Influence of Juvenile and Adult Experiences on Tributary Overshoot and Fallback by Steelhead in the Columbia River Basin

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Abstract

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Tributary overshoot occurs when adult fishes homing to natal sites continue upstream past the mouth of their natal stream. Using multistate release-recapture models, I examined the prevalence of overshooting and fallback to home by 37,806 PIT-tagged steelhead from 14 tributaries of the Columbia River basin in the years 2005—2015. For stocks that overshot at rates > 5%, I used generalized linear models and conditional inference trees to examine the influence of juvenile and adult experiences on overshooting and fallback to home. More than 40% of adult John Day, Umatilla, Walla Walla, Wenatchee, and Tucannon river steelhead overshot upstream dams. Average annual fallback rates to home ranged from 17.8% (SE 1.9%) for Walla Walla hatchery steelhead to 75.0% (SE 2.6%) for Umatilla wild steelhead. Overshooting was associated with factors related to the reservoir environment. Incorrect shoreline orientation within 24 rkm of the natal stream resulted in increased overshooting. Steelhead were also more likely to overshoot when water temperatures were higher (significant in 5 of 7 tributaries, $P < 0.05$). In contrast with adult experiences, juvenile experiences linked to imprinting disruption did not consistently increase overshooting. Hatchery steelhead were more likely to overshoot and less likely to fall back home than their wild counterparts. However, overshooting was only elevated in hatchery stocks reared upstream of release sites. Attraction to upstream areas was decreased with endemic broodstock and long-term acclimation. Juvenile barging was found to decrease overshooting relative to in-river out-migration. Longer ocean residency was associated with increased overshooting, but effects were biologically small. Finally, there was some evidence that spill during March increased fallback to home. A significant positive effect of spill during March was found for hatchery ($\chi^2_8 = 15.82$, $P = 0.032$) but not for wild steelhead ($\chi^2_{10} = 12.87$, $P = 0.231$).

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Chapter 1: Introduction to Tributary Overshoot and Fallback by Steelhead in the Columbia River Basin

Homing is a general pattern in many migratory animals in which reproductive adults return to natal sites, or the site of previous reproduction. Orientation mechanisms used to locate natal sites can include geomagnetic or celestial compass orientation, navigation based on an animal's position on a learned or inherited internal map, and piloting based on local landmarks or odors (Åkesson and Hedenström 2007; Alerstam et al. 2003). Orientation in rivers presents a special challenge compared to lakes or marine environments; decisions must be made at each branch of the river and homeward migrations may include movement in many compass directions depending on the structure of the watershed. While adult salmon *Oncorhynchus* spp. and steelhead *Oncorhynchus mykiss* use multiple types of oriented movement during different stages of their spawning migrations, piloting based on olfactory clues guides them through river systems (reviewed by Bett and Hinch 2016). However, these clues may be difficult to discern and follow in large, complex environments (Keefer et al. 2008b). Immediate river conditions experienced during the adult migration may affect migratory trajectories. Additionally, prior experiences during developmental periods could hinder the piloting abilities of salmonids.

In riverine fishes, tributary overshoot occurs when adult fishes homing to natal sites continue upstream past the mouth of their natal stream (Ricker 1972). A return to downstream sites after overshooting is overshoot fallback (Boggs et al. 2004; Naughton et al. 2006). Overshooting has been documented in steelhead (Copeland et al. 2015; Keefer et al. 2008a), Chinook salmon *O. tshawytscha* (Boggs et al. 2004; Gallinat and Ross 2009; Keefer et al. 2008b), sockeye salmon *O. nerka* (Ricker and Robertson 1935), and Atlantic salmon *Salmo salar* (Økland et al. 2001).

Observed overshoot distances range from less than 1 rkm (Ricker and Robertson 1935) to 200 rkm or more (Boggs et al. 2004).

There is growing awareness that tributary overshoot is a common behavior by steelhead in the Columbia River basin. For example, each year, approximately 50% of Tucannon River steelhead swim past their natal river and ascend Lower Granite Dam 73 km upstream (Bumgarner and Dedloff 2011; Copeland et al. 2015). Unless steelhead successfully fall back at dams to return downstream to natal sites, overshooting rates this extreme may significantly deplete naturally spawning populations. While tributaries may also receive overshooting steelhead from other rivers, large influxes of strays, particularly hatchery strays, may have negative impacts on population fitness (Chilcote 2003; Chilcote et al. 2011). Despite the potential issues involved with tributary overshoot, overshooting has not been characterized for many populations, and previous primary studies (Boggs et al. 2004; Keefer et al. 2008a) may have underreported overshooting rates because they assumed fish origin based on final location. This study is the first to estimate rates of overshooting and fallback to home using robust statistical methods. It is also the first to test hypotheses related to overshooting. In Chapter 2, I use multistate release-recapture estimation to characterize overshooting and fallback to home. In Chapters 3 and 4, I examine whether overshooting is related to imperfect imprinting during juvenile stages, or the river environment during the spawning migration. I also test the hypothesis that late-winter spill increases fallback to home after overshooting.

The goals of this thesis are to: quantify overshooting and fallback to home for multiple populations of steelhead, understand the mechanisms behind overshooting, and evaluate possible management strategies for reducing overshooting or improving fallback to home. To fulfill these goals I will address four primary objectives: (1) document tributary overshoot and fallback for multiple populations of adult steelhead in the Columbia River basin using existing PIT-tag data, (2) determine the extent to which tributary overshoot and fallback are associated with juvenile rearing and barging experiences, (3) characterize the degree to which tributary overshoot is related to shoreline orientation and water temperatures experienced by adults, and (4) determine whether surface passage options promote dam fallback and homing success. It must be noted that potential mechanisms are not mutually exclusive; many juvenile and adult experiences may contribute to these behaviors.

Due to the non-direct nature of the homing process, some overshooting will naturally occur. In order to successfully home, salmon and steelhead must navigate a complex river system and identify waters that contain memorized olfactory stimuli (Johnsen and Hasler 1980; Quinn 2005). Salmon and steelhead are believed to imprint or learn multiple “landmarks” along their out-migration route as juveniles, a process called sequential imprinting (Bett and Hinch 2016; Keefer and Caudill 2014; Ueda 2012). Surges of thyroid hormones, which have been connected to memory formation (Lema and Nevitt 2004), are released in response to novel environments during the juvenile out-migration (Dittman and Quinn 1996). As adults, homing sometimes requires exploration of multiple pathways to determine the correct route (Keefer et al. 2008b; Ricker 1972). In the absence of olfactory clues, salmon display lateral and downstream movement within the channel until the home scent is picked up again (Johnsen and Hasler 1980; Keefer and Caudill 2014; Quinn 2005). When a fish reaches a branch in the river, movement may occur up one branch but be followed by a downstream retreat if the wrong branch is chosen and olfactory clues are lost (Quinn 2005). Under this model, a fish may stray past its natal tributary, move some distance upstream, and then determine that it has lost the home odor and attempt to fall back downstream.

If steelhead overshoot their natal river, they may attempt to return downstream. However, downstream dam passage related mortality is a major concern for adult salmonids (Ferguson et al. 2008; Harnish et al. 2015). Steelhead that fall back at dams are less likely to reach spawning tributaries or hatcheries than steelhead that do not (Boggs et al. 2004). While steelhead are iteroparous, very few steelhead from the interior Columbia River basin actually make repeat migrations (Keefer et al. 2008d). One of the primary reasons that interior Columbia steelhead rarely make repeat migrations is that safely navigating downstream through the hydrosystem is difficult. Not only can downstream dam passage be hazardous for adult fish, it can also add significant delays. Downstream movement rates by kelts slow greatly just above dams, possibly because steelhead are trying to identify downstream passage routes or waiting for flow or spill conditions to change (Harnish et al. 2015; Rayamajhi et al. 2013; Wertheimer and Evans 2005).

The effects of human-induced modifications of river systems and hatchery production on overshoot tendencies are unknown. The Federal Columbia River Power System (FCRPS) has altered river channels, flow regimes, and water temperatures in the Columbia and Snake rivers (Quinn and Adams 1996). There have been extensive efforts to mitigate for the impact of dams in the Columbia River basin, including fish hatcheries and juvenile barging (Keefer et al. 2008c; Mobrand et al. 2005). A combination of dam related mortality, failed artificial propagation programs, overfishing, and continued freshwater habitat loss and degradation have led to considerable declines in salmon and steelhead abundance (Mobrand et al. 2005; Reisenbichler and Rubin 1999). Many wild populations are now listed under the U.S. Endangered Species Act (NMFS 2012), so high levels of tributary overshoot not accompanied by overshoot fallback may affect the viability of naturally spawning populations. Consequently, a greater understanding of this process may be important for the conservation of depleted or listed populations.

Imperfect imprinting.—First, insufficient memories of the juvenile out-migration may lead to increased overshooting. Juvenile experiences including hatchery rearing and barge transportation may produce fish with lower imprinting strength. Normal levels of hormones associated with imprinting and memory development may not be stimulated in hatchery settings (Nishioka et al. 1985). This hypothesis has been supported by other authors (Dickhoff et al. 1978; Dittman et al. 1996). Hatchery produced juveniles exhibit less brain development and reduced olfactory activity (Marchetti and Nevitt 2003), leading to decreased imprinting strength (reviewed by Keefer and Caudill 2014). Because they do not imprint as strongly, hatchery reared individuals may be more likely to overshoot.

In addition to hatchery rearing, unnatural downriver migration may affect learning. Transportation downstream by barge has been used for decades to improve the survival of juvenile salmonids through the FCRPS (Keefer et al. 2008c). Annually, millions of wild and hatchery origin salmon and steelhead smolts are barged hundreds of kilometers down the Snake and Columbia rivers to be released below dams (Keefer et al. 2008c). Barging is utilized to increase juvenile survival and adult returns, but studies have emerged indicating that barging is associated with delayed mortality and impaired adult migrations (Bond et al. 2017; Chapman et al. 1997; Keefer et al. 2008c; Muir et al. 2006). Barging greatly speeds out-migration movement (Muir et al. 2006), which is a critical period for imprinting (Ueda 2012). Due to imprinting disruption, barging is associated with higher rates of straying in adults (Bond et al. 2017; Bugert and Mendel 1997; Keefer et al. 2008c). Steelhead that are barged as juveniles may also be more likely to overshoot as adults, because they failed to properly establish memories needed to find and follow the route to home.

Memories needed to successfully find home may decay naturally with age. There is evidence that salmon that spend more years in the ocean stray more frequently than younger fish in the same run year (Labelle 1992; Pascual et al. 1995; Quinn and Fresh 1984; Quinn et al. 1991), however the opposite pattern has also been found (Hard and Heard 1999). Memory failure may cause older migrants to struggle to recognize scents learned on their out-migration (Quinn 1993). Over longer time periods rivers may also change so that scents learned as juveniles no longer match the current waters (Keefer and Caudill 2014). Difficulty identifying the route to home may lead older steelhead to overshoot.

The hypothesis that imperfect imprinting leads to overshooting is tested in Chapter 3. Overshoot and fallback rates are examined with respect to rearing and barging history, as well as the number of years the fish spend in the ocean. For several tributaries, I sub-divided hatchery meta-populations to investigate behavioral differences between stocks derived from local and out-of-basin broodstock. For one population, I examined the effect of within-basin acclimation prior to release. While hatchery rearing or fish age may make homing more difficult, it may also result in more frequent intentional straying in response to environmental conditions. Variation in run timing among age classes or rear types may systematically expose groups to different environmental conditions. Run timings between rear types and ocean age classes were therefore compared to determine if differences in overshoot rates may be due to environmental factors rather than inherent differences.

Reservoir environment.—Following imprinted scents may be more difficult in wide, slow moving reservoirs, because the home scent may be diffuse and widely mixed. Salmon and steelhead tend to be shore oriented during their spawning migrations (Daum and Osborne 1998; Hughes 2004; Reischel and Bjornn 2003), and incorrect shoreline orientation may result in overshooting within wide, regulated rivers (Keefer et al. 2006a). As Chinook salmon approach their natal stream, they express a strong preference for dam ladders on the same shore as the mouth of their natal stream (Keefer et al. 2006a). However, wide river channels or attraction to high-flow areas may cause lateral olfactory clues to be missed (Keefer et al. 2006a). A fish may more easily overshoot their natal stream and ascend an upstream dam if they fail to orient to the correct shoreline (Keefer et al. 2006a; Keefer et al. 2008b). In Chapter 4, I compare overshooting rates to the shoreline orientation of steelhead at dams prior to their home tributary. If overshooting was related to shoreline orientation, steelhead that ascended ladders on the shore opposite their natal tributary mouth should have been more likely to overshoot.

Water temperature.—In addition to altered river channels, steelhead in the Columbia River basin now face elevated summer water temperatures (Quinn and Adams 1996; Quinn et al. 1997). High water temperatures may spur steelhead to make non-direct homing movements, including overshooting, as they seek out thermal refuge. Steelhead are highly affected by water temperature (Baigun et al. 2000; High et al. 2006; Keefer et al. 2008a; Keefer et al. 2004a). As water temperatures rise, migration rates slow dramatically and many steelhead seek out thermal refuge until conditions improve (High et al. 2006; Keefer et al. 2008a). High et al. (2006) found that 61% of steelhead in the Columbia River basin staged temporarily in at least one cool tributary along their migration. Keefer et al. (2009) found that cool water refuge use was correlated with mainstem water temperatures. Because water temperatures have risen due to the hydrosystem and prevailing climate, it is likely that more steelhead exhibit thermoregulatory behavior today than historically (Keefer et al. 2009).

Interior Columbia River basin steelhead are stream maturing, meaning that they enter freshwater before they are fully mature, overwinter in rivers, and spawn the following spring

(Robards and Quinn 2002). Thermal refuges may not only allow steelhead to escape stressful conditions, but also achieve lower basal metabolic rates in order to conserve energy (Berman and Quinn 1991). Low-velocity pool habitats can serve as thermal refuges, and low current velocity would further increase the metabolic benefit of holding in such refuges prior to spawning. Berman and Quinn (1991) observed spring Chinook salmon in the Yakima River to hold in thermal refuges for four months prior to spawning. As spawning dates neared, fish left refuges and traveled to spawning sites located both up and downstream. Some fish even fell back at Roza Dam to reach downstream spawning sites.

In Chapter 4, I investigate the relationship between overshooting and water temperature in the mainstem and natal rivers. Higher rates of overshooting during warmer periods would support the thermal refuge hypothesis. High rates of fallback to home in spring may indicate that steelhead are holding in upstream areas until the spawning season.

Late-winter spill.—General options for downstream dam passage include turbines, locks, spillways, and sluiceways (Khan et al. 2013; Wertheimer 2007). Dams vary in the availability of options, and passage routes are often only operated during certain times of the year (Khan et al. 2013). Survival of steelhead kelts moving through dams is lowest through turbines and juvenile bypass systems (Harnish et al. 2015). Fallback through turbines and juvenile bypass systems is more dangerous for adult steelhead than smolts (Ferguson et al. 2008; Harnish et al. 2015). Both lethal and sub-lethal injuries obtained during turbine or bypass passage are a concern (Wagner and Hillson 1993; Wertheimer 2007).

Non-turbine, surface-flow passage options are likely the safest and most efficient route for fallback at dams (Khan et al. 2013; Wertheimer 2007; Wertheimer and Evans 2005). Experimental studies estimated adult survival through surface-flow routes at Bonneville and McNary dams to be

98% (Normandeau Associates 2011; Normandeau Associates 2014). Post-spawn steelhead can be effectively routed away from turbines using even a small amount of surface flow (Wertheimer 2007). When available, steelhead kelts exhibit a very strong preference for surface rather than turbine passage (Harnish et al. 2015; Khan et al. 2013; Rayamajhi et al. 2013; Wertheimer 2007). When sluiceway operations at The Dalles Dam were experimentally maintained throughout late winter and early spring, Khan et al. (2013) found 91%—99% of steelhead kelts to fall back through the sluiceway rather than turbines. Forebay residence times of kelts are also decreased through the operation of surface flow routes (Wertheimer and Evans 2005). While these studies focus on post-spawn steelhead, it is likely that pre-spawn steelhead that overshoot their natal streams would benefit from the same operations. Beginning spillway operations in late winter may enhance the fallback of overshooting steelhead, and contribute to increased rates of fallback to home. A true experiment to test the benefits of surface flow at dams to overshooting steelhead is beyond the reach of this study. However, fallback to home rates and timing will be compared to the frequency of late-winter spill in Chapter 4.

This thesis characterizes tributary overshoot and fallback for multiple populations of adult steelhead in the Columbia River basin using existing PIT-tag data. It also investigates the degree to which tributary overshoot and fallback are related to juvenile experiences of rearing and barging history, as well as adult experiences of shoreline orientation, water temperature, and the late-winter spill. Together, these analyses provide a novel and thorough examination relevant to the management and conservation of steelhead in the Columbia River basin.

Chapter 2: Characterization of Tributary Overshoot and Fallback Rates for Steelhead in the Columbia River Basin

Abstract

Overshooting is a poorly understood behavior that has not been widely characterized. This chapter estimates overshoot and fallback rates to home for steelhead from 14 tributaries of the Columbia River basin using multistate release-recapture models. It also compares tally and multistate movement rate estimates based on the migration histories of 37,806 adult steelhead from 14 tributaries in the years 2005—2015. Average detection efficiencies ranged greatly between tributary sites (44.2% (SE 2.8%)—97.1% (SE 3.4%)), and between years at individual sites (35.7% (SE 14.1%)—100%). Because detection efficiencies varied spatially and annually, tally based estimates were not viable indices of return rates. John Day, Umatilla, Walla Walla, Wenatchee, and Tucannon populations overshot at rates greater than 40%. Successful homing declined with increasing overshooting rate. Poor return rates may be due to many steelhead straying to upstream spawning locations, or insufficient downstream dam passage options for adult steelhead in late winter and early spring. On average, 13.2% (SE 2.7%) of overshooting steelhead were observed in upstream where spawning could occur. Average annual fallback rates to home ranged from 17.8% (SE 1.9%) for Walla Walla hatchery steelhead to 75.0% (SE 2.6%) for Umatilla wild steelhead. Concentrated fallback to home in late winter and early spring indicates that steelhead may be holding in refuge areas upstream. Because of its high prevalence in threatened and endangered populations, tributary overshoot merits further attention as managers work to recover steelhead in the Columbia River basin.

Introduction

Overshooting is a poorly understood behavior that has not been widely characterized. Quantitative studies on straying in general are very limited for wild salmon and steelhead. Previous primary studies on overshooting (Boggs et al. 2004; Keefer et al. 2008b) may have underreported overshooting rates because home tributaries of individual fish were unknown, therefore overshooting was only detectable for fish that subsequently fell back and entered a downstream tributary. Additionally, reporting on overshooting and fallback to home by steelhead with known home rivers (Bumgarner and Dedloff 2011; Keefer et al. 2016; Murdoch et al. 2012) utilized a tally-based approach that ignored detection efficiencies. If detection efficiencies are not 100%, tally-based methods underestimate movement rates. Many populations of Pacific salmon and steelhead are at risk of extinction (NMFS 2012), and high levels of tributary overshoot not accompanied by overshoot fallback may affect the viability of naturally spawning populations. Consequently, robust overshoot and fallback estimates are important for the management and conservation of steelhead in the Columbia River basin.

This chapter estimates overshoot and fallback rates to home for multiple populations of steelhead in the Columbia River basin using multistate release-recapture methods. Characterizing steelhead overshoot patterns helps to identify which steelhead populations in the Columbia River basin are most at risk from overshooting, and whether losses are permanent or if fish manage to fall back downstream to home. Overshooting may lead to decreased rates of steelhead that successfully return home to spawn, therefore limiting the recovery of threatened or endangered populations. If overshooting represents a significant sink to a population, awareness of the phenomenon is important for management of those populations

In addition to depleting at risk populations, overshooting may lead to influxes of strays into native populations in upstream tributaries. Influxes of hatchery fish have a negative impact on the recruitment performance of natural populations (Chilcote 2003; Chilcote et al. 2011). While strays often have lower reproductive success than native fish, they can comprise much of the spawning population, increase competition for spawning areas, and produce a significant fraction of a stream’s juvenile fish (Chilcote et al. 1986).

Poor conditions in the natal stream may motivate steelhead to stray in search of superior spawning grounds. Tributaries vary in their attractiveness to salmon and steelhead (Keefer et al. 2009; Quinn et al. 1991), and less stable and poorer quality habitats produce higher proportions of strays (Cram et al. 2013; Leider 1989). Following the eruption of Mount St. Helens, many nearby tributaries were unsuitable for spawning. Steelhead from affected tributaries strayed at higher rates to the nearest upstream river, while rivers downstream did not receive increased numbers of strays (Leider 1989). This is an extreme example of habitat disturbance, but steelhead may also overshoot in response to subtler aspects of stream quality. In this chapter, I investigate post-overshoot movements to determine whether overshooting fish strayed into non-natal tributaries where they could potentially spawn.

The contents of this chapter prepare for subsequent analysis in later chapters into the mechanisms behind overshooting and potential management strategies for reducing overshooting or improving fallback to home. Characterizing the spatial and temporal patterns in overshooting increases knowledge about overshooting in the Columbia River basin, allowing agencies to create informed strategies for the management of threatened and endangered populations.

Methods

Passive integrated transponder (PIT) tags have been used in the Columbia River basin for more than three decades to monitor the movements and survival of juvenile and adult salmon and steelhead (McCutcheon et al. 1994). PIT-tags have distinct identification codes that can be detected from outside of the fish without requiring an internal power source (Gibbons and Andrews 2004; McCutcheon et al. 1994). These tags are small (10-14 mm long, 2 mm wide), and remain with the fish for its entire life (Gibbons and Andrews 2004). PIT-tag monitoring systems are in place in many dams and small stream sites throughout the Columbia River basin. This study made use of existing tagging and observation data in the Columbia Basin PIT Tag Information System (PTAGIS) (www.ptagis.org), which is run by the Pacific States Marine Fisheries Commission.

Nine tributaries of the Columbia River and five tributaries of the Snake River were selected based on sample size of PIT-tagged steelhead and presence of in-stream detection sites from 2005 to 2015. Columbia River tributaries included Fifteenmile Creek (rkm 309), and the Hood (rkm 273), Deschutes (rkm 328), John Day (rkm 351), Umatilla (rkm 465), Walla Walla (rkm 509), Yakima (rkm 539), Wenatchee (rkm 754), and Entiat (rkm 778) river basins (Figure 2.1). Snake River tributaries included the Tucannon (rkm 622), Clearwater (rkm 746), Grande Ronde (rkm 793), Salmon (rkm 825), and Imnaha (rkm 830) river basins.

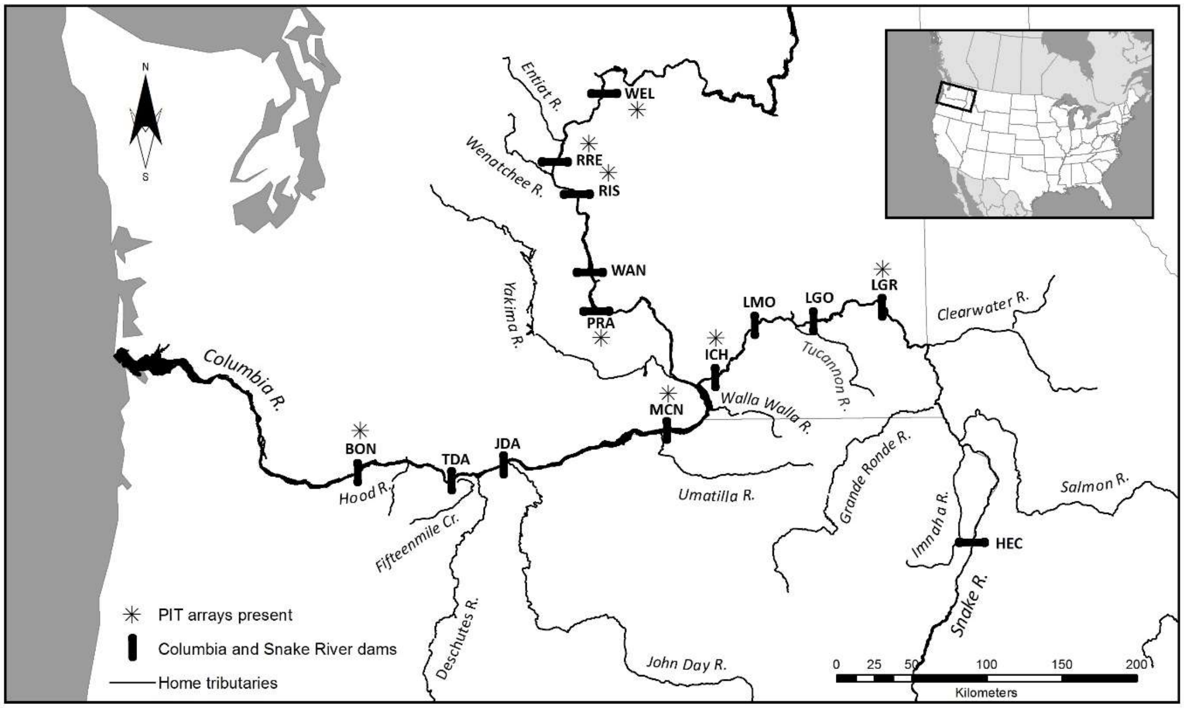

FIGURE 2.1.—Map of the Columbia River basin, including home tributaries of study populations. BON = Bonneville Dam, TDA = The Dalles Dam, JDA = John Day Dam, MCN = McNary Dam, PRA = Priest Rapids Dam, WAN = Wanapum Dam, RIS = Rock Island Dam, RRE = Rocky Reach Dam, WEL = Wells Dam, ICH = Ice Harbor Dam, LMO = Lower Monumental Dam, LGO = Little Goose Dam, LGR = Lower Granite Dam, HEC = Hells Canyon Dam.

Steelhead tagged as adults were excluded because their natal streams were unknown. This study utilized observation data from both hatchery and wild origin steelhead PIT-tagged and released as juveniles within tributaries of the Columbia and Snake rivers. This method of sample selection permitted the natal-origin of each fish to be known with reasonable certainty. Juvenile steelhead do move, but studies have only noted small scale movements within and between creeks (Bramblett et al. 2002; Kahler et al. 2001) rather than movements between major tributaries in a large basin. Steelhead tagged as juveniles were distinguished by filtering on length and detection history. I first removed all steelhead greater than 350 mm at release, as well as those not detected at the Bonneville fishway following release. I examined the meta-data of individual mark files for fish whose tagging information lacked a length parameter. These often contained notes such as “adult tagging” or “out-migration study” that were indicative of juvenile or adult status. Steelhead tagged as adults were removed from the sample.

To characterize when overshooting and fallback to home occurred, I examined the annual run timing of each population. Timing was determined based on the date and time of the first observation at specific locations. I found the timing of arrival at Bonneville Dam, overshoot dams (i.e. the first dam with PIT detection capabilities upstream of the natural tributary in question), and at home without and after overshooting. If fish were not detected in the adult ladder at the overshoot dam, the time of the first observation above the overshoot dam was used. Density plots of the annual run timing for each population were created (Appendix A).

Next, observations were sorted into run years. Because most populations of interior Columbia River basin steelhead normally begin their upstream migration in summer and spawn the following spring (Robards and Quinn 2002), 1 June was used as the division between run years. No date would be a perfect division between runs for all fish in all tributaries. To account for this, I manually examined the individual capture histories of all fish that had observations in consecutive run years and assigned fish to the correct run year or years. Some fish had single migrations that overlapped run years, with either early detections at downstream sites, or late detections indicating downstream movement after the spawning season. Other fish made multiple consecutive upstream migrations (successful kelts that returned as repeat spawners) and were kept in both run years.

Tally v. multistate estimation.—The behavior of each fish was classified based on its capture history. From the data, I generated estimates of overshooting, fallback to home, total success, and use of alternative sites. I also conducted a comparative analysis of multistate release-recapture estimation and less rigorous tally based estimation. A raw tally based approach is straightforward, but is sensitive to missed detection. Undetected fish will not be accounted for, resulting in biased estimates. Rather than an estimate of the probability of overshooting, it will be an estimate of the probability of overshooting *and* being seen doing it. The two estimates will only be equal if the probability of detection is 1. Despite these disadvantages, tally-based approaches are commonly used with PIT-tag data, especially in gray literature.

An alternative approach is to translate the detection history into a release-recapture framework that can be interpreted using a multinomial likelihood model, such as the Cormack-Jolly-Seber model (Cormack 1964; Jolly 1965; Seber 1965). Overshooting can be estimated with the model diagramed in Figure 2.2. Fish are "released" (R) from Bonneville dam. They have a probability (p) of moving upstream to the overshoot dam. At the dam, they have a probability (d) of being detected. Afterward, they have a probability (λ) of moving to and being detected at a site further upstream.

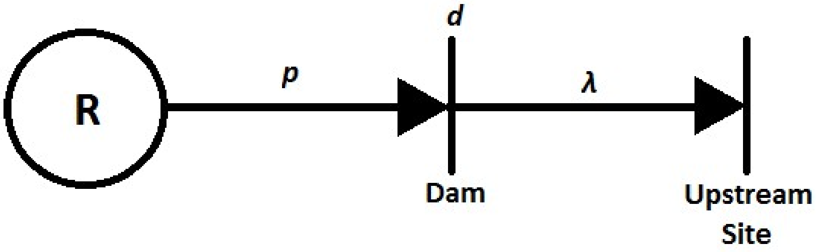

FIGURE 2.2.—Two-period Cormack-Jolly-Seber model to estimate overshooting (p). The detection efficiency at the overshoot dam is d, and the probability of moving to and being seen at a site further upstream is λ.

Every fish has a two period Bernoulli detection history. In the first period, they are either seen (1) or not seen (0) at the upstream dam. In the second period fish are either seen or not seen at a site further upstream. Each history has an associated probability. For example, the probability of history 11 (being seen at the overshoot dam and at a site upstream) is $pd\lambda$. The multinomial likelihood is presented in Equation 2.1.

$$L(x_i|n,p,\lambda) = \tag{2.1}$$

$$\binom{n}{x_{11},\ x_{10},x_{01},x_{01}}(pd\lambda)^{x_{11}}\big(pd(1-\lambda)\big)^{x_{10}}(p(1-d)\lambda)^{x_{01}}\big((1-p)+p(1-d)(1-\lambda)\big)^{x_{00}}$$

where

$p =$ probability of overshooting,

$d =$ probability of being detected,

$\lambda =$ probability of moving to and being observed upstream of the overshoot dam,

$n =$ number of fish “released” from Bonneville,

$x_{11} =$ number of fish observed at the overshoot dam and at a site upstream of it,

$x_{10} =$ number of fish observed at the overshoot dam but not a site upstream of it,

$x_{01} =$ number of fish observed only upstream of the overshoot dam, and

$x_{00} =$ number of fish not observed at the overshoot dam or upstream of it.

The Cormack-Jolly-Seber model is limited to one migration pathway and the fish have only one choice of movement. In the previous example, fish can only move upstream. However, adult steelhead behavior is much more complex. Multistate models, an extension of Cormack-Jolly-Seber models, allow animals to migrate between different states between recapture events

(Brownie et al. 1993; Hestbeck et al. 1991; Schwarz and Arnason 2000). A multistate model allows for multiple movement choices at one or more locations. They can be designed to permit fish to choose between branches of a river, or between moving upstream or downstream. Arnason-Swartz multi-state models assume that transition probabilities between states are independent of the prior capture history (Schwarz and Arnason 2000). These models can be built and analyzed in the program Branch (Lockhart et al. 2015). Program Branch creates multistate likelihoods based on a user-drawn diagram of the model structure to estimate movement and survival parameters.

The graphical interface of the program Branch is demonstrated in Figure 2.3. In this example, a schematic was drawn to model the upstream migration of adult Tucannon River steelhead. Detection "gates" are represented by parallel lines, which are separated by stretches. Detection efficiencies are associated with each gate, and survival probabilities are associated with each stretch between detection gates. Steelhead are "released" from Bonneville Dam (BON). They move upstream through McNary (MCN) and Ice Harbor (ICH), where they are faced with a choice between different states. They can continue on to the Tucannon River (HOME1 and HOME2), or they can overshoot Lower Granite Dam (LGR). After overshooting, steelhead may remain in the upper Snake River (USR), or they may switch states and fall back to home.

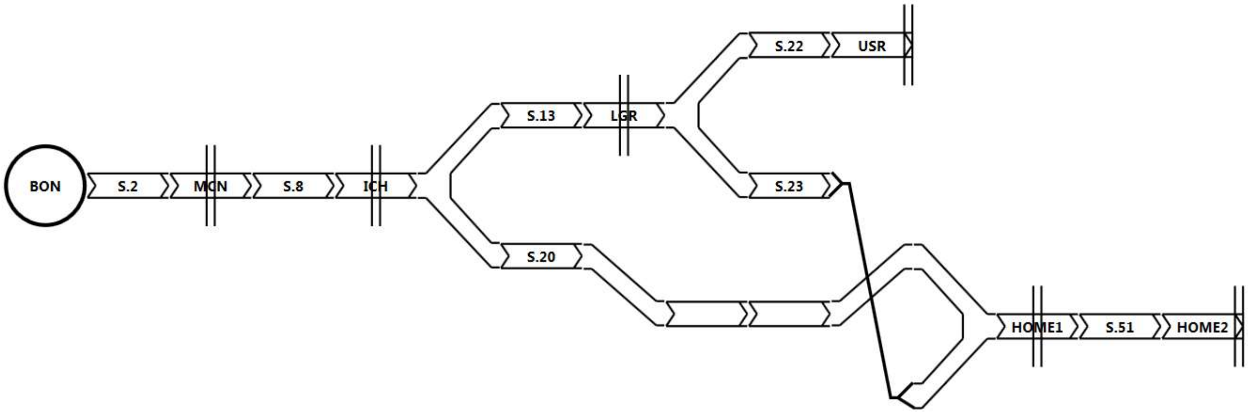

FIGURE 2.3.—Schematic drawn in the program Branch model the adult migration behavior of Tucannon River steelhead. BON = Bonneville, MCN = McNary, ICH = Ice Harbor, LGR = Lower Granite, USR = upper Snake River, HOME1 = Lower Tucannon River, HOME2 = upper Tucannon River.

In this chapter, the behaviors of overshooting, total success, and fallback to home were estimated using both tally and multinomial likelihood/multistate approaches. Estimates were compared using signed-rank tests to determine the appropriateness of using tally results as indices. Differences between the estimates would indicate that a tally approach fails to accurately estimate behavior rates. Spatial and annual variation in log-differences would indicate that tally estimates would not serve as reliable indices of behavior rates across areas or between years.

Overshooting.—Within the study period, the distribution of PIT-arrays allowed overshooting to be calculated at McNary, Priest Rapids, Rock Island, Rocky Reach, Wells, Ice Harbor, and Lower Granite dams. For each population, overshooting was measured over dams upstream of the mouth of the home tributary. For steelhead from the Clearwater, Grande Ronde, Salmon, and Imnaha rivers, overshooting was measured in the upper Columbia River, starting at Priest Rapids Dam. Priest Rapids Dam is not strictly above the natal tributary mouth for these tributaries, but it is upstream of the shortest distance route to home. Other authors have previously classified these movements as overshooting (Keefer et al. 2008b).

To adjust observed rates of overshooting for under-detection, it was necessary to estimate the detection efficiencies at the dams in each run year. To do this I used capture histories based on the Manly-Parr technique. All fish were "released" from the Bonneville Dam fishway. The first period was traveling to and being observed in the adult fish ladder at the upstream dam. The second period was being observed at any site above the dam. Because annual sample sizes of PIT-tagged steelhead from individual populations were often small, fish from all tributaries were pooled. This invokes the assumption that detection probabilities are independent of fish origin. This assumption is reasonable if run timing is similar, or if detection probabilities do not change much throughout the year. Annual probabilities of detection and associated variances were estimated for each dam with the program USER (Lady and Skalski 2009) using the likelihood in Equation 2.1.

Unconditional overshooting rates were calculated as the proportion of fish seen in the fish ladder of the overshot dam out of the number of fish seen at Bonneville, divided by the detection efficiency at the overshot dam in that run year (Eq. 2.2). Variance of the ratio estimator was calculated using the delta method (Eq. 2.3). No covariance term is included; the independence of detection efficiency and observed overshoot rate was assumed. Adjustment by detection efficiency provides an estimate of the actual overshooting rate, rather than simply the perceived overshooting rate.

$$p_i = \frac{\left(\frac{x_i}{n_i}\right)}{d_i} \tag{2.2}$$

$$Var(p_i) = \left(\frac{\left(\frac{x_i}{n_i}\right)}{d_i}\right)^2 \left[\left(\frac{\left(\frac{x_i}{n_i}\right)\left(1-\frac{x_i}{n_i}\right)}{n_i}\right)\left(\frac{1}{\left(\frac{x_i}{n_i}\right)^2}\right) + Var(d_i)\left(\frac{1}{(d_i)^2}\right)\right] \tag{2.3}$$

where

p_i = probability of overshooting in the *i*th year,

n_i = number of fish "released" from Bonneville in the *i*th year,

x_i = number of fish detected at the dam in the *i*th year, and

d_i = detection efficiency at the dam in the *i*th year.

I also estimated conditional overshooting rates using just the fish known to have reached the nearest dam with adult detectors downstream of the overshoot dam. This second estimate excludes early mortalities, harvests, and strays into non-natal hatcheries.

Total success and fallback to home.—"Total success" is the proportion of steelhead that successfully migrated from Bonneville Dam to their home tributary. This could occur along any potential migration pathway, including moving straight to the home tributary or overshooting and then falling back to the home tributary after overshooting. "Fallback to home" is the conditional probability that fish returned to their home tributary after overshooting. While nearly all steelhead were detected moving upstream through dams, few were detected while moving downstream. This is because downstream pathways had very limited detection efficiency. Adult steelhead may utilize juvenile bypass systems that contain PIT detectors, but they are were likely to travel through turbines, spillways, or sluiceways and completely elude detection. Additionally, detection at the dam while a fish falls back did not necessarily indicate fallback success. Fish may die while falling back or prior to reaching their natal stream. Therefore, I estimated fallback to home rather than simply fallback.

Fallback to home was estimated for each dam with PIT detectors that a population overshot. Fallback to home could occur along any pathway, even if it involved overshooting further before falling back. For instance, the fallback rate to home of John Day steelhead that overshot McNary is out of all fish that overshot McNary, including the ones that went on to overshoot Ice Harbor or Priest Rapids as well.

To estimate the proportion of steelhead that return to home, in-stream arrays in the home tributary must be present in the tributary near the confluence with the Columbia (or Snake) River. Additionally, a multiple antenna or array layout is required to estimate detection efficiencies. This means that fish must have the possibility of being detected at a minimum of two successive locations within their natal tributary as they move upstream. This allows for the estimation of detection efficiency at the home site. Finally, sufficient numbers of fish are needed to precisely estimate detection efficiencies and return rates. I did not attempt to calculate total success or fallback to home for any samples comprised of less than 5 fish. I calculated total success and fallback to home in every year that satisfied these requirements.

Total success and fallback to home rates are an estimation of the proportion of fish that moved far enough into the home tributary to cross the first PIT-tag array. The location of the initial detection site may be important, therefore I have supplied the distance (rkm) this site is from the tributary mouth with the results. Most of the anterior home sites are within 10 rkm of the tributary mouth, but a few are located as far as 76 rkm.

Total success and fallback to home were estimated using multistate models in the program Branch (Lockhart et al. 2015). A schematic diagram, like that illustrated in Figure 2.3, was drawn to represent the potential adult migration pathways for each tributary. Models were simplified or expanded to fit the data in each year as needed. Pathways not utilized by at least five fish were not included in that year's model.

Regression analyses.—To evaluate whether overshooting contributed to decreased return to home, I used weighted linear regression. Total success and fallback rates were regressed against overshooting rate, after accounting for population and run year factors. Return rates were weighted by the inverse of their variance. A weighted regression was also used to compare total success across major river basin sections (lower Columbia, upper Columbia, and Snake). The analysis accounted for rear type and run year, using basin location as the final term. The analysis accounted for rear type and run year, using basin location as the final term.

I also performed a series of regression analyses to investigate the effects of distance between the home tributary mouth and upstream dam on rates of overshooting and falling back to home. I modeled the probability of overshooting versus distance (rkm) between the mouth of the home tributary and the overshoot dam for steelhead using binary, logit link models. I modeled lower Columbia and upper Columbia populations separately. To account for seasonal variation, these models first included a run timing covariate. Run timing was represented as the number of months "early" the steelhead was; or the number of months before April that the steelhead was first seen in the Bonneville adult fish ladder. To determine whether overshooting decreased exponentially with distance, I fit both linear and quadratic models for distance.

I tested whether distance affected overshoot rates by combining P-values across multiple years (Eq. 2.4 and 2.5). In the Upper Columbia, there was only adequate data to model the run years 2007/2008—2014/2015. One-tailed P-values testing for the effects of distance in individual models were transformed into χ^2_2 statistics and then summed to a χ^2_{2K} statistic, where K was the number of independent tests.

$$-2lnp_i \sim \chi^2_2 \tag{2.4}$$

$$\sum_{i=1}^{K} y_i \sim \chi^2_{2K} \tag{2.5}$$

where

p_i = the ith p-value and

K = the number of tributaries.

Alternative spawning sites.—After overshooting, steelhead may not necessarily attempt to fall back to home. Steelhead visiting "alternative sites" is of interest because it sheds light on whether overshooting fish that do not return home may be spawning in other locations. Moreover, if a fish enters a non-natal hatchery, travels above a one-way weir, or is harvested in a non-natal stream, it has no opportunity to make a subsequent choice and cannot fall back at all.

While rates are presented in this section, these are only observation rates and are not indicative of actual movement rates. Presented rates are unavoidably biased because there are many areas that steelhead could stray to where there are no instream arrays or traps. Observations reported are presented only to give a general sense that some steelhead are moving to alternative sites, and where some of those alternative sites are located.

The capture history of each overshooting fish was examined for subsequent observations in non-home tributary sites up or downstream of the overshot dam. The proportion seen at up and downstream alternative sites was estimated as the number observed at alternative sites out of the total number that overshot. Due to small sample sizes and spatial array layout limitations, calculation of detection efficiencies at alternative sites was not attempted. I only examined the use of alternative sites by populations in run years fallback to home was estimated.

Many overshooting steelhead are not observed in an alternative spawning location or estimated to return home. This remaining proportion, or undetermined loss, represents an unknown combination of mortalities, strays, and harvests. Undetermined loss (L) was calculated using Equation 2.7.

$$L = 1 - (F + A_u + A_d) \tag{2.7}$$

where

$L =$ undetermined loss,

$F =$ estimated proportion of overshooting fish that fell back to home,

$A_u =$ proportion of overshooting fish seen at alternative spawning site upstream of overshot dam, and

$A_d =$ proportion of overshooting fish seen at alternative spawning site downstream of overshot dam

Results

The PTAGIS database yielded 37,806 adult steelhead migration histories from the 14 selected tributaries in the run years 2005/2006—2014/2015 (Table 2.1). A few steelhead were made repeat migrations, so 37,686 individual steelhead were in this study. Annual numbers of PIT-tagged adults ranged from 898 in 2005/2006 to 7,395 in 2009/2010, with a mean of 3,781. Total numbers of steelhead from individual populations ranged from 278 (Deschutes River, natural) to 7,661 (Salmon River, hatchery), with a mean of 1,644.

TABLE 2.1.—Sample sizes of adult steelhead tagged as juveniles and subsequently detected on the Bonneville adult fishway during run years 2005/2006—2014/2015. Run year was defined as June 1–May 31 each year. Origin refers to the rearing history of the fish, hatchery or wild.

		Run Year										
Tributary	Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Total**
						Lower Columbia						
Hood	*hatchery*	2	31	106	251	430	231	333	144	149	151	**1828**
	wild	1	12	15	8	31	24	30	40	28	89	**278**
Fifteenmile	*wild*	0	1	0	12	47	92	96	34	32	38	**352**
Deschutes	*wild*	0	0	38	68	118	115	109	82	180	97	**807**
John Day	*wild*	68	121	114	248	348	280	287	151	261	243	**2121**
Umatilla	*hatchery*	9	15	60	80	115	76	64	24	16	37	**496**
	wild	3	10	17	22	14	13	81	68	69	173	**470**
Walla Walla	*hatchery*	33	36	25	300	416	223	261	120	111	167	**1692**
	wild	11	11	10	8	61	95	115	92	57	75	**535**
						Upper Columbia						
Yakima	*wild*	15	12	18	17	33	23	40	20	46	78	**302**
Wenatchee	*hatchery*	408	404	338	468	819	526	422	384	188	190	**4147**
	wild	0	0	2	8	69	75	53	33	31	39	**310**
Entiat	*wild*	0	4	8	8	75	74	55	26	44	66	**360**
						Snake						
Tucannon	*hatchery*	60	84	549	425	633	266	163	87	121	145	**2533**
	wild	35	24	39	16	50	45	51	55	44	60	**419**
Clearwater	*hatchery*	38	35	50	178	96	683	726	656	322	391	**3175**
	wild	37	30	50	80	139	200	140	112	89	286	**1163**
Grande Ronde	*hatchery*	19	103	164	153	1137	622	657	419	389	576	**4239**
	wild	35	16	36	37	65	83	83	69	63	62	**549**
Salmon	*hatchery*	37	21	68	83	1656	1237	1471	968	973	1147	**7661**
	wild	17	22	19	49	158	104	126	70	118	148	**831**
Imnaha	*hatchery*	32	36	33	33	734	442	392	163	340	408	**2613**
	wild	38	14	36	124	151	124	143	71	94	130	**925**
Total		**898**	**1042**	**1795**	**2676**	**7395**	**5653**	**5898**	**3888**	**3765**	**4796**	**37806**

Migration timing.—Fallback to home generally occurred much later than overshooting. In all populations, overshooting primarily occurred in late summer and early fall (Figure 2.4). The average median date of overshooting for all populations was 11 September. In contrast, fallback to home after overshooting occurred most often in early spring, with 20 March as the average date between populations. The distribution of fallback to home was bimodal in a few populations, including the Wenatchee hatchery (Figure B.11) and John Day wild (Figure B.5) populations. In these populations one peak occurred in October, followed by a second in April. Similar bimodal distributions were suggested in some of the other populations (Appendix B). Only fish that overshot in fall experienced a delay in average date of home arrival. Populations whose non-overshooting fish overwinter in the mainstem river and enter the home tributary in spring have similar arrivals timing of overshooting and non-overshooting fish (Figure 2.5).

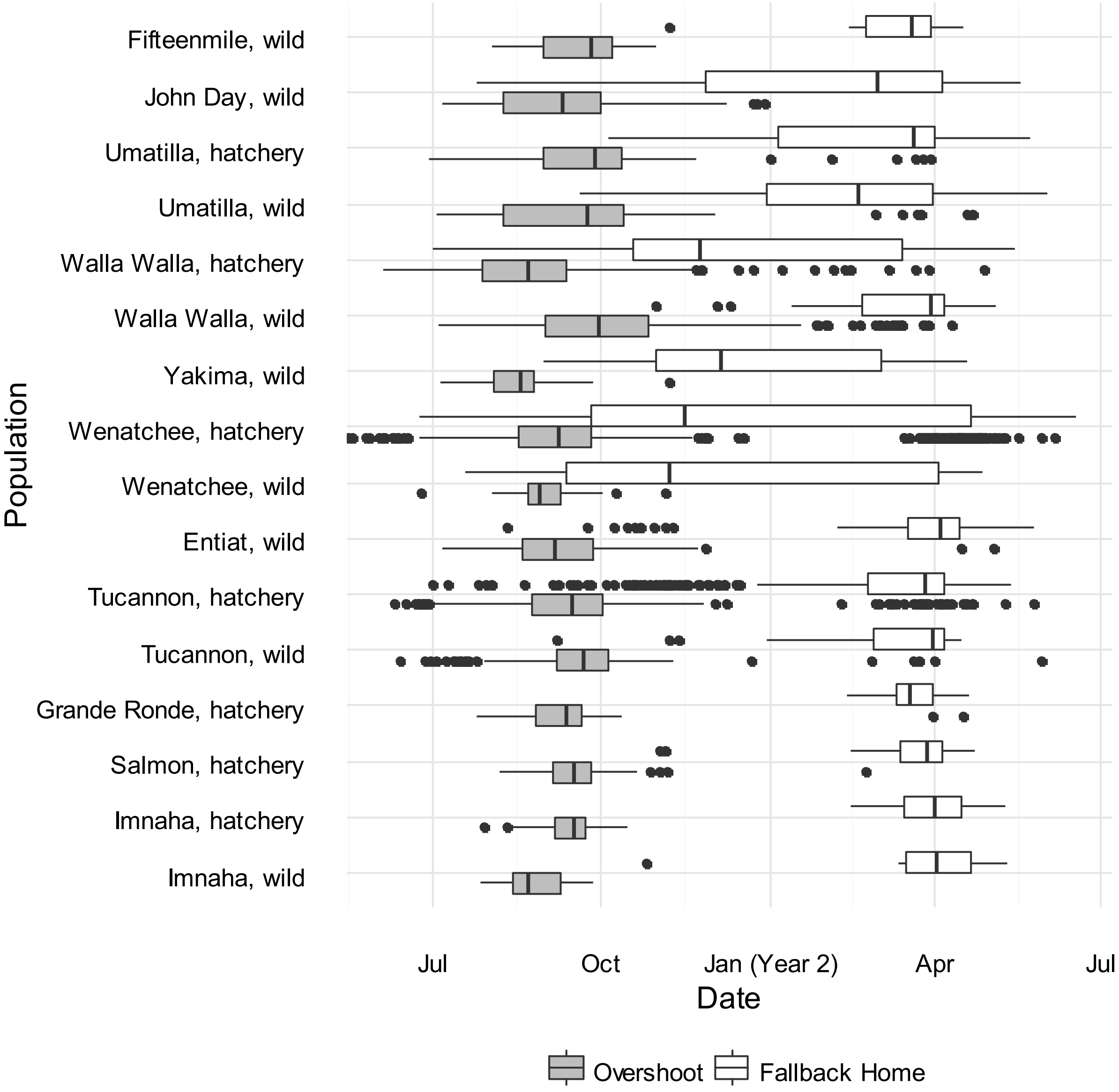

FIGURE 2.4.—Timing of overshoot and fallback to home by Columbia River basin steelhead population from run years 2005/2006—2014/2015. Populations presented in order of distance from Bonneville Dam, with Snake River populations listed last.

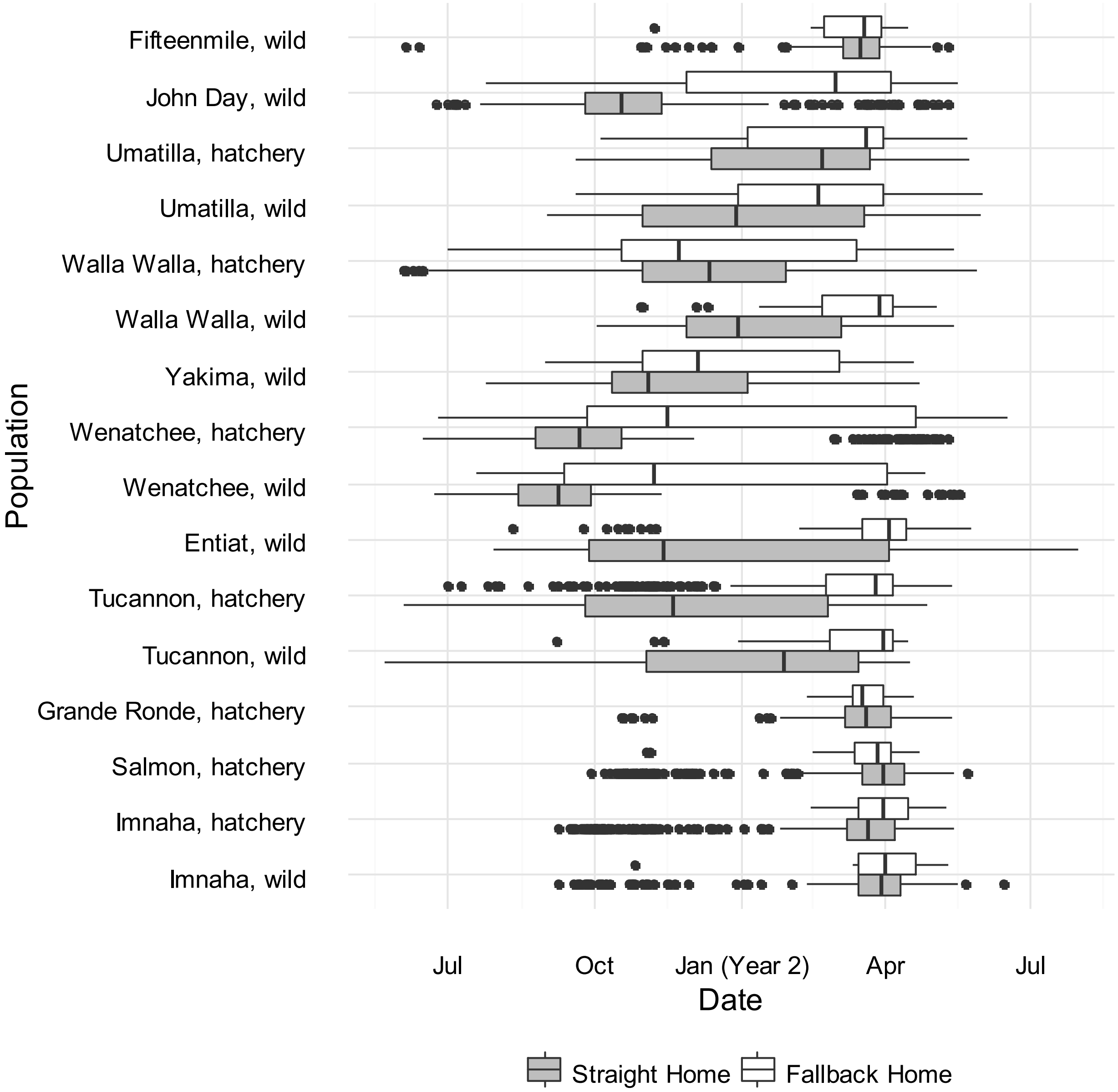

FIGURE 2.5.—Timing of arrival at home either by moving straight to home or falling back to home after overshooting by Columbia River basin steelhead populations from run years 2005/2006—2014/2015. Populations presented in order of distance from Bonneville Dam, with Snake River populations listed last.

Tally v. multistate estimation.— On average, tally estimates of overshooting rates were less than 0.05 percentage points lower than multistate estimates (Figure 2.6, T- = 234, T+ = 24, P = 0.001). Annual PIT-tag detection efficiencies for all dams averaged 97.2% (SE 0.8%). The efficiencies for McNary, Priest Rapids, Wells, Ice Harbor, and Lower Granite were close to 100% in all years (Appendix A). The lowest detection efficiencies were at Rock Island Dam, which averaged 84.8% (SE 3.7%) and was as low as 60.3% (SE 3.1%) in 2014/2015. In 2014, a crack was discovered in the Wanapum Dam downstream of Rocky Reach. Lowering of the reservoir behind Wanapum compromised the Rock Island adult fishway in that year. Additionally, high noise in 2015 prompted the decommission and replacement of four antennas in the right ladder at Rock Island.

