 2 yr 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 1000 times. Annual values for WRS escapement were provided by a larger radiotelemetry 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 ($\chi^2 = 1.7$, 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 ($\chi^2 = 2.55$, df = 1, $P = 0.11$; Table 1). 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

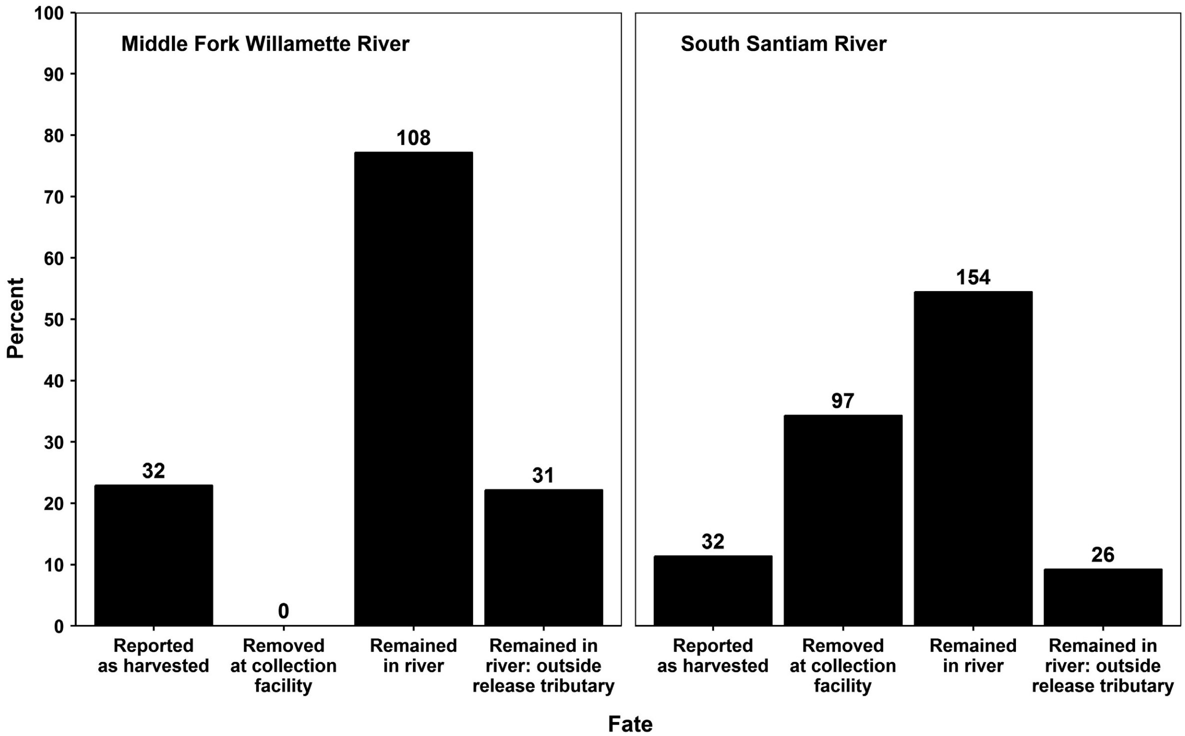

Fig. 2. Fate of non-local radio-tagged summer-run steelhead recycled in the Middle Fork Willamette River (left) and South Santiam River (right), Oregon 2012–2014. Sample size of each fate category is above each bar. The percent of fish remaining in a river other than their release tributary are included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

[IQR]; Table 2), 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 d (median ± IQR; Table 2), 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 (χ^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 1) and the odds of being reported as harvested was 2.72 times higher for males recycled below Dexter Dam than females (χ^2 = 3.95, df = 1, P = 0.047; Table 3). Neither release day nor year were significantly associated with fate