In contrast with dam sites, tributary site detection efficiencies were lower and exceedingly more variable by location and year (Appendix A). Average annual detection efficiencies ranged from 44.2% (SE 2.8%) at the Deschutes River mouth to 97.1% (SE 3.4%) at Prosser Dam in the Yakima River. Inter-annual variation was high for many sites. For instance, detection efficiencies at the Lower Tucannon River site ranged from 35.7% (SE 14.1%) to 100% depending on the year. Tally based estimates of total successful return to home were on average 5.6 percentage points lower than multistate estimates (T- = 144, T+ = 9, P = 0.001, Figure 2.6). Due to one outlier, tally estimates of fallback to home after overshooting were not significantly different from the multistate estimates (T- = 49, T+ = 17, P = 0.175), however tally based estimates underestimated rates of fallback to home in 9 out of 11 populations.

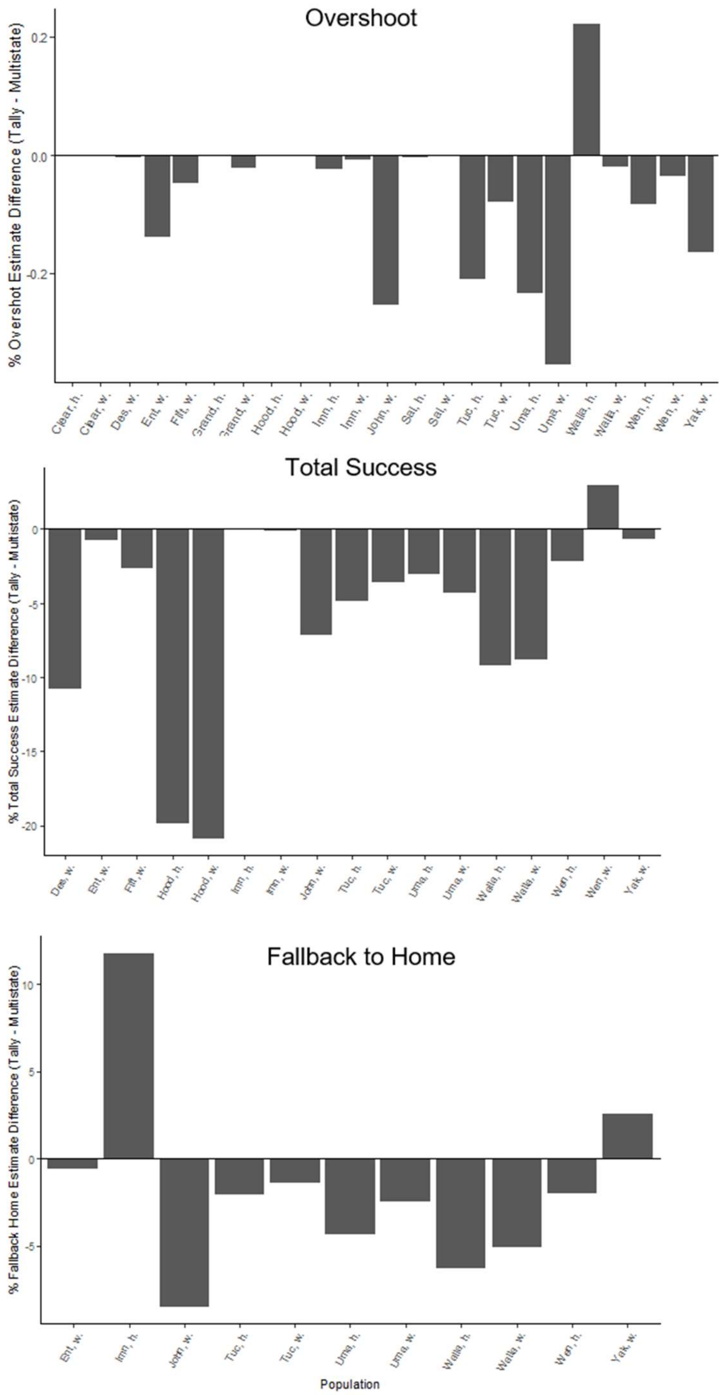

FIGURE 2.6.—Comparison of tally and multistate estimates Estimates were averaged across all run years with available data within a tributary. Estimated differences were calculated by subtracting the multistate estimate from the tally estimate.

Total success rates.—The overall average of the estimates of total success for all populations was 53.9% (SE 4.1%), from a high for Deschutes wild steelhead at 80.8% (SE 3.9%), to a low for Umatilla hatchery steelhead at 25.6% (SE 1.4%) (Appendix C). Steelhead from the upper Columbia River had moderately higher total success than steelhead from the lower Columbia or Snake rivers ($F_{2,68} = 9.68$, $P = 0.0002$). Divided by basin location, the average of the mean annual estimates of total success was 53.6% (SE 5.7%) for lower Columbia populations, 66.1% (SE 6.1%) for upper Columbia populations, and 42.3% (SE 7.1%) for Snake populations. Finally, total success rates were found to decrease in response to overshooting rates (Figure 2.7, $F_{1,54} = 41.5$, $P < 0.0001$). The coefficient of partial determination for overshooting rate in the model was 0.43.

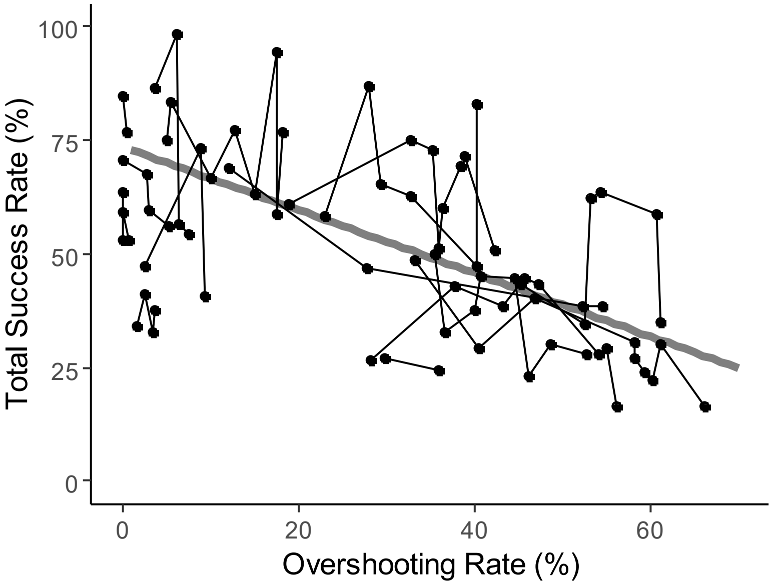

FIGURE 2.7.—Relationship between total success rate and overshooting rate , grouped by 17 steelhead populations investigated. Black lines connect annual values from the same population. Overshooting was measured at the nearest upstream dam with PIT-tag detectors. Overshooting and total success rates are adjusted by estimates of detection efficiencies.

Overshooting rates.—Overshooting occurred at high rates in multiple populations (Appendix D). The highest annual overshooting estimate was 70.8% (SE 9.1%), for Umatilla wild steelhead over McNary Dam in 2006/2007. Eight populations had overshooting rates exceeding 50% in at least one year (Figure 2.8). These estimates were out of the entire run that passed Bonneville; conditional overshooting rates, using just the fish that ascended the dam before the overshoot dam, are even higher (Appendix E). For instance, in 2014/2015, 85.7% (3.1%) of Walla Walla hatchery steelhead that passed McNary Dam went on to overshoot Ice Harbor Dam and 66.1% (SE 6.6%) of Tucannon wild steelhead that passed Ice Harbor Dam went on to overshoot Lower Granite Dam. Although overshooting rates varied year to year, there was no discernable temporal trend (Figure 2.8).

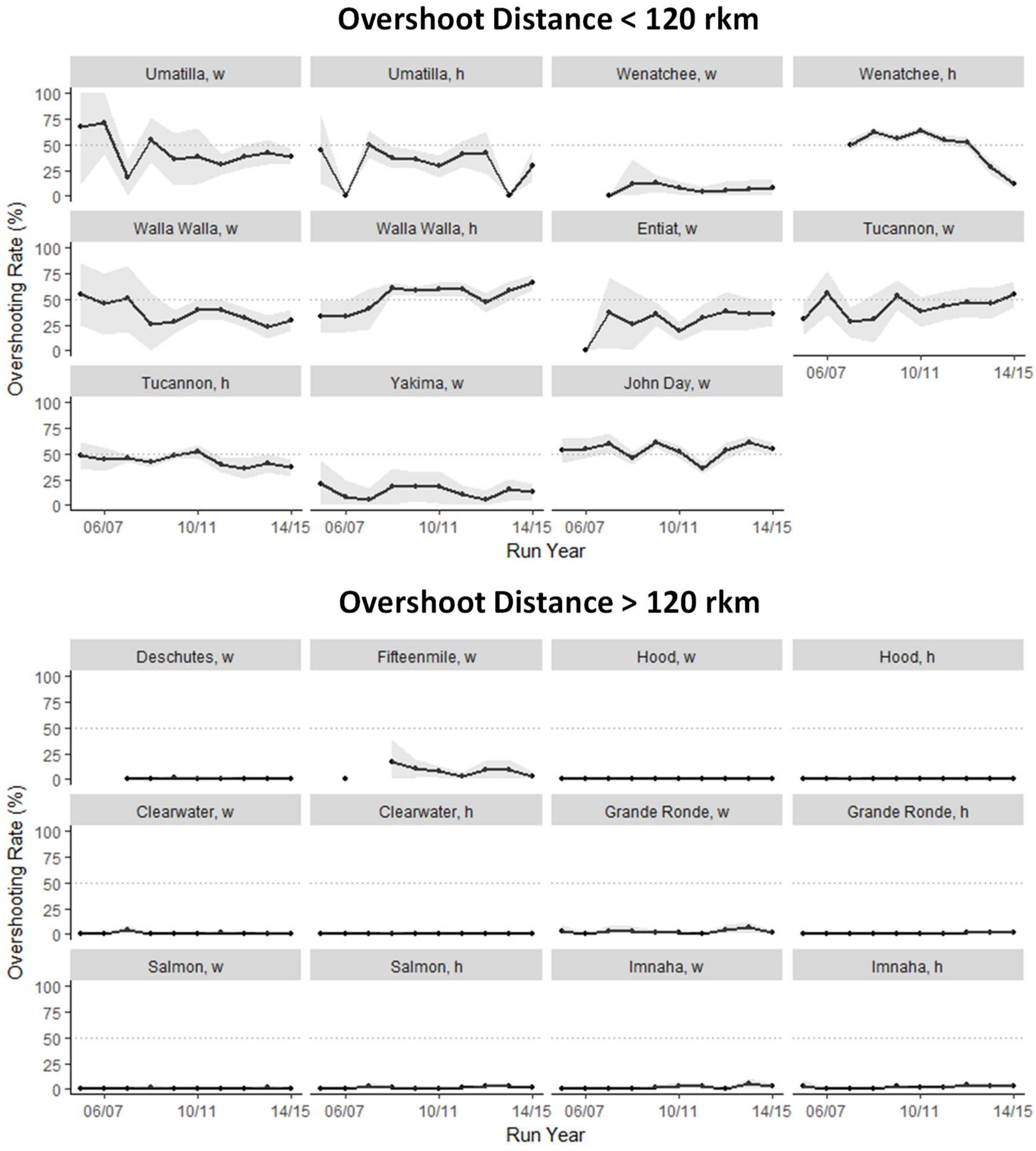

FIGURE 2.8.—Plots of overshoot rates, and 95% confidence intervals, over the nearest upstream dam with adult detection capabilities versus run year. Organized by distance between the upstream dam and the home tributary mouth. Percentage is out of the number of fish that passed Bonneville Dam. Overshoot percentages are adjusted by detection efficiencies at the dams. “w” indicates a wild population and “h” indicates a hatchery population.

A few geographic patterns in overshooting emerged. All populations from tributaries of the lower Columbia River were more likely to overshoot Ice Harbor on the Snake River than Priest Rapids on the upper Columbia River (Figure 2.9). Steelhead from Snake River tributaries were also unlikely to overshoot Priest Rapids into the upper Columbia. In contrast, steelhead from upper Columbia tributaries consistently entered the upper Columbia and almost never overshot into Snake River (Figure 2.9).

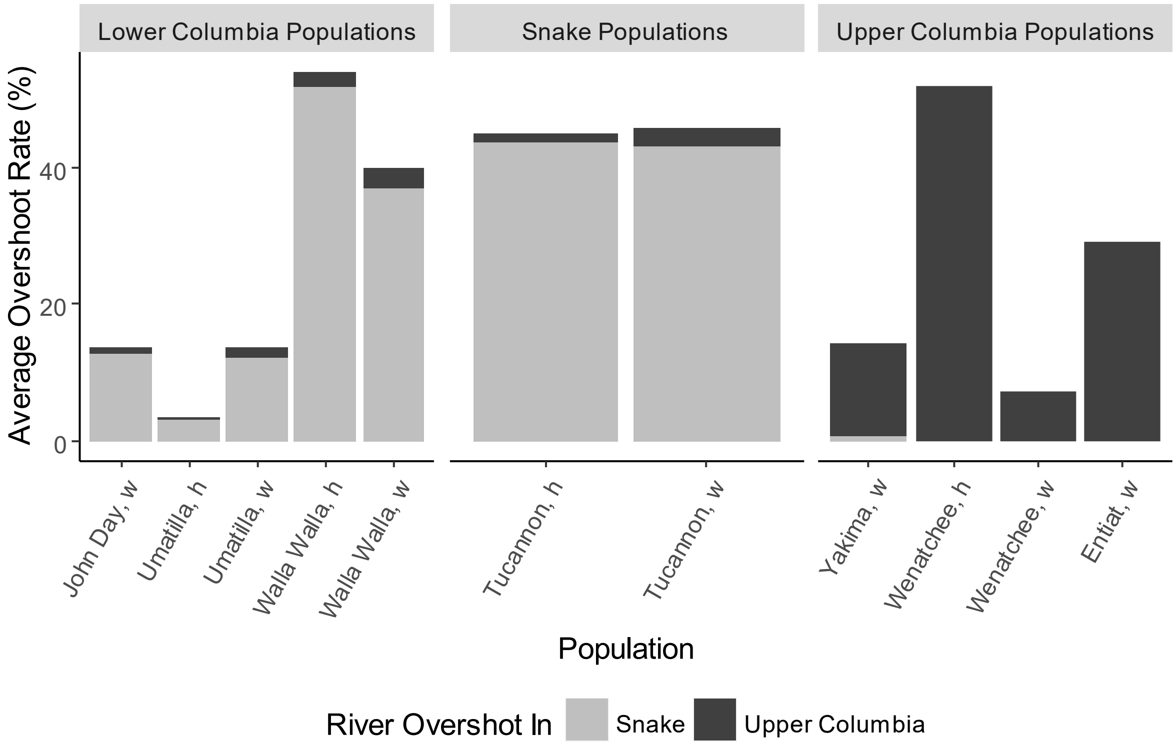

FIGURE 2.9.—Average annual overshoot rates in the Snake and upper Columbia rivers by steelhead from lower Columbia, Snake, and upper Columbia populations that have the opportunity to overshoot dams with PIT detectors in both the upper Columbia and lower Snake rivers.

Overshooting rate decreased sharply with distance to the upstream dam (Lower Columbia: $\chi^2_{20} = 191.96$, $P < 0.0001$, upper Columbia: $\chi^2_{16} = 217.80$, $P < 0.0001$). Distance to the upstream dam had a significant negative linear effect on overshooting rate (lower Columbia combined $\chi^2_{20} = 160.60$, $P < 0.0001$, upper Columbia combined $\chi^2 = 161.09$, $P < 0.0001$). Evidence for a quadratic distance term was inconsistent between analyses because overshooting over McNary did not monotonically decrease with distance (Figure 2.10). John Day steelhead (119 rkm below McNary) overshoot more than Umatilla steelhead (5 rkm below McNary).

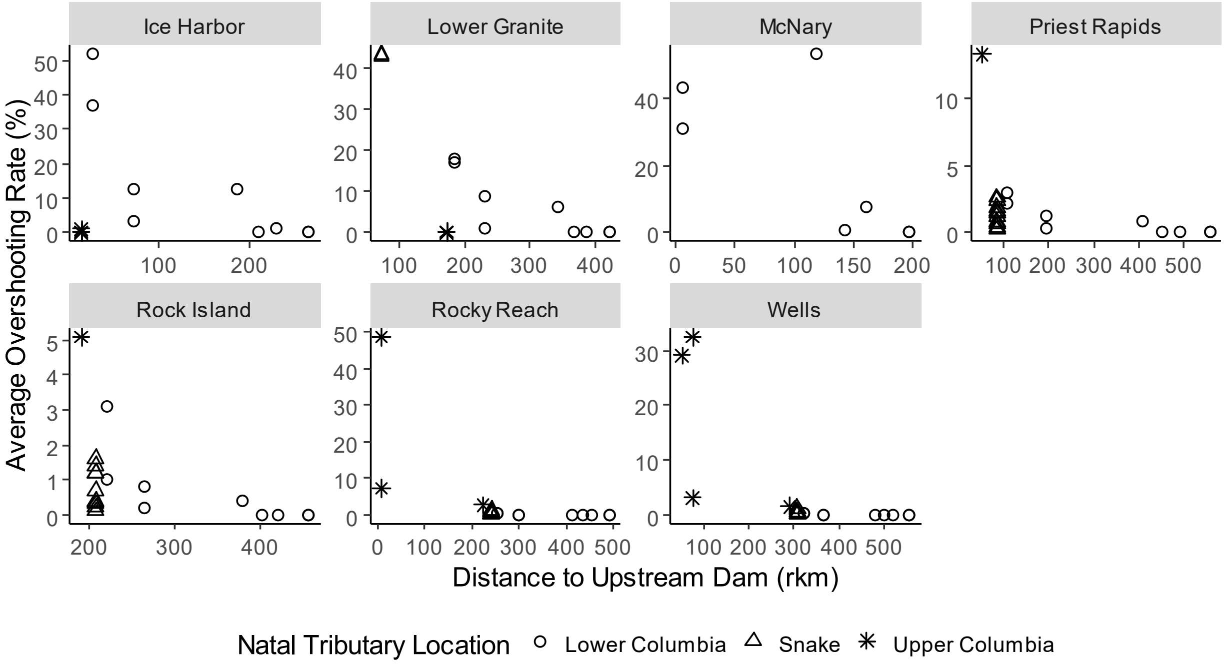

FIGURE 2.10.—Average overshooting rate versus distance to the upstream dam (rkm) from home or the shortest distance route to home. Annual overshooting rates were adjusted by detection efficiencies at the dams.

Fallback rates to home.—Fallback rates to home were estimable in at least one year in 11 of the populations (Figure 2.11). Annual fallback rates to home ranged from 7.7% (SE 7.7%) for Tucannon wild steelhead in 2006/2007 to 93.4% (SE 6.3%) for Entiat wild steelhead in 2013/2014. Fallback rates varied annually and were not related to overshooting rates ($F_{1,33}$ = 0.299, P = 0.588).

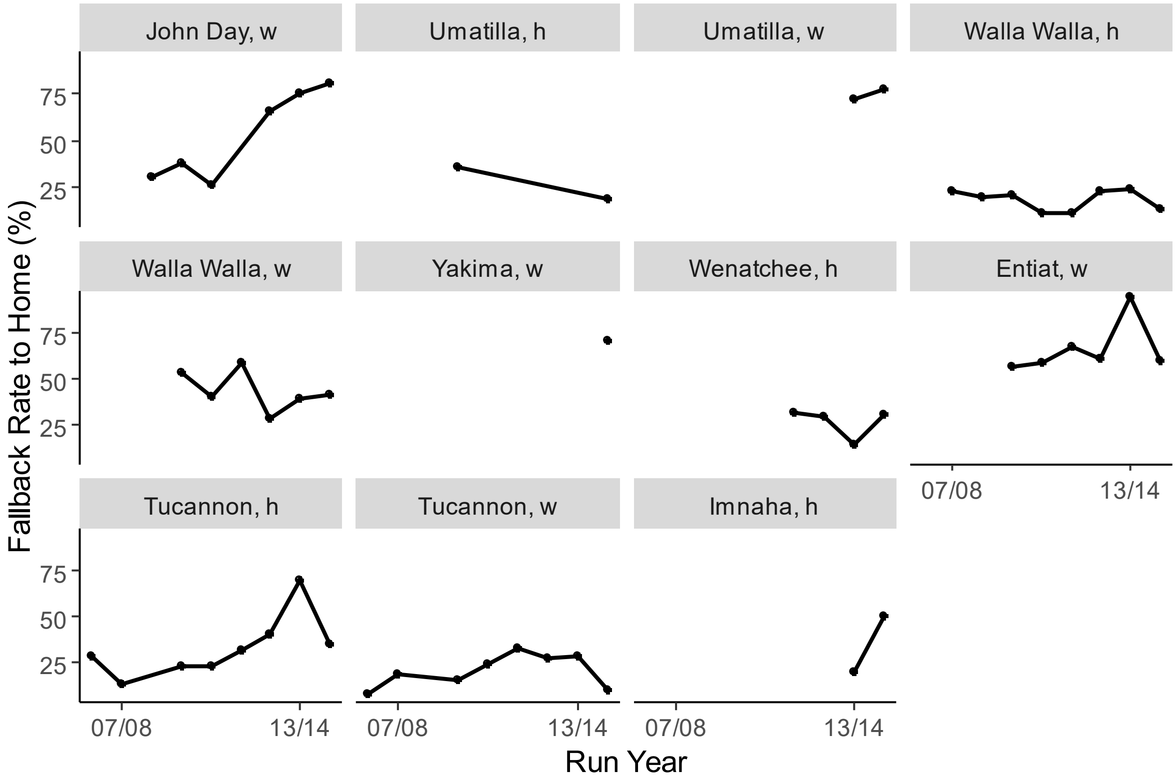

FIGURE 2.11.—Fallback rates (adjusted by detection efficiencies) to home after overshooting the nearest upstream dam with adult detectors.

*Alternative spawning sites.—*Some steelhead were observed in upstream tributaries where spawning could occur. After overshooting, the proportion of steelhead observed at upstream tributary sites ranged from 1.2% (SE 1.2%) for Umatilla hatchery steelhead to 29.1% (SE 4.3%) for Tucannon wild steelhead (Appendix H). For the Tucannon wild and Walla Walla hatchery populations, more fish were observed in upstream alternative tributaries than returned home. Tucannon wild steelhead were seen most frequently in Asotin Creek after overshooting, while the Walla Walla hatchery steelhead were seen primarily in the Tucannon River. Rather than being attracted to the Tucannon River or Asotin Creek, John Day steelhead had an attraction to the Grande Ronde River that was not seen for other populations. Few steelhead were seen at non-home tributary locations downstream of an overshot dam after overshooting. Undetermined losses were greater for hatchery populations than wild populations (Figure 2.12), in part at least to lower rates of fallback to home. Differences between rear types are likely due to differential harvest rates. Annual trends in undetermined losses and observations in alternative tributaries are present (Appendix H), but indicative primarily of changes in array layout throughout time.

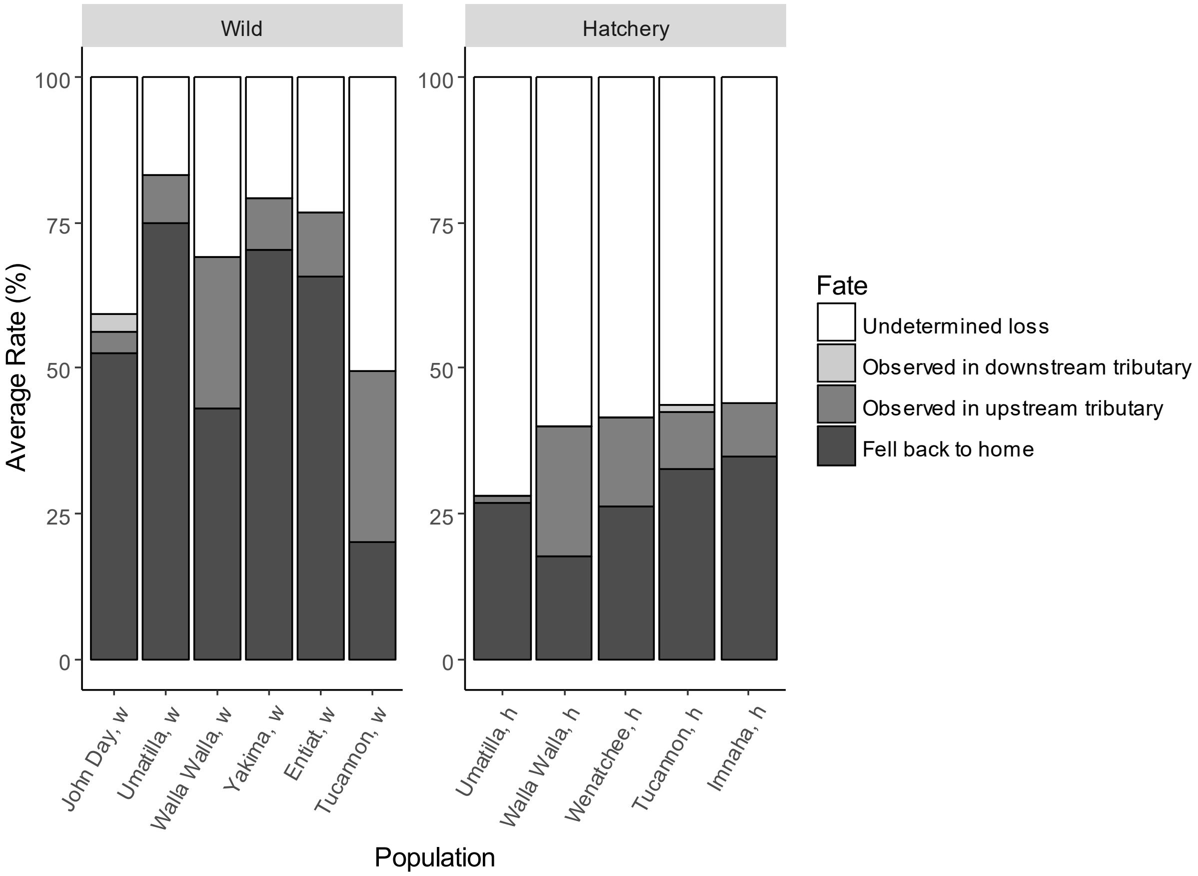

FIGURE 2.12.—Subsequent fates of overshooting steelhead. Fallback rates to home were adjusted by estimates of detection efficiencies, but observations in alternative tributaries were not. Undetermined loss is the remaining proportion of overshooting steelhead, whose fates are unknown.

Discussion

Tributary overshoot is a pervasive behavior in many hatchery and wild Columbia River basin steelhead populations. I identified nine populations for which on average more than a quarter of the adult run overshot an upstream detector dam from 2005/2006—2014/2015. Not only did overshooting occur at high levels in multiple populations, it was associated with decreased successful return to home. Some overshooting steelhead were observed in alternative tributaries upstream where spawning could occur. However, many steelhead did fallback to home, indicating that for many fish, overshooting was only temporary straying. The results presented in this chapter are unique, because they are the first analysis of tributary overshoot and fallback by Columbia River steelhead using robust statistical methods.

Tally v. multistate estimation.—Unless detection efficiencies are 100%, tally-based methods underestimate movement rates from PIT-tag data. In this study, overshooting rates were underestimated by a tally approach, but average differences were very small (< 0.2%) because for the detection efficiencies at all dams except Rock Island Dam were very close to 100%. In contrast, detection efficiencies at tributary sites were highly variable. Average detection efficiencies ranged greatly between the tributaries (44.2% (SE 2.8%)—97.1% (SE 3.4%)), and between years at individual sites (35.7% (SE 14.1%)—100%). Tributary arrays are commonly affected by events such as high flows or loss of power, and are occasionally completely washed away. Installation, replacement, and removal of antennas over time also contributes to variability in detection efficiencies. Because detection efficiencies varied at tributary sites, tally-based estimates of home return rates were not comparable annually or spatially, and therefore were unreliable even as indices of migration success or stock health. Multistate estimates were more appropriate for tracking trends in homing and straying through time.

Multistate release-recapture estimation had not previously been used to estimate rates of overshooting and fallback to home. Previous reporting on overshooting and fallback to home by steelhead in the Columbia River basin (Bumgarner and Dedloff 2011; Keefer et al. 2016; Murdoch et al. 2012) had utilized a tally based approach that did not consider detection efficiencies. These estimates likely to be negatively biased, and they do not include any measure of uncertainty. In this chapter, I presented estimates of overshooting and fallback to home, with associated standard errors, calculated using multistate release-recapture methods.

Overshoot rates.—For six different Columbia River basin tributaries, more than a quarter of adult steelhead overshot upstream dams. These included hatchery and wild steelhead from the Umatilla, Walla Walla, and Tucannon rivers as well as wild steelhead from the John Day and Entiat rivers and hatchery steelhead from the Wenatchee River. These rates are out of the run at Bonneville Dam; overshoot rates out of the run closer to the mouth of the home tributary are even higher, because they exclude early strays or mortalities. In multiple populations, more steelhead overshot than entered their home tributary. For instance, on average 66.4% (SE 5.0%) of Walla Walla hatchery steelhead that passed McNary Dam, the dam before their home tributary, continued past home to overshoot Ice Harbor Dam. Also, 65.6.0% (SE 7.5%) of Wenatchee hatchery steelhead that passed Rock Island Dam overshot Rocky Reach Dam and 60.7% (SE 2.6%) of Tucannon hatchery steelhead that passed Ice Harbor overshot Lower Granite. Overshooting rates this extreme are concerning, because they may deplete small native populations, or lead to large influxes of hatchery strays into upstream areas. It is therefore important to develop an understanding of overshoot behavior, and its relationship to human activities.

Variation in overshoot rates may be due to geographic, population, and seasonal differences. Overshooting declined with increasing distance to the upstream dam. However, some populations did not follow the pattern as expected. Natural origin John Day steelhead overshot McNary Dam at higher rates that Umatilla steelhead, even though the John Day River was 114 rkm further from McNary Dam than the Umatilla River. Inter-annual variation was also found within populations. Some populations, such as hatchery Wenatchee steelhead, exhibited clear trends in movement rates, while others varied but did not consistently increase or decrease within the study period. Overshoot trends may be explained by juvenile experiences including hatchery rearing, acclimation, and barge transportation, as well as adult experiences of shoreline orientation and water temperature. The association between these factors and overshooting and fallback to home will be explored in Chapters 3 and 4.

Alternative spawning sites.—Observations of steelhead at alternative upstream tributary sites suggests that some overshooting fish may permanently stray to and spawn at upstream locations. Many overshooting steelhead were observed in alternative tributaries upstream where spawning could occur. For instance, in 2014/2015, 39.4% of Tucannon wild steelhead that overshot Lower Granite were detected at upstream sites, primarily in the Asotin Creek watershed. This is the relative percent observed, and has not been adjusted by detection efficiencies at the upstream sites. The actual percent of overshooting steelhead entering alternative upstream tributaries, especially those without instream detectors, is likely higher. Other populations commonly observed at upstream sites included the Walla Walla wild (26.0%) and hatchery (22.4%) steelhead.

Fallback rates to home.—While some steelhead entered alternative spawning locations upstream, others were fell back and returned to their natal tributary. Fallback provides evidence that overshooting can be a non-direct homing behavior, where fish fall back after overshooting accidentally, or to find temporary holding areas. Every population examined in this study had at least some fish fall back to home after overshooting. Average annual fallback rates to home after overshooting the nearest upstream dam with detectors ranged from 17.8% (SE 1.9%) for Walla Walla hatchery steelhead to 75.0% (SE 2.6%) for Umatilla wild steelhead. While overshooting primarily occurred in late summer, fallback to home was delayed until late winter. Concentrated fallback to home in late winter and early spring indicates that steelhead may be holding in refuge areas upstream.

Total success rates.—On the West Coast, 11 distinct population segments of steelhead are currently listed as threatened under the Endangered Species Act. These include the Snake River and the lower, middle, and upper Columbia steelhead (Northwest Fisheries Science Center 2015). High overshooting rates may impede improvement in these stocks. Populations with higher overshooting rates had fewer fish successfully return to their natal tributary. Additionally, when overshooting by Wenatchee hatchery steelhead decreased during the study period, total success increased dramatically. From 2011/2012 to 2014/2015, overshooting by Wenatchee hatchery steelhead that passed Bonneville dam dropped from 54.7% (SE 2.5%) to 12.1% (SE 2.3%) and total success increased from 38.4% (SE 2.9%) to 68.8% (SE 3.7%).

Total success rates were higher for upper Columbia steelhead than lower Columbia or Snake River steelhead, despite having to travel further than lower Columbia steelhead and similar distances to Snake River steelhead. This may be due to a combination of lower overshooting and higher downstream passage rates. Downstream passage may be easier through dams on the upper Columbia. Keefer et al. (2005) found that survival rates to home of radio-tagged Snake River steelhead that fell back at dams were less than those that did not fall back at dams. In contrast, upper Columbia steelhead that fell back at dams were as likely to survive to tributaries as those that did not fall back (Keefer et al. 2005). In this study, populations that overshot in both the upper Columbia and lower Snake appeared more likely to return to home after overshooting Priest Rapids Dam than Ice Harbor Dam. However, limited data was available for downstream passage at Priest Rapids Dam because nearly all overshooting lower Columbia steelhead move into the Snake River rather than the upper Columbia River.

Unlike total success, fallback rates to home were not significantly related to overshoot rates, suggesting that whatever is driving overshooting is not necessarily influencing fallback. While overshooting may be related to a number of factors, fallback may be more related to the level of connectivity between up and downstream stretches. The ability of adult steelhead to move through downstream through dams most likely limits their ability to correct non-direct homing movements, and descend from upstream stretches after overwintering. The lack of surface-flow routes at dams during late winter may prevent or delay many steelhead from descending to natal tributaries to spawn in spring.

Conclusions.—Tributary overshoot merits more attention as managers work to recover threatened and endangered steelhead populations in the Columbia River basin. Not only does overshooting occur at high levels in multiple populations, it is also associated with lower migration success rates. Poor return rates may be due to many steelhead straying to upstream spawning locations, or insufficient downstream dam passage options for adult steelhead in late winter and early spring. Later chapters of this thesis will investigate factors that may drive overshooting or facilitate fallback to home. This investigation will begin to answer some of the numerous biological and management-related questions that remain about non-direct homing movements of anadromous salmonids.

Chapter 3: Influence of Juvenile Experiences on Tributary Overshoot and Fallback by Steelhead in the Columbia River Basin

Abstract

In salmonids, homing ability depends on chemosensory memories established as juveniles. This chapter investigates whether steelhead overshooting results from imperfect imprinting caused by hatchery rearing, barge transportation, or longer ocean residency. To test this, I built 33 logistic regression models examining five migration behaviors in seven Columbia River basin steelhead populations. After model fitting, I estimated the average effects of rearing, barging, and ocean age. Contrary to my hypothesis, juvenile barging was found to decrease overshooting and increase rates of migrating directly to home. Longer ocean residency was associated with increased overshooting, but effects were biologically small and age did not affect fallback to home. Hatchery steelhead were more likely to overshoot and less likely to fall back home than their wild counterparts. However, much of the effect on fallback may be explained by harvest. Additionally, overshooting was only elevated in stocks reared at hatcheries upriver of release sites. Attraction to upstream rearing areas may be moderated by producing fish in manners more akin to natural steelhead. Endemic, integrated stocks performed more similarly to wild stocks. Additionally, acclimation within the release basin decreased overshooting in the Wenatchee hatchery population by 41 percentage points compared to direct release. Instead of resulting in extended upstream movements, difficulty identifying olfactory clues may discourage steelhead from continuing further upstream.

Introduction

In salmonids, homing ability depends on chemosensory memories established as juveniles. Salmon and steelhead are believed to imprint using multiple “landmarks” along their out-migration route as juveniles, a process called sequential imprinting (Bett and Hinch 2016; Keefer and Caudill 2014; Ueda 2012). Surges of thyroid hormones, which have been connected to memory formation (Lema and Nevitt 2004), are released in response to novel environments during the juvenile out-migration (Dittman and Quinn 1996; Nishioka et al. 1985). As adults, salmon and steelhead navigate a complex river system by identifying waters that contain memorized olfactory stimuli (Johnsen and Hasler 1980; Quinn 2005). Disruption of memory development during imprinting, or the decay of memories over time, may inhibit the homing abilities of salmonids. Difficulty identifying olfactory clues may lead to greater straying, and potentially overshooting.

In multiple populations of Columbia River steelhead, more than 40% of returning adult fish swim past their natal stream and ascend upstream dams (See Chapter 2). This behavior has received little attention until recently (see Bumgarner 2013; Bumgarner and Dedloff 2011; Copeland et al. 2015; Keefer et al. 2016), and is concerning because a lack of passage options may inhibit fallback through dams during winter. Additionally, overshooting may contribute large influxes of hatchery strays to upstream areas. This chapter investigates the hypothesis that overshooting results from imprinting disruption or memory failure. If overshooting is related to imprinting disruption, there should be higher overshooting rates, and lower fallback to home rates, among individuals raised in hatcheries and transported downriver by barge, as well as steelhead that spend greater time in the ocean.

Hatchery rearing, barge transportation, and longer ocean residence may result in fish with weaker imprinting strength. Normal levels of hormones associated with imprinting and memory development are not stimulated in hatchery settings (Bett and Hinch 2016; Nishioka et al. 1985). Hatchery produced juveniles exhibit less brain development and reduced olfactory activity (Marchetti and Nevitt 2003), leading to decreased imprinting strength (Keefer and Caudill 2014). Hatchery rearing likely plays a role in homing ability, but additional factors may complicate the effects. Broodstock origin, rearing location, and transportation from rearing sites to release locations affects straying rates (Candy and Beacham 2000; Keefer and Caudill 2014; Pascual et al. 1995; Quinn 1993), and may also influence overshooting. Diversity in overshooting rates may even exist between hatchery stocks in the same tributary, if stocks are produced and reared differently.

Barge transportation and ocean residence time may also affect homing ability. Barging is utilized to increase downriver juvenile survival and adult returns, but studies have indicated that barging is associated with delayed mortality and impaired adult migrations (Bond et al. 2017; Chapman et al. 1997; Keefer et al. 2008c; Muir et al. 2006; Williams 2008). Barging greatly accelerates the out-migration stage (Muir et al. 2006), which is a critical period for imprinting (Ueda 2012). Finally, there is evidence that salmon that spend more years in the ocean stray more frequently than younger fish in the same run year (Labelle 1992; Pascual et al. 1995; Quinn and Fresh 1984; Quinn et al. 1991). Memory failure may prevent older migrants from recognizing scents learned on their out-migration (Quinn 1993). Over longer time periods rivers may also change so that scents learned as juveniles no longer match the current waters (Keefer and Caudill 2014)

A primary conservation objective in the Columbia River Basin is to promote the recovery of threatened and endangered natural-origin steelhead consistent with the Endangered Species Act mandate (WFWC 2013). This can be done in part by increasing the numbers of fish that successfully home. Higher homing success may increase the number of wild fish that successfully spawn and help to avoid negative interactions between hatchery and wild populations. Identifying hatchery or barging strategies that lessen overshooting could benefit threatened and endangered populations and allow managers to facilitate higher homing success.

Methods

Tributary selection.—I examined the influence of juvenile experiences on adult migration behavior in populations that overshot at rates greater than 10%, as estimated in Chapter 2. These included seven populations from the John Day, Umatilla, Walla Walla, Yakima, Wenatchee, Entiat, and Tucannon rivers.

Determination of factors.—I used tag records to determine ocean age, stock, barging history, and run timing for each fish. Ocean age was calculated as the time between the last juvenile detection and the first detection of the adult migration in the Bonneville adult ladder, rounded to the nearest whole year.

Hatchery stocks were determined based on tagging information in PTAGIS and additional information from the Washington Department of Fish and Wildlife (WDFW). For Tucannon and Walla Walla populations, hatchery steelhead were further separated into endemic and non-endemic stocks based on mark file names provided by Joseph Bumgarner (WDFW). Both the Tucannon and Walla Walla Rivers received outplants of a non-endemic stock referred to as the “Lyon’s Ferry” stock, as well as endemic stocks derived from the wild steelhead in each tributary.

Wenatchee hatchery steelhead were also further sub-divided into two stocks. During the study period, the Wenatchee hatchery program shifted from directly releasing juveniles to acclimating all juveniles in the Wenatchee River basin over winter prior to release in spring. Wenatchee steelhead were designated as “acclimated” or “not acclimated” based on brood year and text comments in mark files. In the brood years 2002, and 2004—2005, all steelhead were reared upstream of the Wenatchee River and then transported and directly released in the Wenatchee River basin in spring (Hillman et al. 2016). In brood years 2003, and 2008—2010, releases were a mix of acclimated and directly released steelhead. Text comments in tagging files were used to differentiate between acclimated and non-acclimated fish. Those transferred to Blackbird, Rohlfing, or Chiwawa ponds were designated as acclimated. In brood years 2011—2014, all juvenile hatchery steelhead were acclimated in the basin over winter (Hillman et al. 2016).

The transportation status of each fish was provided by Columbia River DART (Data Access in Real Time, www.cbr.washington.edu/dart). DART transport analysis examined fish seen at transport sites within Lower Granite, Little Goose, Lower Monumental, and McNary dams. Fish were assigned a transport status based on the date and location of their last detection at the transport site. Observations at transport sites were compared to transport dates reported by Fish Passage Center, as well as days when fish were collected, but bypass or transport was recorded for the following day. Incorrect assignments were filtered by looking for subsequent downstream detections that indicated bypass rather than transport. If 25% of a group assigned a transport status were detected downstream, all fish from that group were reassigned a bypass status. Finally, additional reported exceptions for specific barge trips or days were used to reassign fish to the most likely transport history.

Run timing was represented by the day of the year that an individual steelhead first seen passed each of four locations: (1) Bonneville Dam, (2) the dam with adult detectors prior to the home stream, (3) the first overshoot dam with adult detectors, and (4) the first detection in the home tributary. For example, run timing of each Tucannon River steelhead was determined at Bonneville Dam, Ice Harbor Dam, Lower Granite Dam, and the home tributary. Bonneville, McNary, Ice Harbor, Lower Granite, Priest Rapids, Rock Island, and Wells dams had adult detectors for entire study period, 2005—2015. Adult detectors were installed in the Rocky Reach fishway in 2006, and Rocky Reach Dam was used in analyses from 2006 on.

Regression analyses.—Five sets of binary, logit-link models were used to examine the relationship between juvenile experiences and adult migration behaviors of steelhead in each tributary. Each tributary was modeled separately. The conceptual framework of the models is diagrammed in Figure 3.1. First, I modeled the probability of moving from Bonneville to the dam with adult detectors prior to the home tributary. Second, I modeled the probability of moving from the lower dam directly to the home tributary. Third, I modeled the probability of overshooting, or moving from the lower dam to first dam with adult detectors upstream of the home tributary. Fourth, I modeled the probability of falling back and being detected in the home tributary after overshooting. Finally, I modeled overall success, or the probability of moving from Bonneville to home along any pathway. All five models were built for Walla Walla, Yakima, Wenatchee, Entiat, and Tucannon populations. Models of John Day and Umatilla populations did not include early migration success, because the first dam with adult detectors below the home tributary was Bonneville Dam.

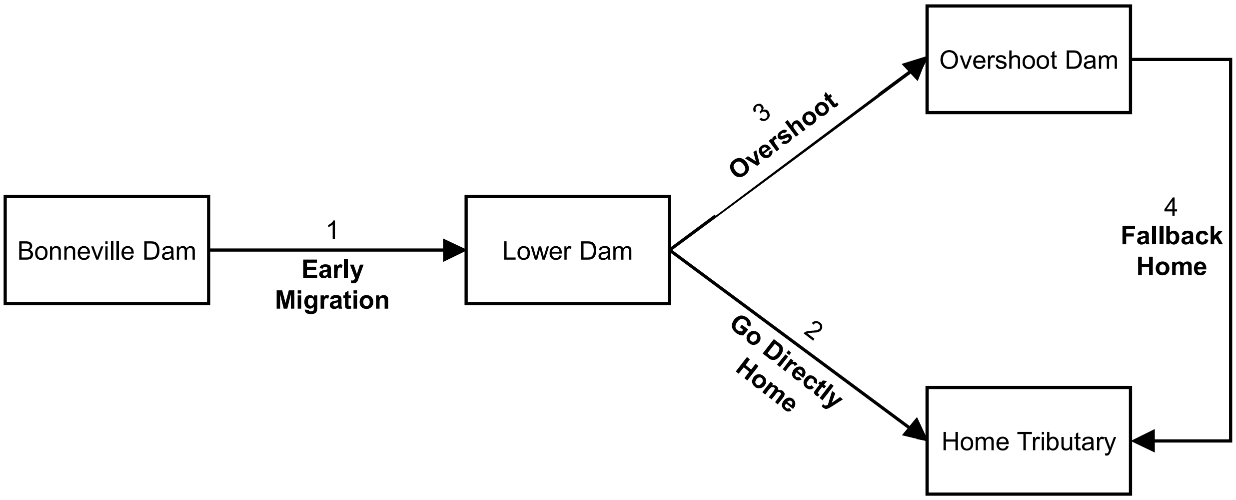

FIGURE 3.1.—Conceptual framework of upstream spawning migration for logistic models. A set of models was created for each labeled stage, as well as for overall success, or moving from Bonneville Dam to the home tributary along either pathway.

Models were constructed using a forward stepwise approach. Variables were added according to significance and lowest AIC values and included if explained a significant ($P < 0.05$) amount of the remaining variation and produced a model with a decrease in AIC value of 1.5 or more. These rules were chosen because some models were underdispersed, and therefore the significance of additional variables was inflated. If the model was overdispersed, standard errors were adjusted by the scale parameter. After all significant variables were added, two-way interactions between accepted variables were considered in the same manner.

Prior to the inclusion of factors related to juvenile experiences, I accounted for annual and seasonal variation. Each model first included run year as a blocking factor. Run year accounted for year-to-year variation, as well as annual variation in detection efficiencies. The importance of home tributary detection efficiencies was demonstrated in Chapter 2. Steelhead that ran during years with no functional array near the home tributary mouth were excluded from analyses involving movement to home (Table 3.1). Seasonal environmental variation was accounted for by including run timing in the models. Linear, quadratic, and cubic terms for run timing and overshoot timing were examined. The highest degree of the polynomial that was significant ($P < 0.05$) was added to the model along with any lower degree terms. I continued adding higher order terms until addition of the next term no longer explained a significant amount of the remaining variation. Only after the inclusion of run year and run timing terms did I test for effects due to ocean age, rear type, and barging history. In populations with more than two stocks, I tested whether each stock had a significantly different effect, and pooled those that were not. For example, Tucannon River endemic hatchery and Lyon's Ferry hatchery stocks were pooled in the fallback model because the two stocks did not have significantly different effects, though both were significantly different than the natural origin stock.

I built 33 logistic regression models examining five migration behaviors in seven steelhead populations and computed Area under ROC Curve or AUC values for each final model. AUC measures the relative predictive performance of a binary regression model (Hosmer and Lemeshow 2000). Values range from 0.5 to 1, with 0.5 indicating performance no better than random assignment and 1 indicating perfect prediction. AUC values for the final models ranged from 0.565 to 0.908, with a mean of 0.707.

TABLE 3.1.—Comprehensive list of 33 models built to examine the effects of juvenile experiences. Run Years indicates the run years utilized in that model. Some run years between 2005/2006 and 2014/2015 were excluded because tributaries lacked sufficient detection capabilities or PIT-tagged steelhead during that year. Additionally, Rocky Reach Dam lacked adult detectors in 2005/2006, impeding the ability to model Wenatchee and Entiat steelhead behavior in that year.

	Population	Migration Stage	Run Years
1	John Day	Go Directly Home	08/09-10/11, 12/13-14/15
2		Overshoot	05/06-14/15
3		Fallback Home	08/09-10/11, 12/13-14/15
4		Overall Success	08/09-10/11, 12/13-14/15
5	Umatilla	Go Directly Home	05/06-14/15
6		Overshoot	05/06-14/15
7		Fallback Home	05/06-14/15
8		Overall Success	05/06-14/15
9	Walla Walla	Pass McNary	05/06-14/15
10		Go Directly Home	05/06-14/15
11		Overshoot	05/06-14/15
12		Fallback Home	05/06-14/15
13		Overall Success	05/06-14/15
14	Yakima	Pass McNary	05/06-14/15
15		Go Directly Home	05/06-14/15
16		Overshoot	05/06-14/15
17		Fallback Home	05/06-14/15
18		Overall Success	05/06-14/15
19	Wenatchee	Pass Rock Island	05/06-14/15
20		Go Directly Home	08/09-14/15
21		Overshoot	06/07-14/15
22		Fallback Home	08/09-14/15
23		Overall Success	08/09-14/15
24	Entiat	Pass Rocky Reach	06/07-14/15
25		Go Directly Home	07/08-14/15
26		Overshoot	06/07-14/15
27		Fallback Home	07/08-14/15
28		Overall Success	07/08-14/15
29	Tucannon	Pass Ice Harbor	05/06-14/15
30		Go Directly Home	05/06-14/15
31		Overshoot	05/06-14/15
32		Fallback Home	05/06-14/15
33		Overall Success	05/06-14/15

Overall effects.—After fitting logistic models, I estimated the overall effects of ocean age, rearing, and barging history by fitting linear models to the predicted values. To do this, I first transformed the fitted logit values produced by each model to the binomial scale. These values represented each fish's estimated probability of performing the behavior predicted by the model. Then, I fit a linear model to the estimated effects for those factors which were significant in logistic modeling. In each linear model, I used the same terms in the corresponding final logistic model, apart from any interaction terms. To lessen the impact of unbalanced designs, any run years that did not include at least 5 fish of each group were excluded from the calculation of overall effects. The effect estimated by the linear model is the average effect found by the logistic model.

Finally, I performed a meta-analysis of the effect of juvenile experiences across tributaries. One-tailed p-values testing for a negative effect of greater ocean age, hatchery rearing, and barge transportation on homing success were transformed into χ^2_2 statistics and then summed to χ^2_{2K} statistics, as follows (Eq. 3.1–3.3). Any extremely significant one-tailed p-values ($P < 0.0001$) were rounded up to 0.0001. Combined p-values testing for a detrimental effect of the memory-related experience were calculated for each migration stage.

$$y_i = -2 ln p_i \tag{3.1}$$

$$y_i \sim \chi^2_2 \tag{3.2}$$

$$\textstyle\sum_{i=1}^{K} y_i \sim \chi^2_{2K} \tag{3.3}$$

where

p_i = the *i*th p-value and

K = the number of tributaries.

Tributary differences.—All seven populations included steelhead with variable ocean ages, allowing for the analysis of ocean age in each. Fewer populations were available for analysis of rearing and barge transportation influences. The influence of barging was only able to be analyzed in a single tributary. The Tucannon River population was the sole available PIT-tagged population comprised partially of steelhead barged downriver as juveniles. Barging histories were queried for Walla Walla, Yakima, Wenatchee, and Entiat steelhead, but no adults within the study period were barged as juveniles. To include more populations with barged fish, I determined the barging histories of PIT-tagged steelhead released directly from the Ringold and Lyon's Ferry hatcheries, on the mainstem upper Columbia and lower Snake rivers respectively. However, only 4 out of nearly 8000 adults from these populations were barged as juveniles. Most barged steelhead likely originate from above Lower Granite Dam, however these populations were not included because they overshot Priest Rapids at rates less than 10%. Additionally, for these populations, movement over Priest Rapids may be better defined as a general straying movement rather than overshooting. Since other researchers have already shown that barging increases straying in adults (Bond et al. 2017; Bugert and Mendel 1997; Keefer et al. 2008c), I did not utilize upper Snake populations. Instead, I focused on the influence of barging on overshooting and falling back to home.

Four tributaries were used to analyze the influence of hatchery rearing; out of the original seven, Umatilla, Walla Walla, Wenatchee, and Tucannon populations included natural origin and hatchery reared individuals, allowing for comparison between rear types. Because the focus of this study is on overshooting, populations from above Lower Granite were not suitable even though they include both hatchery and natural origin PIT-tagged steelhead. Multiple other tributaries, including the Klickitat, were investigated for inclusion in analyses to increase the number of replicates. However, while these tributaries may have yielded adequate numbers of PIT-tagged hatchery steelhead, corresponding sample sizes of natural origin steelhead in individual years were quite limited.

The hatchery stocks investigated in this analysis have unique histories, which are important to consider when interpreting the results. Hatchery Umatilla steelhead were all marked at the Irrigon and Umatilla hatcheries, located several kilometers downstream of the Umatilla River. Hatchery steelhead from the Tucannon and Walla Walla rivers included steelhead from endemic and out-of-basin stocks. Finally, the Wenatchee River hatchery program shifted from direct releases to long-term acclimation within the study period. Because of these differences, Tucannon, Walla Walla, and Wenatchee hatchery stocks were further split into endemic and non-endemic or acclimated and direct release stocks.

Both the Tucannon and Walla Walla rivers received outplants of a non-endemic stock referred to as the “Lyon’s Ferry” stock. Original broodstock for “Lyon’s Ferry” steelhead released in the Walla Walla and Tucannon rivers consisted of an approximate mix of 85—90% upper Columbia and 10—15% Snake River steelhead (personal communication, Joseph Bumgarner, WDFW). Following the listing of Snake River and Mid-Columbia summer steelhead under the Endangered Species Act in 1997, endemic brood stocks were established with the goal of eventual replacement of the Lyon’s Ferry stock (Bumgarner and Schuck 2012). To establish endemic stocks, managers collected natural origin steelhead in the Walla Walla and Tucannon rivers. After collection, wild fish were spawned and young were reared at Lyon’s Ferry Hatchery on the mainstem Snake River. Juveniles were transported for release into the Walla Walla and Tucannon rivers (Bumgarner and Schuck 2012). The endemic programs continue to operate as integrated stocks, do not have adipose fin clips, and are not open to harvest (personal communication, Joseph Bumgarner, WDFW). In recent years, the non-endemic Lyon’s Ferry stock was ended. Due to poor performance of the endemic Walla Walla stock, however, releases of the Lyon's Ferry stock within the Walla Walla River were replaced with the segregated Wallowa stock, derived steelhead collected at lower Snake dams (personal communication, Joseph Bumgarner, WDFW). Only three Walla Walla steelhead within the dataset were of Wallowa origin, therefore the Wallowa stock was not able to be represented in analyses.

Major changes to hatchery stocks during the study period are also important to consider. Between 2005 and 2015, the Wenatchee hatchery program shifted from direct releasing juveniles to acclimating all juveniles in the Wenatchee River basin over winter prior to release in spring. Most early brood years were directly released into the basin. Acclimation ramped up in 2008, however acclimation periods were inconsistent between release groups until 2011. Since 2011, all juvenile hatchery steelhead released in the Wenatchee River have been acclimated within the basin overwinter and released in spring (Hillman et al. 2016). For this analysis, Wenatchee River hatchery steelhead were divided into acclimated and direct-release groups based on release year and location, as well as tag file metadata. Meta-analyses of juvenile experiences across tributaries are presented in the results section below. The results for individual tributaries, such as the Wenatchee River, are in Appendix I.

Results

Juvenile barging effects.—Of the seven populations examined in this chapter, only the Tucannon River population was barged downriver, and that had a significant negative overall effect on overall migration success to home (Table 3.2, $F_{1,2905} = 16.58$, $P < 0.0001$). Within this population, barging was associated with a 10 percentage points decline in successful migration from Bonneville Dam to the Tucannon River (Figure 3.2). This decrease in overall success is due to poor success during the early migration between Bonneville Dam and Ice Harbor Dam. Barging decreased successful movement from Bonneville Dam to Ice Harbor Dam by 37 percentage points. After passing Ice Harbor, however, barged fish performed as well or better than non-transported fish. Contrary to my working hypothesis, juvenile barging decreased overshooting ($F_{1,2107} = 9.24$, $P = 0.002$) and increased rates of direct migration to home ($F_{1,2097} = 4.07$, $P = 0.044$). After passing Ice Harbor, barged steelhead had rates of overshooting 12 percentage points lower and rates of direction migration to home 6 percentage points higher than in-river steelhead. After overshooting, juvenile transportation status did not have a significant impact on fallback probability ($F_{1,1119} = 0.29$, $P = 0.593$).

TABLE 3.2.—One-tailed P-values testing for a negative association between juvenile barging and homing success during four migration stages, as well as the combined effects on overall successful migration from Bonneville Dam to the home tributary. P-values < 0.05 indicate that steelhead barged as juveniles were significantly less likely to home successfully, compared to steelhead that out-migrated in-river, during that stage.

	Migration Stage				
Population	Early Migration	Go Directly Home	Overshoot	Fallback Home	Overall Success
Tucannon	< 0.0001	0.978	0.999	0.296	< 0.0001

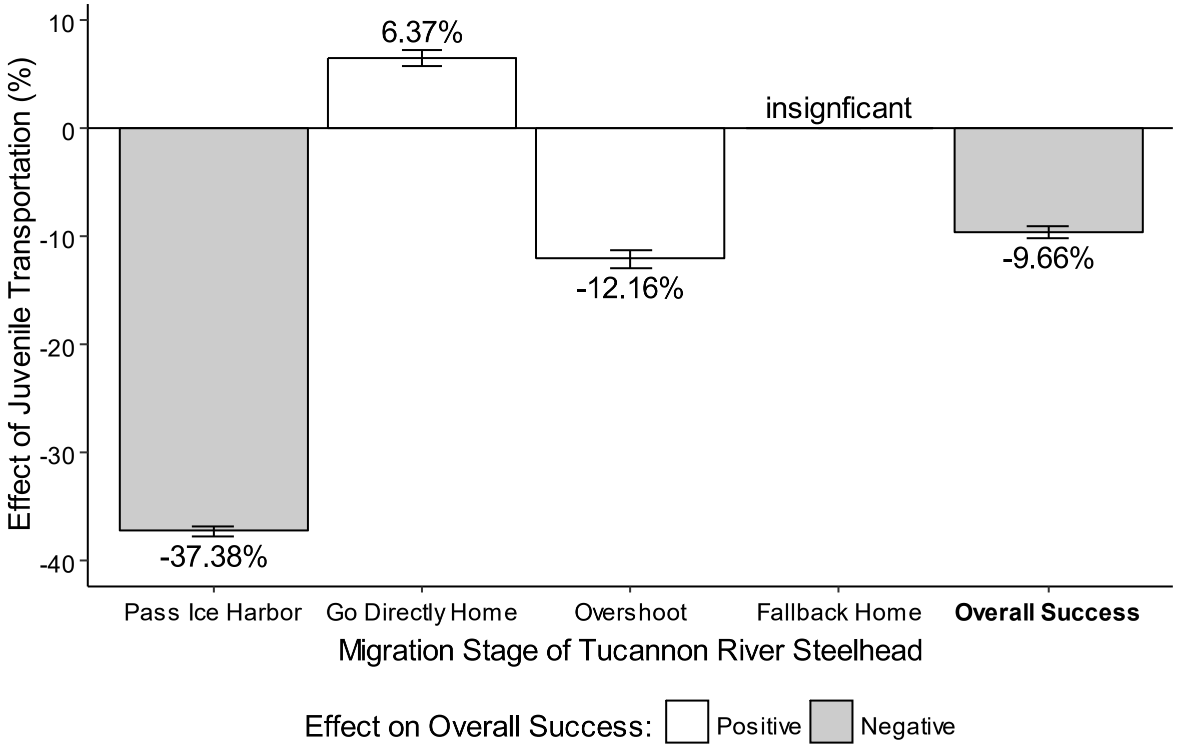

FIGURE 3.2.—Overall effects of juvenile transportation on each stage of adult migration by Tucannon River steelhead, 2005/2006—2014/2015. Steelhead that out-migrated in-river are the baseline. Effects represent percentage point differences. Estimated effect is the percentage point change in successful homing during the indicated migration stage. Error bars represent ± two standard errors.

Rearing effects.—I examined the effects of hatchery rearing in four tributaries: Umatilla, Walla Walla, Wenatchee, and Tucannon. In the meta-analysis, hatchery rearing decreased homing success in every migration stage, including early migration ($\chi^2_6 = 17.46$, $P = 0.008$), movement directly to home ($\chi^2_8 = 46.75$, $P < 0.0001$), overshooting ($\chi^2_8 = 43.42$, $P < 0.0001$), fallback to home ($\chi^2_8 = 55.27$, $P < 0.0001$), and overall success ($\chi^2_8 = 55.65$, $P < 0.0001$). Hatchery produced fish experienced poorer homing success than their natural origin counter parts in the Walla Walla, Wenatchee, and Umatilla populations, but not in the Tucannon population (Table 3.3). Some of the differences in home return rates between hatchery and wild steelhead were most likely due to higher harvest pressure on hatchery fish.

TABLE 3.3.—One-tailed P-values testing for a negative association between hatchery rearing and homing success during four migration stages, as well as the combined effects on overall successful migration from Bonneville Dam to the home tributary. P-values < 0.05 indicate that hatchery reared steelhead were significantly less likely to home successfully, compared to naturally reared steelhead, during that stage.

	Migration Stage				
Population	Early Migration	Go Directly Home	Overshoot	Fallback Home	Overall Success
Umatilla	--	0.004	0.076	< 0.0001	< 0.0001
Walla Walla	0.002	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Wenatchee	0.106	0.001	< 0.0001	< 0.0001	< 0.0001
Tucannon	0.679	0.168	0.488	0.998	0.822
Combined	0.008	< 0.0001	< 0.0001	< 0.0001	< 0.0001

Release location (upstream vs. downstream) relative to hatchery location appeared to affect overshooting. Both the Tucannon and Walla Walla rivers received outplants of Lyon’s Ferry steelhead reared at Lyon’s Ferry Hatchery. The hatchery is located on the Snake River 108 rkm upstream of the Walla Walla River and 5 rkm downstream of the Tucannon River. Lyon’s Ferry hatchery steelhead exhibited different overshooting rates depending on whether they were released up or downstream of the hatchery. Lyon’s Ferry hatchery steelhead released in the Walla Walla River had overshooting rates 15 percentage points higher than their native counterparts. In contrast, overshooting probability was 7 percentage points lower on average, compared to native steelhead, for Lyon’s Ferry hatchery steelhead released in the Tucannon River (Figure 3.3). Steelhead reared upstream of their release tributary may continue upstream after reaching the release tributary, following the landmarks imprinted upon during sequential imprinting. This may occur if steelhead partially imprinted upon upstream hatchery waters. However, unlike the Lyon’s Ferry stock, endemic hatchery steelhead raised at Lyon’s Ferry and released in the Walla Walla River were not more likely to overshoot than natural origin fish.

Except for the Walla Walla endemic stock, fish raised at hatcheries upstream of the natal tributary were more likely to overshoot than natural origin steelhead, while steelhead raised at hatcheries downstream of the natal basin were not. Umatilla hatchery steelhead, which were not raised at upstream hatcheries, did not have significantly different overshooting rates than natal origin steelhead ($F_{1,953} = 2.05$, $P = 0.153$). Similarly, hatchery Tucannon steelhead raised within the release basin or downstream were not more likely to overshoot (Figure 3.3). In contrast, two of three stocks reared at upstream areas, Walla Walla-released Lyon’s Ferry steelhead and Wenatchee River steelhead, had increased likelihood of overshooting and decreased likelihood of returning directly to home (Figure 3.3).

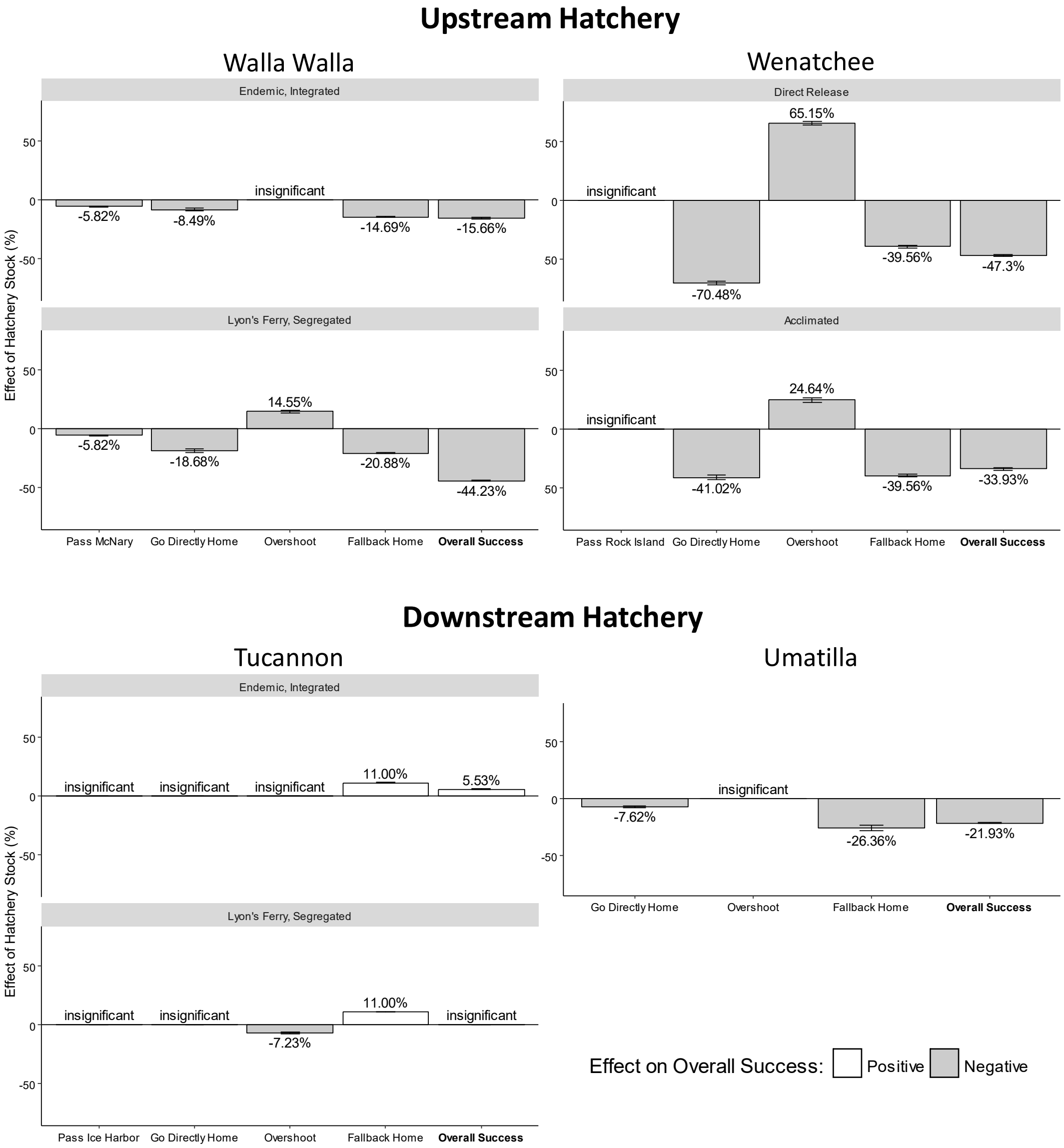

FIGURE 3.3.—Overall hatchery rearing effects on each stage of adult migration by steelhead reared at hatcheries far upstream and shortly downstream of release sites. Effects represent percentage point differences relative to wild steelhead. Tucannon and Walla Walla populations included hatchery steelhead from endemic, integrated stocks and non-endemic, segregated stocks (Lyon’s Ferry). The Wenatchee population included hatchery fish directly released as juveniles or acclimated within basin prior to release. Error bars represent two standard errors.

Attraction to upstream rearing locations may be reduced by using endemic broodstock and acclimating juveniles in the release basin overwinter prior to release. Endemic hatchery Walla Walla steelhead were reared, like the other Walla Walla hatchery stock, at the upstream Lyon's Ferry Hatchery and then transported downriver for release. While Lyon's Ferry hatchery steelhead overshooting rates were 15 percentage points higher than natural origin steelhead, overshooting by endemic hatchery Walla Walla steelhead was not significantly different than the natural origin stock.

Acclimation greatly reduced overshooting and increased successful homing by Wenatchee hatchery steelhead. On average, acclimating hatchery fish within the release basin decreased overshooting in the Wenatchee hatchery population by 41 percentage points compared to directly releasing juveniles in spring. Directly released juveniles were more likely to overshoot, by 65 percentage points, than natural origin Wenatchee River steelhead, while acclimated juveniles were more likely to overshoot by only 25 percentage points (Figure 3.3). While acclimation provided great benefits to movement directly to home, it did not significantly affect fallback to home.

In three out of the four tributaries, hatchery steelhead were less likely to fall back than wild steelhead. Much of this effect may be due to harvest pressure on hatchery fish. Compared to their natural counterparts, the probability of falling back to home was 40 percentage points lower for hatchery Wenatchee steelhead, 15 percentage points lower for endemic hatchery Walla Walla steelhead, 21 percentage points lower for Lyon's Ferry hatchery Walla Walla steelhead, and 26 percentage points lower for hatchery Umatilla steelhead (Figure 3.3). Additionally, despite the substantial benefits of acclimation to homing prior to overshooting, no significant difference was found in fallback to home rates between acclimated or directly released Wenatchee hatchery steelhead. Selective harvest of hatchery fish may contribute to lower fallback to home rates. In contrast, however, Tucannon River hatchery steelhead actually fell back to home more often than natural origin fish. Tucannon River hatchery steelhead were more likely to fall back, by 11 percentage points, possibly because they were less likely to stray to upstream tributaries after overshooting. Additionally, not all hatchery stocks were fin clipped and open to harvest. The endemic Walla Walla and Tucannon hatchery stocks were never fin clipped during the study period (personal communication, Joseph Bumgarner, WDFW). Despite not being available to harvest, the Walla Walla endemic hatchery stock had fallback rates 16 percentage points lower than the naturally reared stock. Therefore, differences in fallback between hatchery and wild stocks cannot be explained by differential harvest pressure alone.

Effects of ocean age.—Individual stage effects due to ocean age were significant in meta-analysis (Table 3.4), but biologically small in most individual tributary models. The effect of ocean age was examined in all seven tributaries, and meta-analysis found increased ocean age reduced homing success during early migration ($\chi^2_{10} = 21.73$, $P = 0.017$), movement directly to home ($\chi^2_{14} = 43.81$, $P < 0.0001$), overshooting ($\chi^2_{14} = 31.67$, $P = 0.005$), and overall success ($\chi^2_{14} = 24.34$, $P = 0.042$). Increased ocean age did not significantly decrease fallback to home ($\chi^2_{14} = 14.39$, $P = 0.421$).

Compared to barging and rearing, ocean age produced smaller effects (Figure 3.4). Steelhead that spend two rather than one year in the ocean were significantly less successful during the early migration, but only in the Wenatchee population ($F_{1,4442} = 6.63$, $P = 0.010$). Even then, Wenatchee steelhead that spent an additional year were less likely to move from Bonneville Dam to Rock Island Dam by only 4 percentage points. In the Umatilla, Walla Walla, and Entiat populations, older steelhead were significantly less likely to return directly to home, by 6, 4, and 12 percentage points respectively. Similar but insignificant effects were found in John Day and

Yakima populations. Steelhead that spend two rather than one year in the ocean were slightly more likely to overshoot in John Day, Yakima, and Entiat populations, but were less likely to overshoot in the Wenatchee population. Effects on fallback were insignificant in all populations except the Walla Walla steelhead, and no significant effects on overall success in individual analyses were found. While significant in the meta-analysis, ocean age appears to play a small role in controlling overshoot probability, and is not responsible for extreme overshooting rates seen in many populations.

TABLE 3.4.—One-tailed P-values testing for a negative association between ocean age and homing success during four migration stages, as well as combined effects on overall successful migration from Bonneville Dam to the home tributary. Values < 0.05 indicate that steelhead that spent two, rather than one, years in the ocean were significantly less likely to home successfully during that stage.

	Migration Stage				
Population	Early Migration	Go Directly Home	Overshoot	Fallback Home	Overall Success
John Day	--	0.064	0.019	0.426	0.377
Umatilla	--	0.015	0.011	0.220	0.070
Walla Walla	0.184	0.005	0.489	0.112	0.067
Yakima	0.232	0.072	0.174	0.475	0.097
Wenatchee	0.005	0.167	0.979	0.914	0.378
Entiat	0.315	0.013	0.013	0.466	0.138
Tucannon	0.285	0.437	0.633	0.353	0.576
Combined	0.017	< 0.0001	0.005	0.421	0.042

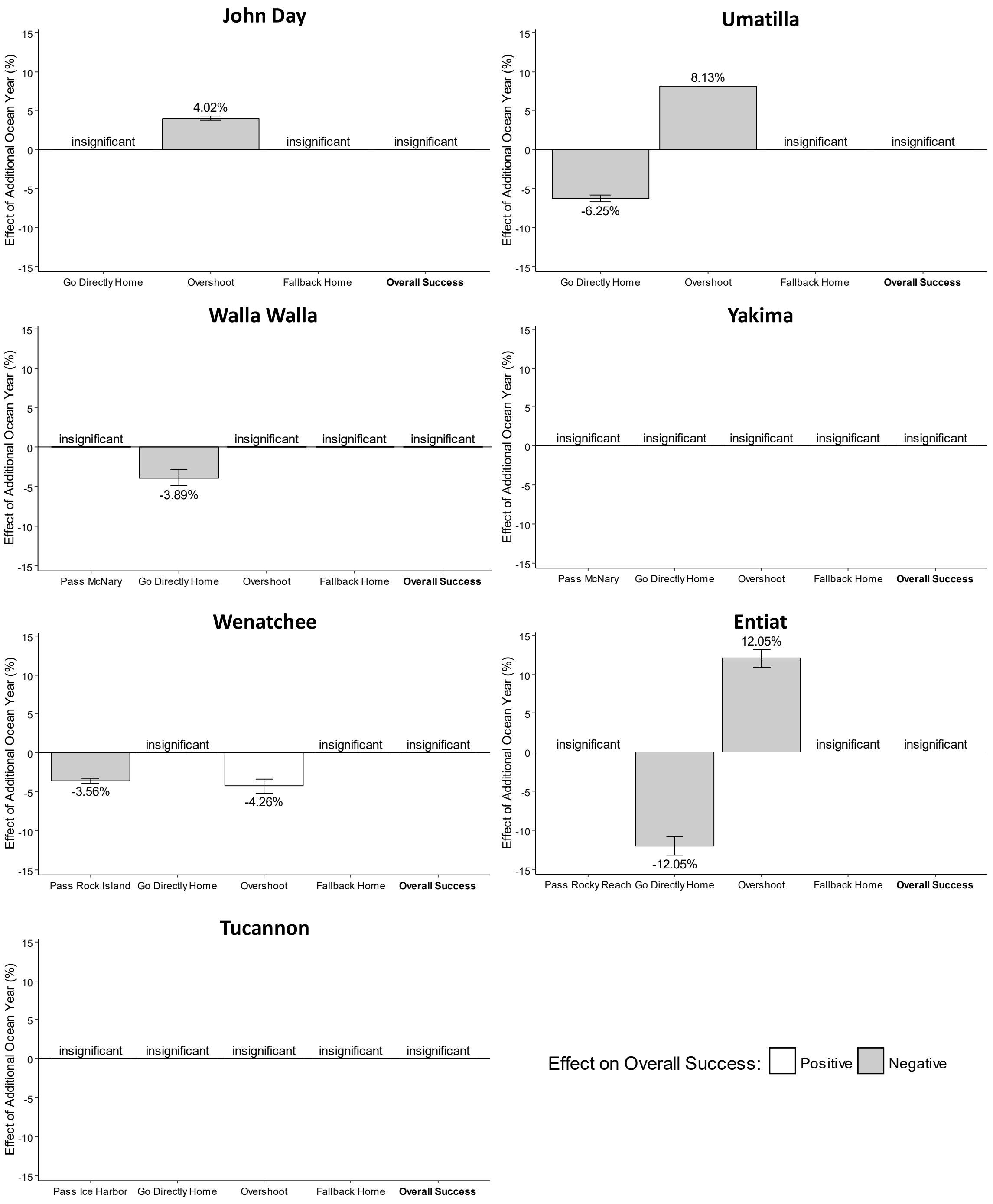

Figure 3.4.—Overall effects of spending 2 years vs. 1 year in the ocean on each stage of adult migration by John Day, Umatilla, Yakima, Wenatchee, Entiat, and Tucannon steelhead. Effects represent percentage point differences.

Discussion

There was little evidence to support the hypothesis that steelhead overshoot due to memory failure linked to barge transportation, hatchery rearing, or ocean age. Instead, barge transportation reduced overshooting and did not affect fallback to home (Figure 3.2). Hatchery rearing was only associated with increased overshooting when fish were reared at upstream hatcheries. The negative effects of hatchery rearing may be moderated by using endemic broodstock and acclimating juveniles overwinter within the release basin prior to release. Fallback to home rates were lower for hatchery stocks (Figure 3.3), but this may be explained by attraction to rearing sites and harvest of hatchery fish within the mainstem river prior to natal tributary entry in spring. Finally, the predicted effects of ocean age were small; spending two rather than one year in the ocean had estimated effects on overshooting ranging from a 4 percentage point decrease for Wenatchee steelhead to a 12 percentage point increase for Entiat steelhead. These effects explain only a fraction of the high overshooting rates estimated for these populations. In most individual models, ocean age failed to explain a significant amount of deviance ($P < 0.05$, Figure 3.4). These findings suggest consideration of alternative hypotheses. Fish may display downstream movement in response to memory failure, leading to decreased rather than increased overshooting. Additionally, proximate environmental conditions may play a more important role than juvenile experiences in determining migratory behavior.

Juvenile barging effects.—Barged Tucannon River steelhead overshot less and moved directly to home more often than steelhead that out-migrated in-river (Figure 3.2). This conflicts with the imperfect imprinting hypothesis, which predicted higher overshooting rates in barged steelhead due to imprinting disruption as juveniles, and difficulty identifying home as adults. Barging increases straying in adults (Bond et al. 2017; Bugert and Mendel 1997; Keefer et al.

2008c), so why did adults not stray at higher rates to upstream areas? In this study, barged steelhead exhibited the greatest disruption to homing during the early migration. If fish successfully neared their home tributary, they were more likely to enter it and less likely to continue upstream.

While barging did not cause overshoot behavior, barged individuals were much less likely to successfully home during the early migration, from Bonneville Dam to Ice Harbor Dam. This marked decline during the early migration resulted in a 10 percentage point decline in overall successful movement from Bonneville Dam to the home tributary. This effect was not due to experience of different conditions as adults, because the two groups had similar run timing (Figure J.27). Additionally, the model included run timing terms prior to the inclusion of transport history.

Steelhead experiencing memory failure may be more likely fall back along their migration, and less likely to move as far inland. In the presence of imprinted scents, salmon and steelhead exhibit positive rheotaxis, or upstream movement (Quinn 2005). Barged Tucannon River steelhead were collected at either Lower Monumental Dam or McNary Dam, transported, and released below Bonneville Dam. As adults, this stretch may be the most challenging portion of the freshwater migration; a lack of recognizable scents could delay and inhibit upstream movement. Barged steelhead may progress upstream more slowly as adults, due to hesitancy while identifying the correct route. The median migration time between Bonneville Dam and Ice Harbor Dam was 18 days for in-river fish, compared with 49 days for barged fish. Tucannon River steelhead that migrated down the river moved upstream 2.7 times faster than barged steelhead. Barged steelhead may be delayed by repeatedly falling back along their upstream migration as they struggle to locate olfactory clues. This is supported by Keefer et al. (2008c), who found that steelhead barged as juveniles were twice as likely to fall back at dams along their upstream migration. Repeated fallback at dams may pose injury and mortality risks in addition to migration delay.

There are two plausible explanations for lower overshooting rates observed in barged Tucannon River steelhead after passing Ice Harbor Dam. First, natal stream conditions may have improved during the period of migration delay, allowing for barged adult steelhead to enter when they arrive. Second, heavy selection on barged fish between Bonneville Dam and Ice Harbor Dam may narrow the population to only fish with the highest homing abilities.

Juvenile transportation provides an initial benefit to juvenile survival, but does that translate to higher adult returns? Buchanan and Skalski (2007) found that Chinook smolts transported from Lower Granite to below Bonneville Dam were approximately twice as likely to return to pass Lower Granite as adults. However, (Dietrich et al. 2011) found that the benefits of barging were not consistent between hatcheries and barging only offset the negative effects of in-river travel when fish were healthy at the time of barging. Even with increased out-migration survival, delayed mortality and impaired adult migrations may out-weigh the initial benefit of transportation. Barging increases stress (Halvorsen et al. 2009) and exposure to pathogens, which may lead to post-barging mortality (Van Gaest et al. 2011). Barging also increases straying in adults (Bugert and Mendel 1997; Keefer and Caudill 2014; Keefer et al. 2008c; Quinn 1993). Keefer et al. (2008c) found Chinook and steelhead that were barged as juveniles to be approximately 10% less likely to successfully home from Bonneville to Lower Granite Dam. This effect is consistent with, though not as pronounced as, the effect observed for Tucannon River steelhead in this study. As adults, barged Tucannon River steelhead experienced a 37 percentage point decline in successful homing between Bonneville and Ice Harbor dams.

Rearing effects.—Because hatchery rearing is associated with reduced brain development (Marchetti and Nevitt 2003), olfactory activity, and imprinting-related hormone levels (Bett and Hinch 2016), I hypothesized that memory failure would cause hatchery steelhead to overshoot more frequently than naturally-reared fish. Hatchery rearing was associated with decreased successful homing during every period of the freshwater migration, including overshooting ($\chi^2_8 = 43.42$, $P < 0.0001$). However, overshooting was only elevated in hatchery stocks reared at hatcheries upstream of release areas. However, I found that overshooting may be reduced by adopting more natural practices. Considerations highlighted by this analysis include rearing location, broodstock origin and run timing, as well as acclimation.

If steelhead are reared at one location and then transported elsewhere for release, they may imprint upon hatchery waters and erroneously seek out scents from early development as adults. Experiments with sockeye salmon indicated that imprinting occurs during early rearing stages (Havey et al. 2016; Quinn et al. 2006). Partial imprinting on the hatchery may lead steelhead to seek out those learned odors as adults. The location of the hatchery relative to the rearing location may determine whether hatchery fish are more prone to overshooting. Within this study, steelhead raised at tributaries slightly downstream of the release basin did not overshoot more than steelhead that reared naturally within their natal stream. Similarly, Pascual et al. (1995) found that when Chinook salmon were transplanted to an upstream release site, fish returned to the place of origin, even though they passed rearing sites to reach release locations. When possible, rearing hatchery steelhead near or within the release tributary may increase successful homing and decrease overshooting.

In two out of three populations, steelhead raised at upstream hatcheries were more likely to overshoot that naturally-reared fish. After nearing the release tributary, fish may seek out scents memorized during early imprinting, leading them to further upstream. However, despite being raised at an upstream hatchery, the endemic Walla Walla stock was not more likely to overshoot. Regardless of rearing location, endemic hatchery stocks may perform more similarly to natural stocks, due to genetic and run timing factors. Other authors have suggested that there is a genetic component to homing (Candy and Beacham 2000; McIsaac and Quinn 1988; Pascual et al. 1995). Candy and Beacham (2000) found that non-natal Chinook salmon stocks in British Columbia were three times more likely to stray than endemic origin stocks.

In addition to other genetic similarities, run timing consistent with natural origin fish may provide a boost to successful homing. Run timing is highly heritable, and hatchery selection often results in earlier arriving fish (Keefer et al. 2004b). Run timing of natural stocks varies by watershed, and timing differences between stocks are reflective of thermal regimes within the migratory route and in the natal stream (Hodgson and Quinn 2002). The run timing of the endemic Tucannon and Walla Walla hatchery stocks was nearly identical to wild steelhead (Figures H.9 and H.28). In contrast, the Lyon's Ferry stock arrived over a month earlier. Different run timing exposes migrating adults to different seasonal conditions. In Chapter 4, I will investigate whether overshooting is driven by proximate conditions, such as water temperature. If water temperature is a primary driving factor behind overshooting, stocks with similar timing may have similar overshoot rates.

New work suggests that the mechanisms behind increased homing in hatchery steelhead sourced from endemic populations extends beyond simply increased site fidelity or run timing appropriate to the thermal regime. In river systems like the Columbia River basin, it may be difficult to locate a small tributary entering a much larger river (Berdahl et al. 2016b). The sensory and navigational ability of an individual are subject to error, however, by traveling in groups fishes may increase migratory accuracy (Berdahl et al. 2016b). The navigational benefits of collective movement are supported by mechanistic models (Berdahl et al. 2016a). Additionally, the collective navigation hypothesis is supported empirical data on straying and abundance (Hard and Heard

1999; Labelle 1992; Quinn and Fresh 1984; Schroeder et al. 2001). Collective navigation with closely-related wild steelhead may boost the homing success of endemic hatchery steelhead to the Walla Walla and Tucannon rivers. The endemic hatchery and natural steelhead are closely related, and run timing between the natural and endemic hatchery stocks is nearly identical. Endemic hatchery steelhead are therefore spatially and temporally poised to identify and migrate with closely-related naturally-reared steelhead. Collective navigation would provide a boost to successful homing, and decrease overshooting towards the upstream hatchery. Here, I found that overshooting rates were consistent between endemic hatchery and naturally reared stocks, regardless of whether fish were released upstream or downstream of the hatchery.

In addition to the use of endemic broodstock, I found long-term acclimation within the release basin to increase homing by steelhead raised at upstream hatcheries. The Wenatchee hatchery program spawns and rears steelhead at hatcheries upstream of the Wenatchee River. Historically, steelhead were reared at Eastbank and Chelan hatcheries, then transferred to Turtle Rock Island, a holding area just above Rocky Reach Dam. From there steelhead were directly planted into the downstream Wenatchee River. Between 2005 and 2015, the Wenatchee steelhead hatchery program shifted from directly releasing all steelhead to acclimating all fish for several months within the Wenatchee River. Since 2011, all release groups have been held in acclimation ponds over winter before release in spring. Acclimation within the release basin was associated with a 41 percentage point reduction in overshooting by hatchery Wenatchee steelhead.

Previous studies on homing and acclimation have not produced consistent results (Clarke et al. 2016; Kenaston et al. 2001). Neither of these studies, however, utilized release groups of steelhead reared upstream of their release sites. Acclimation may provide a greater benefit to homing, through a reduction in overshooting, for fish reared at upstream tributaries. Also, longer term acclimation appears to be better than short term. As Wenatchee hatchery program practices shifted from direct release, to patchy and variable length acclimation, to consistent long term acclimation over winter, overshooting rates dropped and direct movement to home increased (Figure J.20).

Acclimation of Wenatchee hatchery steelhead did not affect fallback rates to home of steelhead that did overshoot (Figure 3.3). Rather than being related to juvenile experiences, fallback to home may be more related simply to the ability of fish to fall back at dams in late winter. For all tributaries, logistic models of fallback to home were the simplest; three of the seven models relied only on run year and did not even include run timing terms. Passage options in late winter may be limited to turbine passage until spill begins in spring for juvenile fish passage. Therefore, fallback to home after overshooting may be unattractive and dangerous to all adult steelhead, regardless of previous experiences. The effects of proximate conditions on fallback to home, including spill and flow, will be explored in Chapter 4.

Harvest pressure on hatchery fish may explain much of the differences fallback rates to home between hatchery and wild fish. However, not all hatchery stocks were fin clipped and subject to harvest. The endemic Walla Walla and Tucannon hatchery stocks were never fin clipped during the study period (personal communication, Joseph Bumgarner, WDFW). Despite not being available to harvest, the Walla Walla endemic stock was still less likely to fall back, by 16 percentage points, compared to the naturally reared stock. Therefore, differences in fallback between hatchery and wild stocks cannot be explained by harvest alone. For other reasons, hatchery steelhead may be less likely to attempt to fall back downstream through dams, or less likely to survive the passage than naturally reared fish. Attraction to upstream rearing areas may make hatchery fish less likely to fall back downstream to their release sites. Wagner and Hillson

(1993) also observed natural origin steelhead to fall back at McNary Dam a higher rate than hatchery steelhead. Hatchery steelhead tagged at the dam were recovered in tributaries primarily above the dam, while natural origin steelhead were recovered primarily in tributaries below the dam (Wagner and Hillson 1993).

Effect of ocean age.—Effects due to ocean residence time were smaller than stock and barging effects. The largest estimated effect occurred in the Entiat River population. In this population, spending 2 years in the ocean rather than 1 year resulted in a 12 percentage point increase in overshoot probability and 12 percentage point decrease in direct migration to home. Like other authors (Labelle 1992; Pascual et al. 1995; Quinn and Fresh 1984; Quinn et al. 1991) have found, older fish appear slightly more likely to stray. Age may have a small effect on overshooting, but it alone does not explain the high overshooting rates found in many Columbia River basin steelhead populations. There was no significant age effect on overall success in any of the seven populations.

Conclusions.—Juvenile experiences linked to imprinting disruption or memory failure were not consistently associated with increased overshooting. High overshooting rates found in Chapter 2 cannot be explained by juvenile transportation, hatchery rearing, or ocean age alone. Even though steelhead barged as juveniles are more likely to stray (Bugert and Mendel 1997; Keefer and Caudill 2014; Keefer et al. 2008c; Quinn 1993), barging was associated with lower overshooting rates in Tucannon River steelhead. Hatchery steelhead were more likely to overshoot than wild steelhead, but only when they were reared at an upstream tributary. That suggests steelhead may have been homing to rearing sites and were not necessarily experiencing memory failure. Attraction to upstream areas may be moderated by producing fish in manners more akin to natural steelhead. Endemic, integrated stocks had overshooting rates similar to wild stocks.

Additionally, homing to release sites was increased by acclimating steelhead within the release basin over winter. Finally, I found that extended ocean residence time produced only small, and mostly insignificant, effects. These findings support an alternate hypothesis, that memory failure reduces rather than increases overshooting. Instead of resulting in extended upstream movements, difficulty identifying olfactory clues may discourage steelhead from continuing further upstream. When olfactory clues are lost, salmon display lateral and downstream movement until the home scent is picked up again (Johnsen and Hasler 1980; Keefer and Caudill 2014; Quinn 2005). Difficulty locating home could result unnecessary downstream retreat. Steelhead with memory failure may hesitant or retreat at lower reaches, and be less likely to move further inland and therefore less likely to overshoot.

Chapter 4: Influence of Adult Experiences on Tributary Overshoot and Fallback by Steelhead in the Columbia River Basin

Abstract

Impoundments and flow regulation in the Columbia River have contributed to the development wide, slow moving reservoirs and elevated summer water temperatures. Here, I used regression and conditional inference tree analyses to investigate the influence of adult experiences, including water temperature, shoreline orientation, and spill on overshooting and fallback to home by steelhead from 7 Columbia River basin tributaries. Orientation to the opposite shoreline 24 rkm below the natal river was associated with decreased movement directly to home and increased overshooting by Wenatchee steelhead. Weaker effects were found for Walla Walla and Yakima steelhead, likely because orientation was measured further from the natal river (39—69 rkm). Water temperature was significant in ($P < 0.05$) in 6 of 7 direct homing and 4 of 7 overshooting logistic models. Temperature also produced significant splits in inference trees for steelhead from 6 of 7 tributaries. As temperatures rose, steelhead were more likely to overshoot and less likely to move directly to home. Temperatures exceeding 16—18 °C may spur steelhead to make non-direct homing movements, including overshooting, as they seek out thermal refuges. Since many adult steelhead may utilize upstream areas for thermal refuge and overwintering, attention should be paid to facilitating downstream dam passage during late winter. Spill during March may facilitate fallback to home; a significant effect was found for hatchery ($\chi^2_8 = 15.82$, $P = 0.032$) but not for wild steelhead ($\chi^2_{10} = 12.87$, $P = 0.231$).

Introduction

Behavioral adaptations allow migrating animals to respond to variable conditions (Alerstam et al. 2003). Changing currents, winds, or weather may necessitate alterations to migration speeds or trajectories (Alerstam et al. 2003; Mandel et al. 2011). The ability of an animal to react with flexibility to its environment promotes migration success. While migration timing is consistent, migratory routes are flexible in many migratory bird species (Mandel et al. 2011; Stanley et al. 2012; Vardanis et al. 2011). Such flexibility suggests that migration routes are fine-tuned in response to local conditions and individual energy reserves (Mandel et al. 2011; Stanley et al. 2012; Vardanis et al. 2011). These factors may also affect the migratory behavior of adult steelhead (High et al. 2006; Keefer et al. 2008a; Keefer et al. 2004a), and overshoot behavior may be an adaptive response to local conditions. This chapter investigates the hypothesis that overshooting by steelhead in the Columbia River basin is a behavioral response to immediate conditions experienced during the adult migration. Additionally, it assesses the influence of spring flow and spill on fallback rates to home.

Like many salmonids, steelhead are highly affected by water (Baigun et al. 2000; High et al. 2006; Keefer et al. 2008a; Keefer et al. 2004a). As water temperatures rise, migration rates slow dramatically and many steelhead seek thermal refuge until conditions improve (High et al. 2006; Keefer et al. 2008a). Since summer migrants now face increased water temperatures and decreased flow in the Columbia River (Quinn and Adams 1996; Quinn et al. 1997), it is likely that more steelhead exhibit thermoregulatory behavior today than historically (Keefer et al. 2009).

Interior Columbia River basin steelhead are stream maturing, meaning that they enter freshwater before they are fully mature, overwinter in rivers, and spawn the following spring (Robards and Quinn 2002). This "premature migration" occurs in many anadromous fishes, potentially because of mortality risks at sea or physical factors in freshwater systems, such as temperature or flow, that seasonally limit access to spawning sites (reviewed by Quinn et al. 2016). Therefore, steelhead must locate freshwater holding areas that are thermally appropriate and energetically efficient for extended occupancy prior to spawning. If steelhead do not encounter suitable holding areas near the mouth of their home tributary, they may travel upstream past natal sites in search of them.

In addition to water temperature, migratory trajectories of steelhead may be influenced by shoreline orientation. Salmon and steelhead tend to be shore oriented during their spawning migrations (Daum and Osborne 1998; Hughes 2004; Reischel and Bjornn 2003), and incorrect shoreline orientation may result in overshooting within wide, regulated rivers (Keefer et al. 2006a). As Chinook salmon approach their natal stream, they express a strong preference for dam ladders on the same shore as the mouth of their natal stream (Keefer et al. 2006a). However, wide river channels or attraction to high-flow areas may cause lateral olfactory clues to be missed (Keefer et al. 2006b). A fish may more easily overshoot their natal stream and ascend an upstream dam if they do not swim along the correct shoreline (Keefer et al. 2008b; Keefer et al. 2006b).

Whether overshooting is a behavioral response to immediate conditions or an unintentional straying behavior, it is possible that fish may attempt to return downstream. Unfortunately, downstream dam passage related mortality is a major concern for adult salmonids (Ferguson et al. 2008; Harnish et al. 2015). Steelhead that fall back at dams are less likely to reach spawning tributaries or hatcheries than steelhead that do not (Boggs et al. 2004). Not only can downstream dam passage be hazardous for adult fish, it can also add significant delays. Downstream movement rates by kelts slow greatly just above dams, possibly because steelhead are trying to identify downstream passage routes or waiting for flow or spill conditions to change (Harnish et al. 2015; Rayamajhi et al. 2013; Wertheimer and Evans 2005).

General options for downstream dam passage include through turbines, locks, spillways, and sluiceways (Khan et al. 2013; Wertheimer 2007). Dams vary in the availability of options, and passage routes are often only operated during certain times of the year (Khan et al. 2013). Survival of post-spawn steelhead moving through dams is lowest through turbines and juvenile bypass systems (Harnish et al. 2015). Instead, non-turbine, surface-flow passage options are likely the safest and most efficient route for fallback at dams (Khan et al. 2013; Wertheimer 2007; Wertheimer and Evans 2005). When available, steelhead kelts exhibit a very strong preference for surface rather than turbine passage (Harnish et al. 2015; Khan et al. 2013; Rayamajhi et al. 2013; Wertheimer 2007). Post-spawn steelhead can be effectively routed away from turbines using even a small amount of surface flow (Wertheimer 2007). While these studies focus on post-spawn steelhead, it is likely that pre-spawn steelhead that overshoot their natal streams would benefit from the same operations. It is possible that spill and flow patterns in late winter and early spring affect the ability of overshooting fish to safely return downstream to home.

In this chapter, I investigate the effects of adult experiences, including water temperature, shoreline orientation, flow, and spill on overshooting and fallback to home by steelhead in the Columbia River basin. Higher rates of overshooting during warmer periods would support the hypothesis that overshooting is a thermoregulatory behavior. If overshooting is related to shoreline orientation, steelhead that ascend ladders on the shore opposite their natal tributary mouth should be more likely to overshoot. Finally, if surface-flow passage options promote fallback of overshooting fish, there should be a positive association between fallback rate to home and late-winter spill. Understanding the mechanisms behind tributary overshoot and fallback is important, especially in the face of continued climate change impacts on river conditions.

Methods

Adult experiences.— I investigated the influence of adult experiences on overshooting and fallback to home in the same populations examined in Chapter 3. These were steelhead from the John Day, Umatilla, Walla Walla, Yakima, Wenatchee, Entiat, and Tucannon rivers, which I estimated to overshoot upstream dams at rates greater than 10% in Chapter 2. In this chapter, I examined the influence of water temperature and shoreline orientation on overshooting and movement directly to home. I also investigated the relationship between fallback rates to home and spring flow and spill at the overshot dam. Water temperature, flow, and spill data were downloaded on 5 January, 2017. Daily water temperatures in the forebay outflow of McNary, Ice Harbor, Lower Granite, Priest Rapids, Rocky Reach, and Wells dams from 2005 to 2015 were downloaded from Columbia River DART (www.cbr.washington.edu/dart). Records of spill and outflow during the months of January, February, and March were also downloaded from Columbia River DART for the same dams. Stream temperature data for each tributary were queried from the U.S. Geological Survey, U.S. Department of the Interior Bureau of Reclamation, and Washington Department of Ecology. Natal stream temperature data were obtained for the mainstem Umatilla, Walla Walla, and Tucannon rivers. Multiple years of stream temperature data from a mainstem site within 75 rkm of the river mouth were not available for the remaining four tributaries. Umatilla data were obtained from the U.S. Department of the Interior Bureau of Reclamation (https://www.usbr.gov). The Umatilla station was located at 45° 54' 00" N, 119° 20' 00" W. Umatilla water temperature data were missing for much of 2013 and 2014. Walla Walla and

Tucannon stream temperatures were obtained from the Washington Department of Ecology (https://fortress.wa.gov/ecy/eap/flows). The Walla Walla station was located at 46° 2' 35.16" N, 118° 29 '25.8" W, 53 rkm above the confluence with the Columbia River. The Tucannon station was located at 46° 26' 25.07996" N, 117° 45' 1.071167" W, 41 rkm above the confluence with the Snake River.

I calculated mean water temperature during the week each steelhead neared and potentially passed its home tributary. To do this, I first predicted when each steelhead approached home. PIT arrays were primarily located at dams on the Columbia and Snake Rivers, and not located in the immediate vicinity of tributary mouths. Therefore, for each tributary, I found the median number of days it took overshooting steelhead to move from the lower dam prior to their home tributary to the overshoot dam. Travel times were estimated between the lower dam and the overshoot dam because many steelhead appeared to overwinter in the mainstem river prior to entering and being detected in the natal stream. Median travel times to home stream detectors were much greater than to overshoot dams, and therefore did not reflect the time steelhead arrived near their tributary mouth. Travel times varied throughout the year, therefore median travel times were estimated on a month-by-month basis. Steelhead moved slower during the summer period of peak water temperatures, consistent with the findings of Keefer et al. (2009).

Next, I estimated mean water temperatures in the period steelhead likely neared their home tributary. By adding the monthly median travel time to the date each steelhead passed the dam prior to the home tributary. To account for variation in travel time, I created a week-long window, centered around the median monthly travel time, during which each steelhead was likely arrive near their home tributary. I found the average water temperature in the outflow of the upstream dam within the one-week window. For steelhead from the Umatilla, Walla Walla, and Tucannon rivers, I estimated the average water temperature in the home stream, and also found the average natal-mainstem water temperature difference by subtracting the mean temperature at the upstream dam from the mean temperature at the tributary monitoring station.

Shoreline orientations were also determined based on observations at the dam prior to the home tributary. Many dams in the Columbia River basin have adult ladders on both shorelines; observations in these ladders indicated shoreline orientation below the natal stream. At dams with adult detectors and multiple fish ladders, I determined shoreline orientation based on the antenna code associated with the first detection at the dam for each steelhead. Antenna codes and layouts, including rearrangements through time, were accessed at http://ptagis.org/sites/interrogation-site-metadata. I determined the shoreline orientations of Walla Walla, Yakima, and Wenatchee River steelhead. For the remaining four populations, the lower dam either lacked adult detectors during the study period or possessed a ladder on only one shoreline. Shoreline orientations of Wenatchee river steelhead were measured at Rocky Reach Dam, 24 rkm downstream of the natal river. For Walla Walla and Yakima steelhead, shoreline orientations were determined at McNary Dam, 39 and 69 rkm prior to the home tributary, respectively.

Lastly, for analyses of fallback to home, I estimated late-winter flow and spill at overshoot dams. For each dam, I found the average amount of outflow during March in each year (2006—2015). I also found the proportion of days with any amount of spill in January, February, and March. Year-to-year variation in spill was represented as the proportion of days with any amount of spill for two reasons. First, at many dams there was very little variation in spill. For instance, continuous spring spill over Lower Granite Dam began on 3 April in 7 of the 10 run years, and little spill was recorded between January and March. From 2006 to 2015, the total number of spill days at Lower Granite prior to 3 April only ranged from 0 to 11. Second, I utilized the presence or absence of spill rather than spill volume because Wertheimer (2007) found that even a small amount of surface flow routed steelhead kelts away from turbines.

Regression analyses.—Logistic regression was used to investigate the relationship between adult experiences and overshooting and movement directly to home, while weighted linear regression was used to analyze the influence of flow and spill on fallback rates to home. Fallback to home was modeled using annual fallback rates to home because the covariates, flow and spill, varied annually rather than on a fish-by-fish basis.

Two sets of binary data, logit-link models were used to examine the relationship between adult experiences and upstream migration behaviors of steelhead in each tributary. Each tributary was modeled separately. Overshoot and direct homing analyses utilized steelhead observed to move successfully between Bonneville Dam and the dam with adult detectors below their home tributary. This excluded steelhead that were not successful during the early migration, which includes early strays, harvests, or mortalities. First, I modeled the probability of moving from the lower dam directly to the home tributary. Second, I modeled the probability of overshooting, or moving from the lower dam to first dam with adult detectors upstream of the home tributary.

Models were constructed using a forward stepwise approach. Variables were added according to significance and lowest AIC values. Variables were only added if they explained a significant ($P < 0.05$) amount of the remaining variation and produced a model with a decrease in AIC value of 1.5 or more. These rules were chosen because some models were underdispersed, and therefore the significance of additional variables was inflated. If the model was overdispersed, standard errors were adjusted by the scale parameter. After all significant variables were added, two-way interactions between accepted variables were considered in the same manner.

Prior to the inclusion of factors related to adult experiences, I accounted for variation due to run year and juvenile experiences. Each model first included run year as a blocking factor. Run year accounted for year-to-year variation, as well as annual variation in detection efficiencies. The importance of home tributary detection efficiencies was demonstrated in Chapter 2. Steelhead that ran during years with no functional array near the home tributary mouth were excluded from analyses involving movement to home (Table 4.1). Next, I included juvenile experiences found to significantly affect overshooting and movement directly to home, based on meta-analysis in Chapter 3. These factors were rearing history, ocean age, and barging history. All seven populations included steelhead with variable ocean ages. Umatilla, Walla Walla, Wenatchee, and Tucannon populations included stocks with different rearing histories, and only the Tucannon River population included steelhead with variable barging histories (see Chapter 3). Only after the inclusion of run year and juvenile experience terms did I test for effects due to water temperature and shoreline orientation. Linear, quadratic, and cubic terms for water temperature were examined. The highest degree of the polynomial that was significant ($P < 0.05$) was added to the model along with any lower degree terms. I continued adding higher order terms until addition of the next term no longer explained a significant amount of the remaining variation.

I built 14 logistic regression models examining overshooting and direct homing behaviors in seven steelhead populations. I computed Area under ROC Curve or AUC values for each final model. AUC measures the relative predictive performance of a binary regression model (Hosmer and Lemeshow 2000). Values range from 0.5 to 1, with 0.5 indicating performance no better than random assignment and 1 indicating perfect prediction. AUC values for models of movement directly to home and overshooting ranged from 0.597 to 0.887, with a mean of 0.748.

TABLE 4.1.—List of overshoot and direct homing logistic models built to examine the effects of adult experiences. Run Years indicates the run years utilized in that model. Some run years between 2005/2006 and 2014/2015 were excluded because tributaries lacked sufficient detection capabilities or PIT-tagged steelhead during that year. Additionally, Rocky Reach Dam lacked adult detectors in 2005/2006, impeding the ability to model Wenatchee and Entiat steelhead behavior in that year.

	Population	Migration Stage	Run Years
1	John Day	Go Directly Home	08/09-10/11, 12/13-14/15
2		Overshoot	05/06-14/15
3	Umatilla	Go Directly Home	05/06-14/15
4		Overshoot	05/06-14/15
5	Walla Walla	Go Directly Home	05/06-14/15
6		Overshoot	05/06-14/15
7	Yakima	Go Directly Home	05/06-14/15
8		Overshoot	05/06-14/15
9	Wenatchee	Go Directly Home	08/09-14/15
10		Overshoot	06/07-14/15
11	Entiat	Go Directly Home	07/08-14/15
12		Overshoot	06/07-14/15
13	Tucannon	Go Directly Home	05/06-14/15
14		Overshoot	05/06-14/15

Fallback rates to home were analyzed using weighted linear regression. Annual fallback rates to home, and standard errors, were estimated for each population in Chapter 2. Fallback rates to home were not estimable in every year either due to insufficient detection capabilities in the home tributary or small sample sizes. I weighted estimates by the inverse of their variance and regressed against flow and spill variables. Since rearing type significantly affected fallback rates to home (Chapter 3), I examined fallback in hatchery and wild stocks separately. In Chapter 3, no differences in fallback to home were found among endemic/non-endemic and acclimated/non-acclimated hatchery stocks in the Tucannon and Wenatchee rivers, however Walla Walla endemic and non-endemic hatchery steelhead were found to fall back at different rates. I therefore grouped hatchery stocks for the Wenatchee and Tucannon rivers, but kept stocks separate for the Walla Walla River.

Next, I performed a meta-analysis of the effect of spill and flow across tributaries. One-tailed P-values testing for a positive effect of increased flow and spill on fallback rates to home were transformed into χ^2_2 statistics and then summed to χ^2_{2K} statistics, as follows: Equations 4.1–4.3. Combined P-values testing for a positive effect of flow and spill were calculated for each rear type (hatchery and wild). Additionally, I performed a sign test to determine whether the frequency of a positive slope between fallback rate to home and flow and spill was significantly different from 0.5.

$$y_i = -2lnp_i \tag{4.1}$$

$$y_i \sim \chi^2_2 \tag{4.2}$$

$$\sum_{i=1}^{K} y_i \sim \chi^2_{2K} \tag{4.3}$$

where

p_i = the ith P-value and

K = the number of tributaries.

Conditional inference trees.—Conditional inference trees were used to examine the combined influence and relative importance of all juvenile and adult experiences investigated in this chapter and in Chapter 3. Like classification trees, conditional inference trees are constructed by selecting cut-points in continuous or categorical variables that best divide observations into known categories. Conditional inference trees make use of unbiased recursive partitioning (Hothorn et al. 2006). Split variables are chosen using P-values from permutation distributions of influence (Loh 2014). Due to disproportion in response groups (such as many steelhead observed to overshoot and few observed to move directly to home), conditional inference trees performed better than classification trees. Conditional inference trees were fit using the “ctree()” function in the R packages “party” and “partykit” (Hothorn et al. 2006) Pruning of the tree was not necessary because ctree() uses Bonferroni-adjusted P-values to determine stopping points (Loh 2014). P-value for variable entry was $P = 0.05$.

Overshooting trees characterized steelhead in three categories: those that overshoot, those that moved directly to home, and those that were not observed to overshoot or move directly to home. Potential split variables included passage day at the lower dam, ocean age, rearing history, barging history, shoreline orientation, mainstem water temperature, natal water temperature, and natal-mainstem water temperature difference. Passage day, ocean age, rearing history, and barging history were determined based on methods presented in Chapter 3. For both overshoot and fallback trees, I only utilized steelhead from years that had home tributary detectors.

Fallback trees modeled two potential outcomes: observed to fall back to home and not observed to fall back to home. Potential split variables included passage day at the overshoot dam, ocean age, rearing history, barging history, as well as average flow during March and the number of spill days in January, February, and March. Fallback trees performed better in populations with large numbers of PIT-tagged steelhead. Due to small sample sizes, fallback trees for Yakima (n = 40) and Entiat (n = 110) populations did identify any significant splits at the $P = 0.05$ cutoff.

Results

Overshooting.—Warm temperature significantly reduced the probability of movement to home. Logistic regression found water temperature in the mainstem or natal rivers to be significant ($P < 0.05$) in 6 of 7 models of movement directly to home and 4 of 7 models for overshooting (Table 4.2). Analysis using conditional inference trees found significant effects of water temperature for steelhead from 6 of 7 tributaries. The probability of movement directly to home decreased with increasing water temperatures. For natural origin Walla Walla steelhead, the probability of moving directly to home decreased from over 90% to less than 25% as water temperature at Ice Harbor Dam increased from 10 °C to 20 °C (Figure 4.1). Regression analysis also found declines in movement directly to home in response to increasing temperature for steelhead from Umatilla, Yakima, Wenatchee, Entiat, and Tucannon River steelhead. The John Day was the only population for which temperature was not found to affect movement directly to home ($F_{1,1456} = 0.13$, $P = 0.715$).

TABLE 4.2.—Inclusion of water temperature terms in final logistic models and conditional inference trees. “X” indicates presence of water temperature term in final model. P-value for variable entry was P = 0.05.