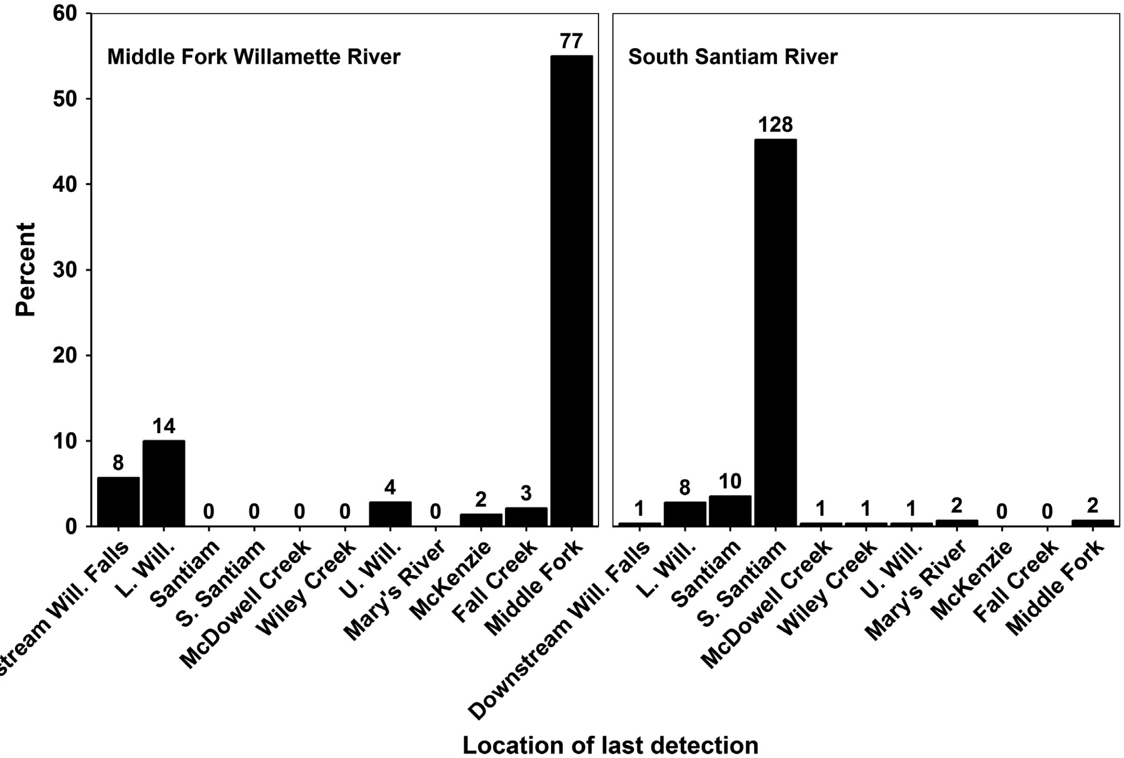

Fig. 3. Locations of last detections for 108 and 154 non-local radio-tagged summer-run steelhead recycled in the Middle Fork Willamette River (left) and South Santiam River (right), Oregon, respectively, that were assigned a fate of remaining in a river. Sample sizes for individual locations are above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

Table 1. The number, size, fate, and straying rate of non-local male and female radio-tagged recycled summer-run steelhead in the Middle Fork Willamette River, 2012–2014.

Sex	No. radio-tagged	Fork length (cm); mean (SD)	Reported as harvested		Remained in river		Remained in river, outside release tributary	
			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

Notes: 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 than their release tributary are included the group classified as remaining in river.

(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

Table 2. 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, USA.

Year	Release site	N (percent)	Distance traveled Median rkm (IQR)	Time elapsed Median days (IQR)	Number of detections 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)

Notes: A recycled fish was classified as a stray if it was last detected in a river outside of its release tributary. En dash indicates that there were no strays from the release site, so there is no median.

PLV, Pleasant Valley; WTL, Waterloo; WLC, Wiley Creek; FST, Foster Dam tailrace; DXD, Dexter; rkm, river kilometer; IQR, interquartile range.

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, USA.

Variable	Estimate	Confidence interval Lower	Confidence interval 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

Notes: Estimates expressed as odds of being harvested. Parameter estimates shown in bold have 95% confidence intervals that do not include 1.

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 (χ^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 UWR 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 2), 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 2), 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 4). 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 4). Overall, sex was associated with fate (χ^2 = 6.78, df = 2, P = 0.03; Table 5). 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 5).

Table 4. The number, size, fate, and straying rate of non-local male and female radio-tagged recycled summer-run steelhead in the South Santiam River, 2012–2014.

Sex	No. radio-tagged	Fork length (cm); mean (SD)	Reported as harvested		Remained in river		Removed at Foster		Remained in river, outside release tributary	
			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

Notes: 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 than their release tributary are included the group classified as remaining in river.

Table 5. 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, USA.

Variable	Estimate	Confidence interval	
		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

Notes: Parameter estimates shown in bold have 95% confidence intervals that do not include 1.

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).

PLV, Pleasant Valley; WLC, Wiley Creek; WTL, Waterloo.

Reported harvest of males (16.1%) was not significantly higher than females (10.8%; $\chi^2 = 0.48$, 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 ($\chi^2 = 0.0003$, df = 2, $P = 0.99$; Table 5) nor release distance from Foster Dam ($\chi^2 = 7.15$, df = 6, $P = 0.31$; Table 5) 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 3901 ± 2651 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 6). The greatest difference occurred in 2012 when the estimated population of SRS remaining in a river (4647; 3961–5256; 95% CI) was approximately six times higher than the estimated WRS escapement (811; 579–1119; 95% CI; Table 6).