	Logistic Models		
Tributary	Direct Home	Overshoot	Inference Tree
John Day			X
Umatilla	X		
Walla Walla	X	X	X
Yakima	X	X	X
Wenatchee	X		X
Entiat	X	X	X
Tucannon	X	X	X
Total	6/7	4/7	6/7

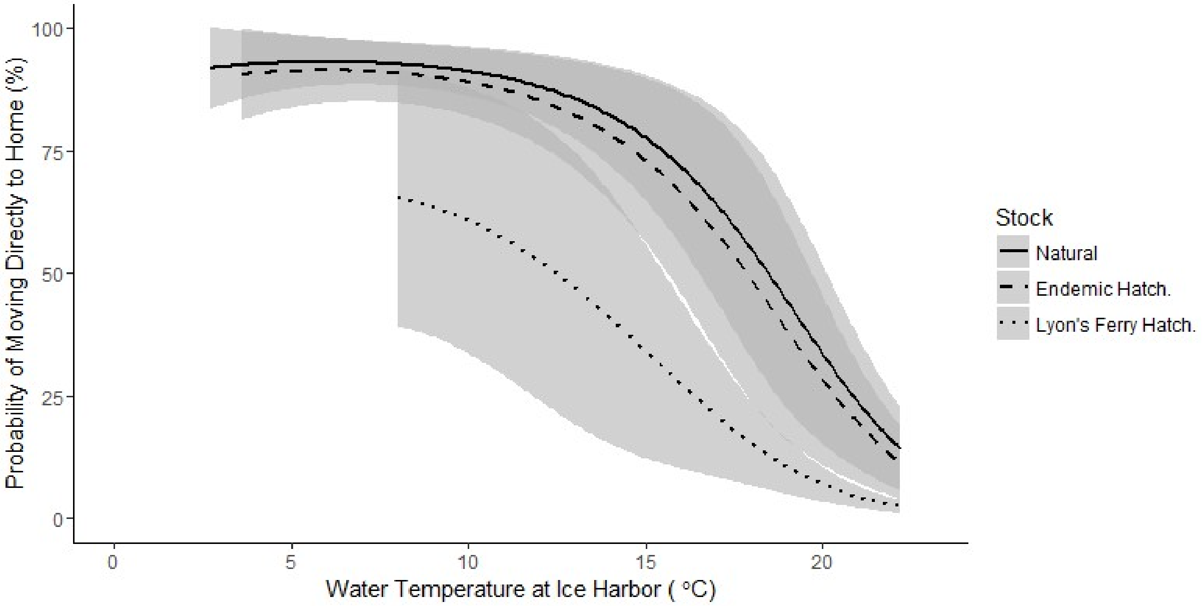

FIGURE 4.1.—Predicted probability of moving directly to home after passing McNary Dam, and 90% confidence interval, at different mainstem water temperatures for Walla Walla River steelhead. Baselines is steelhead that spent one year in the ocean and returned to freshwater in the run year

Logistic regression found that water temperature significantly ($P < 0.05$) affected overshooting by steelhead from 4 of 7 tributaries (Table 4.2). The exceptions were the John Day ($F_{2,2033} = 2.31$, $P = 0.100$), Umatilla ($F_{1,823} = 2.08$, $P = 0.150$), and Wenatchee steelhead ($F_{1,2074} = 2.73$, $P = 0.098$). Overshooting generally increased with increasing water temperature, though in some populations, such as the Tucannon (Figure 4.2) and Walla Walla, overshooting rates leveled off or declined after reaching a threshold temperature.

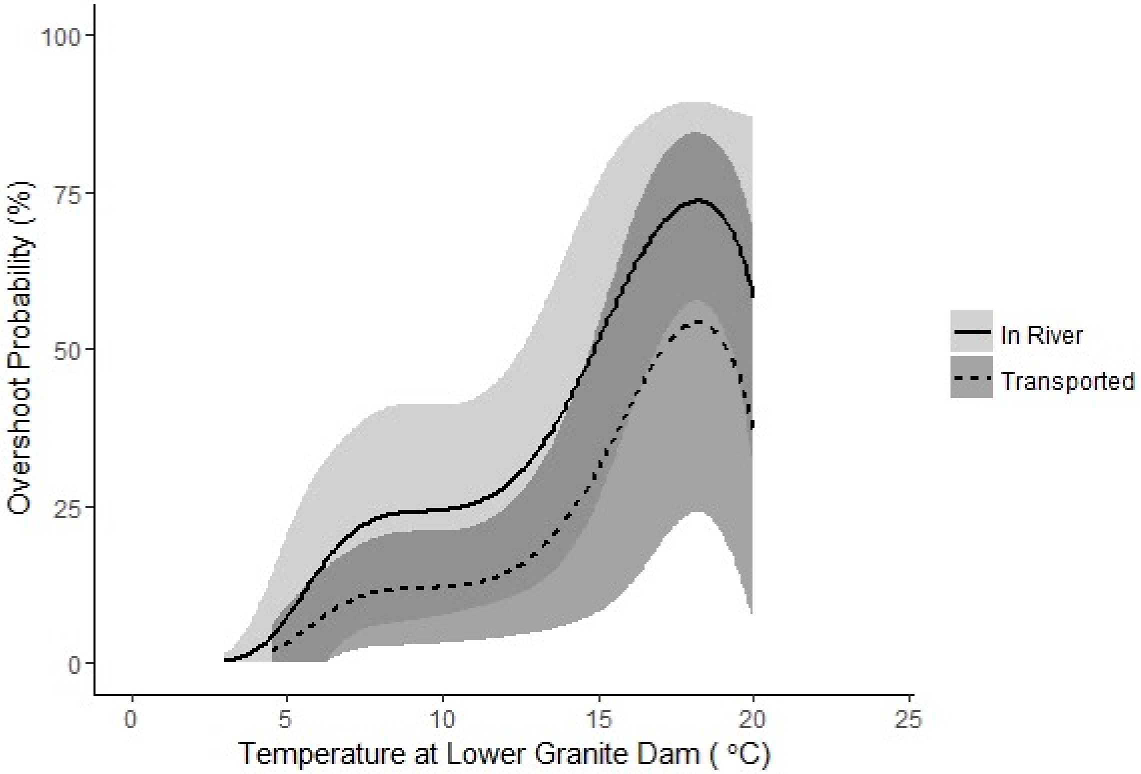

FIGURE 4.2.—Predicted probability of overshooting after passing Ice Harbor Dam, and 90% confidence interval, at different mainstem water temperatures for Tucannon River steelhead. Baseline is natural origin steelhead that spent one year in the ocean and returned to freshwater in the run year 2014/2015. In River = in-river out-migration as a juvenile, Transported = barged downriver as a juvenile.

While mainstem temperature was examined in each tributary, the influence of natal water temperature could only be examined for steelhead from the Umatilla, Walla Walla, and Tucannon rivers. Increasing natal temperature decreased movement directly to home by Tucannon and Umatilla steelhead, and increased overshooting by Walla Walla steelhead (Table 4.3). In most models, mainstem water temperature was accepted into the model before natal water temperature because it had more significant P-values.

TABLE 4.3.—Inclusion of natal water temperature terms in final logistic models and conditional inference trees. “X” indicates presence of natal water temperature or natal-mainstem water temperature difference in final model. P-value for variable entry was P = 0.05.

	Logistic Models		
Tributary	Direct Home	Overshoot	Inference Tree
Umatilla	X		
Walla Walla		X	X
Tucannon	X		X
Total	2/3	1/3	2/3

Tributary and mainstem temperatures were highly correlated, therefore the likelihood of variable entry for both factors was reduced. In Tucannon and Walla Walla models, mainstem temperature had a larger estimated effect than natal temperature. However, natal temperature produced the first split in the conditional inference tree examining behavior by Walla Walla steelhead (Figure 4.3). Walla Walla steelhead that encountered higher natal temperatures were likely to overshoot, while steelhead that encountered lower natal temperatures were likely to move directly to home. Mainstem temperature produced four further splits within the tree. In each split, higher mainstem temperatures resulted in higher overshooting rates and lower rates of direct homing. The highest rates of movement directly to home belonged to steelhead that encountered natal temperatures less than 14.9 °C and mainstem temperatures less than 11.2 °C (Figure 4.3). In contrast, the final node with the most extreme overshooting rate (> 90%) was comprised of fish that experienced mainstem temperatures exceeding 18.3 °C.

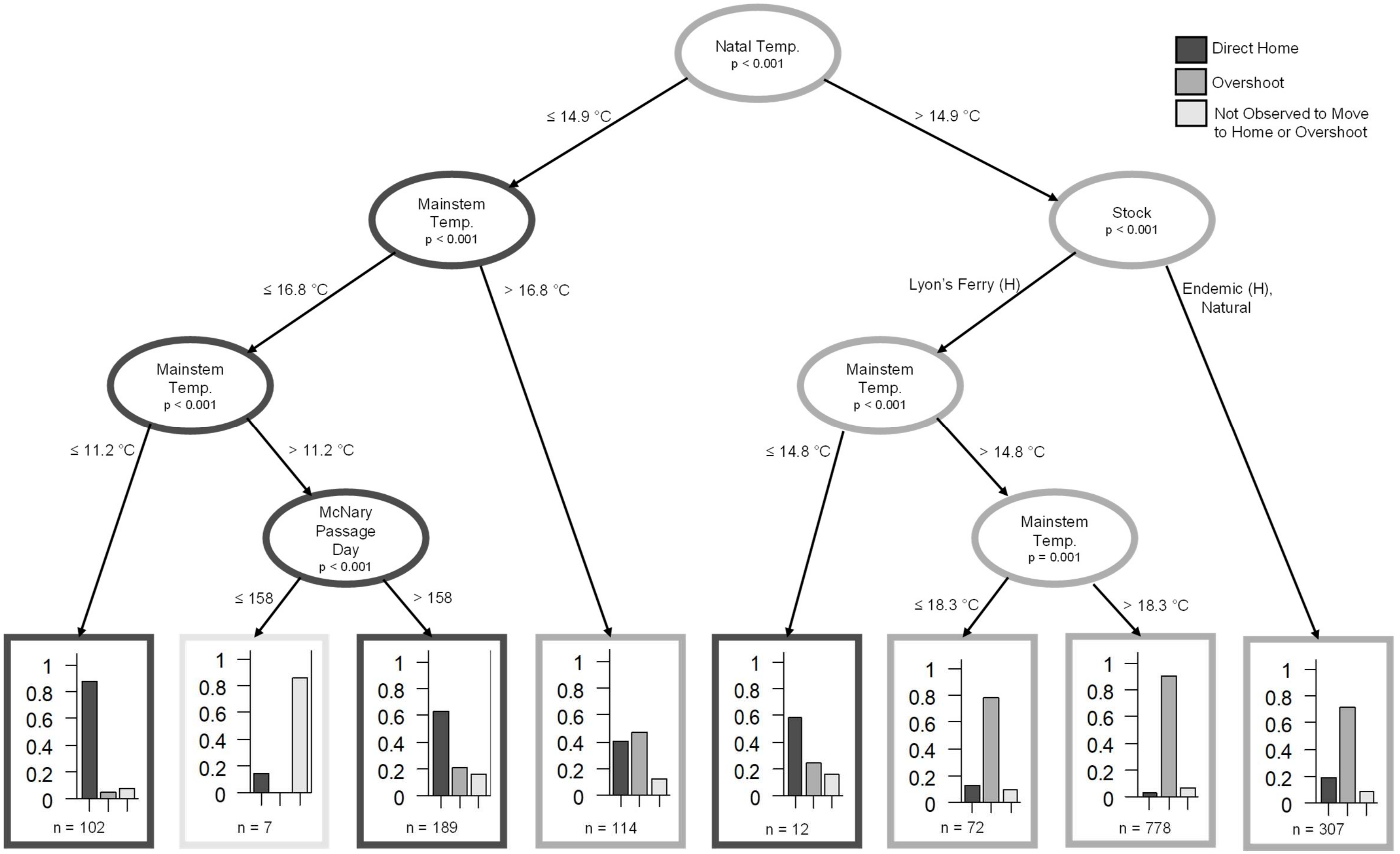

FIGURE 4.3.—Conditional inference tree of Walla Walla steelhead behavior between McNary and Ice Harbor. Direct Home = migrated to home without overshooting, Overshoot = overshot Ice Harbor Dam, Natal Temp. = temperature at Walla Walla monitoring station, Mainstem Temp. = temperature of Ice Harbor Dam tailwater, McNary Passage Day = calendar day of McNary Dam passage, Stock = rearing history, natural, endemic hatchery, or Lyon's Ferry hatchery.

I tested the significance of both natal temperature and the natal-mainstem temperature difference. The natal temperature was accepted into the Tucannon model of movement directly to home, while the final Walla Walla overshooting and Umatilla direct homing models instead included the temperature difference between the mainstem and natal rivers. For Umatilla steelhead, the probability of moving directly to home decreased as natal temperatures increased relative to the mainstem river (Figure 4.4). Tucannon River steelhead also exhibited a decline in direct homing with increasing natal temperatures (Figure 4.5).

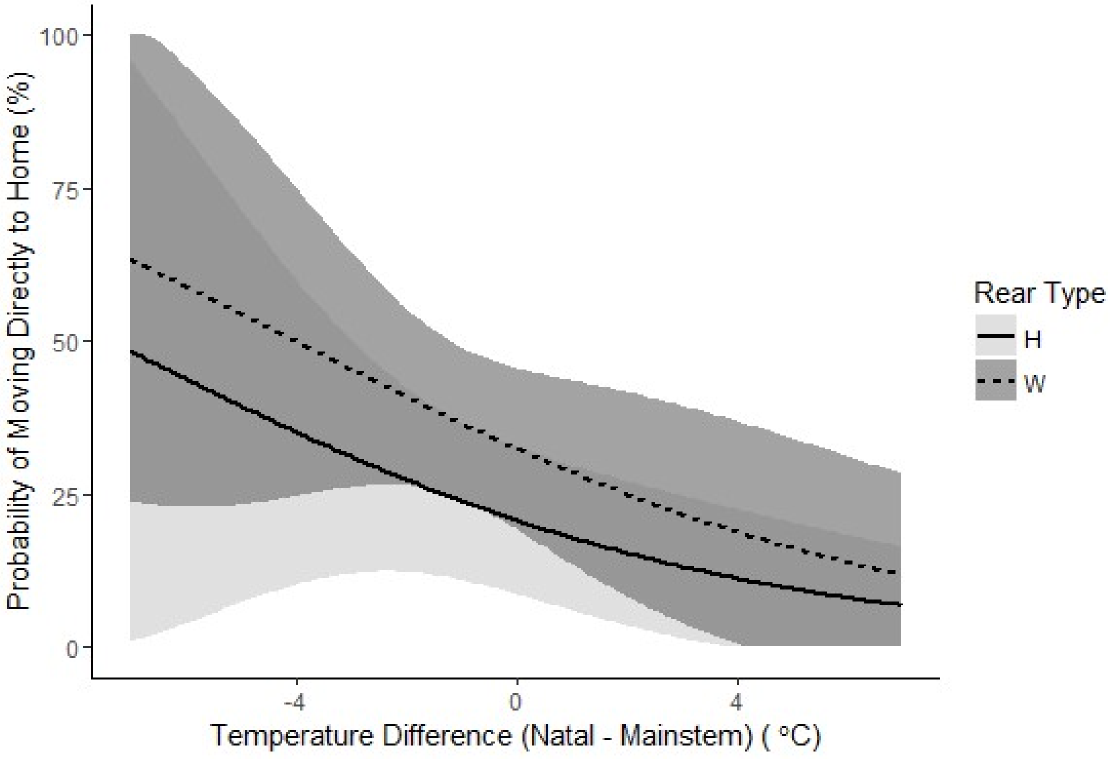

FIGURE 4.4.—Predicted probability of moving directly to home after passing Bonneville Dam, and 90% confidence interval, given the temperature difference between the Umatilla River monitoring station and McNary Dam outflow for Umatilla River steelhead. Baseline is steelhead that spent one year in the ocean and returned to freshwater in the run year 2014/2015. Rear type = rearing history, H = hatchery, W = wild.

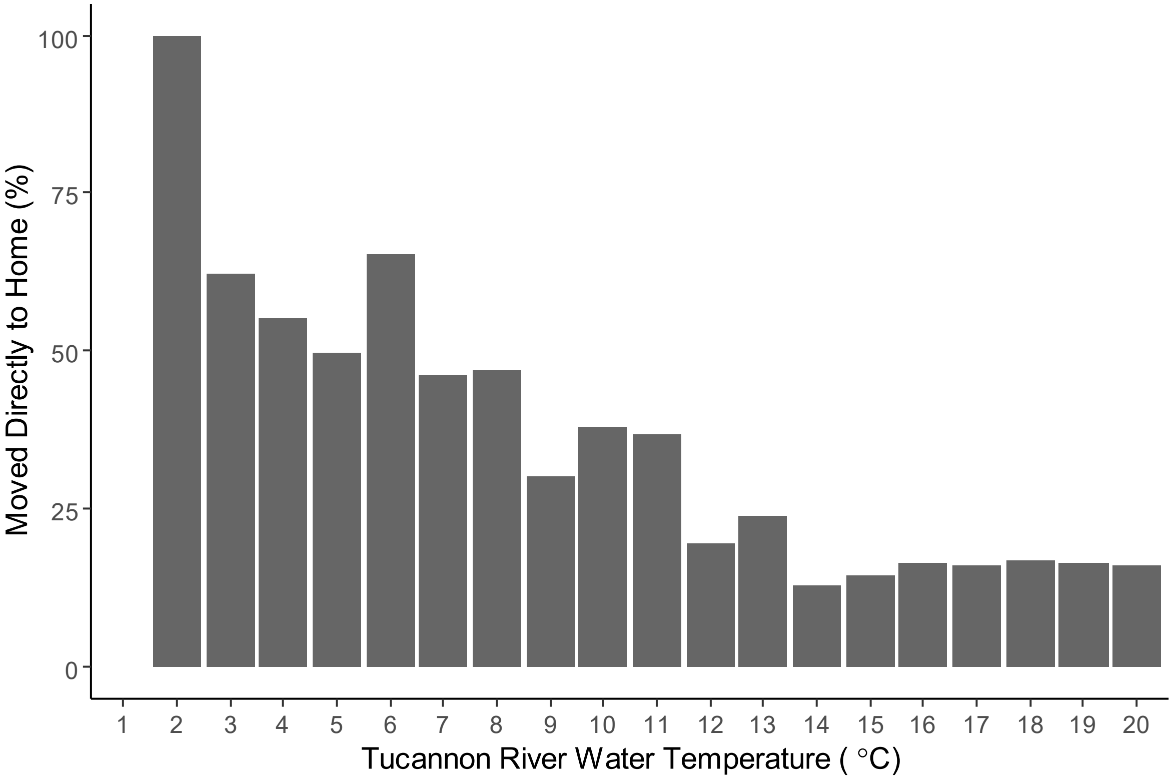

FIGURE 4.5.—Percent of PIT-tagged Tucannon River steelhead observed to move directly to home from 2005—2015 after passing Ice Harbor Dam versus water temperature in the Tucannon River at rkm 41.

In addition to water temperature, I examined the influence of shoreline orientation on direct homing and overshooting. Shoreline orientation was determined by the dam ladder steelhead utilized at the dam prior to the home tributary. Shoreline orientation was examined for Walla Walla, Yakima, and Wenatchee River steelhead. For other populations, the lower dam either lacked adult detectors or possessed a ladder on only one shoreline.

Incorrect shoreline orientation reduced direct homing ($F_{2,1594} = 28.47$, $P < 0.0001$) and increased overshooting ($F_{2,2075} = 24.97$, $P < 0.0001$) by Wenatchee River steelhead. Steelhead that passed in the eastern ladder, on the opposite shore of the natal river mouth, returned directly to home less and overshot more often than steelhead that passed in the middle or western ladders at Rock Island Dam. Those that passed in the middle ladder experienced a smaller decline in probability of direct homing than those that passed in the eastern ladder (Figure 4.6). Analysis using conditional inference trees produced results consistent with the regression analysis (Appendix J).

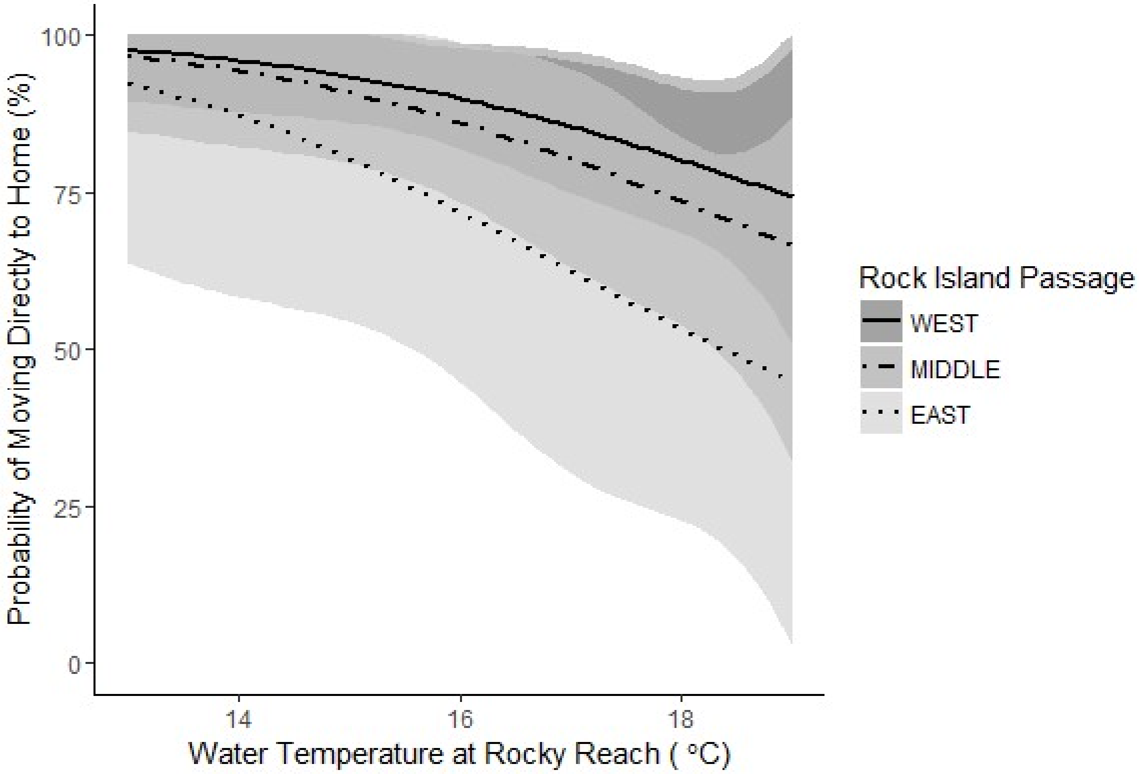

FIGURE 4.6.—Predicted probability of moving directly to home after passing Rock Island Dam, and 90% confidence interval, at different mainstem water temperatures for Wenatchee River steelhead. Baseline is natural origin steelhead that spent two years in the ocean and returned to freshwater in the run year 2010/2011. Rock Island Dam passage occurred in the western, middle, or eastern dam ladder. The western ladder is on the same side of the river as the Wenatchee River.

Shoreline orientation did not exert as strong as an effect on behavior by Walla Walla and Yakima River steelhead, likely because orientation was measured further from the natal stream. Shoreline orientation of Wenatchee river steelhead was measured at Rocky Reach Dam, 24 rkm downstream of the natal river. In contrast, shoreline orientation was determined for Walla Walla and Yakima steelhead at McNary Dam, 39 and 69 rkm prior to the home tributary, respectively. For Walla Walla steelhead, shoreline orientation was not included in the final model for overshooting ($F_{1,1545} = 1.84$, $P = 0.176$) or movement directly to home ($F_{1,1567} = 2.35$, $P = 0.125$). However, the direction of the effect suggested higher homing rates for steelhead that were oriented the same shore as the Walla Walla River. This pattern was not found for Yakima River steelhead. Shoreline orientation at McNary Dam was not significant enough to be included in the final model for overshooting ($F_{1,201} = 2.70$, $P = 0.102$) or movement directly to home ($F_{1,201} = 1.15$, $P = 0.285$) for Yakima River steelhead.

Analysis of overshoot behavior with conditional inference trees supported the regression analysis in this chapter and Chapter 3 for all experiences except ocean age (Table 4.4). I found wholly consistent results between the two analysis methods for three of five factors (rearing history, barging, and shoreline orientation). Water temperature inclusion in final models matched in 5 of 7 tributaries. In contrast, the inclusion of ocean age into inference trees was not consistent with regression analysis. Though it was significant in overshoot or direct homing models for 5 populations, ocean age only produced a significant split in one tree examining overshoot behavior. In both analysis methods, ocean age was one of the last variables to enter the model. This supports the conclusion that longer ocean residence time increased overshooting by only a small amount relative to higher water temperature, incorrect shoreline orientation, or rearing at upstream hatcheries.

TABLE 4.4.—Summary of logistic regression and conditional inference tree analysis of direct homing and overshoot behavior. Regression analysis of rearing history, barging, and ocean age was presented in Chapter 3. R = inclusion in final logistic regression model for overshooting or direct homing, T = inclusion in conditional inference tree. Rearing history, barging, and shoreline orientation were not able to be investigated in all tributaries. P-value for variable entry was P = 0.05.

Tributary	Rearing History	Barging	Ocean Age	Temperature	Shoreline
John Day	*N/A*	*N/A*	R/T	T	*N/A*
Umatilla	R/T	*N/A*	R	R	*N/A*
Walla Walla	R/T	*N/A*	R	R/T	-/-
Yakima	*N/A*	*N/A*	-/-	R/T	-/-
Wenatchee	R/T	*N/A*	R	R/T	R/T
Entiat	*N/A*	*N/A*	R	R/T	*N/A*
Tucannon	R/T	R/T	-/-	R/T	*N/A*
Agreement (%)	100%	100%	42.9%	71.40%	100%

Analysis using conditional inference trees found water temperature and rearing history to most affect overshoot behavior. At least one significant split based on water temperature was found for 6 of the 7 populations. Water temperature produced the first split in three of these trees and rearing history produced the first split in two. In the remaining tree, the first split occurred on passage timing. John Day River steelhead that passed Bonneville Dam after 19 July were more likely to overshoot than those that arrived earlier. As water temperatures vary seasonally, passage timing likely accounts for at least a partial response to temperature. Both analysis methods indicated lower overshooting by steelhead that were reared more naturally as juveniles and exposed to lower water temperatures as adults. More natural rearing of hatchery fish includes the use of endemic broodstock, rearing close to the release stream rather than far upstream, and long-term acclimation prior to release.

Fallback to home.—I examined the influence of flow during March and spill during January, February, and March on annual fallback rates to home estimated in Chapter 2 using weighted linear regression. For many populations, statistical power was limited due to the small number of years in which fallback rates to home were estimable. Fallback rates to home were not estimable in every year either due to insufficient detection capabilities in the home tributary or small sample sizes. Since rearing type significantly affect fallback rates to home (Chapter 3), I examined fallback in hatchery and wild stocks separately. In Chapter 3, no differences in fallback to home were found among hatchery stocks in the Wenatchee and Tucannon River. However endemic and Lyon's Ferry hatchery steelhead fell back at different rates. I therefore grouped hatchery stocks for the Wenatchee and Tucannon rivers, but kept stocks separate for the Walla Walla River.

Three significant, positive associations were found between fallback to home rate and spill or flow for individual stocks (Table 4.5). Walla Walla endemic hatchery steelhead were more likely to fall back to home in years with more spill days during February ($F_{1,5} = 1.61$, $P = 0.014$). Additionally, increasing numbers of spill days during March were associated with higher fallback rates to home in Tucannon hatchery ($F_{1,6} = 4.03$, $P = 0.046$) and Walla Walla Lyon's Ferry hatchery steelhead ($F_{1,5} = 7.19$, $P = 0.022$). These stocks had the largest sample sizes and the greatest degrees of freedom.

TABLE 4.5.—One-tailed P-values testing for a positive association between estimated fallback rate and January, February, or March spill, as well as March flow at overshot dams. Values < 0.05 indicate a significant positive relationship (*) between fallback and spill or flow. Walla Walla endemic and Lyon's Ferry hatchery stocks are separated because they were found to have significantly different fallback rates to home in Chapter 2.

	One-tailed P-value			
Tributary, Stock	January Spill	February Spill	March Spill	March Flow
John Day, Wild	0.293	0.530	0.465	0.378
Walla Walla, Wild	0.931	0.309	0.380	0.263
Yakima, Wild	0.609	0.620	0.189	0.407
Entiat, Wild	0.061	0.814	0.191	0.284
Tucannon, Wild	0.567	0.710	0.253	0.169
Walla Walla, Endemic Hatchery	0.430	0.014*	0.693	0.793
Walla Walla, Lyon's Ferry Hatch.	0.264	0.774	0.022*	0.148
Wenatchee Hatchery	0.849	0.530	0.320	0.580
Tucannon Hatchery	0.132	0.571	0.046*	0.303
Combined Wild	0.412	0.842	0.231	0.253
Combined Hatchery	0.366	0.174	0.032*	0.303

Meta-analysis found March spill to be positively associated with fallback rates to home for hatchery steelhead ($\chi^2_8 = 16.83$, P = 0.032). A similar relationship was suggested for wild steelhead ($\chi^2_{10} = 12.87$, P = 0.231), but was not significant. The slope of the regression line was positive in 8 of 11 stocks (Figure 4.7, P = 0.113, one-tailed sign test).

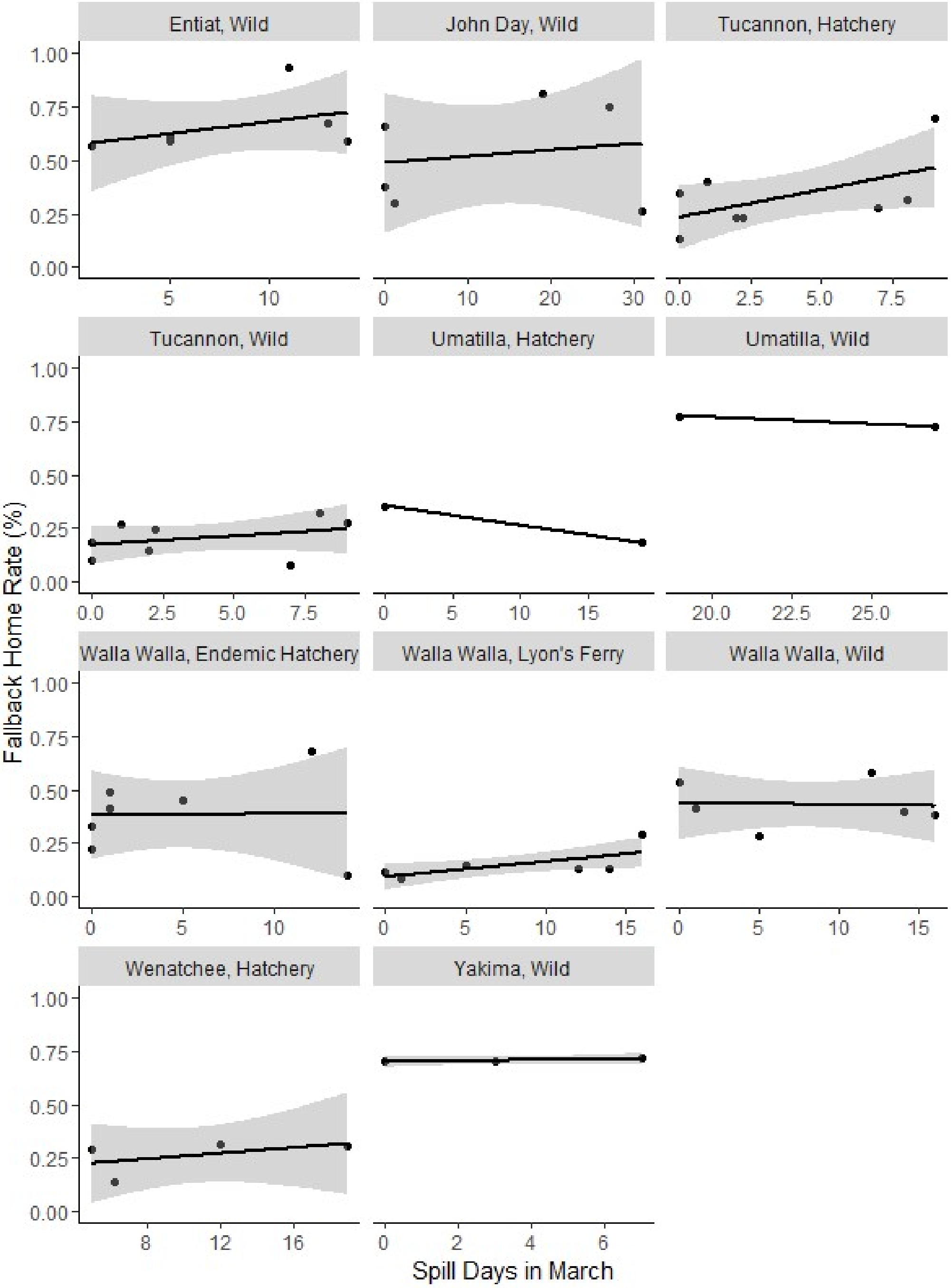

FIGURE 4.7.—Fallback to home rates versus number of spill days in March at the overshot dam for hatchery and wild Columbia River basin steelhead populations. Fallback to home rates are adjusted by detection efficiencies in the home tributaries. Regression and 90% confidence intervals are plotted.

Analysis of fallback to home using conditional inference trees was also limited by small sample sizes. No tree included more than 3 significant splits, and no splits were found for Entiat (n = 110) and Yakima (n = 40) populations, which had fewest PIT-tagged steelhead that overshot. Conditional inference trees did not match regression analyses as closely for fallback to home as for overshooting models (Table 4.6). However, regression analysis of flow and spill were conducted using weighted regression of estimated annual fallback rates rather than individual steelhead behaviors. Logistic regression may more closely match conditional inference trees because the methods use the same sampling units.

TABLE 4.6.—Summary of regression and conditional inference tree analysis of fallback to home. Regression analysis of rearing history, barging, and ocean age was presented in Chapter 3. R = significant in the regression model of fallback to home, T = inclusion in conditional inference tree. Rearing history and barging were not able to be investigated in all tributaries. P-value for variable entry was P = 0.05.

Tributary	Rearing History	Barging	Ocean Age	Flow	Spill
John Day	*N/A*	*N/A*	-/-	T	T
Umatilla	R/T	*N/A*	-/-	-/-	-/-
Walla Walla	R/T	*N/A*	-/-	-/-	R
Yakima	*N/A*	*N/A*	-/-	-/-	-/-
Wenatchee	R/T	*N/A*	T	T	-/-
Entiat	*N/A*	*N/A*	-/-	-/-	-/-
Tucannon	R/T	-/-	-/-	-/-	R/T
Agreement (%)	100%	100%	85.7%	71.4%	71.4%

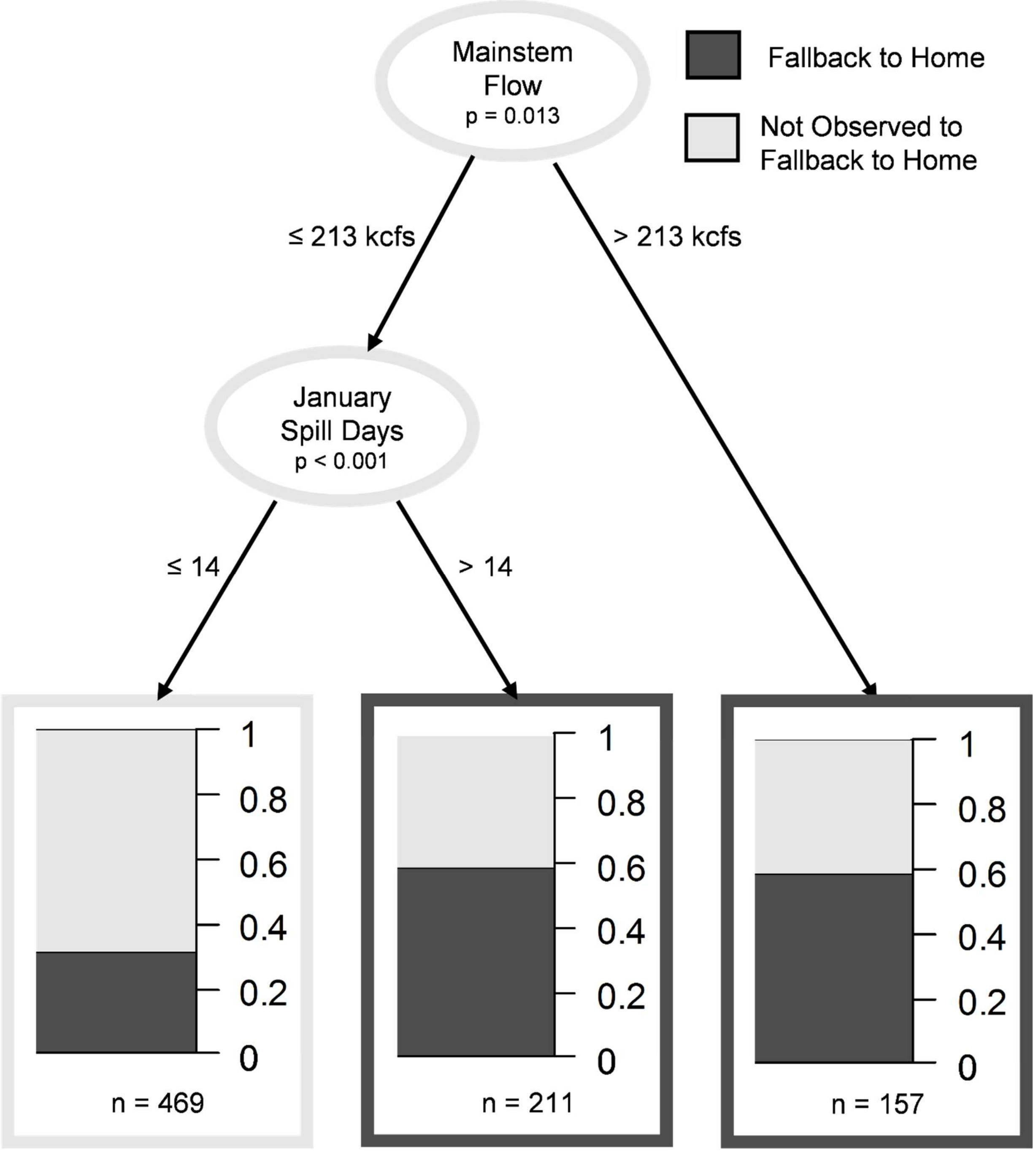

FIGURE 4.8.—Conditional inference tree of adult John Day River steelhead migratory after overshooting McNary Dam. Fallback to Home = fell back downstream to home, Mainstem Flow = average flow at McNary Dam during March, January Spill Days = number of days in January during which any amount of water was spilled over McNary Dam.

In two of the inference trees, higher flows were significantly associated with higher fallback rates to home. Analysis of fallback to home by John Day River steelhead found mainstem flow and January spill to produce significant splits (Figure 4.8). More steelhead fell back to home in years with higher flow during March. Within the low flow group, greater spill in January was associated with higher fallback to home. Of the three final nodes, the only node not assigned to fallback to home was the low flow, low spill group (Figure 4.8). A similar, smaller effect of flow was found for Wenatchee River steelhead.

Spill also produced a significant split in the inference tree for Tucannon River steelhead (Figure 4.9). Steelhead that overshot during run years where water was spilled over Lower Granite Dam for more than 8 days in March were predicted to have high fallback rates to home, while those that overshot in years with 8 or fewer spill days in March were not predicted to fall back to home. However, within the high spill group, natural origin steelhead responded much less strongly than endemic hatchery steelhead. Greater spill may affect wild Tucannon River steelhead less strongly, due to the strong tendency to stray to upstream tributaries (Chapter 2).

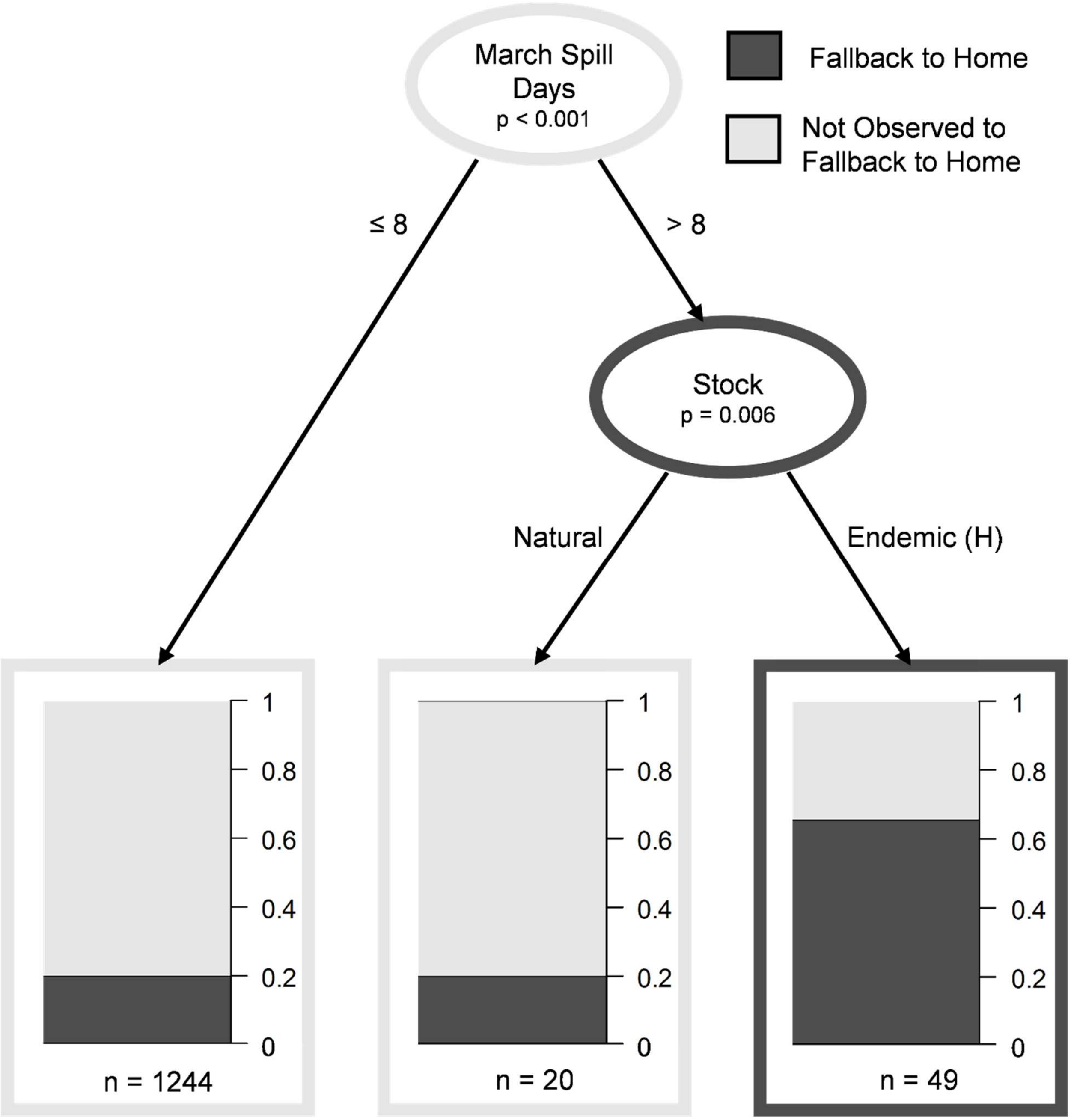

FIGURE 4.9.—Conditional inference tree of adult Tucannon River steelhead migratory after overshooting Lower Granite Dam. Fallback to Home = fell back downstream to home, March Spill Days = number of days during March during which any amount of water was spilled over Lower Granite Dam, Stock = rearing history (natural, endemic hatchery, Lyon's Ferry hatchery).

Together, the results of analysis using regression and conditional inference trees suggests higher fallback rates to home by natural origin and non-adipose fin clipped PIT-tagged hatchery steelhead. Marked hatchery steelhead generally fell back to home at reduced levels, indicating harvest in upstream areas. There is also some evidence to suggest that higher flows and more spill days during March aids fallback rates to home.

Discussion

This chapter characterized the degree to which tributary overshoot is related to adult experiences of water temperature and shoreline orientation, and examined whether late-winter spill and flow promote dam fallback and homing success. Overshoot behavior was strongly related to adult experiences. Shoreline orientation within 24 rkm of the natal stream exerted a significant effect on direct homing and overshooting, while shoreline orientations measured farther downstream did not. I also found a strong relationship between homing behavior and water temperature by steelhead from 6 out of 7 tributaries. As water temperatures in the mainstem and natal rivers rose, movement directly to home decreased and overshooting increased. Finally, I some evidence suggested that prolonged periods of spill during March facilitated fallback to home. The relationship was significant for hatchery steelhead ($\chi^2_8 = 16.83$, P = 0.032), but not significant for wild steelhead ($\chi^2_{10} = 12.87$, P = 0.231).

Shoreline orientation.—When measured within 24 rkm of the natal stream, shoreline orientation exerted a significant effect on direct homing and overshooting. Orientation to the opposite shoreline may cause steelhead to miss the natal stream mouth and incoming water plume (Keefer et al. 2008b; Keefer et al. 2006b). Wenatchee River steelhead that passed in the middle ladder experienced a smaller decline in probability of direct homing, after controlling for blocking factors, than those that passed in the eastern ladder (Figure 4.6). Analysis using conditional inference trees produced results consistent with the regression analysis (Appendix J).

Shoreline orientation did not exert as strong as an effect on behavior by Walla Walla and Yakima River steelhead, likely because orientation occurred further from the natal stream. Shoreline orientation of Wenatchee river steelhead was measured at Rocky Reach Dam, 24 rkm downstream of the natal river. In contrast, shoreline orientation was determined for Walla Walla and Yakima steelhead at McNary Dam, 39 and 69 rkm prior to the home tributary, respectively. Though insignificant, the direction of the effect suggested higher homing rates for Walla Walla steelhead that swam along the southern shore, the same as the Walla Walla River. This pattern was not found for Yakima steelhead, however, Yakima steelhead may have plenty of time to orient correctly after passing McNary Dam, as the Yakima River is 69 rkm upstream.

My findings for Wenatchee River steelhead are consistent with the suggestion Keefer et al. (2006b) and Keefer et al. (2008b): fish may more easily overshoot their natal stream and ascend an upstream dam if they fail to orient to the correct shoreline. Overshooting due to improper shoreline orientation may be exacerbated by the hydrosystem. Fish express a preference for their natal shorelines, which may confer energetic and survival advantages (Keefer et al. 2006b). However, wide river channels or attraction to high-flow areas may cause lateral olfactory clues to be missed (Keefer et al. 2006b). Steelhead moving through reservoirs may have difficulty following or locating olfactory clues and orienting to the correct shoreline, either due to distance or indistinct olfactory gradients created by wide, slow moving environments. Within altered river channels, olfactory homing may be more difficult, resulting in more frequent non-direct homing behaviors including overshooting (Keefer et al. 2006b).

Water temperature.—In addition to altered river channels, summer migrants now face increased summer water temperature and decreased overall flow in the Columbia River (Quinn and Adams 1996; Quinn et al. 1997). In this study, I found that overshooting rates increased and movement directly to home decreased as water temperatures rose. Logistic regression found that water temperature was significant in 6 of 7 models of movement directly to home and 4 of 7 models of overshooting (Table 4.2). Analysis using conditional inference trees found significant effects of water temperature for steelhead from 6 of 7 tributaries. While other authors have observed adult steelhead in the Columbia River to be highly affected by water temperature (Baigun et al. 2000; High et al. 2006; Keefer et al. 2008a; Keefer et al. 2004a), this is the first reported link between water temperature and tributary overshoot. The probability of movement directly to home decreased with increasing temperature; for natural origin Walla Walla steelhead, the probability of moving directly to home decreased from over 90% to less than 25% as water temperature at Ice Harbor Dam increased from 10 °C to 20 °C (Figure 4.1). Regression analysis also found declines in movement directly to home in response to increasing temperature for steelhead from Umatilla, Yakima, Wenatchee, Entiat, and Tucannon rivers. Overshooting generally increased with increasing water temperature, though in some populations, such as the Tucannon (Figure 4.2) and Walla Walla, overshooting rates leveled off or declined after reaching a high threshold temperature.

As water temperatures rise, steelhead migration rates slow dramatically and many steelhead seek out thermal refuge until conditions improve (High et al. 2006; Keefer et al. 2008a; Keefer and Caudill 2014; Salinger and Anderson 2006). Steelhead are highly affected by water temperature (Baigun et al. 2000; High et al. 2006; Keefer et al. 2004a). While summer flow is another important factor, steelhead migration rates seem to be more affected by temperature than discharge (Keefer et al. 2004a). One reason for decreased migration rates is that steelhead seek out thermal refuge until temperatures fall. High et al. (2006) found that 61% of steelhead in the Columbia River basin staged temporarily in at least one cool tributary along their migration. Cool water refuge use is correlated with mainstem water temperatures (Keefer et al. 2009). If steelhead do not encounter holding areas suitable for both thermal tolerance and energetic efficiency near the mouth of their home tributary, they may travel upstream past natal sites in search of them. Higher rates of overshooting observed in this study during warmer periods supports the hypothesis that steelhead overshoot to locate thermally appropriate holding areas. However, overshooting may drop off if mainstem temperatures rise high enough to create impassable barriers.

Peak water temperatures may create migratory barriers (McCullough 1999; Richter and Kolmes 2006; Stabler 1981), preventing entry into the natal stream or passage over upstream dams. Movement directly to home generally declined monotonically with increasing temperature. However, rising temperatures did not always result in higher overshooting rates. For John Day, Walla Walla, and Tucannon River steelhead, overshooting increased with rising temperatures, but leveled off or even declined when average temperatures exceeded 18 °C to 20 °C in the mainstem river. This is consistent with previous authors, who report migration blockages to steelhead arising when water temperatures exceed 19 °C (McCullough 1999; Richter and Kolmes 2006; Stabler 1981). Nielson et al. (1994) reported that temperatures exceeding 22 °C resulted in avoidance behavior in adult steelhead, and Fish and Hanavan (1948) noted that steelhead gathered in cool water refuges when temperatures passed 21.7 °C. Hicks (2000) recommended that daily maximum temperatures should not exceed 16 °C to 17 °C in refuge areas.

Temperatures between 21 °C and 22 °C can be lethal to migrating adult steelhead (Coutant 1970). To avoid direct lethality, Hicks (2000) recommended that daily maximum temperatures remain below 19 °C to 20 °C. Temperatures experienced by steelhead in this study exceeded these recommendations. Mean mainstem temperatures experienced by the 7 populations near their natal stream ranged 18.3 °C for Yakima and Wenatchee River steelhead to 20.6 °C for John Day River steelhead. In the three populations for which natal temperatures were available, natal water temperatures at monitoring sites were on average 1.5 °C to 2.9 °C cooler than the mainstem river. The temperature difference between the mainstem and natal rivers was significant in the final Walla Walla overshooting and Umatilla direct homing models, and natal water temperature was significant in the final Tucannon direct homing model. Umatilla, Walla Walla, and Tucannon River steelhead were more likely to return directly to home or less likely to overshoot when natal water temperatures were lower. This suggests that steelhead react flexibly to local water temperatures.

Rather than homing failure, overshoot behavior may be an adaptive response to local conditions that allows steelhead to temporarily escape unfavorable water temperatures. Overshooting increased and direct homing decreased with increasing water temperatures. Similarly, Workman et al. (2002) found that the probability of upstream movement by adult steelhead in Lake Michigan tributaries increased with rising water temperatures. If steelhead do not encounter holding areas suitable for both thermal tolerance and energetic efficiency near the mouth of their home tributary, they may travel upstream past natal sites in search of them.

Thermal refuges may not only allow steelhead to escape stressful conditions, but also achieve lower basal metabolic rates in order to conserve energy (Berman and Quinn 1991). Apart from lower temperatures, thermal refuges may also have reduced current velocity, which would further increase the metabolic benefit of holding in such refuges prior to spawning. As winter approaches and waters cool, steelhead transition into overwintering behavior and hold in deep, reduced flow areas (Keefer et al. 2008a). Movement towards spawning sites resumes after water temperatures rise in late winter. Berman and Quinn (1991) observed spring Chinook salmon in the Yakima River to hold in thermal refuges for four months prior to spawning. As spawning dates neared, fish left refuges and traveled to spawning sites located both up and downstream. Some fish even fell back at Roza Dam, a dam on the mainstem Yakima River, to reach downstream spawning sites.

While thermal refuge may provide an escape for steelhead, it does not guarantee survival. Keefer et al. (2009) found that steelhead that utilized cool water refuge had lower survival rates to natal streams due to harvest and additional unknown mortality in the mainstem river. Harvest rates ranged from 4% to 17% for steelhead staging in non-natal tributaries for thermal refuge (Keefer et al. 2009). In addition to harvest risks, steelhead that seek out thermal refuge may have delayed survival effects due to previous temperature stress. Crossin et al. (2008) found that exposure to high temperatures had negative effects on the subsequent survival of sockeye salmon, particularly among females. Apart from increased risk of delayed mortality, sockeye exposed to high temperatures were less likely to successfully complete their migration (Crossin et al. 2008).

As spawning dates near, steelhead may leave refuge areas and resume their migrations to home. In Chapter 2, I found that fallback to home after overshooting occurred most often in early spring. The average median fallback to home date was 20 March. High rates of fallback to home in spring indicate that steelhead are overwintering in upstream areas and then descending back downstream in spring. Keefer et al. (2008a) also found some radio-tagged steelhead from the John Day, Umatilla, and Walla Walla rivers to overwinter in Snake River reservoirs, several dams above their natal stream. Additionally, Poxon and Faber (2014) reported that many Fifteenmile Creek steelhead mostly likely overwinter above The Dalles Dam.

Summer migrants now face increased summer water temperature and decreased overall flow in the Columbia River (Quinn and Adams 1996; Quinn et al. 1997). Quinn et al. (1997) found that river warming began 30 days earlier in 1993 than in 1938, and between 1949 and 1993 annual maximum temperatures rose by 1.8 °C. Overshooting may be more common than it once was, and continued increases in temperature may exacerbate the behavior further. Since water temperatures have risen due to the hydrosystem and prevailing climate, it is likely that more steelhead exhibit thermoregulatory behavior today than historically (Keefer et al. 2009). Since upstream areas may be used by many adult steelhead as holding areas, attention should be paid to facilitating downstream dam passage during late winter and early spring.

Spill.—Whether steelhead overshoot due to homing difficulty or to find appropriate holding areas, they may still fall back though overshot dams and successfully return to home. In Chapter 3, the probability of falling back to home after overshooting was poorly explained by juvenile experiences. Most hatchery stocks were less likely to fall back to home, but much of the effect may be due to harvest while fish are in upstream reaches or to partial imprinting on upstream rearing areas. Fallback to home after overshooting may be unattractive and dangerous to all adult steelhead because passage options in late winter can be limited to turbine passage, at least until spill begins in spring for juvenile fish passage. Based on studies of downstream passage by steelhead kelts (Harnish et al. 2015; Khan et al. 2013; Normandeau Associates 2011; Normandeau Associates 2014; Rayamajhi et al. 2013; Wertheimer 2007; Wertheimer and Evans 2005), I hypothesized that late-winter spill may aid overshoot fallback. Annual variation in fallback rates to home found in Chapter 2 support the hypothesis that year to year variation may affect downstream passage rates. In this chapter, I found evidence that more days of spill at the overshot dam during the month of March facilitated overshoot fallback.

Meta-analysis found that March spill was positively associated with fallback rates to home for hatchery steelhead, and to a lesser extent for wild steelhead. Regression analysis did not find fallback to be significantly related to spill during January or February, or flow during March, but analysis with conditional inference trees found increased March flow to be associated with higher fallback rates to home in two populations.

Inference power in both analyses was limited due to small sample sizes of overshooting fish, issues with tributary arrays in some years, and relatively low variation in spill patterns at some dams. The strongest effects were found for populations with the most number of replicate years for which fallback rates to home were estimable (Walla Walla and Tucannon River steelhead). Walla Walla endemic hatchery steelhead were more likely to fall back to home in years with more spill days during February ($F_{1,5} = 1.61$, $P = 0.014$). Additionally, increasing numbers of spill days during March were associated with higher fallback rates to home in Tucannon hatchery ($F_{1,6} = 4.03$, $P = 0.046$) and Walla Walla Lyon's Ferry hatchery steelhead ($F_{1,5} = 7.19$, $P = 0.022$). These stocks had the largest sample sizes and the greatest degrees of freedom. Though small sample sizes resulted in low significance, the slope of the regression line between March spill and fallback to home was positive in 8 of 11 stocks (Figure 4.7, $P = 0.113$, one-tailed sign-test).

The effect of spill on fallback to home was also difficult to evaluate because at some dams there was little variation in spill during late winter and early spring from 2006 to 2015. For instance, in 7 of the 10 years, continuous spring spill at Lower Granite Dam began on 3 April, and the earliest continuous spill began in any year was 26 March. Between the years, the total number of spill days at Lower Granite prior to 3 April only ranged from 0 to 11. Despite little range in the amount of late winter spill, it was still an important predictor for Tucannon River hatchery steelhead within the fallback tree and regression model. Experimentally spilling water during late winter and early spring would provide further insight into how effective it may be for increasing fallback to home rates.

In Chapter 2, estimates of average annual fallback rates to home ranged from 17.8% (SE 1.9%) for Walla Walla hatchery steelhead to 75.0% (SE 2.6%) for Umatilla wild steelhead. While some steelhead that did not fallback to home were likely strays or harvests, many may have been steelhead that failed to find safe downstream passage through dams. Fallback through turbines and juvenile bypass systems is more dangerous for adult steelhead than smolts (Ferguson et al. 2008; Harnish et al. 2015). Both lethal and sub-lethal injuries obtained during turbine or bypass passage are a concern (Wagner and Hillson 1993; Wertheimer 2007). In addition to injury concerns, downstream dam passage can also add significant migration delays. Movement rates of steelhead kelts slow greatly just above dams, possibly because steelhead are trying to identify downstream passage routes or waiting for flow or spill conditions to change (Harnish et al. 2015; Rayamajhi et al. 2013; Wertheimer and Evans 2005).

Non-turbine, surface-flow passage options including spillways and sluiceways are likely the safest and most efficient route for fallback at dams (Khan et al. 2013; Wertheimer 2007; Wertheimer and Evans 2005). Experimental studies estimated adult survival through surface-flow routes at Bonneville and McNary dams to be 98% (Normandeau Associates 2011; Normandeau Associates 2014). When available, steelhead kelts exhibit a very strong preference for surface rather than turbine passage (Harnish et al. 2015; Khan et al. 2013; Rayamajhi et al. 2013; Wertheimer 2007). When sluiceway operations at The Dalles Dam were experimentally maintained throughout late winter and early spring, Khan et al. (2013) found 91%—99% of kelts to fall back through the sluiceway rather than turbines. Forebay residence times of kelts are also decreased through the operation of surface flow routes (Wertheimer and Evans 2005). While these studies focus on post-spawn steelhead, it is likely that pre-spawn steelhead that overshoot their natal streams would benefit from the same operations. Here, I found that greater time spent spilling water, of any amount, during March was associated with higher rates of fallback to home in hatchery steelhead. While not significant, the same pattern was observed for wild steelhead. Beginning spillway operations in late winter may enhance the fallback of overshooting steelhead, and contribute to increased rates of fallback to home.

Conclusions.—Overshoot behavior by steelhead in the Columbia River basin was strongly related to adult experiences. Analysis using logistic regression and conditional inference trees indicated lower overshooting by steelhead exposed to lower water temperatures as adults. Shoreline orientation near the home tributary also played a significant role in Wenatchee River steelhead. Combined analysis of juvenile and adult experiences using conditional inference trees indicates that the most important predictors of overshoot behavior were water temperature and rearing history. More natural rearing of hatchery fish, including the use of endemic broodstock, rearing close to the release stream rather than far upstream, and long-term acclimation prior to release, result in lower overshooting and higher homing success. Conditional inference trees of fallback to home also indicated a strong effect of rearing history, consistent with the results of Chapter 3. In most stocks, I found higher fallback rates to home by natural origin and non-adipose clipped hatchery steelhead. Marked hatchery steelhead generally fell back to home at reduced levels, indicating harvest in upstream areas. Lastly, I found evidence to suggest that higher flows and more spill days during March aids fallback rates to home.

Impoundments and flow regulation in the Columbia River have contributed to the development wide, slow moving reservoirs and elevated summer water temperatures. Wide reservoir environments may make olfactory homing more difficult. Here, I found evidence that steelhead oriented to the opposite shoreline near their home tributary were more likely to overshoot. Additionally, steelhead were more likely to overshoot and less likely to return directly to home when water temperatures were higher. This suggests that overshoot behavior can be an adaptive response to local conditions. Temperatures exceeding 16—18 °C may spur steelhead to make non-direct homing movements, including overshooting, as they seek out thermal refuges. Since upstream areas may be used by many adult steelhead for thermal refuge or overwintering sites, attention should be paid to facilitating downstream dam passage during late winter and early spring. Beginning spillway operations in late winter may enhance the fallback of overshooting steelhead, and contribute to increased rates of fallback to home. Experimentally spilling water during late winter and early spring would provide further insight into how effective it may be for increasing the homing success of overshooting fish.

Chapter 5: Synthesis of Findings on Tributary Overshoot and Fallback by Steelhead in the Columbia River Basin

This study is the first to estimate rates of overshooting and fallback to home using robust statistical methods, link overshooting to potential mechanisms, as well as quantitatively evaluate possible management strategies for reducing overshooting or increasing fallback to home. The primary objectives of this thesis were to: (1) document tributary overshoot and fallback for multiple populations of adult steelhead in the Columbia River basin using existing PIT-tag data, (2) determine the extent to which tributary overshoot and fallback are associated with juvenile rearing and barging experiences, (3) characterize the degree to which tributary overshoot is related to shoreline orientation and water temperature, and (4) determine whether surface passage options promote dam fallback and homing success. In Chapter 2, I estimated rates of overshooting and fallback to home using multistate release-recapture models. In Chapters 3 and 4, I utilized generalized linear models and conditional inference trees to assess a variety of potential mechanisms, as well as highlight what management strategies may enable greater rates of successful homing. These analyses have expanded our knowledge about the migratory behavior of adult steelhead, and have provided a stepping stone to improved management and conservation of threatened and endangered populations.

Prior to this thesis, steelhead overshooting was a puzzling behavior that had not been adequately quantified or explained. It was a subject of interest, but had not been characterized using robust statistical methods. Quantitative estimates of straying in general are very limited for natural origin salmon and steelhead (Keefer and Caudill 2014). Additionally, previous primary studies on overshooting (Boggs et al. 2004; Keefer et al. 2008b) may have underreported overshooting rates because home tributaries of individual fish were unknown, therefore overshooting was only detectable for fish that subsequently fell back and entered a downstream tributary. Given that many populations of Pacific salmon and steelhead are at risk of extinction, high levels of tributary overshoot not accompanied by overshoot fallback may affect the viability of naturally spawning populations. Consequently, a greater understanding of this process was important for the conservation of depleted or listed populations.

Previous reporting on overshooting and fallback to home by steelhead in the Columbia River basin (Bumgarner and Dedloff 2011; Keefer et al. 2016; Murdoch et al. 2012) has utilized a tally-based approach that ignored detection efficiencies. Here, I showed the extent of bias associated with tally-based estimates (Chapter 2). While the amount of bias was relatively small for overshooting over each dam except Rock Island Dam, the degree of bias in tally-based estimates of fallback to home after overshooting was very high for many populations. Average detection efficiencies ranged greatly between tributary sites (44.2% (SE 2.8%)—97.1% (SE 3.4%)), and between years at individual sites (35.7% (SE 14.1%)—100%). Because detection efficiencies varied spatially and annually, tally-based estimates were not viable estimates or even reliable indices of return rates. In the technical report by Keefer et al. (2016), proportions of steelhead that fell back to home after overshooting were reported, however, these rates were not adjusted for any sort of detection efficiency. Not only were these estimates likely to be negatively biased, they also did not include any measure of uncertainty. In Chapter 2, I presented estimates of overshooting and fallback to home, with associated standard errors, calculated using multistate release-recapture methods. Unlike tally-based estimates, multistate estimates of movement rates are comparable between populations and between years.

Major findings.—There was a range in overshooting rates over the study dams. Some populations far from dams with PIT-tag detectors overshot very little, and Snake River populations were found to rarely overshoot into the upper Columbia. However, other populations nearer to mainstem dams overshot at higher rates. Average annual overshooting rates ranging from 7.2% to 51.8% were found for steelhead from the John Day, Umatilla, Walla Walla, Yakima, Wenatchee, Entiat, and Tucannon rivers. These rates are out of all steelhead that passed Bonneville Dam. Overshoot rates out of the run closer to the mouth of the home tributary are even higher. For instance, on average 66.4% (SE 5.0%) of Walla Walla hatchery steelhead that passed McNary Dam, the dam before their home tributary, continued past home to overshoot Ice Harbor Dam. Also, 65.6% (SE 7.5%) of Wenatchee hatchery steelhead that passed Rock Island Dam overshot Rocky Reach Dam and 60.7% (SE 2.6%) of Tucannon hatchery steelhead that passed Ice Harbor Dam overshot Lower Granite Dam.

Excessive overshooting may lead to decreased numbers of steelhead that successfully return home to spawn, therefore limiting the recovery of threatened or endangered populations. Average annual fallback rates to home ranged greatly, from 17% to 75%. Low fallback rates contributed to lower homing success in populations with high levels of overshooting. Not only does overshooting occur at high levels in multiple populations, it is associated with decreased successful return to home. Therefore, a greater understanding of this behavior could be critical to steelhead management in the Columbia River basin.

Overshooting rates were highly affected by dam proximity, shoreline orientation, water temperature, and hatchery practices. Distance to the upstream dam had a highly significant negative effect on overshooting rate for steelhead from the lower and upper Columbia rivers. Aside from dam proximity, fish position within the reservoir played a role in overshooting. Salmon and steelhead tend to be shore oriented during their spawning migrations (Daum and Osborne 1998; Hughes 2004; Reischel and Bjornn 2003), and I determined shoreline orientation of steelhead approaching their natal stream by which dam ladder they used at downstream dams. Shoreline orientation was highly significant in direct homing and overshooting models for Wenatchee River. Shoreline orientation was measured at Rock Island Dam, 24 kilometers below the Wenatchee River mouth. Steelhead that passed in the eastern ladder, on the opposite shore of the natal river mouth, returned directly to home less and overshot more than steelhead that passed in the middle or western ladders. Weaker effects were found for Walla Walla and Yakima steelhead, likely because orientation was measured further from the natal river (39—69 rkm). Within reservoirs, orientation of adult steelhead to the opposite shoreline where the natal tributary is located may cause steelhead to miss the natal stream mouth.

This study focused on summer steelhead, which migrate through the Columbia River hydrosystem during the summer period of elevated water temperatures. I found that as water temperatures rose, steelhead were less likely to move directly to home. A significant effect was found for steelhead from 6 of 7 tributaries. Additionally, steelhead that experienced higher water temperatures near their natal stream were more likely to overshoot. Temperature was found to be associated with steelhead behavior for 6 of 7 tributaries. Specifically, temperatures exceeding 16—18 °C may spur steelhead to make non-direct homing movements, including overshooting, as they seek out thermal refuges. For John Day, Walla Walla, and Tucannon River steelhead, overshooting increased with rising temperatures, but leveled off or even declined when average temperatures exceeded 18 °C to 20 °C in the mainstem river. Peak temperatures may create migratory barriers, preventing passage over upstream dams.

Extensive efforts to mitigate for the impact of dams in the Columbia River basin, including fish hatcheries and juvenile barging, have been enacted (Keefer et al. 2008c; Mobrand et al. 2005). However, these practices may have unintended effects on adult behavior. Hatchery rearing was associated with decreased successful homing during every period of the freshwater migration, including overshooting. However, overshooting was only elevated in hatchery stocks reared at hatcheries upstream of release sites. Hatchery steelhead raised at upstream hatcheries may be attracted to rearing areas, making them more likely to overshoot. For steelhead reared at upstream areas, I found that overshooting may be reduced by adopting more natural rearing practices.

Hatchery steelhead sourced from endemic, integrated broodstocks performed more similarly to natural origin steelhead than hatchery fish sourced from out-of-basin, segregated stocks. Out-of-basin stock released in the Walla Walla River were more likely to overshoot than the endemic hatchery stock, even though both were raised at the same hatchery. In addition to the use of endemic broodstock, long-term acclimation may be used to reduce overshooting by steelhead reared at upstream tributaries. Since 2011, all juvenile hatchery steelhead released in the Wenatchee River have been acclimated within the basin overwinter and released in spring (Hillman et al. 2016). The shift from direct release to long-term acclimation was associated with a major decline in overshooting by Wenatchee hatchery steelhead, which are reared upstream of the Wenatchee River. On average, long-term acclimation within the release basin reduced overshooting by Wenatchee hatchery steelhead by 41 percentage points.

Extended ocean residence time and juvenile barging did not consistently lead to increased overshooting. Spending two rather than one year in the ocean had estimated effects on overshooting ranging from a 4 percentage point decrease for Wenatchee steelhead to a 12 percentage point increase for Entiat steelhead. Like other authors (Labelle 1992; Pascual et al.

1995; Quinn and Fresh 1984; Quinn et al. 1991) have found, older fish appeared slightly more likely to stray. Age may have had a small effect on overshooting, but it alone did not explain the high overshooting rates found in many Columbia River basin steelhead populations.

Steelhead barged as juveniles were found to overshoot less than steelhead that out-migrated in-river. The effects of juvenile barging were evaluated for Tucannon River steelhead. Barging was associated with a positive effect on moving directly to home and a negative effect on overshooting. Barging had no effect on fallback to home after overshooting. While barging was linked to beneficial effects in the late migration, barging greatly reduced early migration success. Barged Tucannon River steelhead were less likely to move from Bonneville Dam to Ice Harbor Dam, by 37 percentage points on average. Barged steelhead may be delayed by repeatedly falling back along their upstream migration as they struggle to locate olfactory clues (Keefer et al. 2008c). The median migration time between Bonneville Dam and Ice Harbor Dam was 18 days for in-river fish, compared with 49 days for barged fish.

My final objective was to determine whether surface passage options promote dam fallback and homing success. I found the number of days of spill during March to be positively associated with fallback rates to home for hatchery steelhead. A similar relationship was suggested for wild steelhead, but was not significant. For many populations, inferential power was limited due to the small number of years in which fallback rates to home were estimable. Though small sample sizes resulted in low levels of significance, the slope of the regression line between March spill and fallback to home was positive in 8 of 11 stocks.

Together, these findings support the hypothesis that steelhead overshoot to find thermal refuge because temperatures are too warm for extended occupancy near their natal stream. Analysis using logistic regression and conditional inference trees indicated lower overshooting by steelhead exposed to lower water temperatures as adults. Additionally, I found evidence to support the hypothesis that overshooting results from difficulty following olfactory clues through reservoirs. When measured within 24 rkm of the natal stream, shoreline orientation exerted a significant effect on direct homing and overshooting. Finally, my findings reinforce the proposal that late-winter spill increases fallback to home by overshooting fish.

In contrast, I did not find consistent evidence to support the hypothesis that steelhead overshoot due to memory failure linked to barge transportation, hatchery rearing, or ocean age. Instead, barge transportation reduced overshooting and did not affect fallback to home. Hatchery rearing was only associated with increased overshooting when fish were reared at upstream hatcheries, and this effect was moderated by using endemic broodstock and acclimating juveniles overwinter. Lastly, the effects of ocean age were biologically small and did not explain high overshooting rates observed in many populations. These findings support an alternate hypothesis, that memory failure reduces rather than increases overshooting. Instead of resulting in extended upstream movements, difficulty identifying olfactory clues may discourage steelhead from continuing further upstream.

Management implications.—My findings indicate that overshooting is exacerbated by human-induced changes to river systems and steelhead populations. Impoundments and flow regulation in the Columbia River have contributed to the development wide, slow moving reservoirs and elevated summer water temperatures. Because water temperatures are likely to rise with climate change, managers should consider adopting hatchery practices that do not further heighten overshooting by hatchery fish, as well as dam operations that enable downstream dam passage during winter.

Rearing of hatchery steelhead in manners more similar to wild steelhead generally resulted in lower overshooting and higher homing success. First, I found hatchery location to play an important role. Hatchery steelhead reared near the release basin, rather than far upstream, were not significantly more likely to overshoot than wild steelhead. Second, I found hatchery steelhead sourced from endemic, integrated broodstocks to perform better than steelhead sourced from out-of-basin, segregated stocks. Local adaptations, including appropriate run timing, may result in endemic hatchery fish performing more similarly to wild fish. Finally, acclimation over winter within the release basin was found to drastically reduce overshooting. On average, long-term acclimation within the release basin reduced overshooting by Wenatchee hatchery steelhead by 41 percentage points. The rise in the proportion of acclimated steelhead explained the steep decline in overshooting by Wenatchee River steelhead, as well as the corresponding increase in overall homing success through time. From 2008 to 2015, successful homing by Wenatchee hatchery steelhead from Bonneville Dam to the Wenatchee River increased from less than 20% to greater than 60%.

Because upstream areas may be used by adult steelhead for thermal refuge or overwintering sites, attention should be paid to facilitating downstream dam passage during late winter and early spring. Here, I found that spillway operations in late winter may enhance the fallback of overshooting steelhead, and contribute to increased rates of fallback to home. The effectiveness of surface flow for downstream dam passage is supported by numerous studies on post-spawn steelhead (Harnish et al. 2015; Khan et al. 2013; Normandeau Associates 2011; Normandeau Associates 2014; Rayamajhi et al. 2013; Wertheimer 2007; Wertheimer and Evans 2005). However, spillways are currently operated primarily for juvenile fish, and are not regularly operated during times of the year when they may be beneficial for fallback by overshooting fish.

In this study, the average median date of overshooting for all populations was 11 September. However, most steelhead did not fall back to home until late winter or early spring. The average median fallback to home date was 20 March.

To facilitate downstream passage during March, there must be water resources available. The completion of this thesis coincides with a recent ruling to increase spill at Columbia River basin dams during April and June. On 27 March, 2017, a judge in the United States District Court ordered water to be spilled up to the "spill cap" for total dissolved gas criteria from 3 April through 20 June at Snake River dams and from 10 April through 15 June at lower Columbia dams (United States District Court 2017). This ruling was issued to improve survival of juvenile fish through the hydrosystem. It may, however, reduce available water resources during other periods of the year, making it more difficult to provide spill for adults.

Despite limited resources, it is still important to consider the potential benefits of providing even a small amount of surface flow during March. First, proper management requires the consideration of survival during all periods of the life cycle. Smolt-to-adult survival ratios of wild Snake River summer steelhead range from 0.004 (SE 0.001) to 0.029 (SE 0.002) (Columbia River DART), meaning that for each returning adult, there were hundreds to thousands of out-migrating juveniles. Enhancing the survival of juvenile steelhead may ultimately have limited effectiveness to population recovery if the small fraction that return as adults are unable to properly home due to a lack of downstream passage options. The court-ordered spill will occur too late in the year to provide additional benefits to overshooting steelhead. By mid-April, most overshoot fallback by adult steelhead has already completed (Appendix B). A larger gain in adult returns may be gained by allocating spill for adults as well as juveniles. Second, only small amounts of spill may be necessary to facilitate downstream passage by adults. Wertheimer (2007) found that 80% of kelts were efficiently routed away from turbines with spill fractions less than 5%. In comparison, spill fractions for juvenile fish during April and June in recent years typically ranged from 20% to 50% (Columbia River DART). Compared to juvenile fish, adult salmonids may require lower spill levels because they are better able to actively search for passage options. Finally, reservoirs in the Columbia River basin have available water during March (Figure 5.1). During late winter and early spring, water supplies are increasing (Columbia River DART). To improve the homing success of adult steelhead, a small amount of spill could be released during this time.

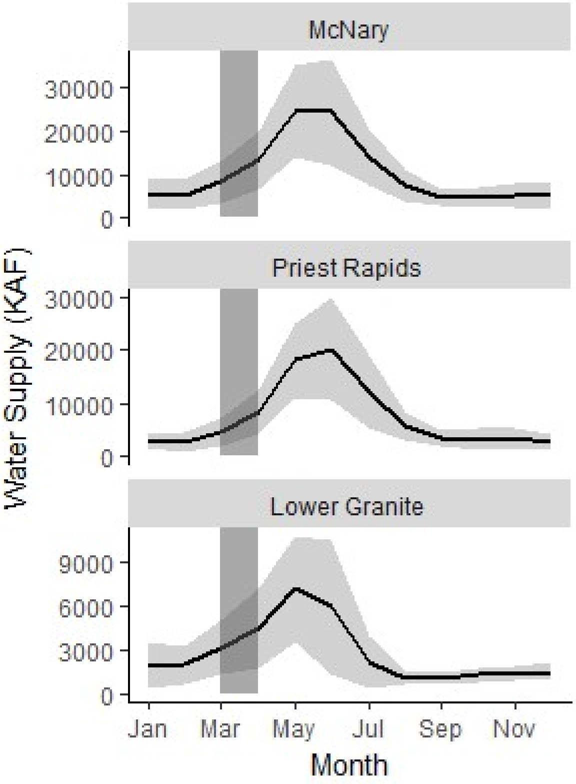

FIGURE 5.1.—Monthly average available water supply from 1997 to 2016 in kilo acre feet at McNary, Priest Rapids, and Lower Granite Dam with 90% confidence interval. Period of suggested spill for overshooting fish (1 March through 31 March) is highlighted. Data accessed from Columbia River DART.

Conclusions.—Because it is a pervasive behavior in many populations, tributary overshoot deserves to receive further attention as managers work to recover steelhead in the Columbia River basin. In this thesis, I verified that overshooting occurs at high levels in multiple Columbia River basin steelhead populations, and that it is associated with lower migration success rates. I found evidence that overshooting is, in part, an adaptive response to local conditions. Steelhead were more likely to overshoot and less likely to return to home when water temperatures were higher. Additionally, I found that more natural rearing of hatchery steelhead, including the use of endemic broodstock, rearing fish near the release basin rather than far upstream, and long-term acclimation prior to release, results in lower overshooting and higher homing success. Since upstream areas may be used by many adults for thermal refuge or overwintering sites, attention should be paid to facilitating downstream dam passage during late winter and early spring. Beginning spillway operations in late winter may enhance the fallback of overshooting steelhead, and contribute to increased rates of fallback to home.

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APPENDIX A.—Detection efficiencies

TABLE A.1.—PIT-tag detection efficiencies in the adult fish ladders of McNary, Priest Rapids, Rock Island, Rocky Reach, Wells, Ice Harbor, and Lower Granite dams for the run years 2005/2006—2014/2015. Standard errors are in parentheses.

	Run Year										
Dam	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Lower Columbia											
McNary	98.9% (0.4%)	98.9% (0.4%)	99.0% (0.3%)	99.5% (0.2%)	99.2% (0.1%)	99.2% (0.1%)	99.4% (0.1%)	99.6% (0.1%)	99.1% (0.2%)	99.3% (0.2%)	**99.2%**
Upper Columbia											
Priest Rapids	94.8% (1.4%)	99.3% (0.5%)	100%	99.7% (0.3%)	99.3% (0.3%)	98.9% (0.4%)	99.1% (0.5%)	99.5% (0.4%)	100%	100%	**99.1%**
Rock Island	78.3% (3.5%)	85.4% (2.2%)	92.0% (1.9%)	81.8% (2.1%)	97.7% (0.6%)	97.0% (0.8%)	93.2% (1.2%)	73.3% (2.3%)	88.9% (2.1%)	60.3% (3.1%)	**84.8%**
Rocky Reach	--	98.5% (1.0%)	100%	100%	99.6% (0.3%)	99.7% (0.3%)	98.7% (0.7%)	98.4% (0.9%)	99.1% (0.9%)	100%	**99.3%**
Wells	100%	100%	100%	95.2% (4.6%)	100%	100%	100%	100%	96.3% (3.6%)	100%	**99.2%**
Snake											
Ice Harbor	98.9% (0.6%)	100%	98.7% (0.4%)	98.7% (0.4%)	99.5% (0.1%)	99.6% (0.1%)	99.3% (0.2%)	99.6% (0.1%)	99.0% (0.2%)	99.5% (0.1%)	**99.3%**
Lower Granite	100%	96.2% (3.8%)	100%	100%	99.8% (0.2%)	99.8% (0.2%)	99.6% (0.2%)	100%	99.5% (0.3%)	99.9% (0.1%)	**99.5%**

TABLE A.2.—PIT-tag detection efficiencies at home tributary sites for lower Columbia River populations for the run years 2006/2007—2014/2015. Origin refers to the rear type of the population, hatchery or wild. Standard errors are in parentheses.

		Run Year									
Home Site	Origin	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Hood											
"HRM" (rkm 0)	*hatchery*	--	--	--	--	--	--	65.0% (6.5%)	41.6% (9.8%)	--	**53.3%**
	wild	--	--	--	--	--	--	56.7% (14.6%)	58.0% (24.9%)	--	**57.4%**
Fifteenmile											
"158" (rkm 5)	*wild*	--	--	--	--	--	--	49.8% (10.1%)	100%	100%	**83.3%**
Deschutes											
"DRM" (rkm 1)	*wild*	--	--	--	--	--	--	--	47.0% (4.7%)	41.4% (6.5%)	**44.2%**
John Day											
"JD1" (rkm 32)[a]	*wild*	--	--	99.6% (0.2%)	98.5% (0.6%)	99.8% (0.2%)	--	48.8% (7.6%)	40.6% (4.8%)	38.8% (4.7%)	**71.0%**
Umatilla											
"TMF" (rkm 5)	*hatchery*	--	--	--	53.9% (13.8%)	--	--	--	--	100%	**76.9%**
	wild	--	--	--	--	--	--	--	100%	76.6% (6.5%)	**88.3%**
Walla Walla											
"ORB" (rkm 10) or "PRV" (rkm 9)[b]	*hatchery*	40.0% (21.9%)	66.7% (27.2%)	33.3% (15.7%)	44.6% (10.6%)	60.0% (21.9%)	64.4% (10.8%)	72.7% (13.4%)	90.3% (11.5%)	95.0% (4.9%)	**63.0%**
	wild	--	--	--	56.8% (10.2%)	40.0% (8.9%)	42.0% (7.1%)	79.7% (6.4%)	96.6% (3.4%)	97.8% (2.2%)	**68.8%**

[a] “JD1” was washed out and replaced in 2011/2012

[b] “ORB” used 07/08—11/12, “PRV” used 12/13—14/15

TABLE A.3.—PIT-tag detection efficiencies at home tributary sites for upper Columbia and Snake River populations for the run years 2006/2007—2014/2015. Origin refers to the rear type of the population, hatchery or wild. Standard errors are in parentheses.

		Run Year									
Home Site	Origin	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
						Upper Columbia					
Yakima											
"PRO" (rkm 76)	*wild*	--	100%	100%	90.9% (8.7%)	87.5% (11.7%)	100%	100%	100%	98.4% (0.8%)	**97.1%**
Wenatchee											
"LWE" (rkm 3)	*hatchery*	--	--	--	--	--	53.8% (4.0%)	69.8% (3.3%)	58.0% (4.8%)	85% (2.3%)	**66.7%**
	wild	--	--	--	--	--	35.0% (7.5%)	54.4% (8.5%)	74.3% (15.7%)	99.2% (1.0%)	**65.7%**
Entiat											
"ENL" (rkm 2)	*wild*	--	--	--	93.3% (4.6%)	90.7% (5.1%)	94.6% (3.7%)	94.1% (5.7%)	96.8% (3.2%)	90.9% (5.0%)	**93.4%**
						Snake					
Tucannon											
"LTR" (rkm 3)	*hatchery*	96.0% (3.1%)	96.6% (1.1%)	**--**	92.8% (2.4%)	86.4% (4.4%)	76.7% (6.4%)	85.3% (5.2%)	67.2% (5.8%)	55.6% (6.9%)	**82.1%**
	wild	100%	97.2% (3.4%)	--	100%	72.7% (16.1%)	88.3% (7.8%)	91.2% (4.9%)	35.7% (14.1%)	67.6% (10.6%)	**81.6%**
Imnaha											
"IR1" (rkm 7)	*hatchery*	--	--	--	--	--	84.0% (3.2%)	100%	89.9% (1.2%)	96.8% (1.4%)	**92.7%**
	wild	--	--	--	--	--	87.8% (3.4%)	93.5% (3.6%)	95.7% (3.0%)	100%	**94.2%**

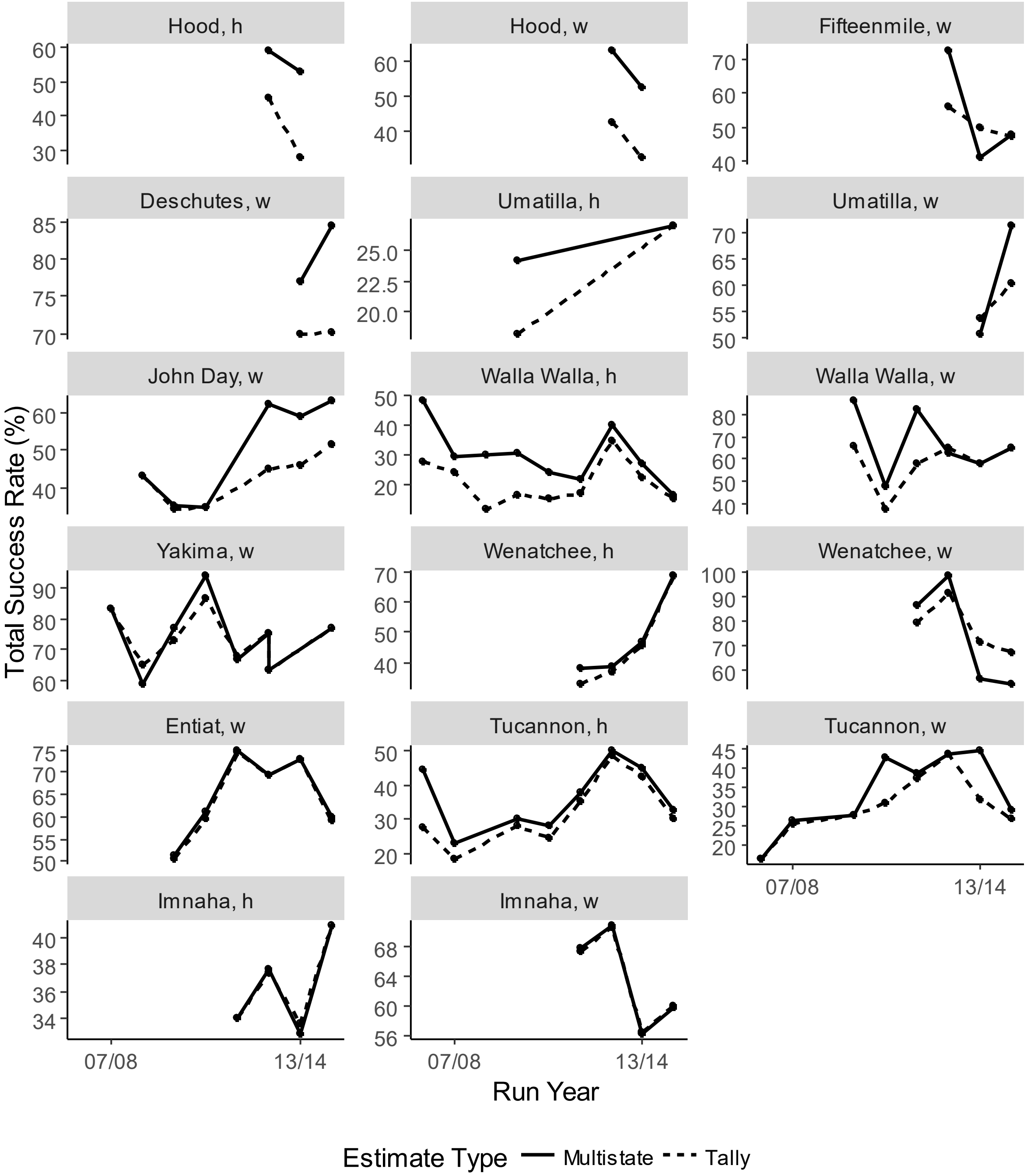

FIGURE A.1.—Annual variability between tally and multistate estimates of total success rates.

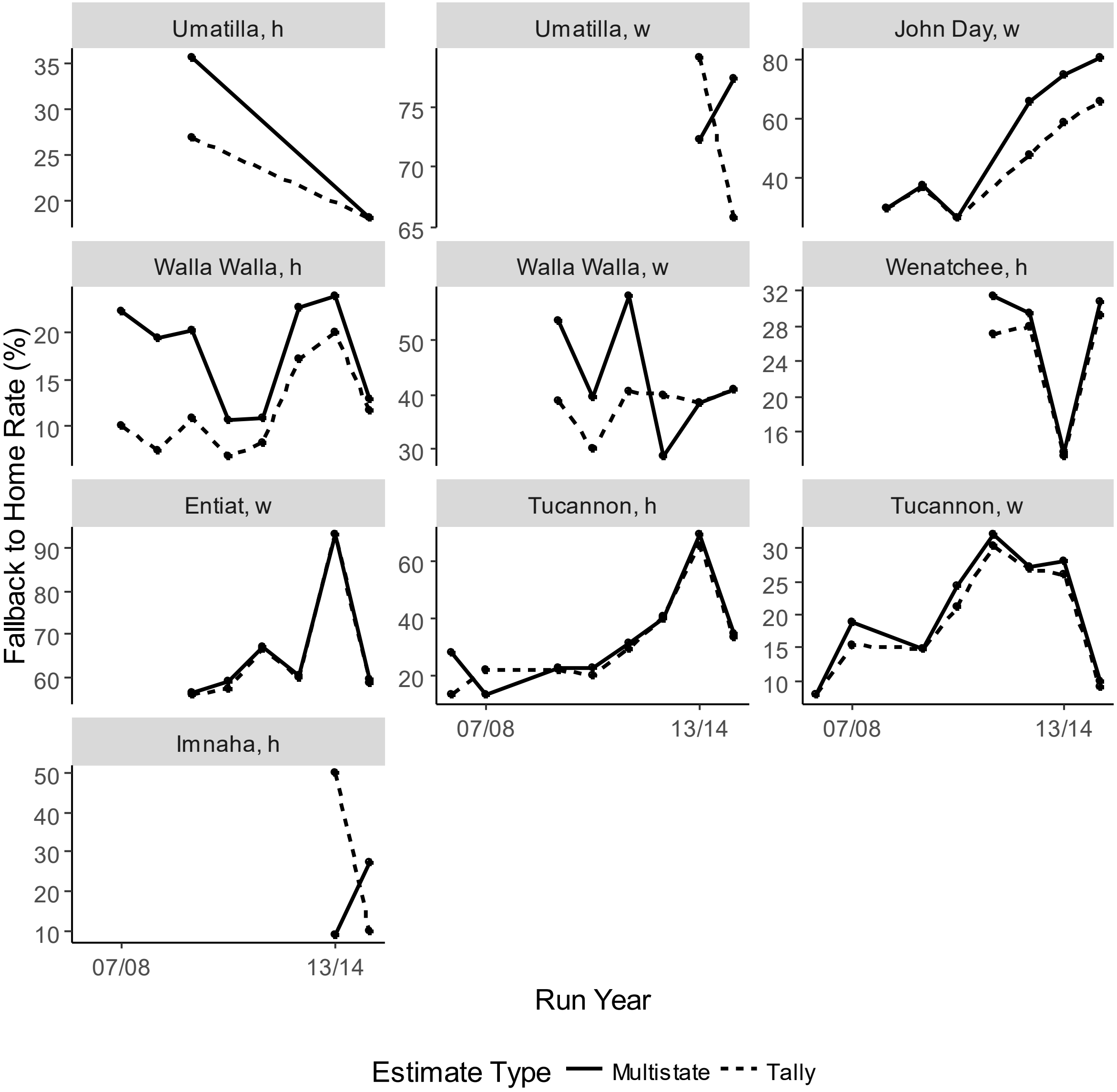

FIGURE A.2.—Annual variability between tally and multistate estimates of fallback to home rates.

A suspicious trend was observed for the John Day wild population (Figure A.3). The detection efficiencies at "JD1" from 2008/2009 to 2010/2011 were over 98%. According to the PTAGIS event log, the array was washed out by high flows in 2011. A new array was installed at the same location in 2012. In the following run years, the efficiencies dropped by more than half to 38.8%—48.8%. This shift in detection efficiencies was mirrored by a similar and opposite shift in estimates of return rate to home. Total success rates jumped from 34.7%—43.3% to 58.9%—63.4%. This trend suggests that detection efficiencies may be overestimated in earlier years or underestimated in later years. However, spawning abundance of John Day River steelhead did increase in the same time period (Northwest Fisheries Science Center 2015).

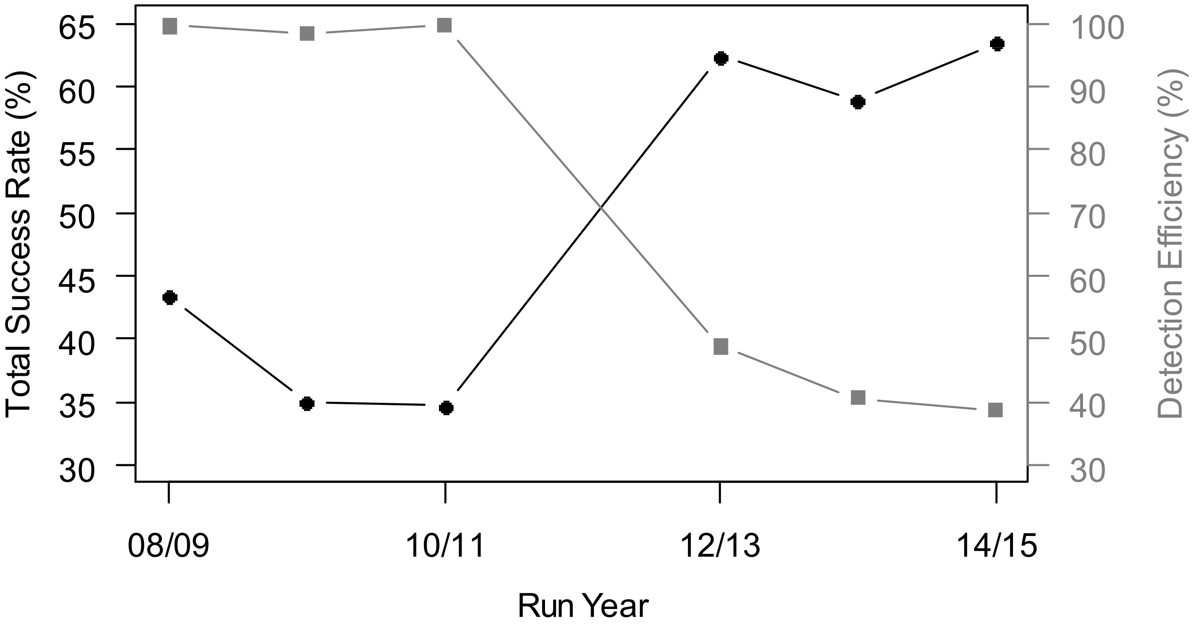

FIGURE A.3.—Total success rates of John Day steelhead compared to detection efficiencies at "JD1" (rkm 32).

APPENDIX B.—Migration timing

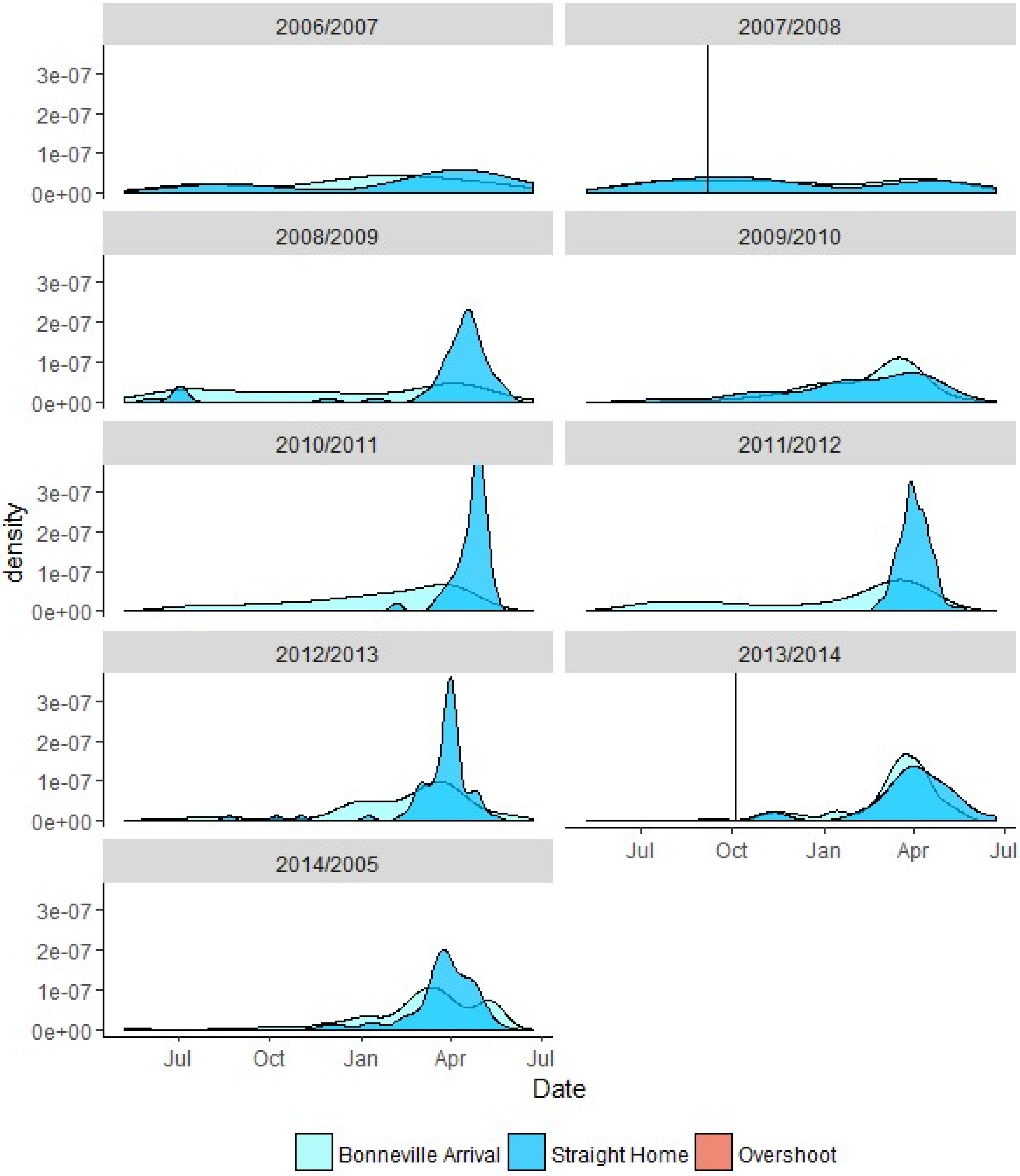

FIGURE B.1.—Density plots of run timing of Hood River hatchery steelhead. Timing is based on the first detection at the location. Area under each curve is equal to 1.

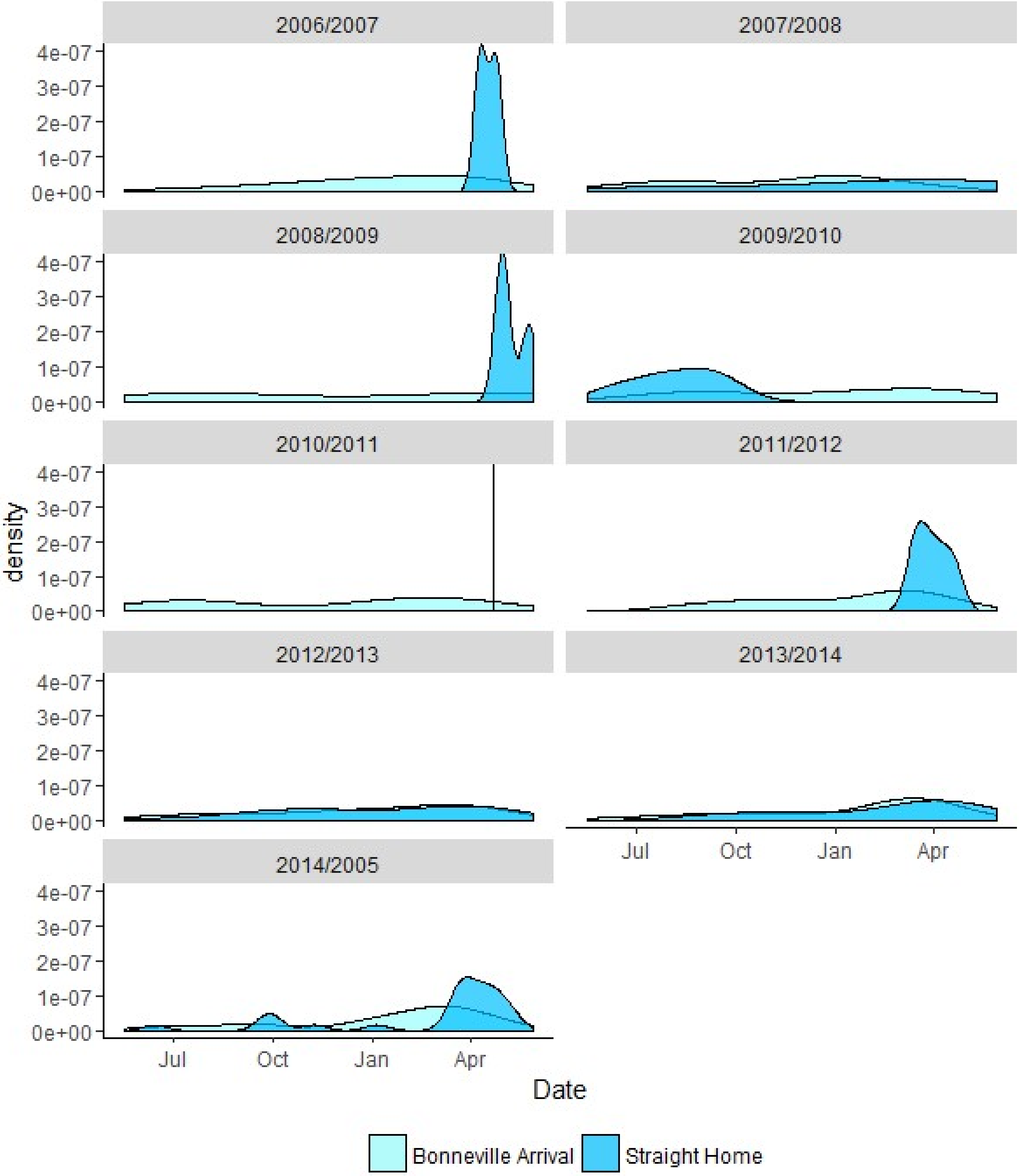

FIGURE B.2.—Density plots of run timing of Hood River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

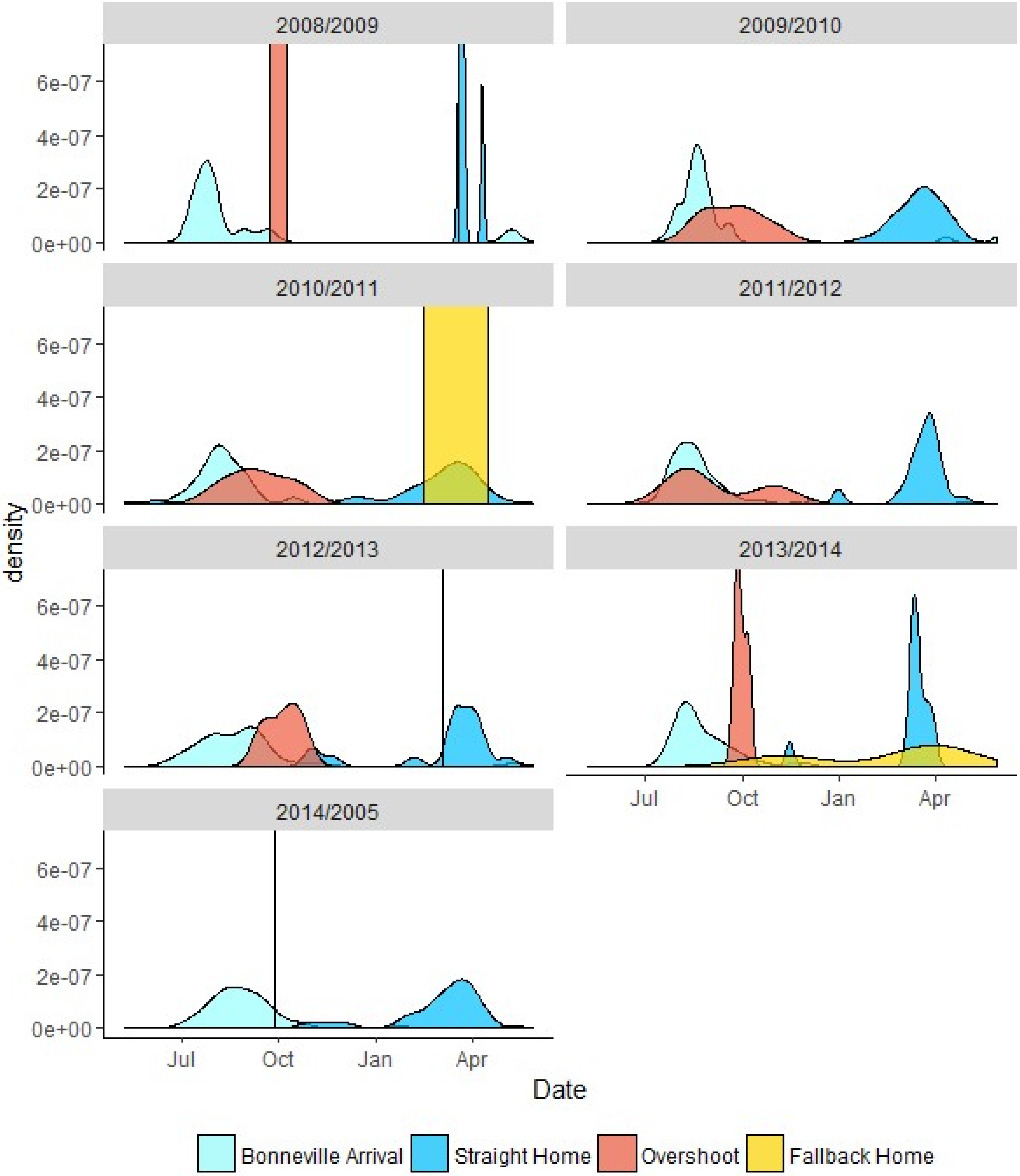

FIGURE B.3.—Density plots of run timing of Fifteenmile Creek wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

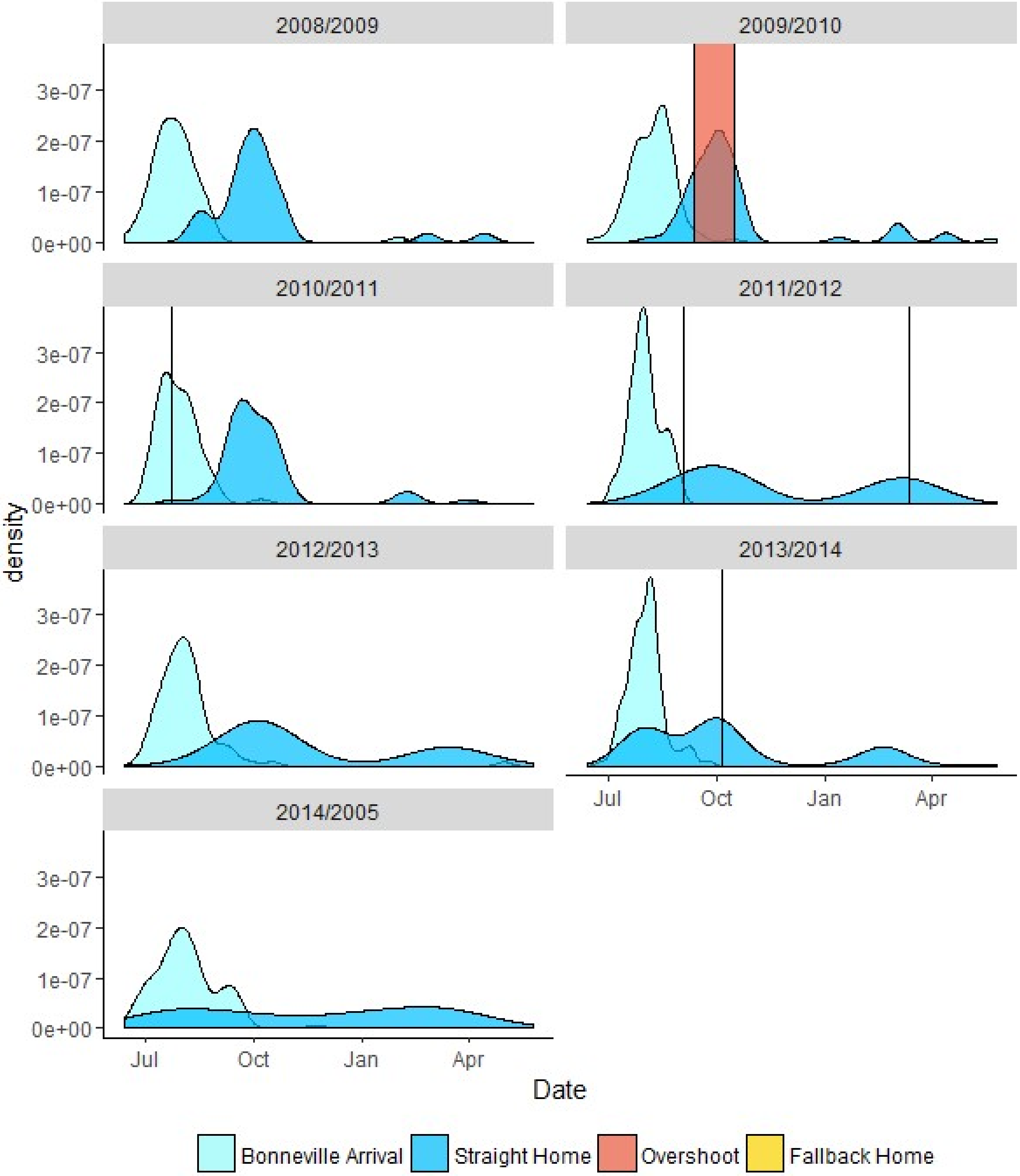

FIGURE B.4.—Density plots of run timing of Deschutes River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