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

Table 6. 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.

Year	No. 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 summer-run steelhead 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)

Notes: 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.

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. 2012*a*). 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 2015*b*). 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. 2012*a*). 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 and

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 and 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 decrease 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, is important for managers to consider (McCormick and Porter 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 and 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 (Putaala and Hissa 1998, Stewart et al. 2005). 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 and Luikart 2007). Unlike salmon, steelhead are iteroparous which could exasperate these potential issues; 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. 2013). 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 and Caudill 2014). Keefer and 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 and 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

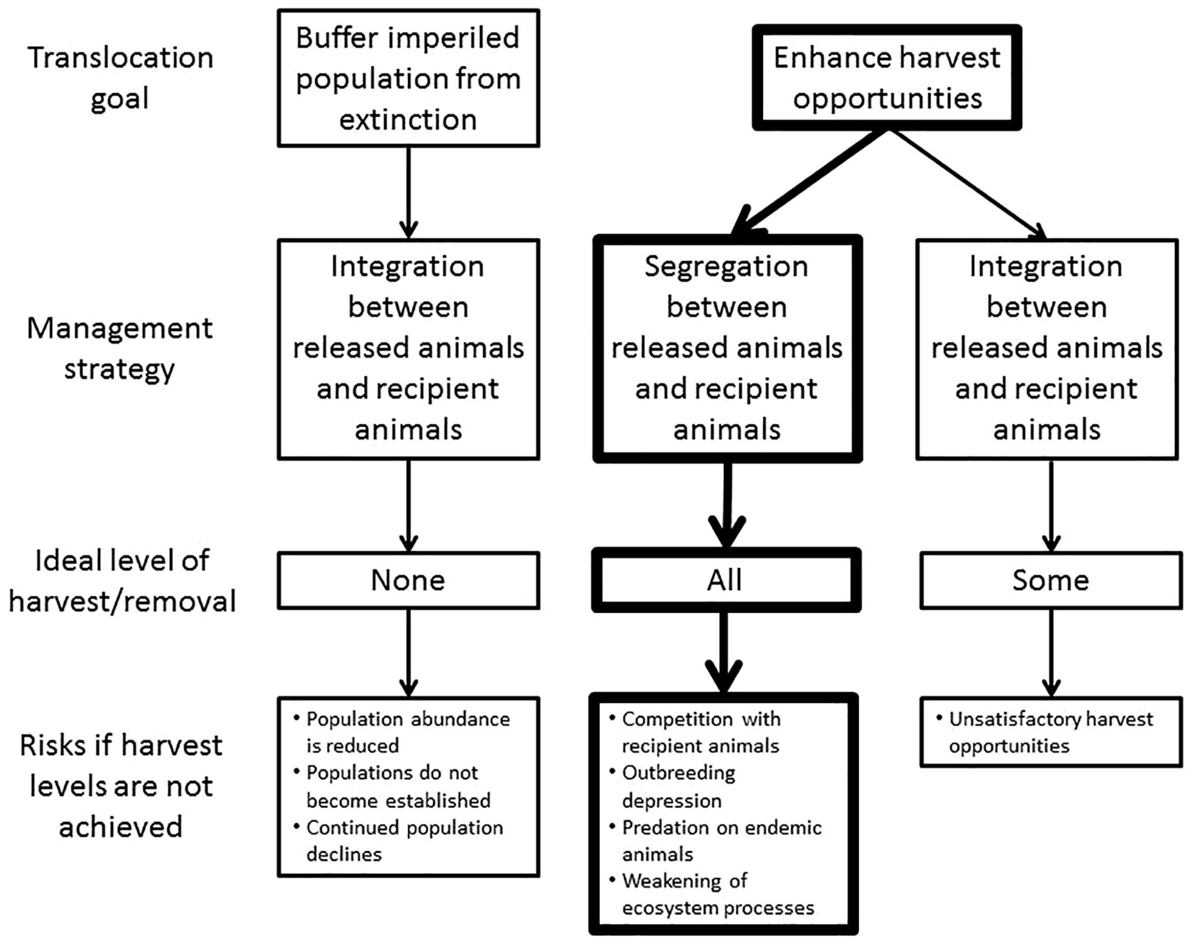

Fig. 4. Diagram illustrating acceptable harvest levels of non-local animals intentionally released and the associated ecological and social costs and benefits. Thicker boxes indicate scenario in Willamette River basin, Oregon, where non-local summer-run steelhead are released and recycled to increase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

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. 2012*b*), 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 framework (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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