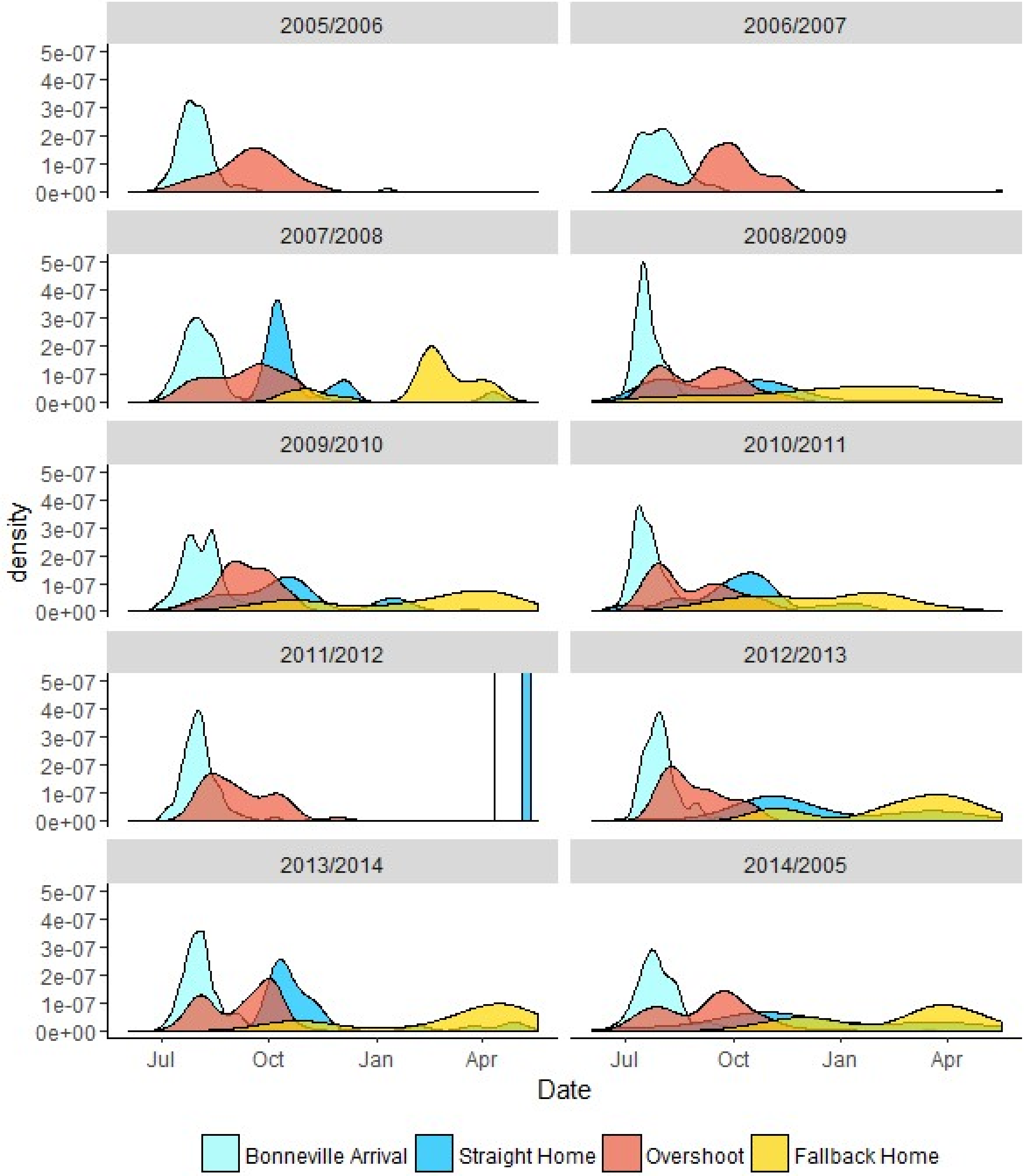

FIGURE B.5.—Density plots of run timing of John Day River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

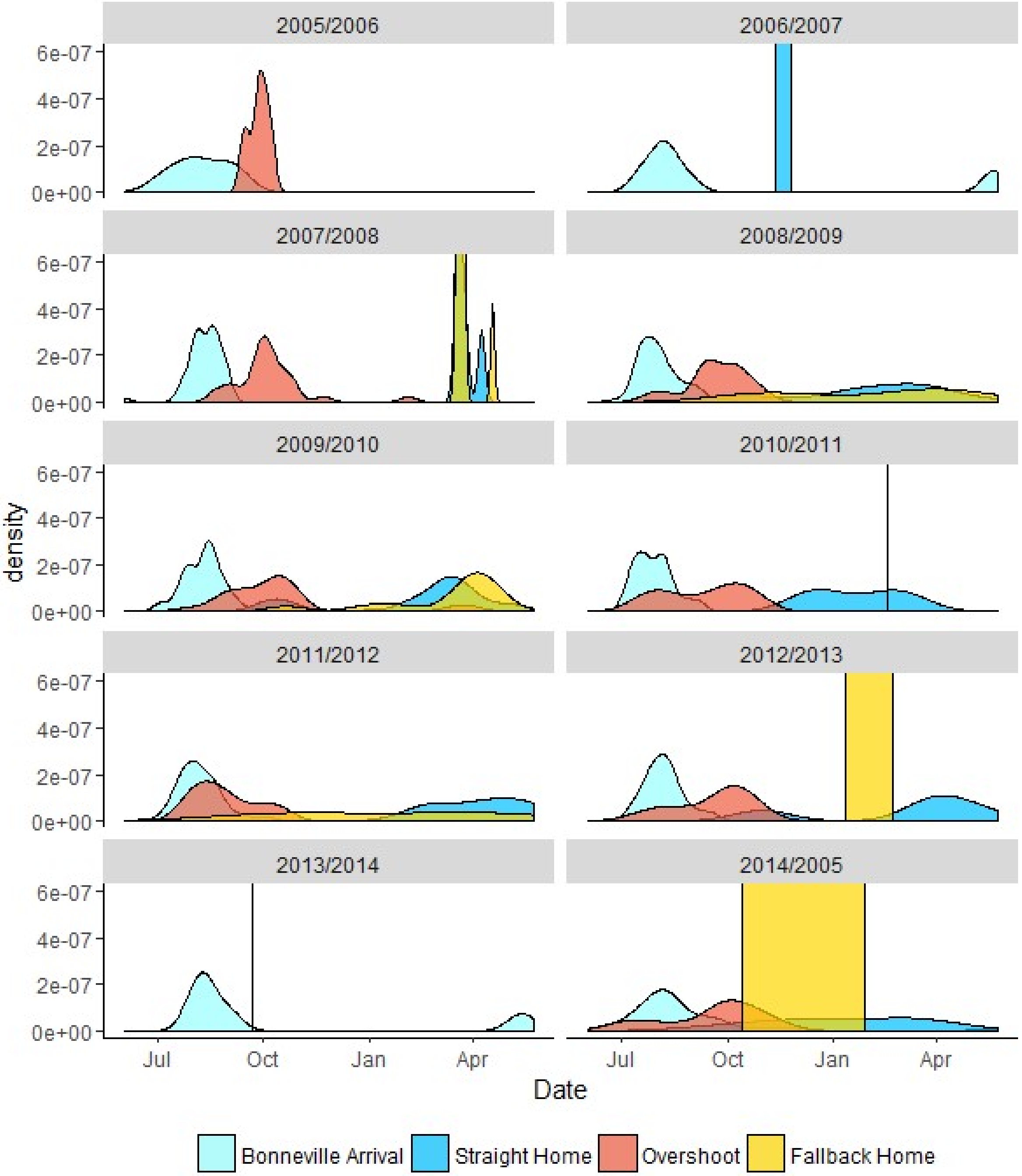

FIGURE B.6.—Density plots of run timing of Umatilla River hatchery steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

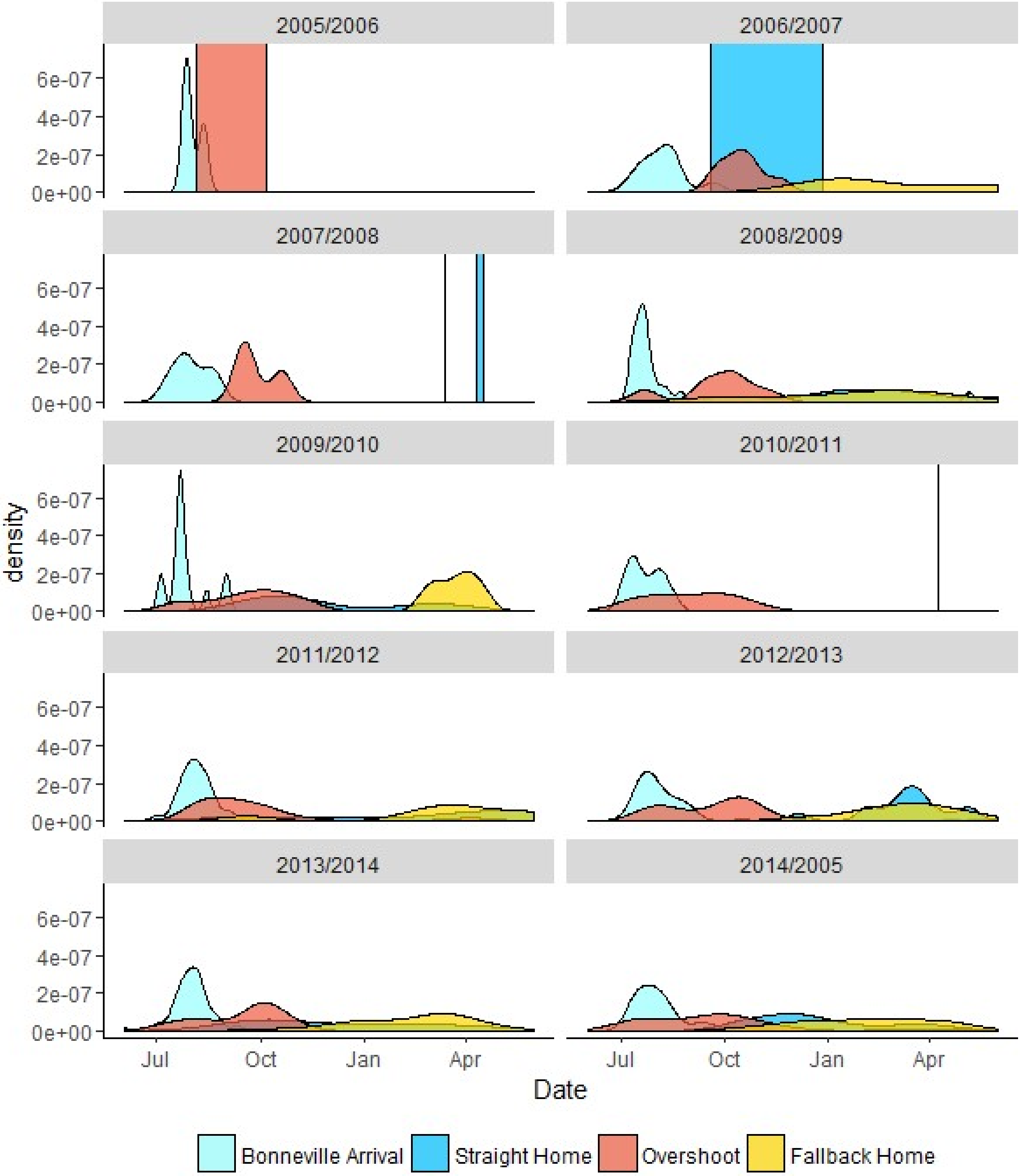

FIGURE B.7.—Density plots of run timing of Umatilla River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

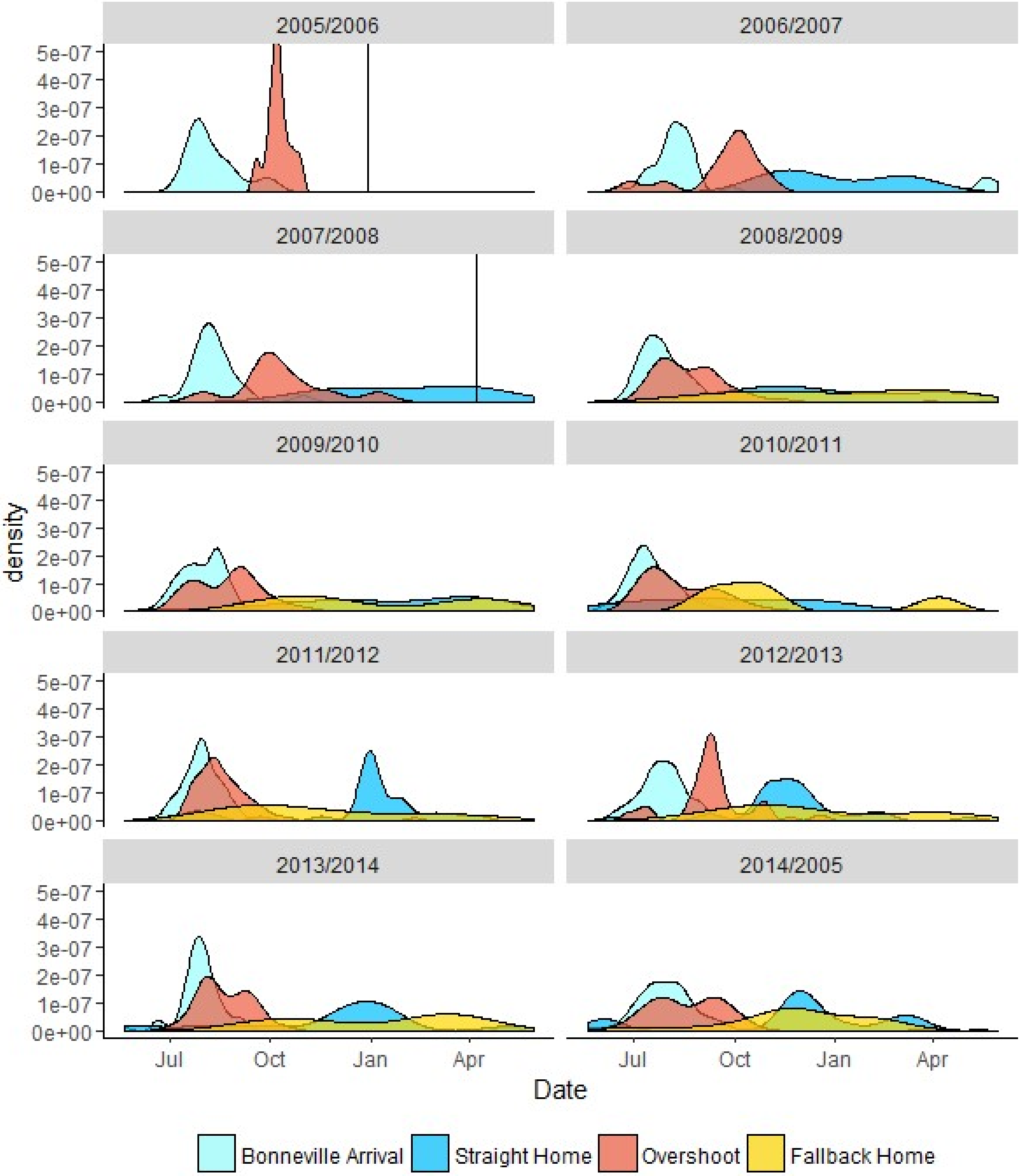

FIGURE B.8.—Density plots of run timing of Walla Walla River hatchery steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

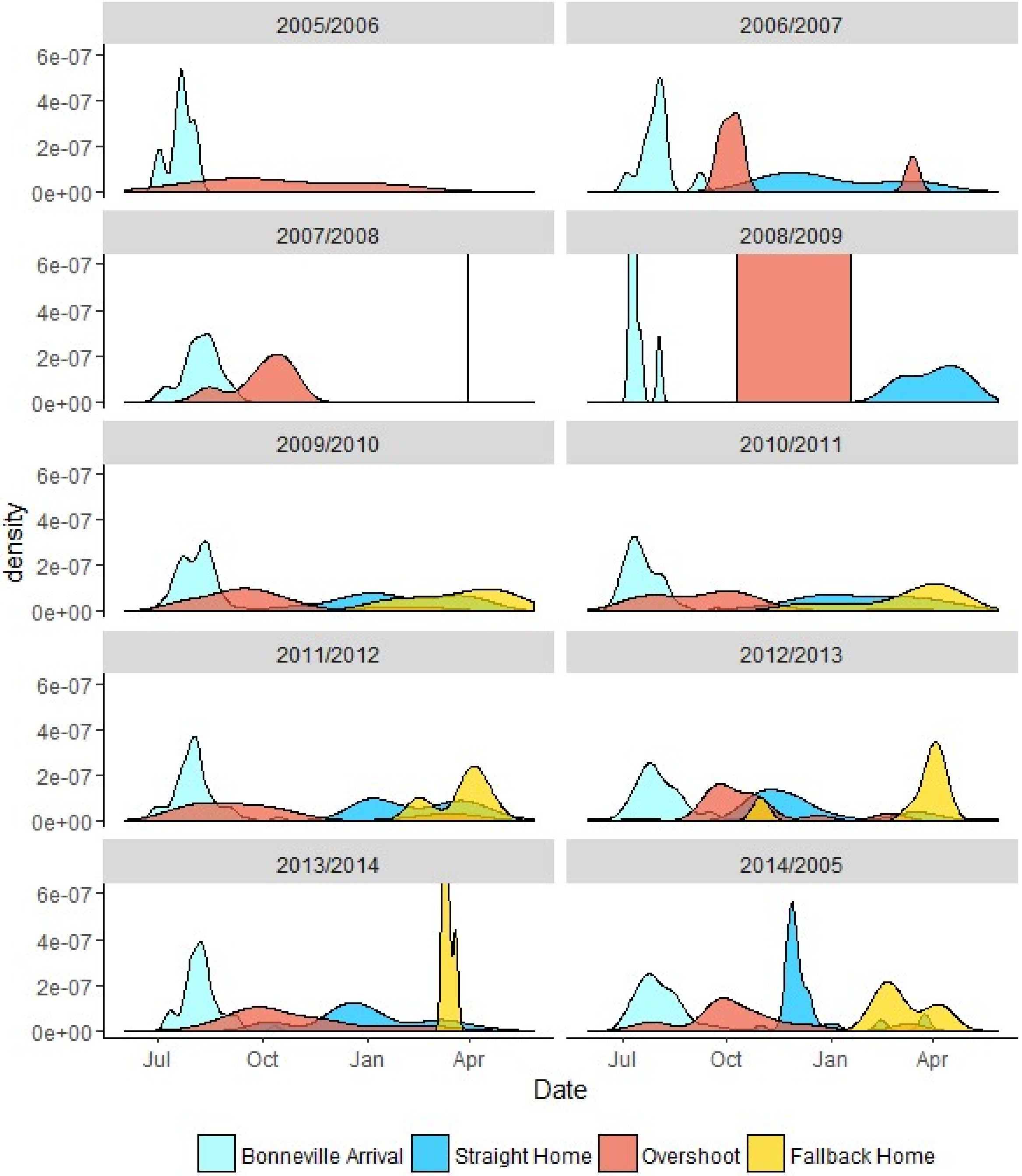

FIGURE B.9.—Density plots of run timing of Walla Walla River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

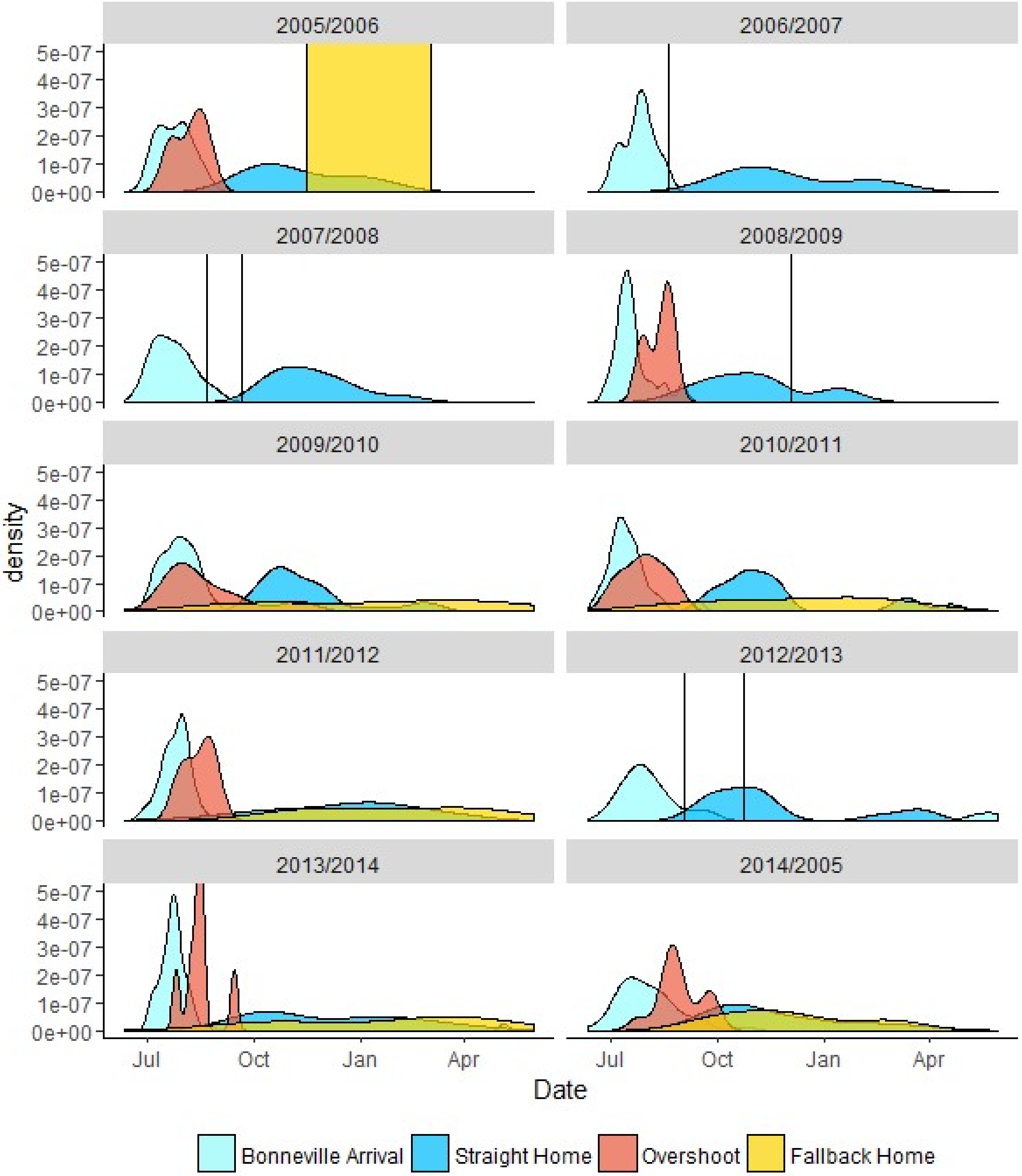

FIGURE B.10.—Density plots of run timing of Yakima River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

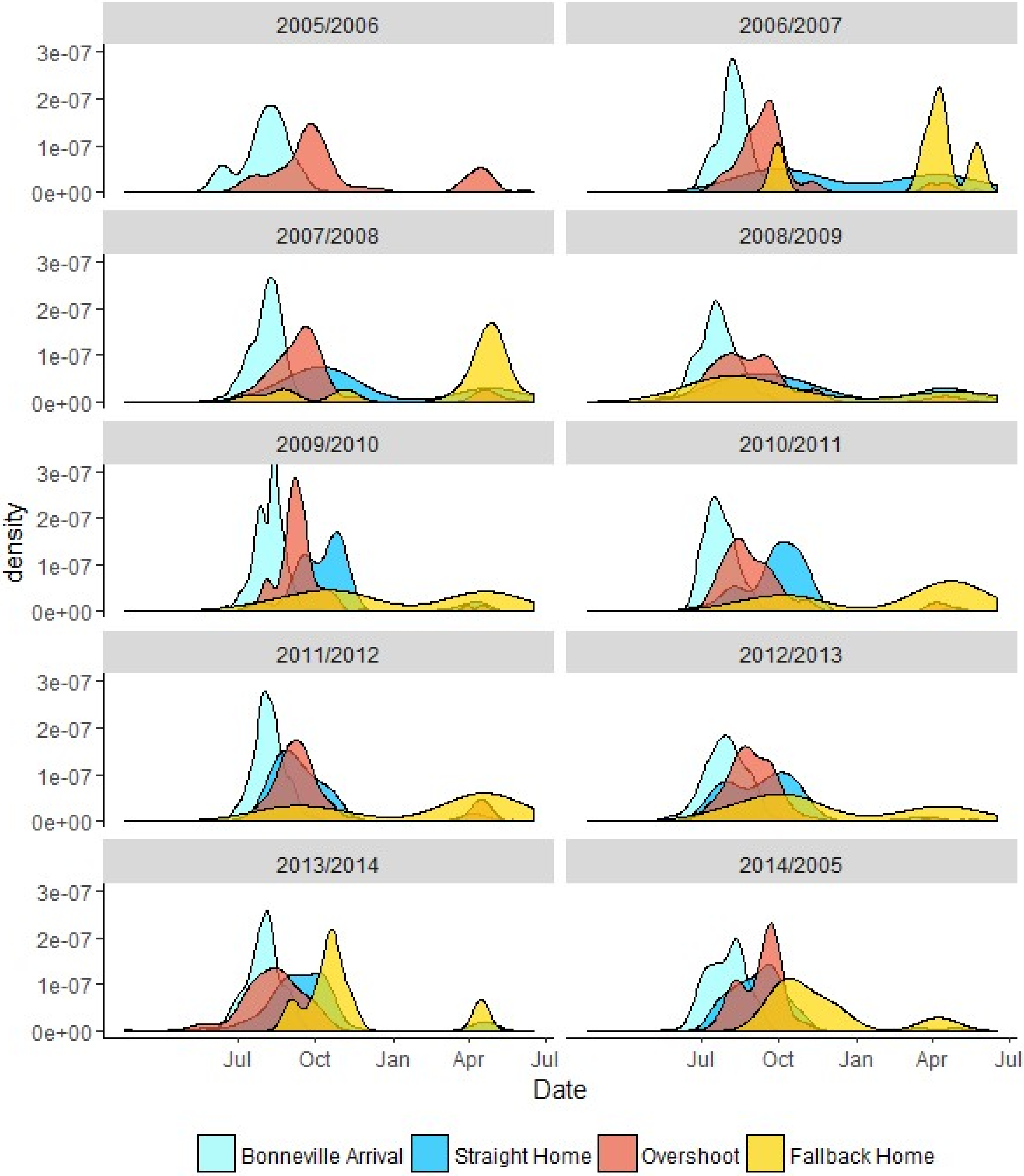

FIGURE B.11.—Density plots of run timing of Wenatchee River hatchery steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

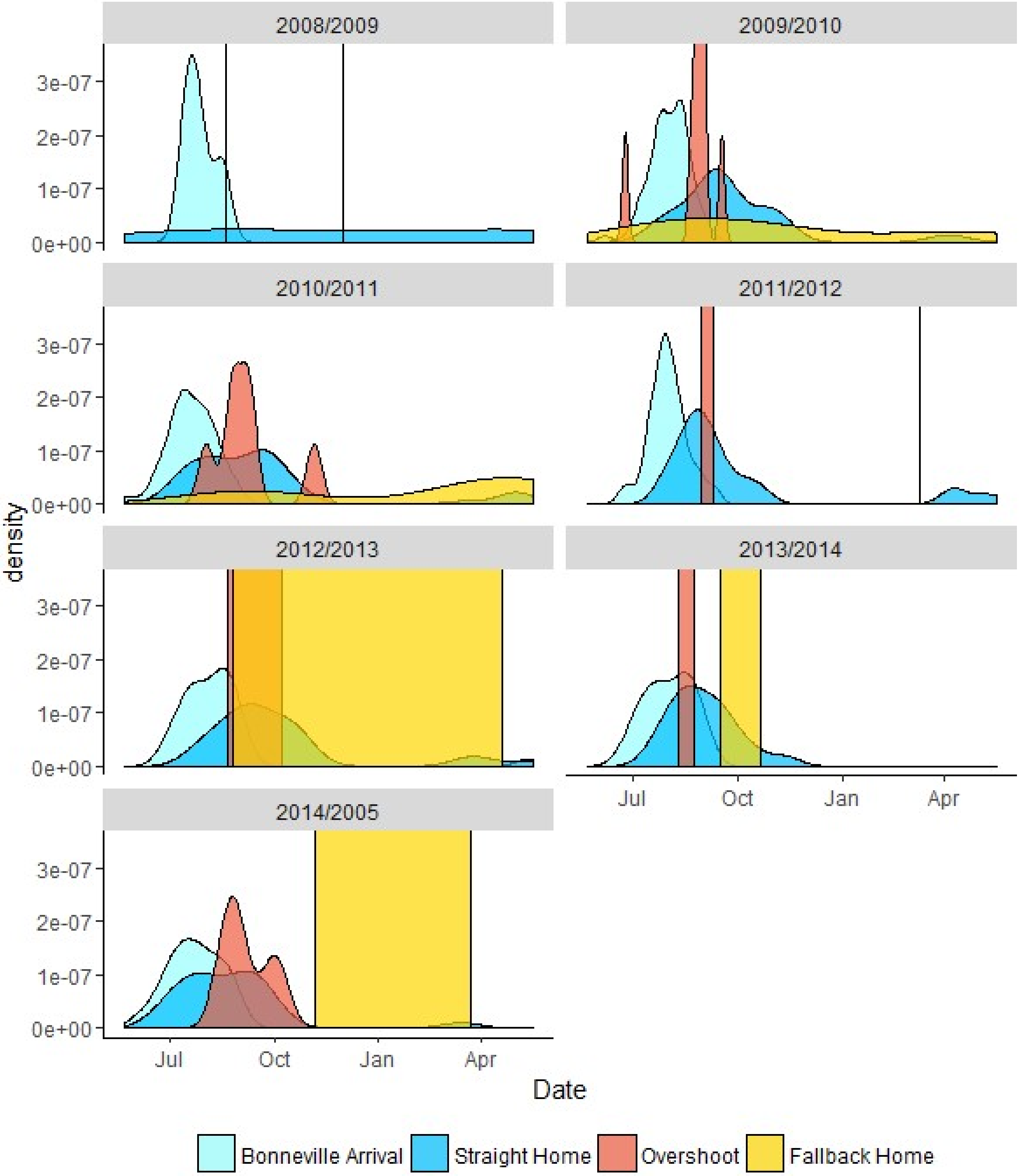

FIGURE B.12.—Density plots of run timing of Wenatchee River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

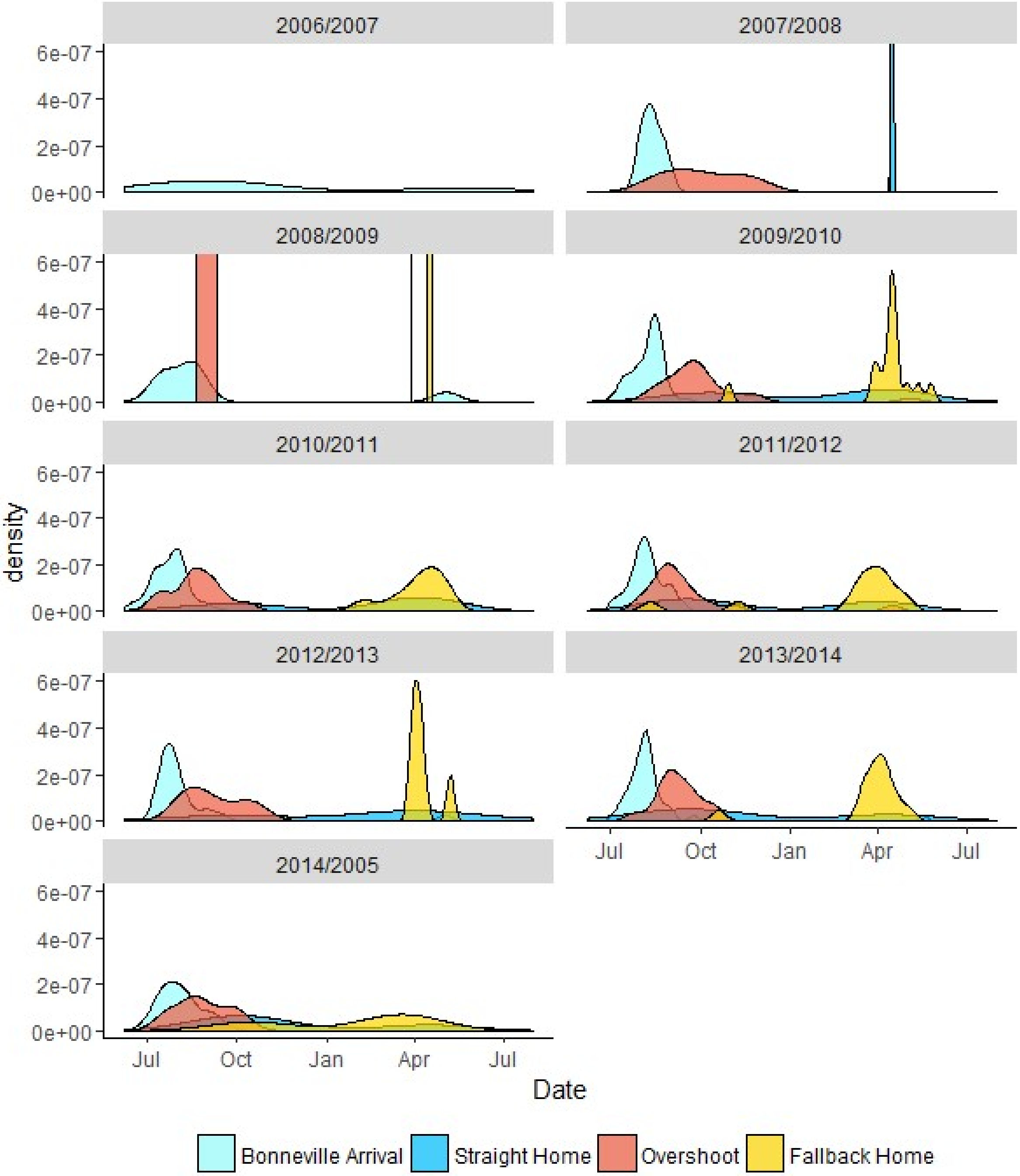

FIGURE B.13.—Density plots of run timing of Entiat River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

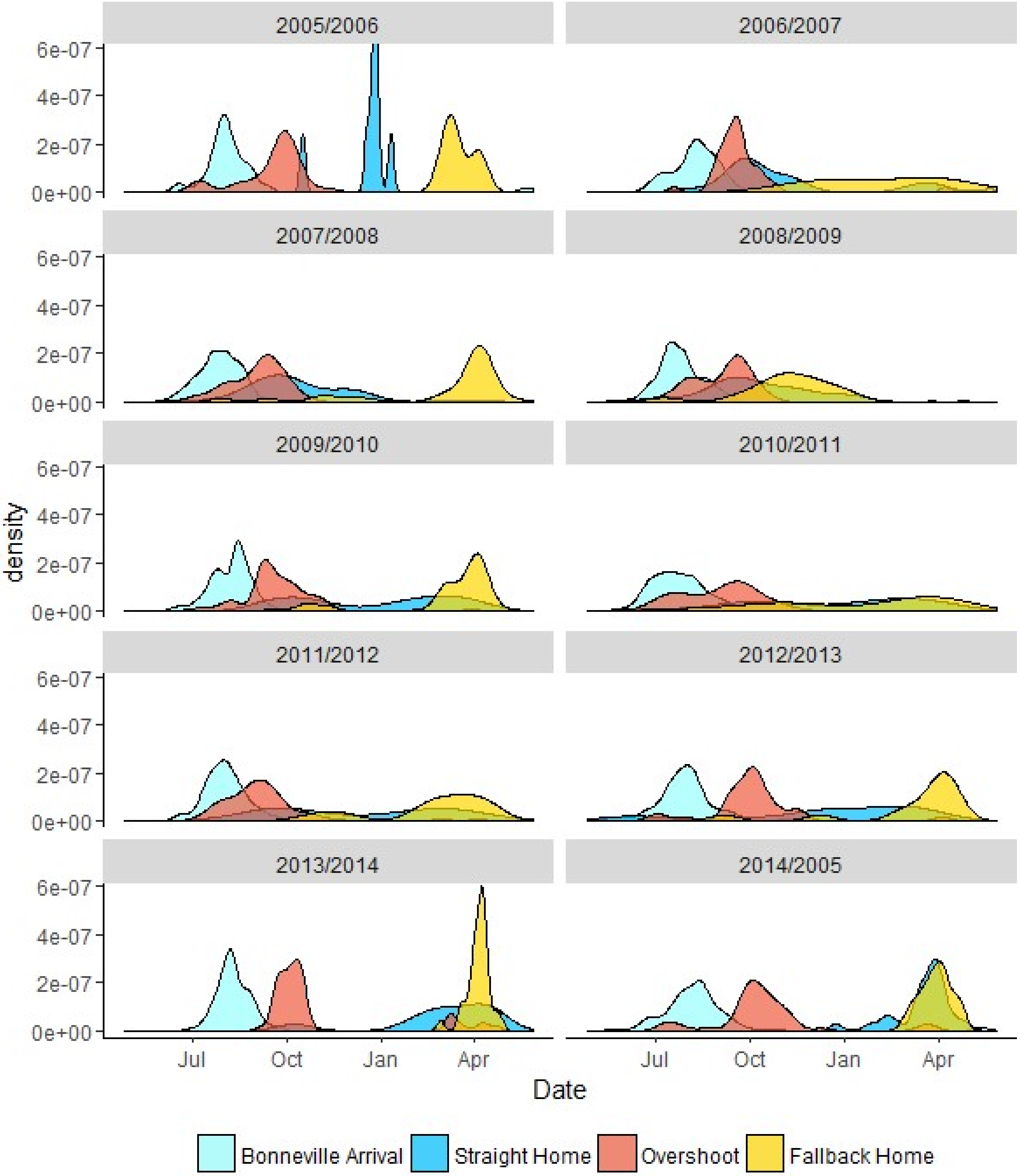

FIGURE B.14.—Density plots of run timing of Tucannon River hatchery steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

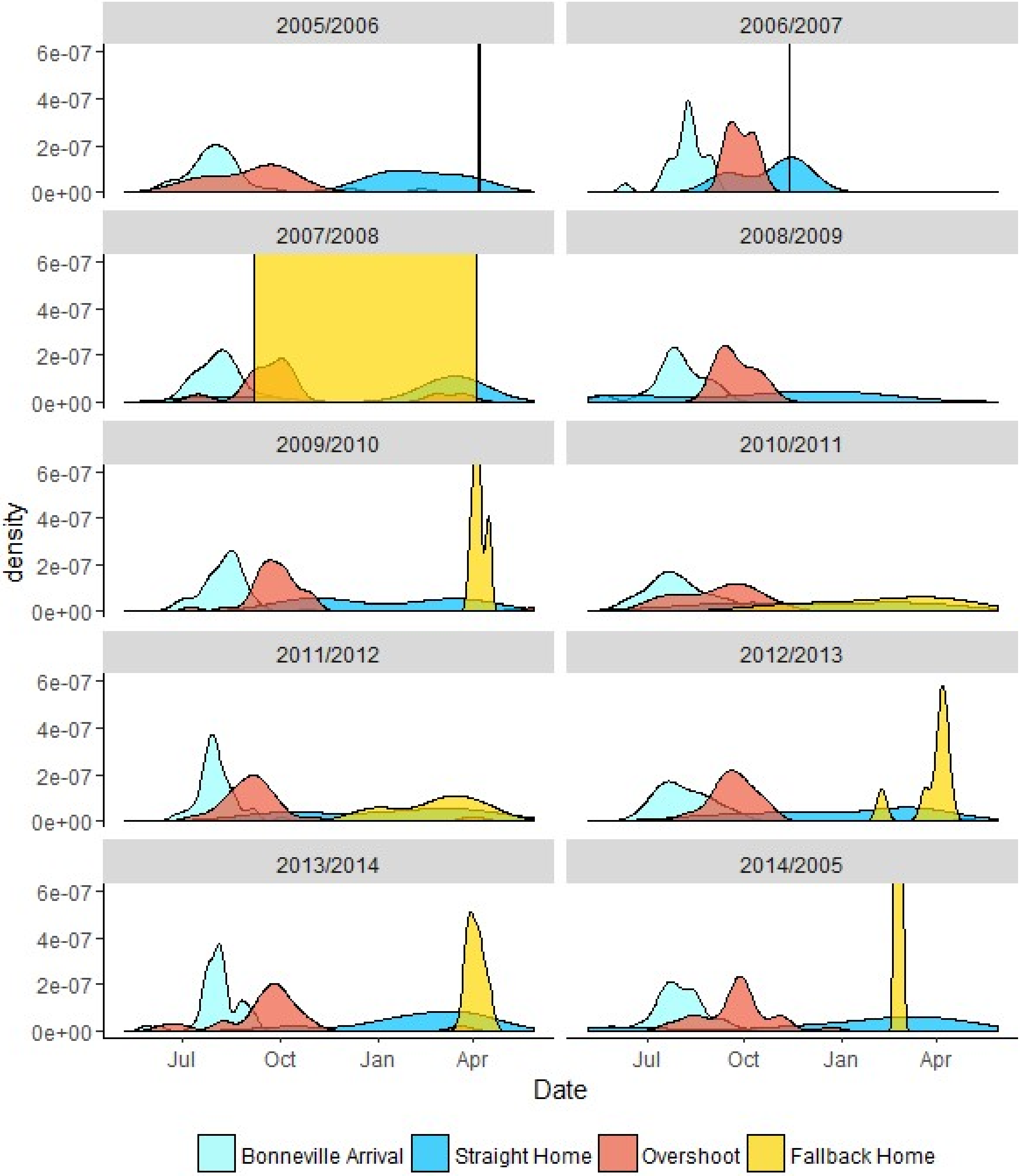

FIGURE B.15.—Density plots of run timing of Tucannon River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

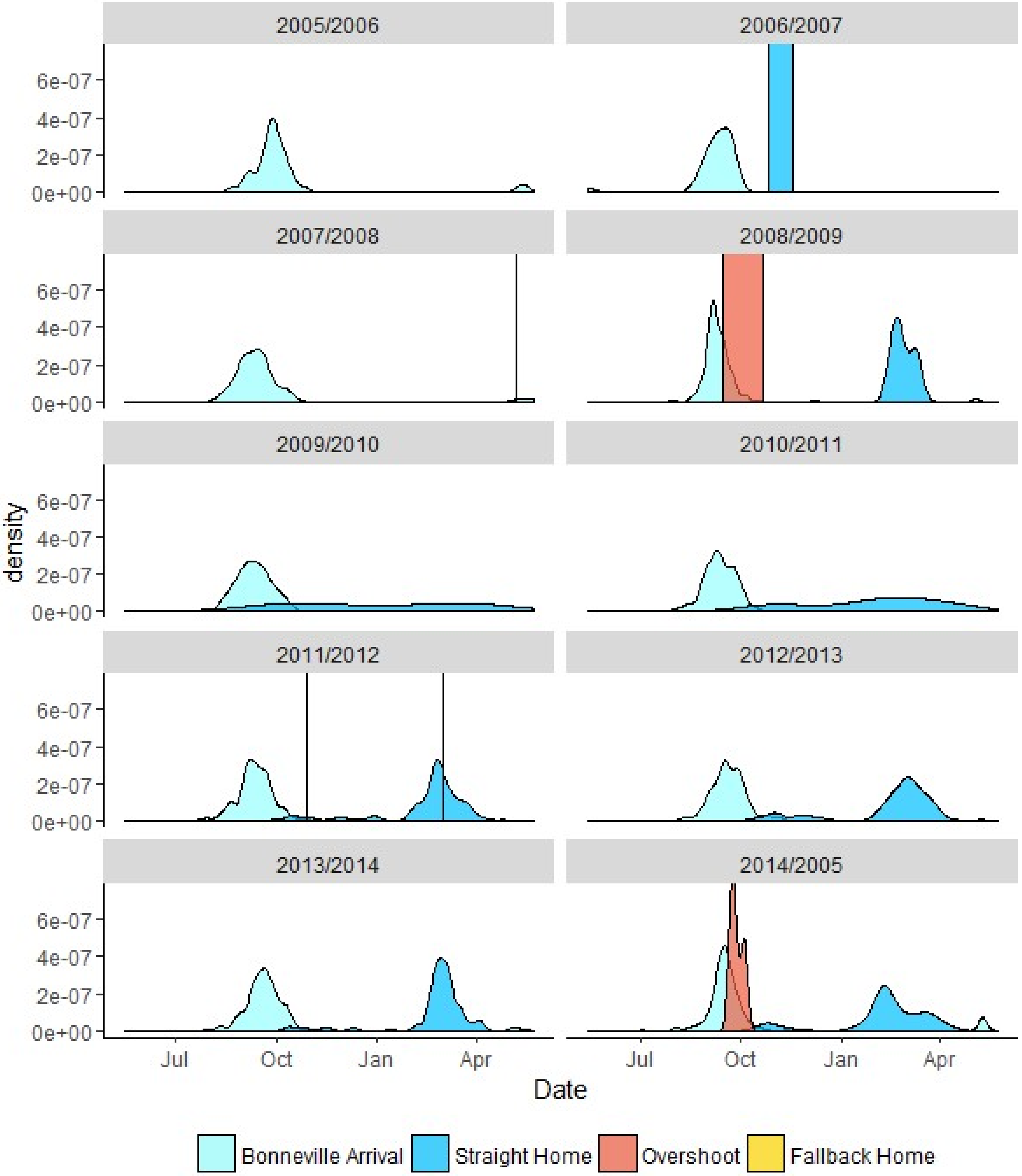

FIGURE B.16.—Density plots of run timing of Clearwater River hatchery steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

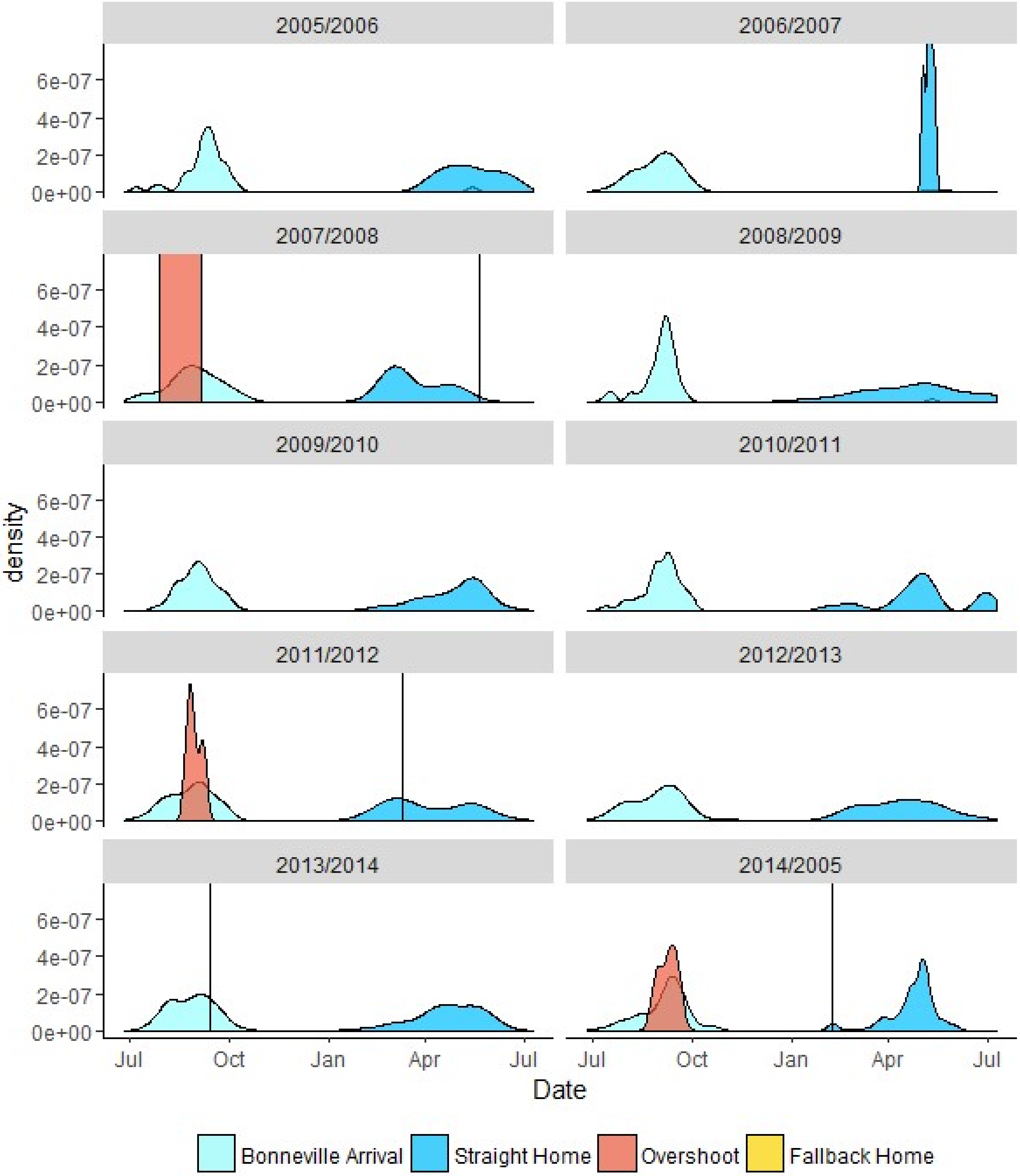

FIGURE B.17.—Density plots of run timing of Clearwater River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

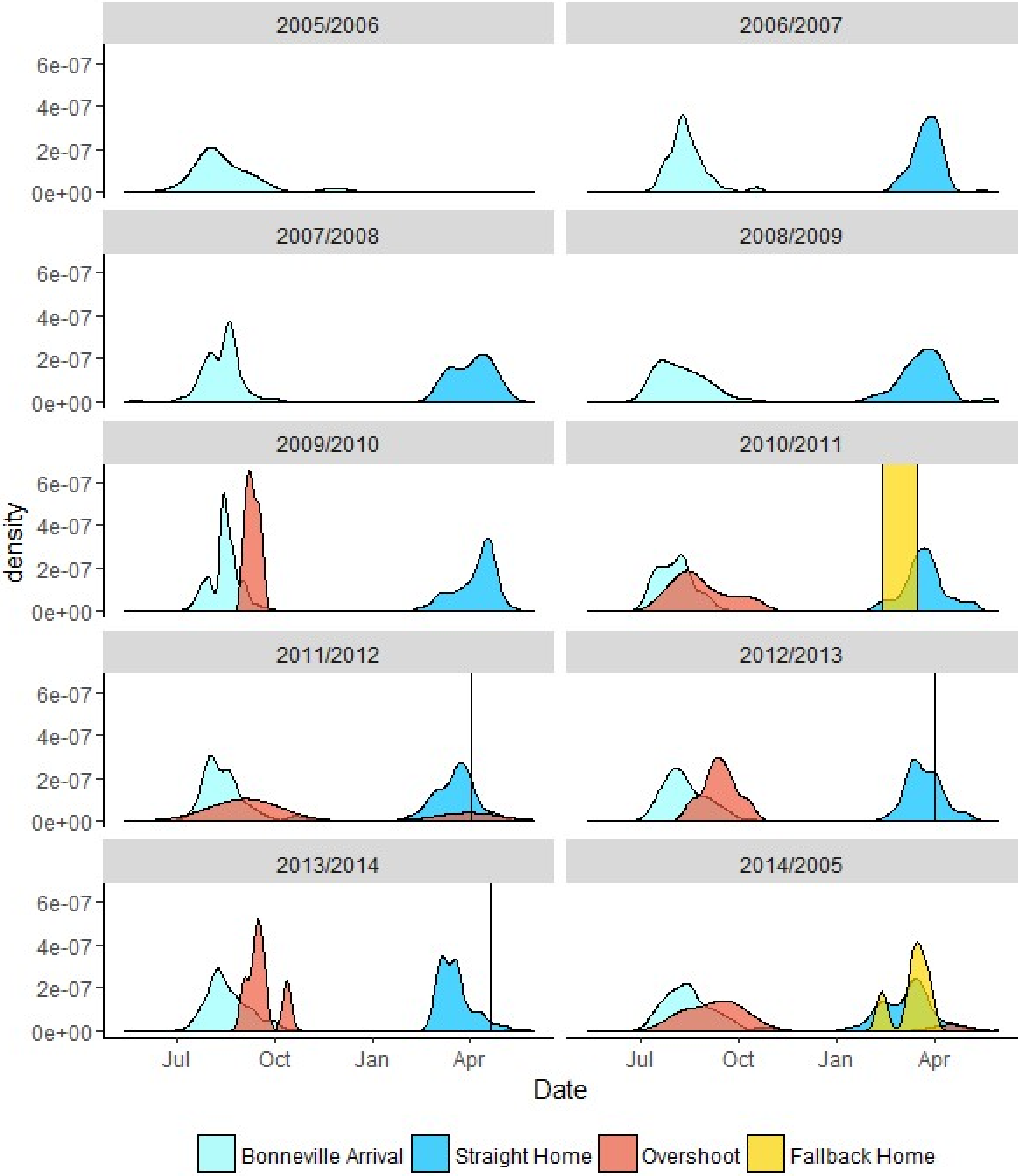

FIGURE B.18.—Density plots of run timing of Grande Ronde River hatchery steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

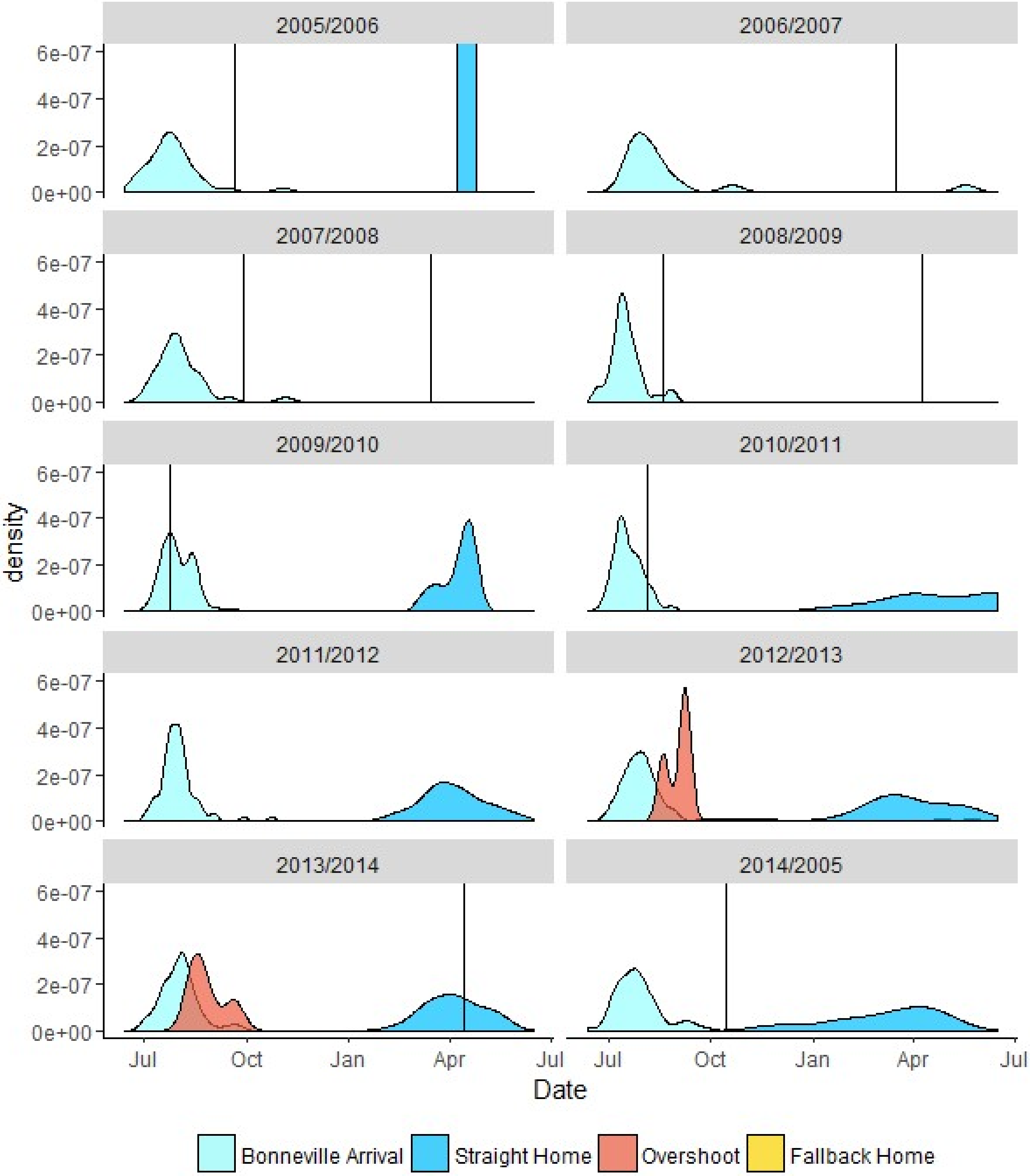

FIGURE B.19.—Density plots of run timing of Grande Ronde River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

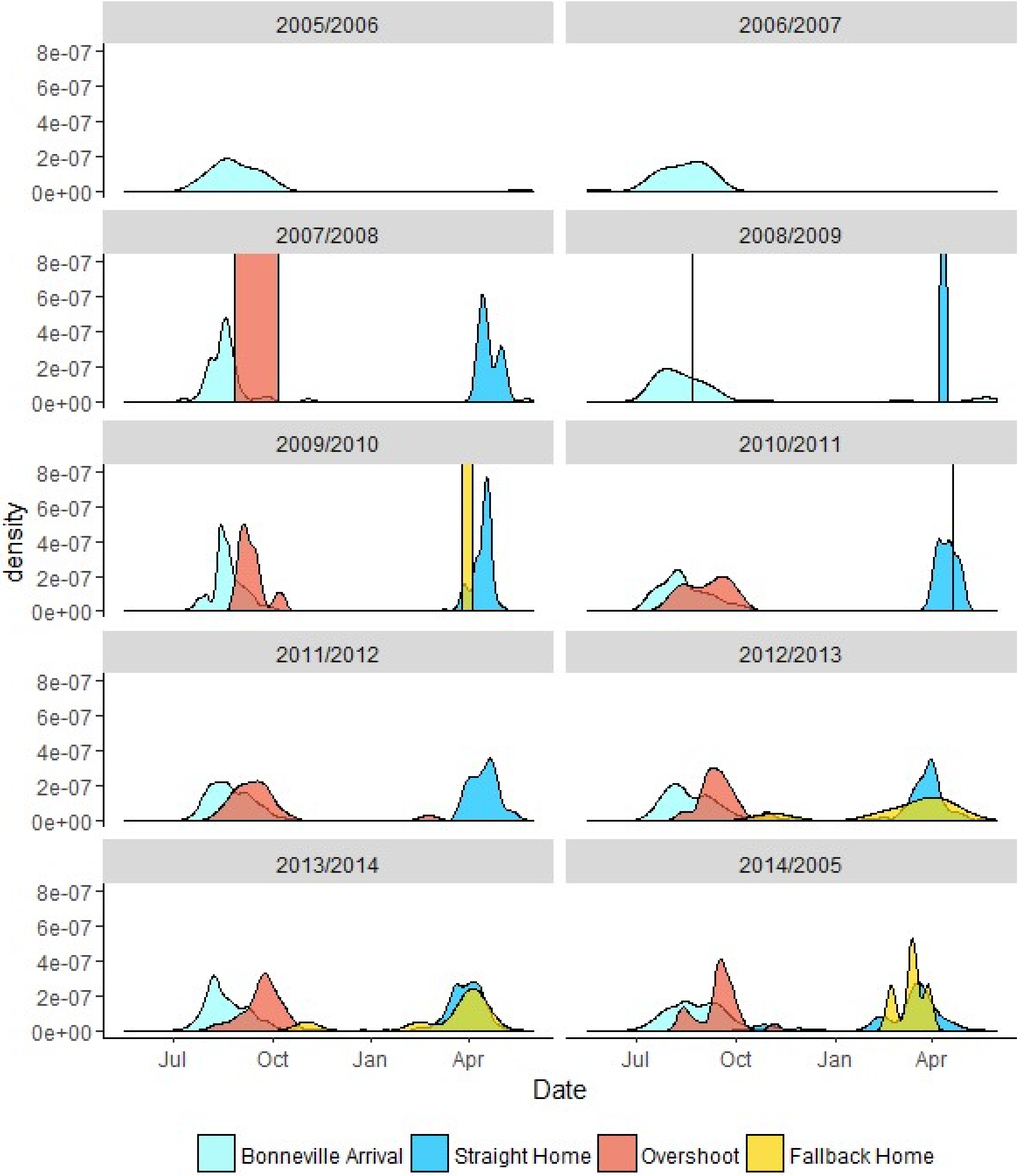

FIGURE B.20.—Density plots of run timing of Salmon River hatchery steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

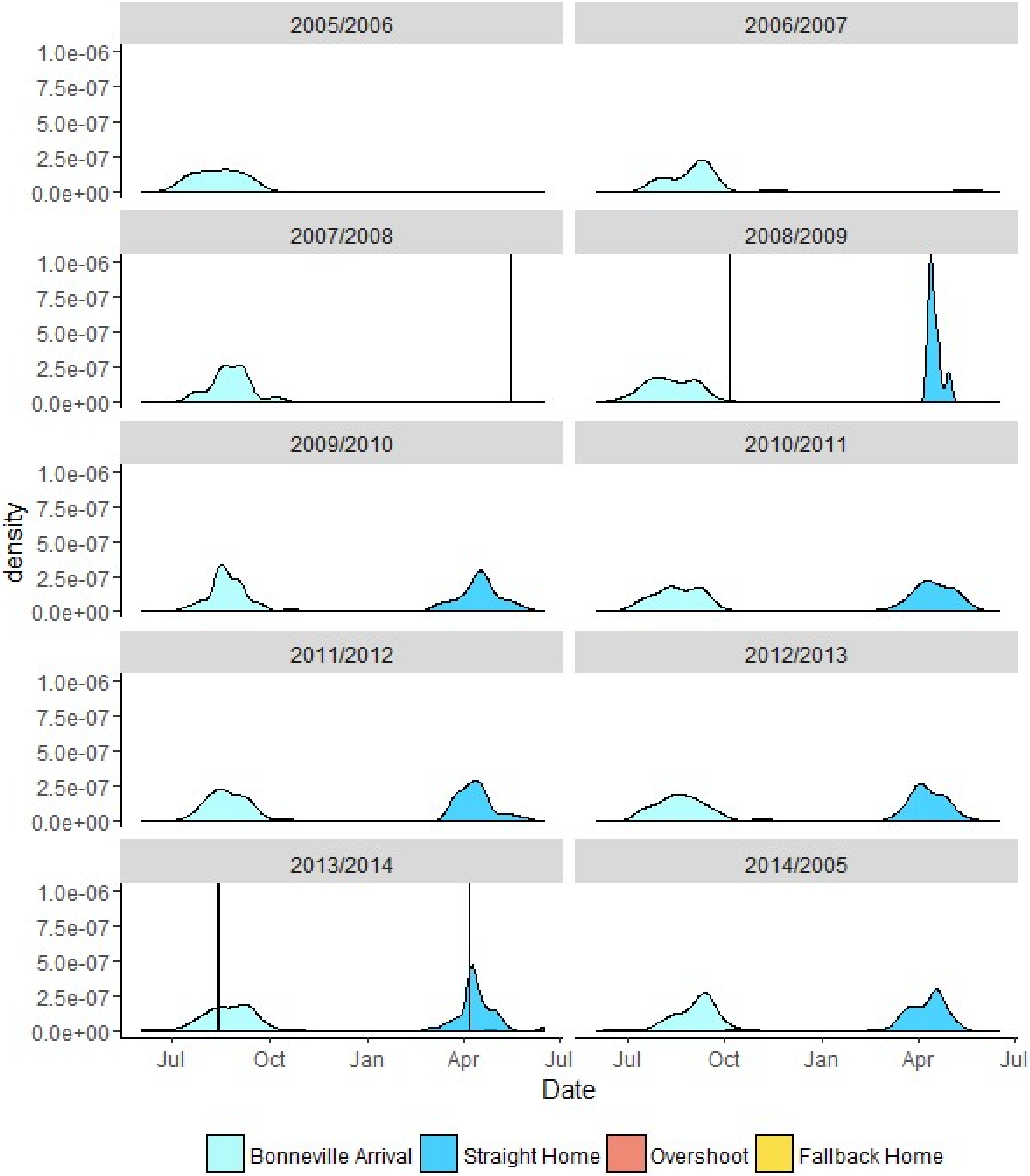

FIGURE B.21.—Density plots of run timing of Salmon River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

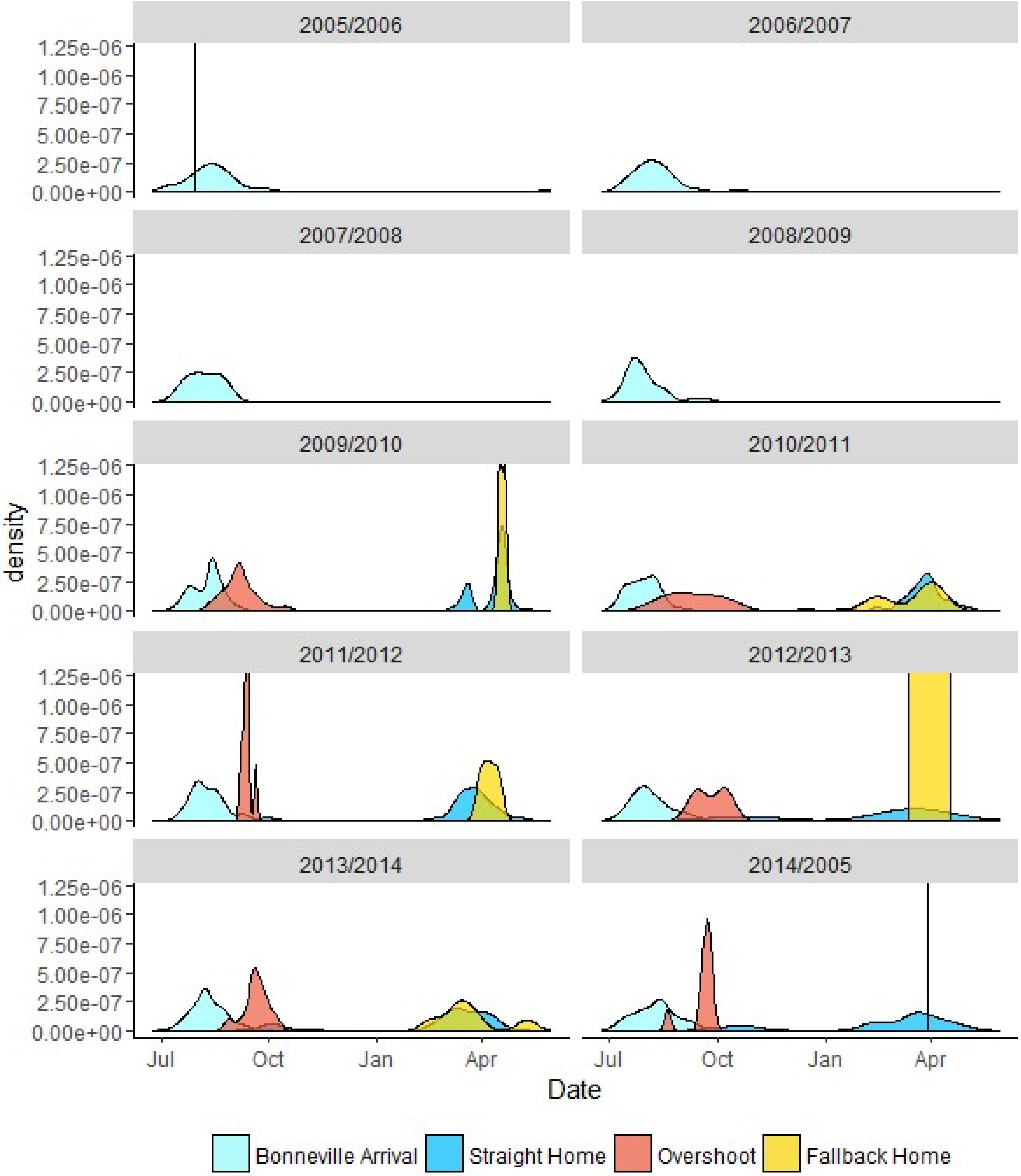

FIGURE B.22.—Density plots of run timing of Imnaha River hatchery steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

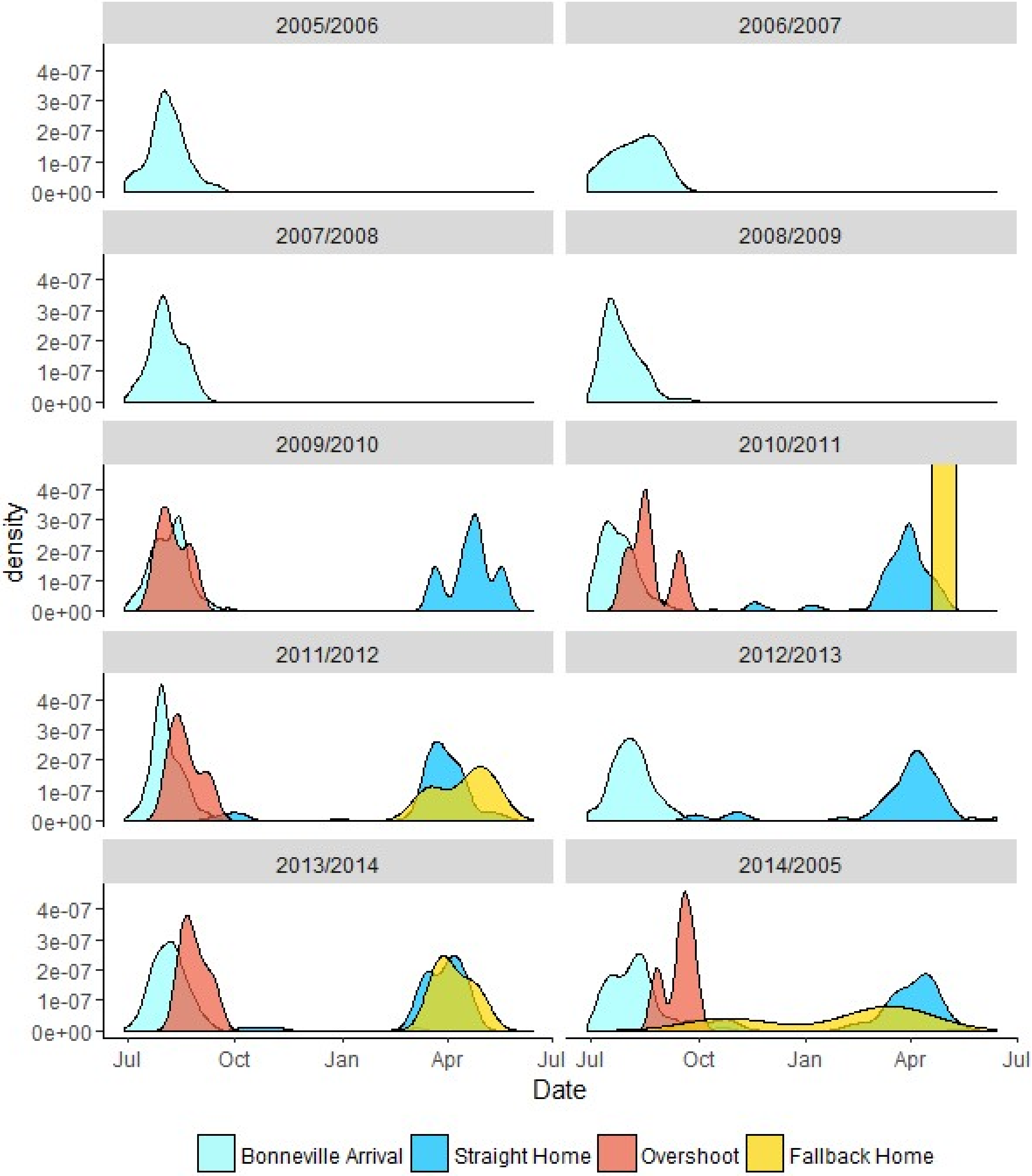

FIGURE B.23.—Density plots of run timing of Imnaha River wild steelhead. Timing is based on the first detection. Area under each curve is equal to 1.

APPENDIX C.—Total success rates

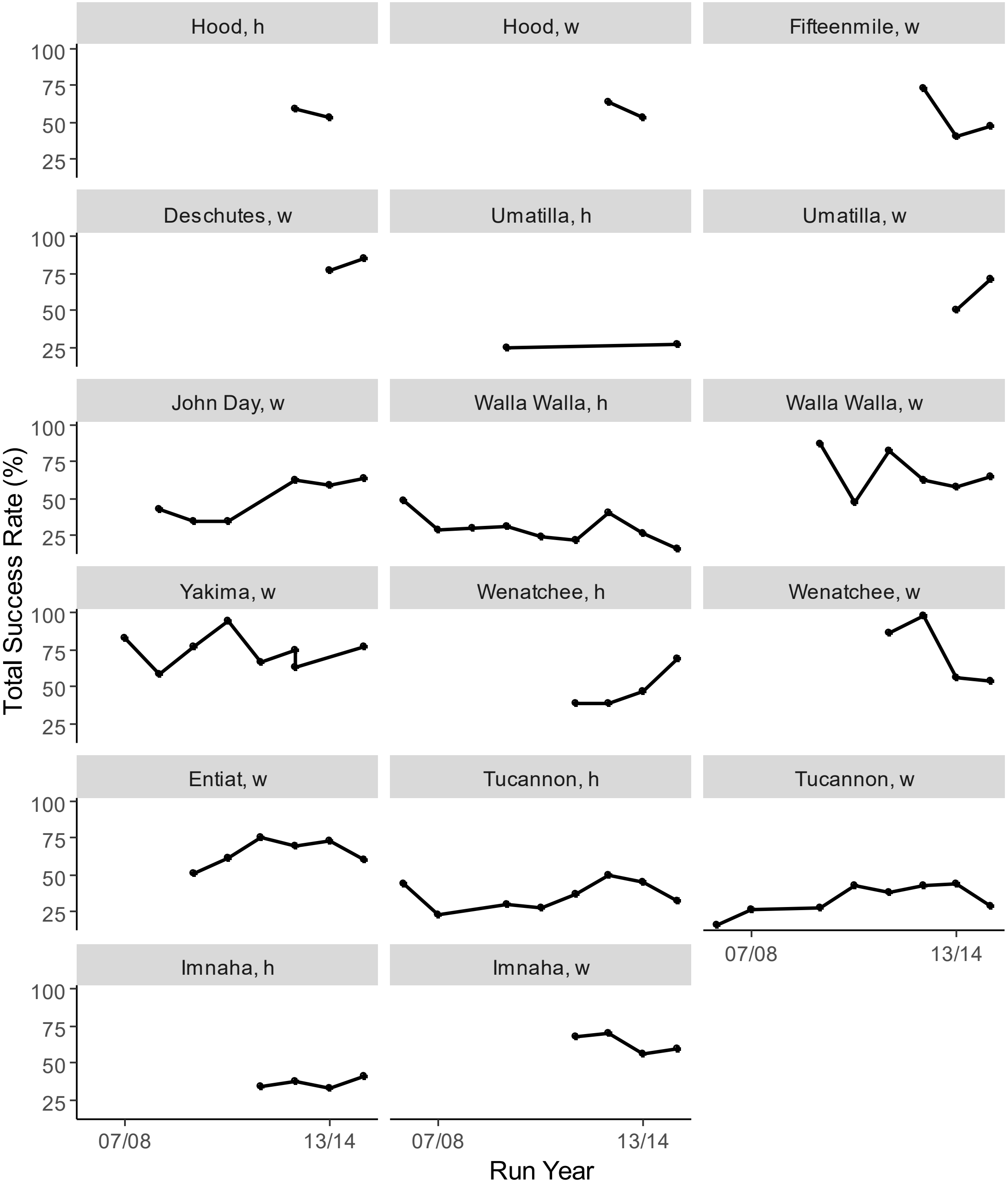

FIGURE C.1.—Annual total success rates (adjusted by detection efficiencies) of Columbia River basin steelhead. “w” indicates a wild population and “h” indicates a hatchery population.

TABLE C.1.—Total success rates (movement from Bonneville to the home tributary) for lower Columbia River steelhead. Parentheses contain ±2 standard errors. Years not estimated lacked sufficient numbers of fish or detection ability in the home tributary.

	Run Year									
Origin	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Hood										
hatchery	--	--	--	--	--	--	59.3% (±13.6%)	53.0% (±25.0%)	--	**56.2%**
wild	--	--	--	--	--	--	63.5% (±34.3%)	52.8% (±50.5%)	--	**58.2%**
Fifteenmile										
wild	--	--	--	--	--	--	73.1% (±28.2%)	40.6% (±17.0%)	47.4% (±15.9%)	**53.7%**
Deschutes										
wild	--	--	--	--	--	--	--	76.9% (±8.7%)	84.7% (±15.8%)	**80.8%**
John Day										
wild	--	--	43.3% (±6.2%)	35.0% (±5.1%)	34.7% (±5.6%)	--	62.4% (±16.1%)	58.9% (±10.4%)	63.4% (±10.4%)	**49.6%**
Umatilla										
hatchery	--	--	--	24.2% (±11.9%)	--	--	--	--	27.0% (±14.3%)	**25.6%**
wild	--	--	--	--	--	--	--	50.7% (±11.8%)	71.4% (±11.7%)	**61.1%**
Walla Walla										
hatchery	48.6% (±47.0%)	29.2% (±4.2%)	30.0% (±26.8%)	30.7% (±13.7%)	23.9% (±17.2%)	22.0% (±7.7%)	40.1% (±15.5%)	26.9% (±10.4%)	16.4% (±5.7%)	**29.8%**
wild	--	--	--	86.7% (±24.3%)	47.4% (±15.6%)	82.8% (±20.5%)	62.8% (±11.3%)	58.2% (±12.9%)	65.4% (±10.8%)	**67.2%**

TABLE C.2.—Total success rates (movement from Bonneville to the home tributary) for upper Columbia and Snake River steelhead. Parentheses contain ±2 standard errors. Success rates not estimated lacked sufficient numbers of fish or detection ability in the home tributary.

	Run Year									
Origin	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
					Upper Columbia					
Yakima										
wild	--	83.3% (±17.2%)	58.8% (±23.4%)	76.7% (±18.0%)	94.4% (±21.8%)	66.7% (±23.9%)	75.0% (±19.0%)	63.0% (±13.9%)	77.1% (±9.4%)	**74.4%**
Wenatchee										
hatchery	--	--	--	--	--	38.4% (±5.8%)	38.7% (±5.1%)	46.9% (±7.4%)	68.8% (±6.7%)	**48.2%**
wild	--	--	--	--	--	86.3% (±15.9%)	98.5% (±14.4%)	56.5% (±33.0%)	54.3% (±15.8%)	**73.9%**
Entiat										
wild	--	--	--	51.4 (±11.5%)	61.1% (±11.7%)	75.0% (±11.6%)	69.5% (±17.8%)	72.8% (±13.2%)	60.0% (±12.1%)	**67.7%**
					Snake					
Tucannon										
hatchery	44.6% (±26.4%)	23.2% (±3.6%)	--	30.0% (±4.0%)	27.9% (±6.4%)	37.6% (±8.2%)	50.1% (±11.0%)	45.1% (±9.7%)	32.9% (±8.5%)	**36.4%**
wild	16.7% (±14.9%)	26.4% (±14.2%)	--	28.0% (±12.4%)	42.8% (±26.2%)	38.5% (±13.7%)	43.4% (±13.2%)	44.6% (±26.4%)	29.1% (±12.6%)	**33.7%**
Imnaha										
hatchery	--	--	--	--	--	34.0% (±4.7%)	37.7% (±7.5%)	32.8% (±2.0%)	41.0% (±4.8%)	**36.4%**
wild	--	--	--	--	--	67.7% (±7.8%)	70.8% (±10.7%)	56.2% (±10.2%)	59.7% (±8.5%)	**63.6%**

APPENDIX D.—Overshoot rates

TABLE D.1.—McNary Dam overshooting by steelhead from lower Columbia tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to McNary, ascending order. Parentheses contain ±2 standard errors.

	Run Year										
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Umatilla											
hatchery	45.0% (±32.8%)	0%	50.5% (±12.8%)	37.7% (±10.7%)	35.9% (±8.8%)	29.2% (±10.3%)	40.9% (±12.1%)	41.8% (±19.8%)	0% (±0%)	29.9% (±14.8%)	**31.1%**
wild	67.4% (±54.0%)	70.8% (±28.7%)	17.8% (±18.3%)	54.8% (±20.9%)	36.0% (±25.3%)	38.8% (±26.6%)	31.0% (±10.1%)	38.4% (±11.6%)	42.4% (±11.8%)	39.0% (±7.3%)	**43.6%**
John Day											
wild	53.6% (±12.0%)	55.2% (±9.0%)	60.3% (±9.1%)	45.4% (±6.2%)	61.1% (±5.2%)	52.5% (±5.9%)	36.4% (±5.6%)	53.2% (±8.0%)	60.7% (±6.0%)	54.3% (±6.3%)	**53.3%**
Deschutes											
wild	**--**	**--**	0%	0%	1.7% (±2.3%)	0.9% (±1.7%)	0.9% (1.8%)	0%	0.6% (±1.1%)	0%	**0.5%**
Fifteenmile											
wild	**--**	0%	--	16.7% (±21.2%)	10.7% (±18.9%)	7.7% (±5.5%)	3.1% (3.5%)	8.9% (±9.6%)	9.5% (±10.2%)	2.7% (±5.1%)	**7.4%**
Hood											
hatchery	0%	0%	1.0% (±1.9%)	0%	0%	0%	0%	0%	0.7% (±1.3%)	0%	**0.2%**
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**

TABLE D.2.—Ice Harbor Dam overshooting by steelhead from lower Columbia tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Ice Harbor, ascending order. Parentheses contain ±2 standard errors.

	Run Year										
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Walla Walla											
hatchery	33.7% (±16.3%)	33.3% (±15.4%)	40.5% (±19.5%)	61.1% (±5.6%)	58.2% (±4.8%)	59.4% (±6.5%)	60.2% (±6.0%)	46.8% (±9.0%)	58.2% (±9.3%)	66.2% (±7.2%)	**51.8%**
wild	55.2% (±29.8%)	45.5% (±29.4%)	50.7% (±31.4%)	25.3% (±30.4%)	28.0% (±11.3%)	40.2% (±9.9%)	40.3% (±9.0%)	32.7% (±9.6%)	23.0% (±11.0%)	29.5% (±10.4%)	**37.0%**
Umatilla											
hatchery	0%	0%	5.1% (±5.6%)	7.6% (±5.8%)	0.9% (±1.7%)	4.0% (±4.4%)	9.4% (±7.2%)	0%	0%	5.4% (±7.3%)	**3.2%**
wild	67.4% (±54.0%)	0%	6.0% (±11.3%)	4.6% (±8.8%)	0%	15.4% (±19.7%)	3.7% (±4.1%)	7.4% (±6.2%)	7.3% (±6.2%)	12.2% (±4.9%)	**12.4%**
John Day											
wild	19.3% (±9.5%)	12.4% (±5.9%)	8.0% (±5.0%)	18.8% (±4.9%)	18.2% (±4.1%)	15.4% (±4.2%)	9.8% (±3.5%)	4.0% (±3.1%)	7.7% (±3.3%)	14.1% (±4.4%)	**12.8%**
Deschutes											
wild	--	--	0%	0%	0.9% (±1.7%)	0%	0%	0%	0.6% (±1.1%)	0%	**0.2%**
Fifteenmile											
wild	--	0%	--	0%	2.1% (±4.1%)	2.2% (±3.0%)	1.0% (±2.0%)	3.0% (±5.7%)	0%	2.6% (±5.1%)	**1.4%**
Hood											
hatchery	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**

TABLE D.3.—Ice Harbor Dam overshooting by steelhead from upper Columbia tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Ice Harbor, ascending order. Parentheses contain ±2 standard errors.

					Run Year						
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Yakima											
wild	0%	0%	0%	0%	6.1% (±8.2%)	0%	2.5% (±4.9%)	0%	0%	1.3% (±2.5%)	**1.0%**
Wenatchee											
hatchery	0%	0%	0%	0%	0%	0%	0%	0%	0%	0.5% (±1.0%)	**0.1%**
wild	--	--	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
Entiat											
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**

TABLE D.4.—Lower Granite Dam overshooting by steelhead from lower Columbia and Snake River tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Lower Granite, ascending order. Parentheses contain ±2 standard errors.

	Run Year										
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Tucannon											
hatchery	48.3% (±12.6%)	44.6% (±11.5%)	46.1% (±4.2%)	41.6% (±4.7%)	48.6% (±3.9%)	52.7% (±6.0%)	40.0% (±7.5%)	35.6% (±10.1%)	40.7% (±8.8%)	36.6% (±7.8%)	**43.5%**
wild	31.4% (±15.4%)	56.3% (±21.2%)	28.2% (±14.1%)	31.3% (±22.7%)	54.1% (±13.8%)	37.8% (±14.2%)	43.3% (±13.6%)	47.3% (±13.2%)	45.7% (±14.8%)	55.1% (±12.6%)	**43.0%**
Walla Walla											
hatchery	6.1% (±8.1%)	5.8% (±7.8%)	8.0% (±10.6%)	24.0% (±4.8%)	26.5% (±4.2%)	23.4% (±5.6%)	20.8% (±4.9%)	15.0% (±6.4%)	23.5% (±7.9%)	26.4% (±6.7%)	**17.9%**
wild	27.3% (±26.3%)	28.4% (±27.5%)	30.0% (±28.4%)	12.5% (±22.9%)	11.5% (±8.0%)	15.8% (±7.3%)	14.0% (±6.3%)	14.1% (±7.1%)	7.1% (±6.7%)	12.0% (±7.4%)	**17.3%**
Umatilla											
hatchery	0%	0%	1.7% (±3.2%)	5.0% (±4.8%)	0.9% (±1.7%)	1.3% (±2.6%)	0%	0%	0%	2.7% (±5.2%)	**1.2%**
wild	66.7% (±53.3%)	0%	5.9% (±11.2%)	0%	0%	7.7% (±14.5%)	2.5% (±3.4%)	0%	1.5% (±2.8%)	4.6% (±3.1%)	**8.9%**
John Day											
wild	13.2% (±8.1%)	6.9% (±4.6%)	0%	7.3% (±3.2%)	9.5% (±3.1%)	7.5% (±3.1%)	7.3% (±3.0%)	3.3% (±2.9%)	2.3% (±1.8%)	4.1% (±2.5%)	**6.1%**
Deschutes											
wild	--	--	0%	0%	0.8% (±1.7%)	0%	0%	0%	0.6% (±1.1%)	0%	**0.2%**

TABLE D.5.—Lower Granite Dam overshooting by steelhead from Columbia tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Lower Granite, ascending order. Parentheses contain ±2 standard errors.

	Run Year										
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
					Lower Columbia						
Fifteenmile											
wild	--	0%	--	0%	0% (±1.7%)	1.1%	0%	2.9%	0% (±1.1%)	0%	**0.5%**
Hood											
hatchery	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
wild	--	--	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
					Upper Columbia						
Yakima											
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	1.3% (±2.5%)	**0.1%**
Wenatchee											
hatchery	0%	0%	0%	0%	0%	0%	0%	0%	0%	0.5% (±1.0%)	**0.1%**
wild	--	--	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
Entiat											
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**

TABLE D.6.—Priest Rapids Dam overshooting by steelhead from Columbia tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Priest Rapids, ascending order. Parentheses contain ±2 standard errors.

	Run Year										
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Yakima											
wild	21.1% (±21.4%)	8.4% (±15.7%)	5.6% (±10.6%)	17.7% (±18.2%)	18.3% (±13.2%)	17.6% (±15.7%)	10.1% (±9.4%)	5.0% (±9.6%)	15.2% (±10.4%)	12.8% (±7.4%)	**13.2%**
Walla Walla											
hatchery	0%	5.6% (±7.5%)	0%	2.3% (±1.7%)	3.1% (±1.7%)	2.7% (±2.1%)	0%	0%	6.3% (±4.5%)	1.2% (±1.6%)	**2.1%**
wild	9.6% (±17.9%)	0%	10.0% (±18.6%)	0%	1.7% (±3.2%)	6.4% (±4.9%)	0.9% (±1.7%)	0%	0%	1.3% (±2.6%)	**3.0%**
Umatilla											
hatchery	0%	0%	3.3% (±4.5%)	0%	0%	0%	0%	0%	0%	0%	**0.3%**
wild	0%	0%	0%	4.6% (±8.7%)	0%	7.8% (±14.6%)	0%	0%	0%	1.2% (±1.6%)	**1.3%**
John Day											
wild	0%	0%	1.8% (±2.4%)	0.4% (±0.8%)	0.9% (±1.0%)	2.5% (±1.8%)	0%	1.3% (±1.8%)	1.1% (±1.3%)	0.8% (±1.1%)	**0.9%**
Deschutes											
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
Fifteenmile											
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
Hood											
hatchery	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**

TABLE D.7.—Priest Rapids Dam overshooting by steelhead from Snake River tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Priest Rapids, ascending order. Parentheses contain ±2 standard errors.

	Run Year										
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Tucannon											
hatchery	0%	3.6% (±4.0%)	2.7% (±1.4%)	0.9% (±0.9%)	2.2% (±1.2%)	1.1% (±1.3%)	0%	1.2% (±2.3%)	0%	0.7% (±1.3%)	**1.2%**
wild	0%	0%	5.1% (±6.9%)	0%	2.0% (±3.9%)	4.5% (±6.1%)	0%	1.8% (±3.6%)	9.1% (±8.5%)	3.3% (±4.5%)	**2.6%**
Clearwater											
hatchery	0%	0%	0%	1.1% (±1.6%)	0%	0%	0.1% (±0.3%)	0%	0%	0.8% (±0.9%)	**0.2%**
wild	0%	0%	4.0% (±5.4%)	0%	0%	0%	2.2% (±2.4%)	0%	1.1% (±2.2%)	1.0% (±1.2%)	**0.8%**
Grande Ronde											
hatchery	0%	0%	0%	0%	0.3% (±0.3%)	1.0% (±0.8%)	0.6% (±0.6%)	1.7% (±1.2%)	1.3% (±1.1%)	1.7% (±1.1%)	**0.7%**
wild	3.0% (±5.8%)	0%	2.8% (±5.4%)	2.7% (±5.2%)	1.5% (±3.0%)	1.2% (±2.4%)	0%	4.4% (±4.8%)	6.3% (±6.0%)	1.6% (±3.1%)	**2.4%**
Salmon											
hatchery	0%	0%	2.9% (±4.0%)	1.2% (±2.4%)	1.0% (±0.5%)	0.9% (±0.5%)	1.2% (±0.6%)	2.8% (±1.0%)	3.0% (±1.1%)	2.0% (±0.8%)	**1.5%**
wild	0%	0%	0%	2.0% (±4.0%)	0%	0%	0%	0%	1.7% (±2.3%)	0%	**0.4%**
Imnaha											
hatchery	3.3% (±6.4%)	0%	0%	0%	2.7% (±1.2%)	1.1% (±1.0%)	1.8% (±1.3%)	3.7% (±2.9%)	3.5% (±2.0%)	2.5% (±1.5%)	**1.9%**
wild	0%	0%	0%	0%	2.0% (±2.2%)	3.3% (±3.1%)	2.8% (±2.7%)	0%	5.3% (±4.5%)	3.1% (±3.0%)	**1.6%**

TABLE D.8.—Rock Island Dam overshooting by steelhead from Columbia River tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Rock Island, ascending order. Parentheses contain ±2 standard errors.

	Run Year										
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Yakima											
wild	8.5% (±16.1%)	0%	0%	7.2% (±13.7%)	9.3% (±10.0%)	4.5% (±8.6%)	2.7% (±5.2%)	0%	12.2% (±10.1%)	6.4% (±7.1%)	**5.1%**
Walla Walla											
hatchery	0%	3.3% (±6.3%)	0%	1.6% (±1.6%)	1.0% (±1.0%)	0.9% (±1.3%)	0%	0%	2.0% (±2.8%)	1.0% (±1.9%)	**1.0%**
wild	11.6% (±21.7%)	0%	10.9% (±20.2%)	0% (±0%)	1.7% (±3.3%)	4.3% (±4.2%)	0%	0%	0%	2.2% (±4.3%)	**3.1%**
Umatilla											
hatchery	0%	0%	1.8% (±3.5%)	0%	0%	0%	0%	0%	0%	0%	**0.2%**
wild	0%	0%	0%	0%	0%	7.9% (±14.9%)	0%	0%	0%	0%	**0.8%**
John Day											
wild	0%	0%	1.9% (±2.6%)	0%	0.3% (±0.6%)	0.4% (±0.7%)	0%	0.9% (±1.8%)	0%	0.7% (±1.3%)	**0.4%**
Deschutes											
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
Fifteenmile											
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
Hood											
hatchery	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**

TABLE D.9.—Rock Island Dam overshooting by steelhead from Snake River tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Rock Island, ascending order. Parentheses contain ±2 standard errors.

	Run Year										
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Tucannon											
hatchery	0%	0%	1.0% (±0.9%)	0.6% (±0.8%)	1.1% (±0.8%)	0.8% (±1.1%)	0%	0%	0%	0%	**0.3%**
wild	0%	0%	5.6% (±7.5%)	0%	0%	0%	0%	2.5% (±4.8%)	5.1% (±6.9%)	2.8% (±5.4%)	**1.6%**
Clearwater											
hatchery	0%	0%	0%	1.4% (±1.9%)	0%	0%	0%	0%	0%	0.8% (±1.2%)	**0.2%**
wild	0%	0%	0%	0%	0%	0%	1.5% (±2.1%)	0%	1.3% (±2.5%)	1.2% (±1.6%)	**0.4%**
Grande Ronde											
hatchery	0%	0%	0%	0%	0.1% (±0.2%)	0%	0.5% (±0.6%)	1.3% (±1.3%)	0.6% (±0.8%)	1.4% (±1.3%)	**0.4%**
wild	0%	0%	3.0% (±5.8%)	0%	1.6% (±3.1%)	0%	0%	4.0% (±5.4%)	3.6% (±4.9%)	0%	**1.2%**
Salmon											
hatchery	0%	0%	3.2% (±4.4%)	1.5% (±2.9%)	0.4% (±0.3%)	0.7% (±0.5%)	0.8% (±0.5%)	1.4% (±0.9%)	2.0% (±0.9%)	2.0% (±1.1%)	**1.2%**
wild	0%	0%	0%	0%	0%	0%	0%	0%	1.0% (±1.9%)	0%	**0.1%**
Imnaha											
hatchery	0%	0%	0%	0%	1.4% (±0.9%)	0.5% (±0.6%)	1.1% (±1.1%)	0.8% (±1.6%)	1.7% (±1.4%)	1.2% (±1.4%)	**0.7%**
wild	0%	0%	0%	0%	0.7% (±1.3%)	1.7% (±2.3%)	3.0% (±2.9%)	0%	4.8% (±4.6%)	3.8% (±4.3%)	**1.4%**

TABLE D.10.—Rocky Reach Dam overshooting by steelhead from Columbia River tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Rocky Reach, ascending order. Parentheses contain ±2 standard errors.

	Run Year									
Origin	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Wenatchee										
hatchery	57.5% (±5.0%)	50.3% (±5.3%)	62.2% (±4.4%)	56.3% (±3.4%)	63.9% (±4.1%)	54.7% (±4.9%)	52.4% (±5.2%)	27.9% (±6.5%)	12.1% (±4.6%)	**48.6%**
wild	--	0%	12.5% (±22.9%)	13.1% (±8.0%)	8.0% (±6.2%)	3.8% (±5.2%)	6.2% (±8.3%)	6.5% (±8.7%)	7.7% (±8.4%)	**7.2%**
Yakima										
wild	0%	0%	5.9% (±11.2%)	6.1% (±8.2%)	4.4% (±8.4%)	0%	0%	4.4% (±5.9%)	2.6% (±3.5%)	**2.6%**
Walla Walla										
hatchery	0%	0%	0.3% (±0.7%)	0.7% (±0.8%)	0.9% (±1.2%)	0%	0%	0.9% (±1.8%)	0%	**0.3%**
wild	0%	0%	0%	1.6% (±3.2%)	3.2% (±3.5%)	0%	0%	0%	0%	**0.5%**
Umatilla										
hatchery	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
John Day										
wild	0%	0%	0%	0%	0%	0%	0%	0%	0.4% (±0.8%)	**0.0%**
Deschutes										
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
Fifteenmile										
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
Hood										
hatchery	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**

TABLE D.11.—Rocky Reach Dam overshooting by steelhead from Snake River tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Rocky Reach, ascending order. Parentheses contain ±2 standard errors.

Origin	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Tucannon										
hatchery	0%	0.7% (±0.7%)	0.2% (±0.5%)	0.8% (±0.7%)	0.4% (±0.7%)	0%	0%	0%	0%	**0.2%**
wild	0%	5.1% (±6.9%)	0%	0%	0%	0%	1.8% (±3.6%)	4.6% (±6.2%)	0%	**1.3%**
Clearwater										
hatchery	0%	0%	0.6% (±1.1%)	0%	0%	0%	0%	0%	0.8% (±0.9%)	**0.1%**
wild	0%	0%	0%	0%	0%	0%	0%	0%	0.3% (±0.7%)	**0.0%**
Grande Ronde										
hatchery	0%	0%	0%	0.1% (±0.2%)	0%	0.5% (±0.5%)	0.2% (±0.5%)	0.3% (±0.5%)	0.5% (±0.6%)	**0.2%**
wild	0%	2.8% (±5.4%)	0%	1.5% (±3.0%)	0%	0%	1.5% (±2.9%)	3.2% (±4.4%)	0%	**1.0%**
Salmon										
hatchery	0%	0%	1.2% (±2.3%)	0.1% (±0.2%)	0.6% (±0.4%)	0.5% (±0.4%)	1.4% (±0.7%)	1.5% (±0.8%)	0.9% (±0.5%)	**0.7%**
wild	0%	0%	0%	0%	0%	0%	0%	0.9% (±1.7%)	0%	**0.1%**
Imnaha										
hatchery	0%	0%	0%	1.1% (±0.8%)	0.2% (±0.4%)	0.8% (±0.9%)	0%	1.8% (±1.4%)	1.2% (±1.1%)	**0.6%**
wild	0%	0%	0%	0.7% (±1.3%)	1.6% (±2.2%)	1.4% (±2.0%)	0%	0%	0.8% (±1.5%)	**0.5%**

TABLE D.12.—Wells Dam overshooting by steelhead from Columbia River tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Wells, ascending order. Parentheses contain ±2 standard errors.

	Run Year										
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Entiat											
wild	--	0%	37.5% (±33.5%)	26.3% (±31.6%)	36.0% (±10.9%)	18.9% (±8.9%)	32.7% (±12.4%)	38.5% (±18.7%)	35.4% (±14.8%)	36.4% (±11.6%)	**29.1%**
Wenatchee											
hatchery	29.9% (±4.4%)	33.4% (±4.6%)	34.3% (±5.1%)	38.6% (±5.9%)	44.7% (±3.4%)	39.0% (±4.2%)	34.6% (±4.5%)	37.2% (±4.8%)	24.3% (±6.5%)	8.9% (±4.1%)	**32.5%**
wild	--	--	0%	0%	11.6% (±7.6%)	2.7% (±3.6%)	1.9% (±3.7%)	0%	3.3% (±6.5%)	5.1% (±6.9%)	**3.1%**
Yakima											
wild	6.7% (±12.6%)	0%	0%	0%	3.0% (±5.8%)	0%	0%	0%	4.5% (±6.1%)	1.3% (±2.5%)	**1.5%**
Walla Walla											
hatchery	0%	0%	0%	0%	0.5% (±0.7%)	0%	0%	0%	0.9% (±1.8%)	0%	**0.1%**
wild	0%	0%	0%	0%	1.6% (±3.2%)	1.1% (±2.1%)	0%	0%	0%	0%	**0.3%**
John Day											
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0.4% (±0.8%)	**0.0%**
Deschutes											
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
Fifteenmile											
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
Hood											
hatchery	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**

TABLE D.13.—Wells Dam overshooting by steelhead from Snake River tributaries. Overshoot percentages are out of the count in the Bonneville fishway. Overshoot rates are adjusted by detection probabilities. Organized by distance to Wells, ascending order. Parentheses contain ±2 standard errors.

	Run Year										
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Tucannon											
hatchery	0%	0%	0.5% (±0.6%)	0.2% (±0.5%)	0.5% (±0.5%)	0%	0%	0%	0%	0%	**0.1%**
wild	0%	0%	5.1% (±6.9%)	0%	0%	0%	0%	1.8% (±3.5%)	4.7% (±6.4%)	0%	**1.2%**
Clearwater											
hatchery	0%	0%	0%	0.6% (±1.2%)	0%	0%	0%	0%	0%	0.8% (±0.9%)	**0.1%**
wild	0%	0%	0%	0%	0%	0%	0%	0%	0%	0.3% (±0.7%)	**0.0%**
Grande Ronde											
hatchery	0%	0%	0%	0%	0%	0%	0.5% (±0.5%)	0%	0.3% (±0.5%)	0.5% (±0.6%)	**0.1%**
wild	0%	0%	0%	0%	0%	0%	0%	1.4% (±2.8%)	3.3% (±4.5%)	0%	**0.5%**
Salmon											
hatchery	0%	0%	0%	1.3% (±2.5%)	0% (±0%)	0.3% (±0.3%)	0.4% (±0.3%)	0.8% (±0.6%)	1.5% (±0.8%)	0.7% (±0.5%)	**0.5%**
wild	0%	0%	0%	0%	0%	0%	0%	0%	0.9% (±1.7%)	0%	**0.1%**
Imnaha											
hatchery	0%	0%	0%	0%	1.0% (±0.7%)	0%	0.5% (±0.7%)	0.6% (±1.2%)	1.8% (±1.5%)	1.0% (±1.0%)	**0.5%**
wild	0%	0%	0%	0%	0%	0.8% (±1.6%)	1.4% (±1.9%)	0%	0%	0.8% (±1.5%)	**0.3%**

APPENDIX E.—Conditional overshooting rates

TABLE E.1.—Conditional overshooting rates for John Day wild steelhead. Conditional overshooting rates are calculated as the proportion of fish that overshoot the next upstream dam with adult detectors out of the number seen at the previous dam with adult detectors. Rates are adjusted by detection efficiencies at the upstream dam. Parentheses contain ± 2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
BON → MCN	53.6% (±12.0%)	55.2% (±9.0%)	60.3% (±9.1%)	45.4% (±6.2%)	61.1% (±5.2%)	52.5% (±5.9%)	36.4% (±5.6%)	53.2% (±8.0%)	60.7% (±6.0%)	54.3% (±6.3%)	**53.3%**
MCN → ICH	33.7% (±15.6%)	22.7% (±10.1%)	13.4% (±8.2%)	41.6% (±9.2%)	29.5% (±6.2%)	29.6% (±7.4%)	27.1% (±8.6%)	7.5% (±5.8%)	12.9% (±5.3%)	26.1% (±7.5%)	**24.4%**
ICH → LGR	69.2% (±25.1%)	55.5% (±26.6%)	0%	39.1% (±14.1%)	52.5% (±12.4%)	48.9% (±15.0%)	75.3% (±16.1%)	83.3% (±29.8%)	30.2% (±20.2%)	29.4% (±15.3%)	**48.3%**
MCN → PRA	0%	0%	2.9% (±4.0%)	0.9% (±1.7%)	1.4% (±1.6%)	4.8% (±3.5%)	0%	2.5% (±3.4%)	1.9% (±2.1%)	1.5% (±2.1%)	**1.6%**

TABLE E.2.—Conditional overshooting rates for Umatilla steelhead. Conditional overshooting rates are calculated as the proportion of fish that overshoot the next upstream dam with adult detectors out of the number seen at the previous dam with adult detectors. Rates are adjusted by detection efficiencies at the upstream dam. Parentheses contain ± 2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
					Hatchery						
BON → MCN	45.0% (±32.8%)	0%	50.5% (±12.8%)	37.7% (±10.7%)	35.9% (±8.8%)	29.2% (±10.3%)	40.9% (±12.1%)	41.8% (±19.8%)	0%	29.9% (±14.8%)	**31.1%**
MCN → ICH	0%	--	10.1% (±10.9%)	20.3% (±14.5%)	2.5% (±4.7%)	13.7% (±14.4%)	23.3% (±16.3%)	0%	--	18.3% (±22.9%)	**11.0%**
ICH → LGR	--	--	33.3% (±53.3%)	66.7% (±37.7%)	100.0%	33.4% (±53.4%)	0%	--	--	50.0% (±69.4%)	**47.2%**
MCN → PRA	0%	--	6.7% (±8.9%)	0%	0%	0%	0%	0%	--	0%	**0.8%**
					Wild						
BON → MCN	67.4% (±54.0%)	70.8% (±28.7%)	17.8% (±18.3%)	54.8% (±20.9%)	36.0% (±25.3%)	38.8% (±26.6%)	31.0% (±10.1%)	38.4% (±11.6%)	42.4% (±11.8%)	39.0% (±7.3%)	**43.6%**
MCN → ICH	100%	0%	33.8% (±54.0%)	8.4% (±15.8%)	0%	40.2% (±43.1%)	12.1% (±12.8%)	19.3% (±15.2%)	17.4% (±13.9%)	31.5% (±11.2%)	**26.3%**
ICH → LGR	100%	--	100%	0%	--	50.1% (±69.4%)	66.9% (±53.5%)	0%	20.1% (±35.2%)	38.1% (±20.8%)	**46.9%**
MCN → PRA	0%	0%	0%	8.4% (±15.7%)	0%	20.2% (±35.5%)	0%	0%	0%	3.0% (±4.1%)	**3.2%**

TABLE E.3.—Conditional overshooting rates for Walla Walla steelhead. Conditional overshooting rates are calculated as the proportion of fish that overshoot the next upstream dam with adult detectors out of the number seen at the previous dam with adult detectors. Rates are adjusted by detection efficiencies at the upstream dam. Parentheses contain ± 2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
					Hatchery						
MCN → ICH	38.4%	46.2%	56.3%	76.0%	76.4%	71.3%	75.9%	57.3%	80.6%	85.7%	**66.4%**
	(±17.9%)	(±19.2%)	(±23.3%)	(±5.6%)	(±4.8%)	(±6.6%)	(±5.9%)	(±9.8%)	(±9.0%)	(±6.2%)	
ICH → LGR	18.2%	17.3%	20.0%	38.1%	44.9%	39.5%	33.5%	32.1%	39.3%	40.0%	**32.3%**
	(±22.8%)	(±22.0%)	(±24.8%)	(±7.1%)	(±6.3%)	(±8.3%)	(±7.4%)	(±12.2%)	(±12.0%)	(±9.2%)	
MCN → PRA	0%	7.7%	0%	2.9%	4.2%	3.3%	0%	0%	8.9%	1.6%	**2.9%**
		(±10.3%)		(±2.1%)	(±2.2%)	(±2.6%)			(±6.3%)	(±2.1%)	
					Wild						
MCN → ICH	60.7%	62.5%	84.4%	33.8%	31.1%	46.5%	47.3%	36.3%	30.5%	35.7%	**46.9%**
	(±30.7%)	(±33.5%)	(±30.2%)	(±38.2%)	(±12.3%)	(±10.8%)	(±10.0%)	(±10.4%)	(±13.9%)	(±12.0%)	
ICH → LGR	50.0%	62.4%	60.0%	50.0%	35.4%	39.5%	32.7%	43.3%	30.9%	40.9%	**44.5%**
	(±40.0%)	(±44.9%)	(±42.9%)	(±69.3%)	(±22.8%)	(±15.6%)	(±13.6%)	(±17.7%)	(±25.2%)	(±20.6%)	
MCN → PRA	10.6%	0%	16.7%	0%	1.8%	7.4%	1.0%	0%	0%	1.6%	**3.9%**
	(±19.6%)		(±29.8%)		(±3.6%)	(±5.7%)	(±2.0%)			(±3.1%)	

TABLE E.4.—Conditional overshooting rates for Yakima wild steelhead. Conditional overshooting rates are calculated as the proportion of fish that overshoot the next upstream dam with adult detectors out of the number seen at the previous dam with adult detectors. Rates are adjusted by detection efficiencies at the upstream dam. Parentheses contain ± 2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
MCN → PRA	26.4% (±25.9%)	10.1% (±18.7%)	6.7% (±12.6%)	20.1% (±20.3%)	21.6% (±15.3%)	20.2% (±17.7%)	13.5% (±12.3%)	6.7% (±12.7%)	22.6% (±14.7%)	15.6% (±8.9%)	**16.3%**
PRA → RIS	42.6% (±68.3%)	0%	0%	40.8% (±65.3%)	51.2% (±41.0%)	25.8% (±43.7%)	26.8% (±45.5%)	0%	80.4% (±37.8%)	49.7% (±47.4%)	**31.7%**
MCN → ICH	0%	0%	0%	0%	7.2% (±9.6%)	0%	3.4% (±6.5%)	0%	0%	1.6% (±3.1%)	**1.2%**

TABLE E.5.—Conditional overshooting rates for Wenatchee steelhead. Conditional overshooting rates are calculated as the proportion of fish that overshoot the next upstream dam with adult detectors out of the number seen at the previous dam with adult detectors. Rates are adjusted by detection efficiencies at the upstream dam. Parentheses contain ± 2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
					Hatchery						
RIS → RRE	--	78.9% (±5.4%)	73.4% (±5.9%)	82.3% (±4.5%)	75.8% (±3.5%)	82.4% (±3.8%)	73.3% (±5.3%)	68.2% (±6.5%)	39.9% (±8.7%)	16.0% (±8.0%)	**65.6%**
RRE → WEL	--	58.1% (±6.4%)	68.2% (±7.0%)	62.1% (±8.4%)	79.5% (±3.7%)	60.9% (±5.2%)	63.6% (±6.2%)	71.2% (±6.3%)	87.9% (±12.1%)	73.9% (±17.9%)	**69.5%**
MCN → ICH	0%	0%	0%	0%	0%	0%	0%	0%	0%	0.7% (±1.3%)	**0.1%**
					Wild						
RIS → RRE	--	--	0%	25.0% (±42.4%)	16.7% (±10.6%)	10.9% (±8.3%)	4.9% (±6.7%)	4.6% (±8.8%)	5.0% (±9.6%)	17.6% (±18.1%)	**10.6%**
RRE → WEL	--	--	--	0%	88.9% (±20.5%)	33.3% (±37.7%)	50.0% (±69.3%)	0%	51.9% (±72.1%)	66.7% (±53.3%)	**41.5%**
MCN → ICH	--	--	0%	0%	0%	0%	0%	0%	0%	0%	**0%**

TABLE E.6.—Conditional overshooting rates for Entiat wild steelhead. Conditional overshooting rates are calculated as the proportion of fish that overshoot the next upstream dam with adult detectors out of the number seen at the previous dam with adult detectors. Rates are adjusted by detection efficiencies at the upstream dam. Parentheses contain ± 2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
RRE → WEL	--	0%	50.0% (±40.0%)	42.0% (±45.3%)	50.9% (±13.5%)	27.5% (±12.2%)	39.1% (±14.1%)	43.5% (±20.3%)	47.2% (±18.0%)	47.1% (±13.7%)	**38.6%**
MCN → ICH	--	0%	0%	0%	0%	0%	0%	0%	0%	0%	**0%**

TABLE E.7.—Conditional overshooting rates for Tucannon steelhead. Conditional overshooting rates are calculated as the proportion of fish that overshoot the next upstream dam with adult detectors out of the number seen at the previous dam with adult detectors. Rates are adjusted by detection efficiencies at the upstream dam. Parentheses contain ± 2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
Hatchery											
ICH → LGR	70.7% (±13.9%)	63.5% (±13.8%)	68.7% (±4.8%)	56.5% (±5.5%)	65.8% (±4.4%)	67.1% (±6.4%)	48.3% (±8.5%)	47.0% (±12.0%)	63.1% (±10.8%)	55.8% (±10.0%)	**60.7%**
MCN → PRA	0%	4.3% (±4.8%)	3.6% (±1.8%)	1.2% (±1.2%)	2.9% (±1.5%)	1.4% (±1.6%)	0%	1.5% (±2.9%)	0%	1.0% (±1.9%)	**1.6%**
Wild											
ICH → LGR	50.0% (±20.9%)	84.5% (±20.9%)	47.8% (±20.4%)	45.5% (±29.4%)	67.6% (±14.5%)	50.1% (±16.8%)	59.7% (±15.9%)	60.5% (±14.6%)	60.9% (±16.8%)	66.1% (±13.1%)	**59.3%**
MCN → PRA	0%	0%	7.1% (±9.5%)	0%	2.5% (±4.8%)	5.6% (±7.6%)	0%	2.3% (±4.5%)	11.8% (±10.8%)	4.0% (±5.4%)	**3.3%**

TABLE E.8.—Conditional overshooting rates for upper Snake River steelhead. Conditional overshooting rates are calculated as the proportion of fish that overshot Priest Rapids Dam of the number seen at McNary Dam. Rates are adjusted by detection efficiencies at Priest Rapids. Parentheses contain ± 2 standard errors. Origin refers to rear type, hatchery or wild.

	Run Year										
Origin	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
					Clearwater						
hatchery	0%	0%	0%	1.1% (±2.1%)	0%	0%	0.1% (±0.4%)	0%	0%	0.8% (±1.1%)	**0.2%**
wild	0%	0%	4.0% (±6.0%)	0%	0%	0%	2.2% (±2.9%)	0%	1.1% (±2.7%)	1.0% (±1.5%)	**0.8%**
					Grande Ronde						
hatchery	0%	0%	0%	0%	0.3% (±0.4%)	1.0% (±1.0%)	0.6% (±0.7%)	1.7% (±1.6%)	1.3% (±1.4%)	1.7% (±1.5%)	**0.7%**
wild	3.0% (±7.5%)	0%	2.8% (±7.4%)	2.7% (±6.9%)	1.5% (±3.9%)	1.2% (±3.2%)	0%	4.4% (±6.0%)	6.3% (±7.8%)	1.6% (±4.1%)	**2.4%**
					Salmon						
hatchery	0%	0%	2.9% (±4.7%)	1.2% (±2.9%)	1.0% (±0.6%)	0.9% (±0.7%)	1.2% (±0.7%)	2.8% (±1.3%)	3.0% (±1.4%)	2.0% (±1.0%)	**1.5%**
wild	0%	0%	0%	2.0% (±4.7%)	0%	0%	0%	0%	1.7% (±3.3%)	0%	**0.4%**
					Imnaha						
hatchery	3.3% (±7.8%)	0%	0%	0%	2.7% (±1.5%)	1.1% (±1.4%)	1.8% (±1.7%)	3.7% (±3.6%)	3.5% (±2.7%)	2.5% (±1.9%)	**1.9%**
wild	0%	0%	0%	0%	2.0% (±2.8%)	3.3% (±4.0%)	2.8% (±3.2%)	0%	5.3% (±6.9%)	3.1% (±4.0%)	**1.6%**

The conditional probability of overshooting the next upstream dam changed as steelhead became further away from their home tributary. Most steelhead populations were less likely to overshoot the second dam than they were to overshoot the first dam. However, steelhead that did overshoot the second dam were more likely to overshoot further dams. This pattern was very consistent between the John Day wild and Umatilla populations (Figure E.1).

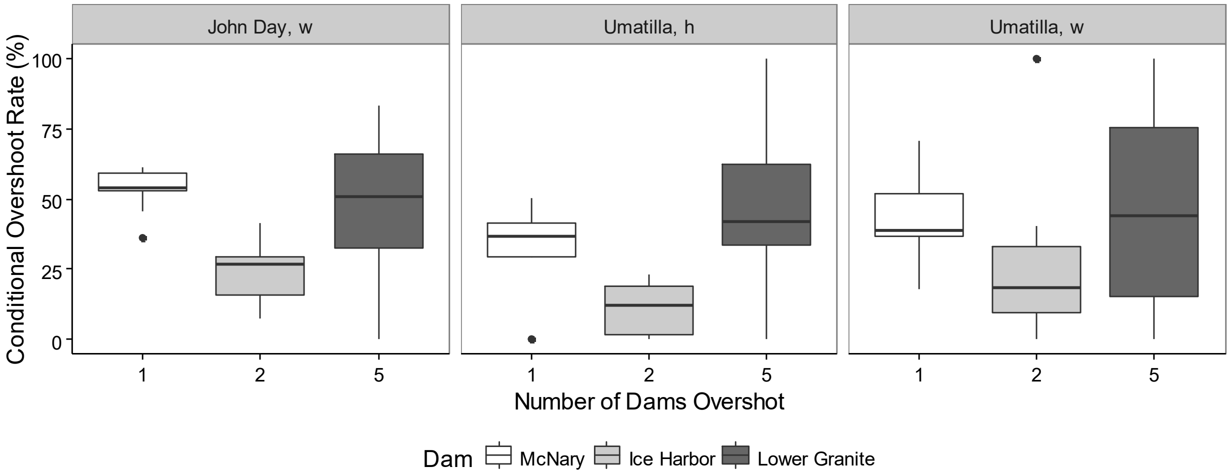

FIGURE E.1.—Conditional overshooting rates by John Day and Umatilla steelhead as they passed the first, second, and fifth upstream dams. Overshooting rates were adjusted by detection efficiencies.

Middle and upper Columbia populations were not as consistent in conditional overshooting patterns (Figure E.2). Conditional overshooting rates for Walla Walla hatchery steelhead declined between the first and the fourth upstream dam, but overshooting rates remained about the same after fish passed the first dam in the Walla Walla wild and Wenatchee hatchery populations. Yakima and Wenatchee wild steelhead were more likely to continue overshooting than they were to overshoot in the first place.

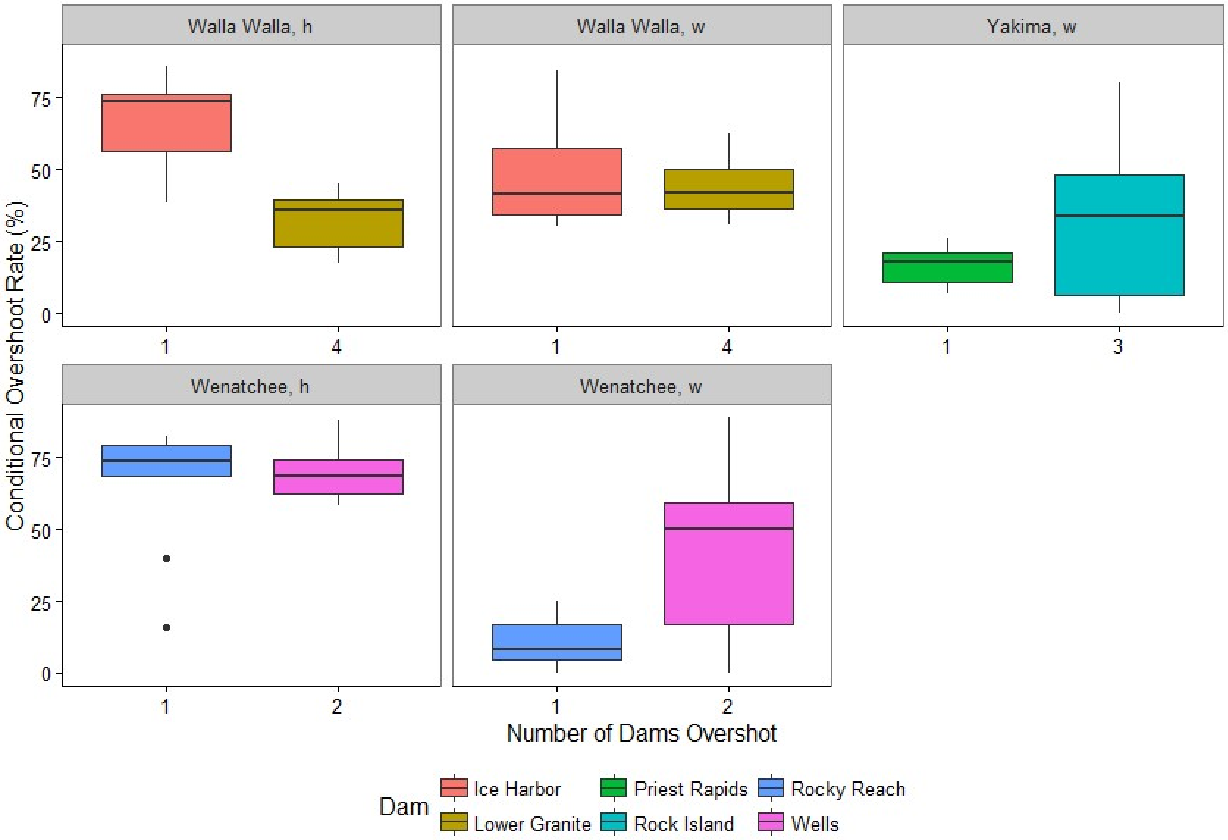

FIGURE E.2.—Conditional overshooting rates for Walla Walla, Yakima, and Wenatchee steelhead as they passed the first and further upstream dams. Overshooting rates are adjusted by detection efficiencies.

APPENDIX F.—Overshooting maps

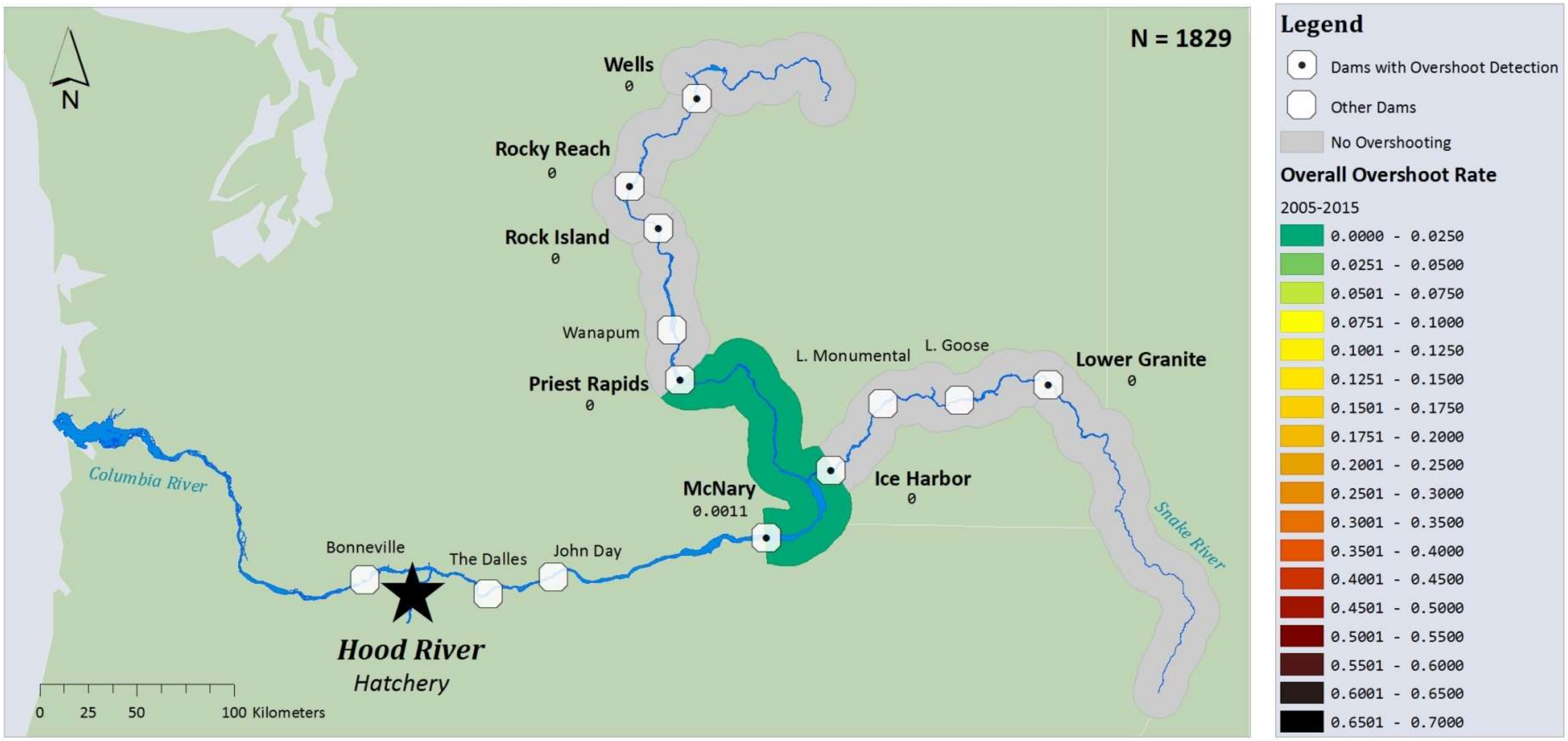

FIGURE F.1.—Map of overshooting by Hood River hatchery steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

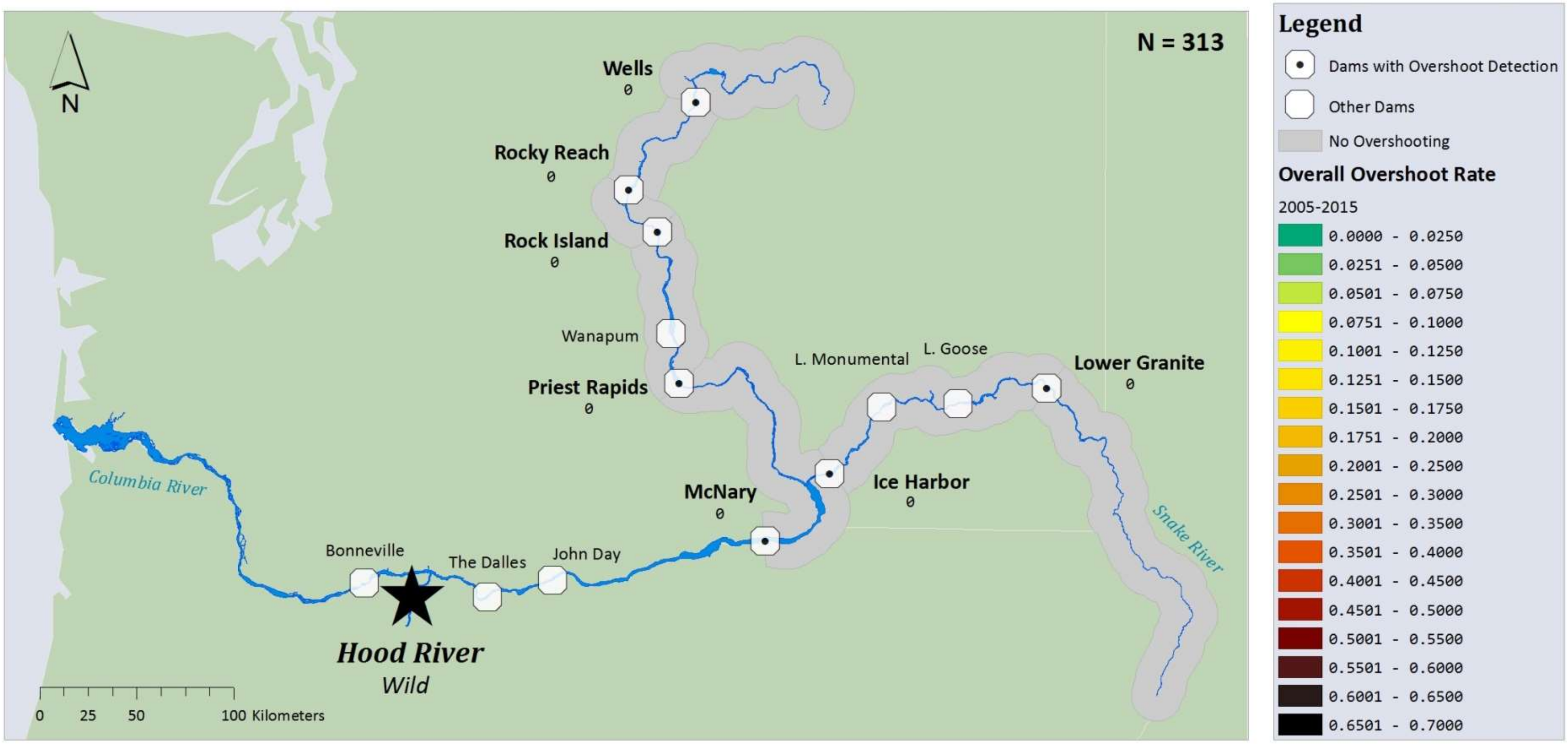

FIGURE F.2.—Map of overshooting by Hood River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

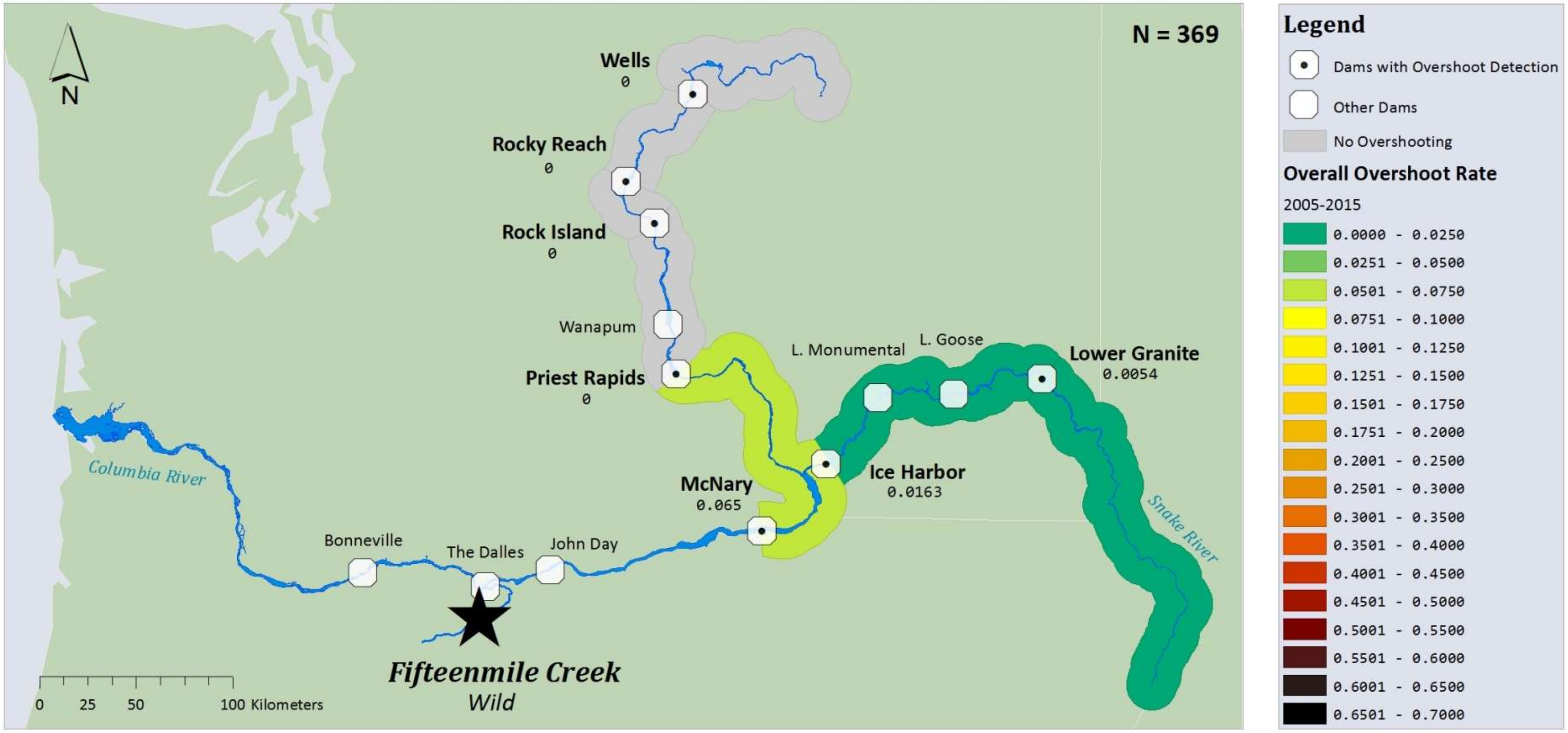

FIGURE F.3.—Map of overshooting by Fifteenmile Creek wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

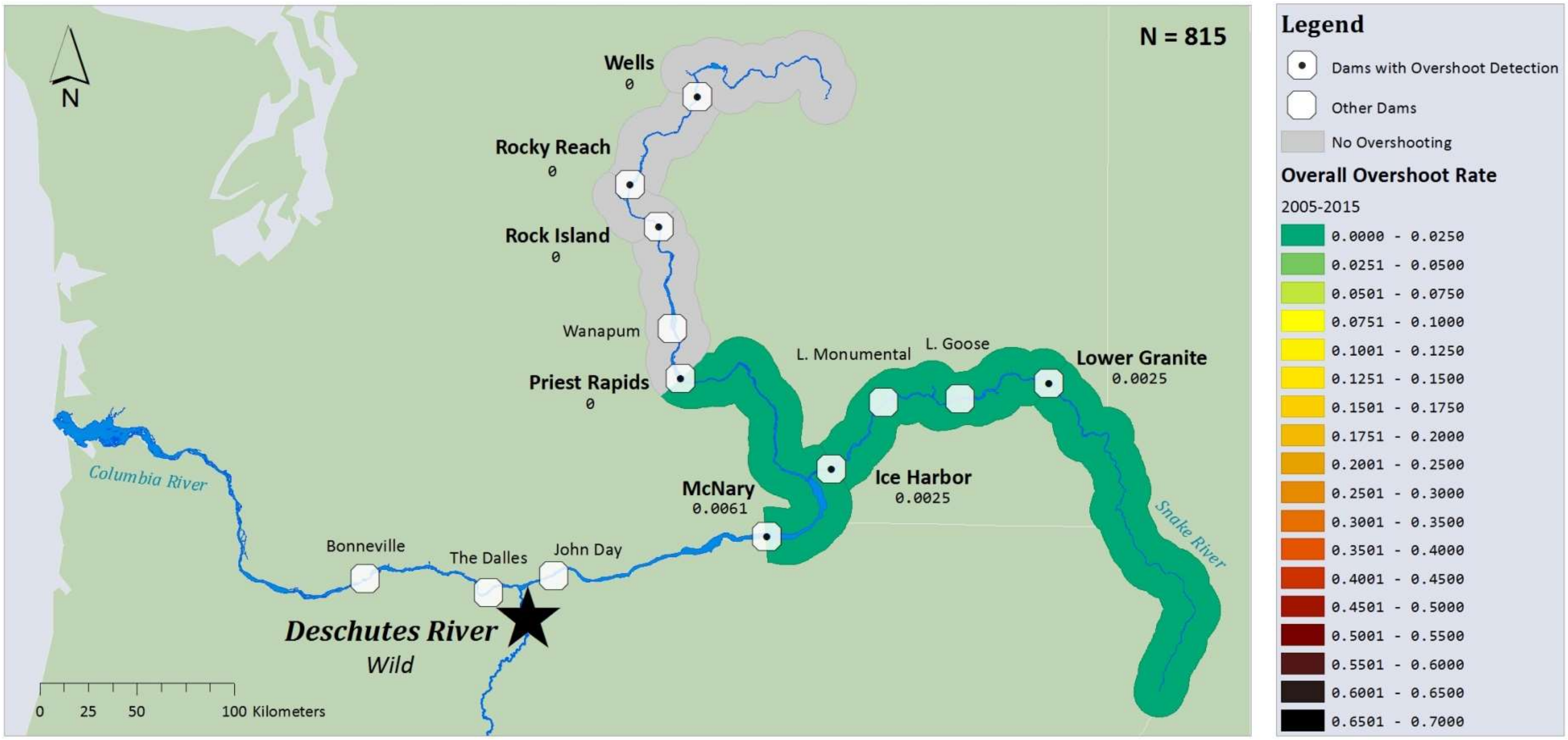

FIGURE F.4.—Map of overshooting by Deschutes River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

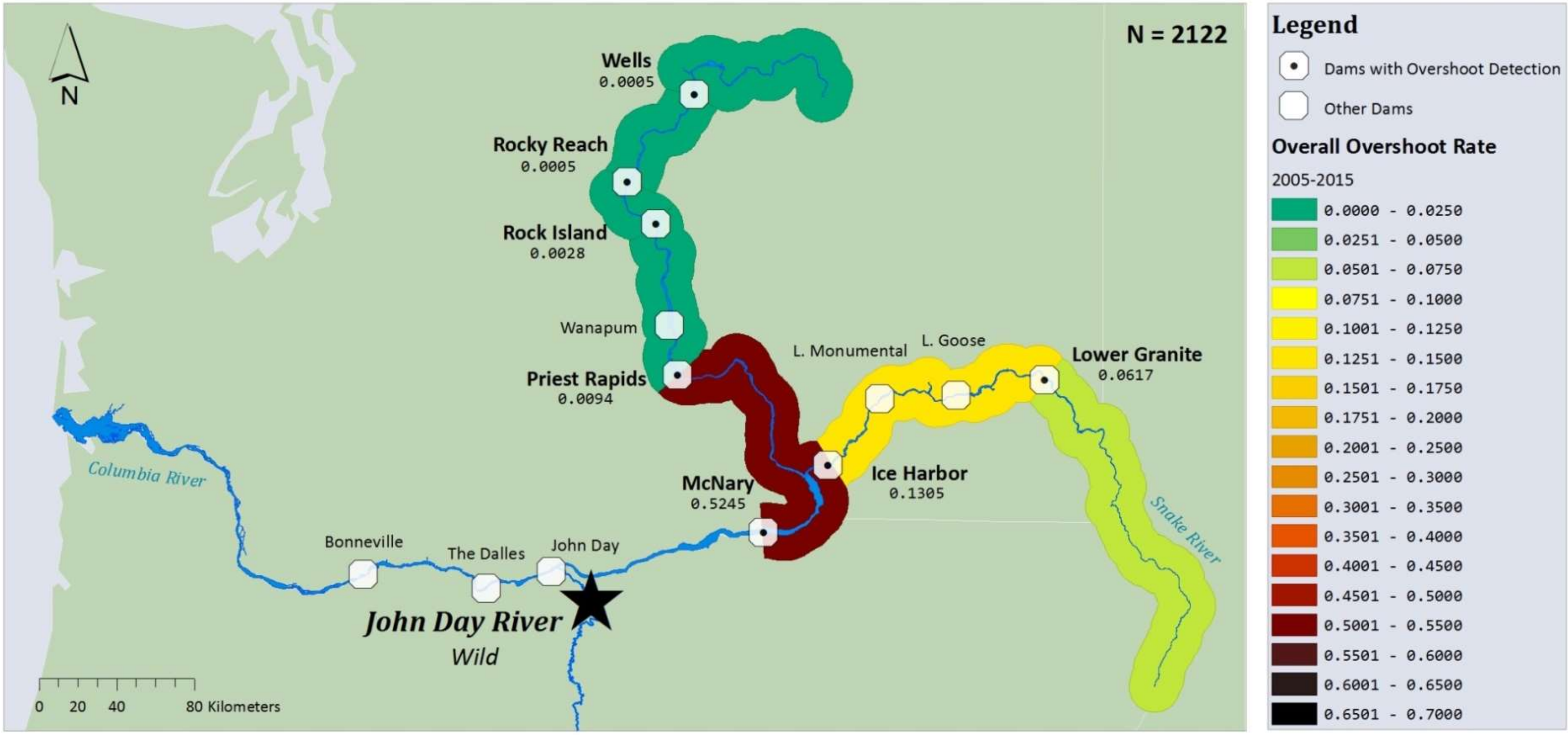

FIGURE F.5.—Map of overshooting by John Day River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

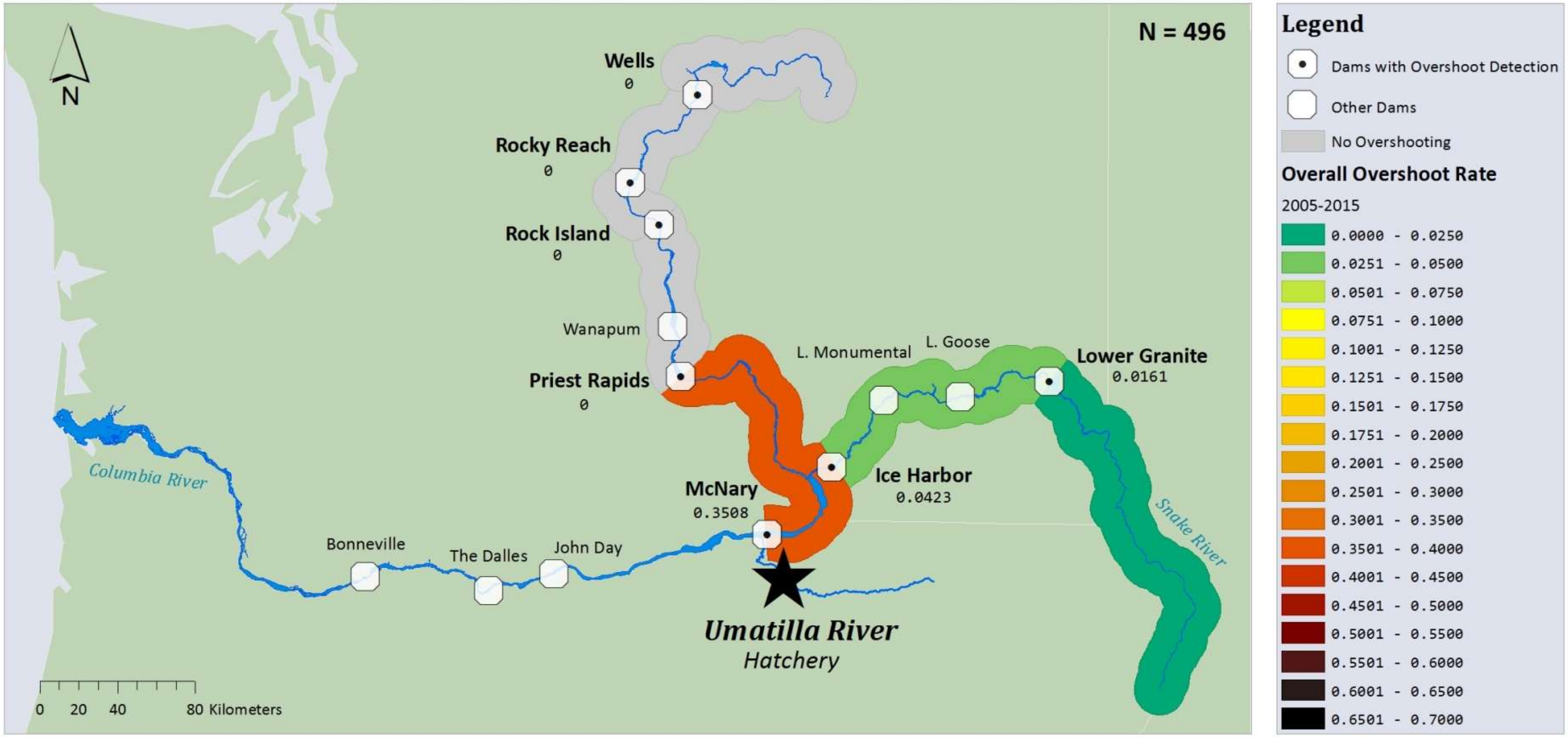

FIGURE F.6.—Map of overshooting by Umatilla River hatchery steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

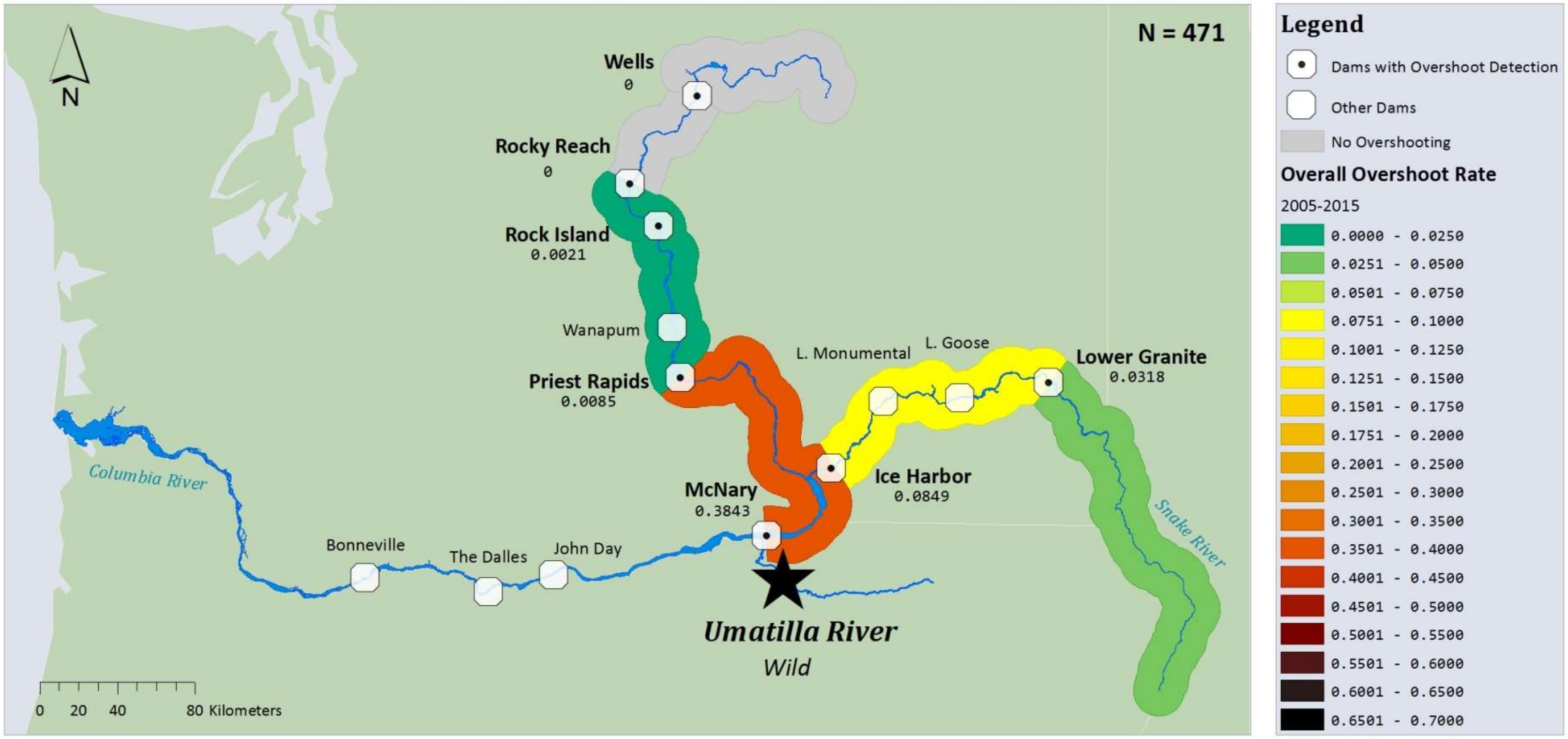

FIGURE F.7.—Map of overshooting by Umatilla River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

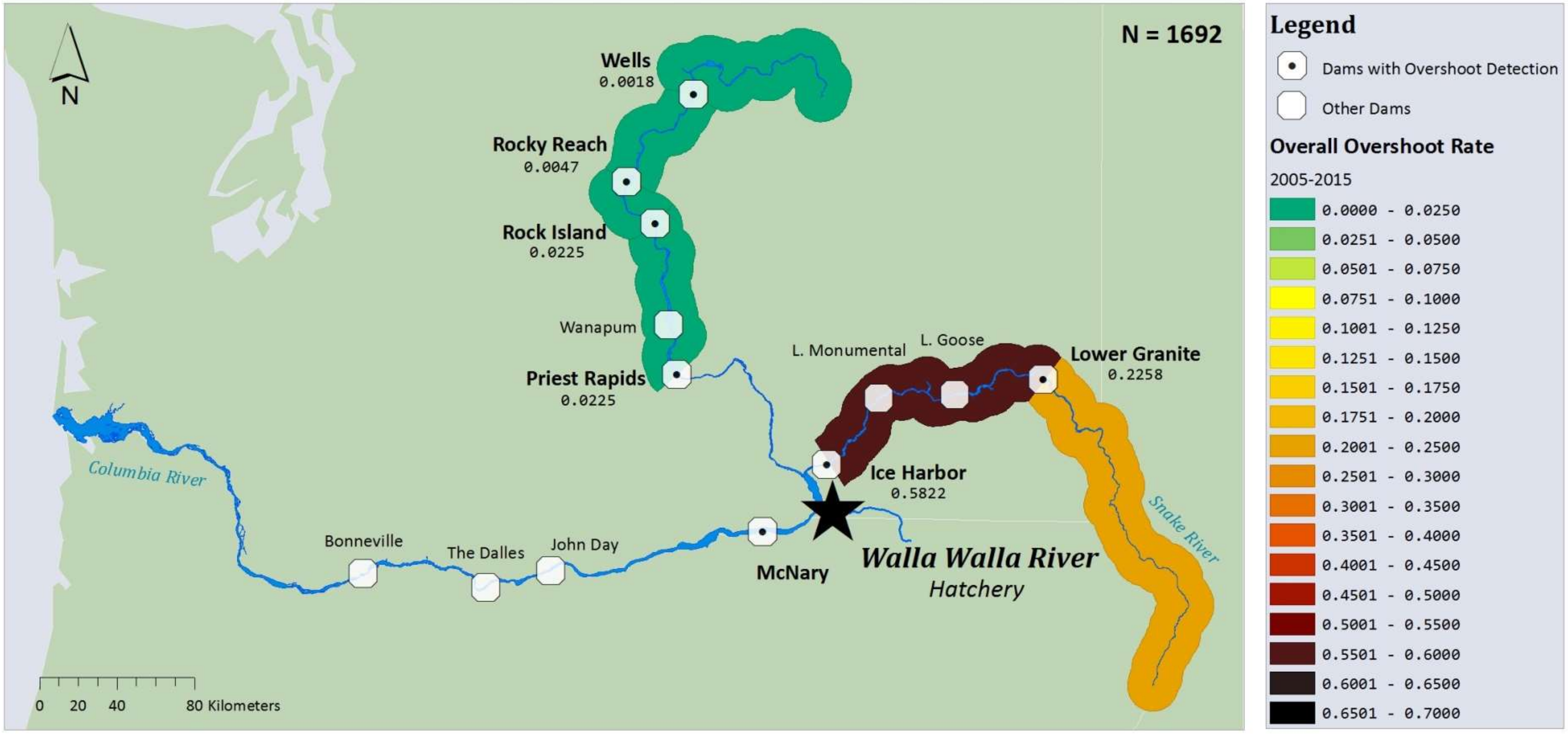

FIGURE F.8.—Map of overshooting by Walla Walla River hatchery steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

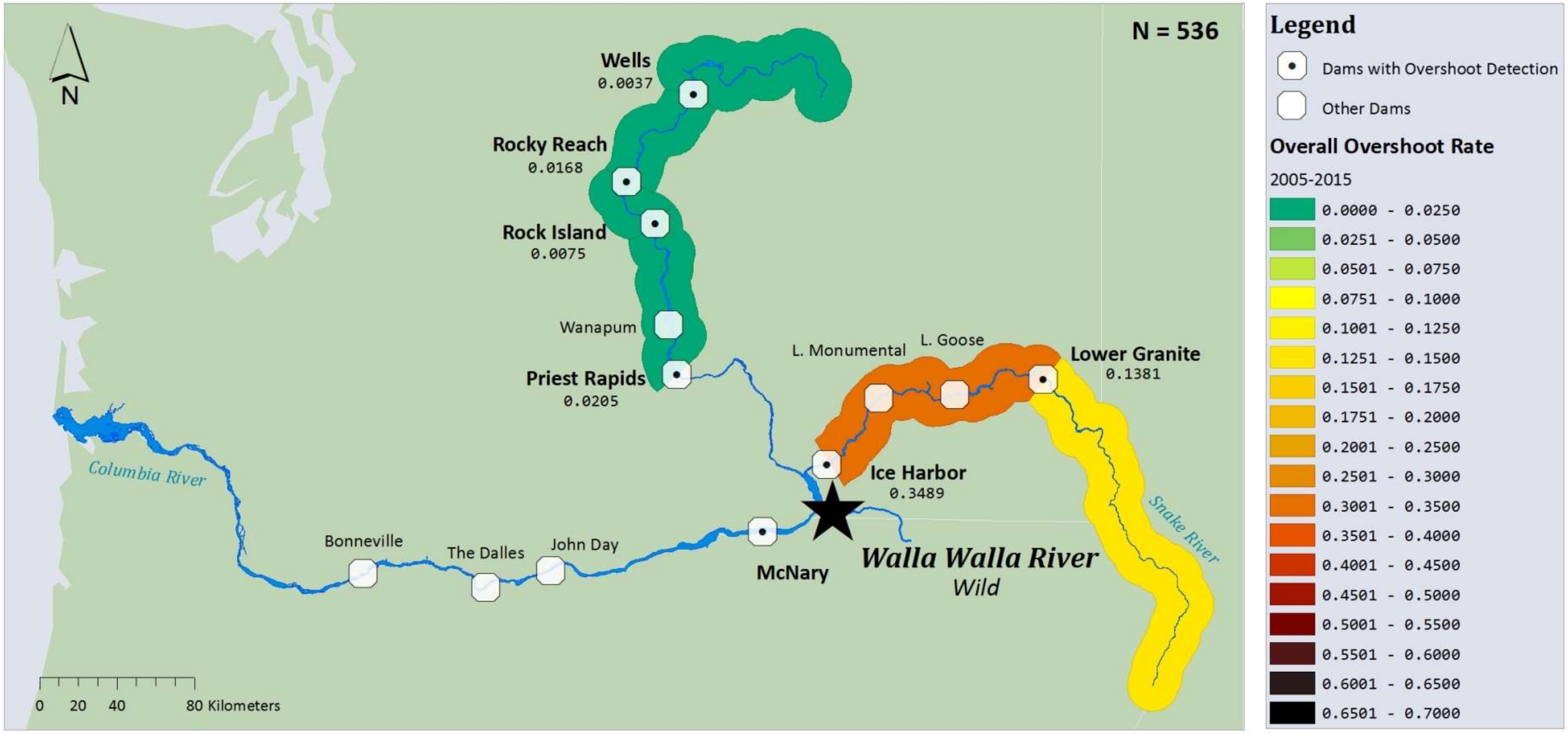

FIGURE F.9.—Map of overshooting by Walla Walla River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

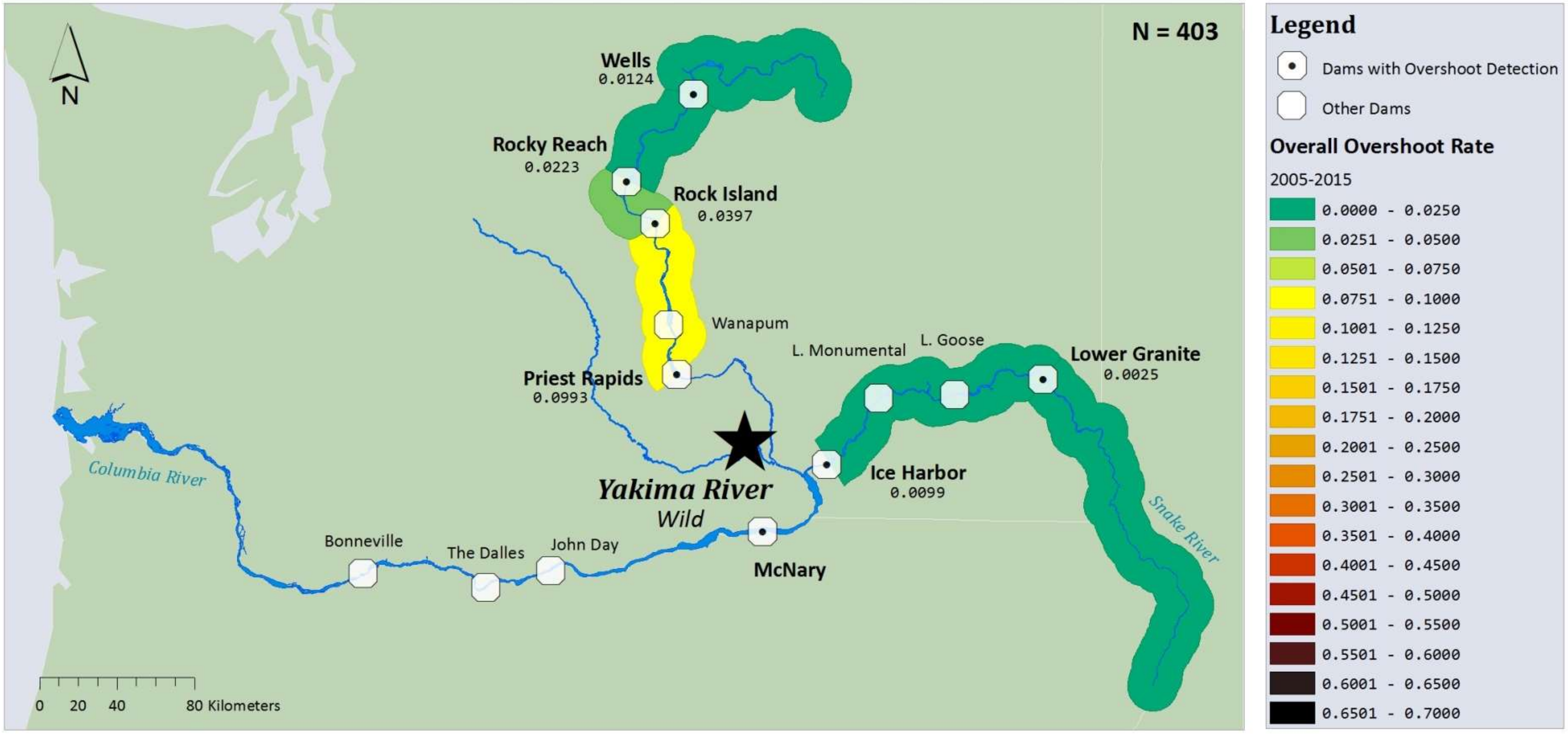

FIGURE F.10.—Map of overshooting by Yakima River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

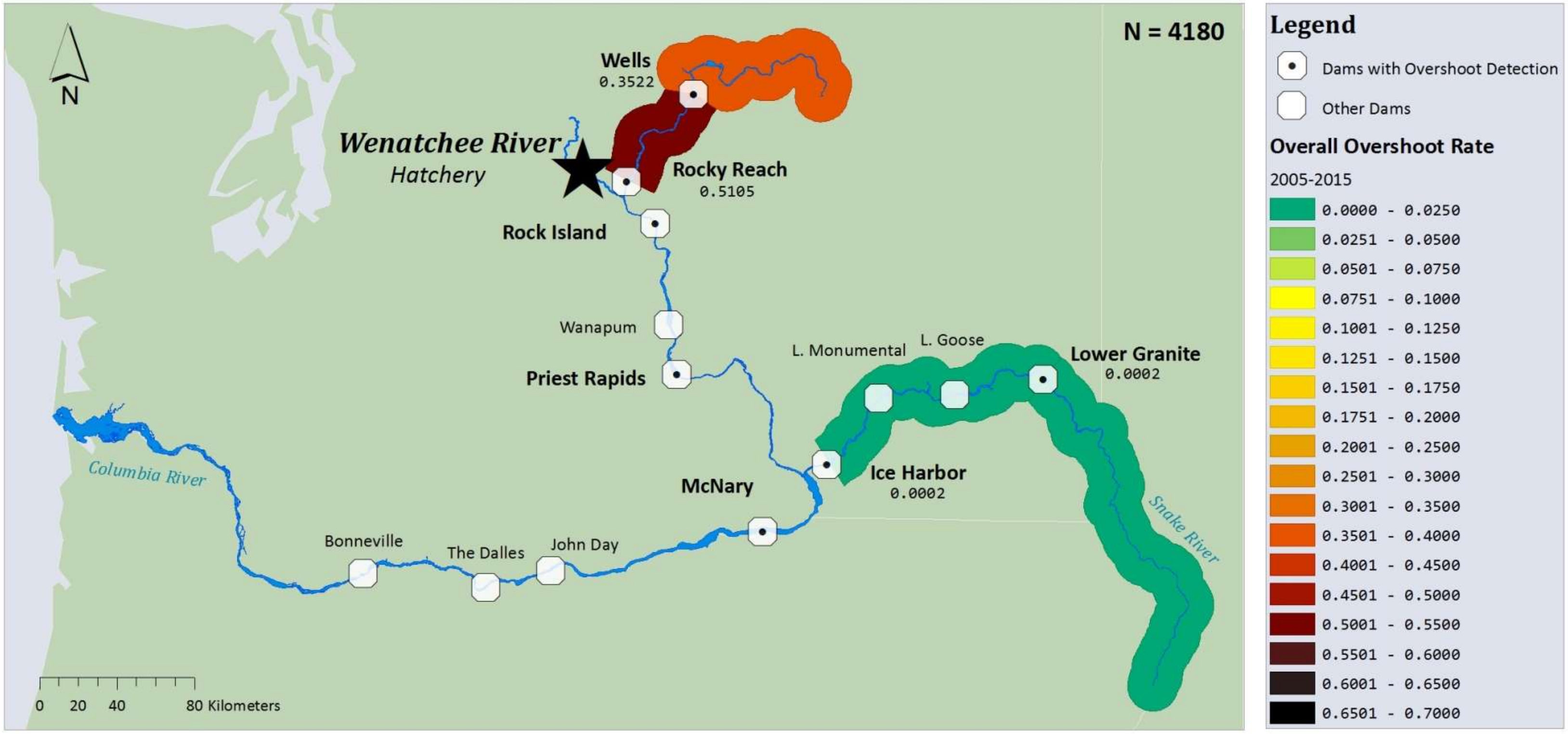

FIGURE F.11.—Map of overshooting by Wenatchee River hatchery steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

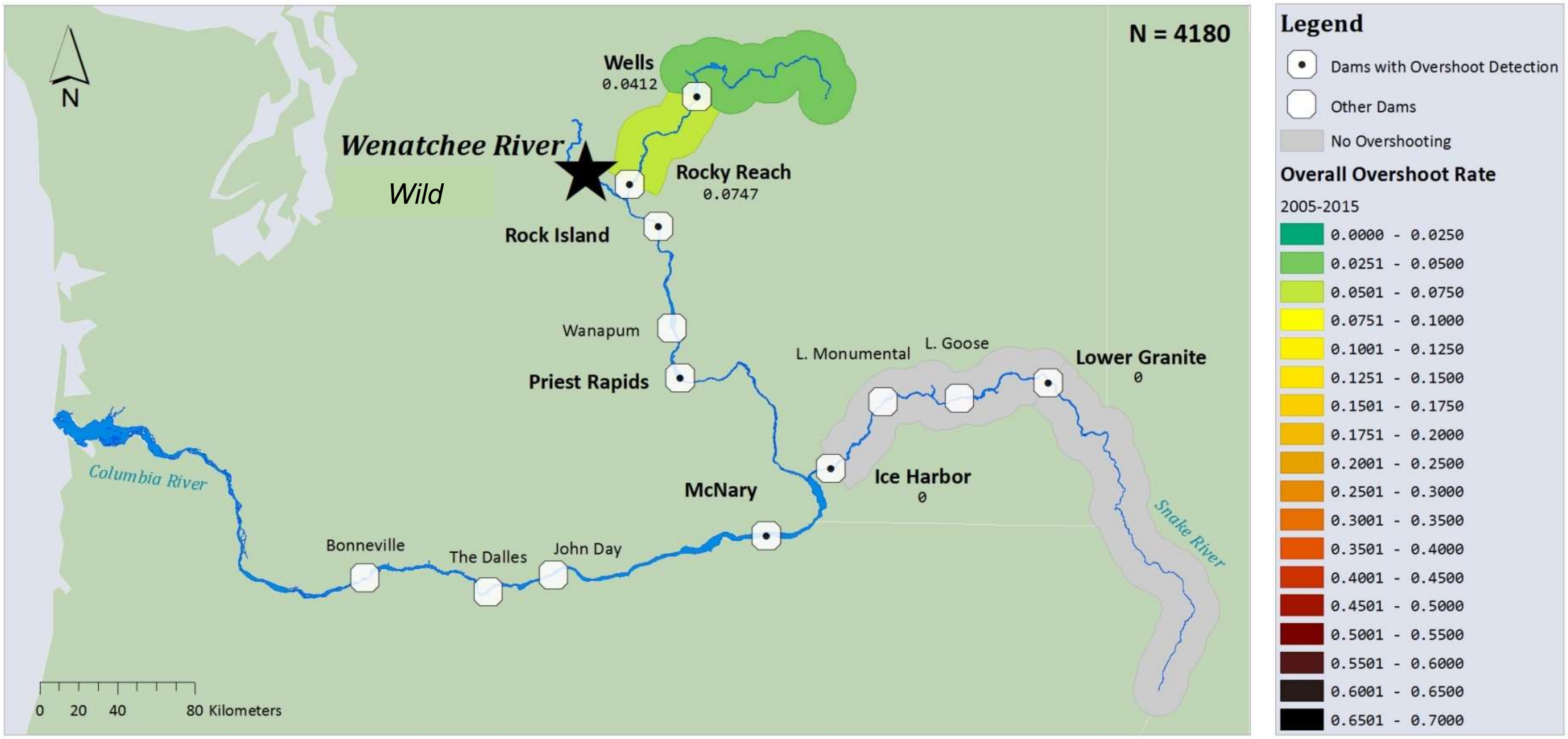

FIGURE F.12.—Map of overshooting by Wenatchee River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

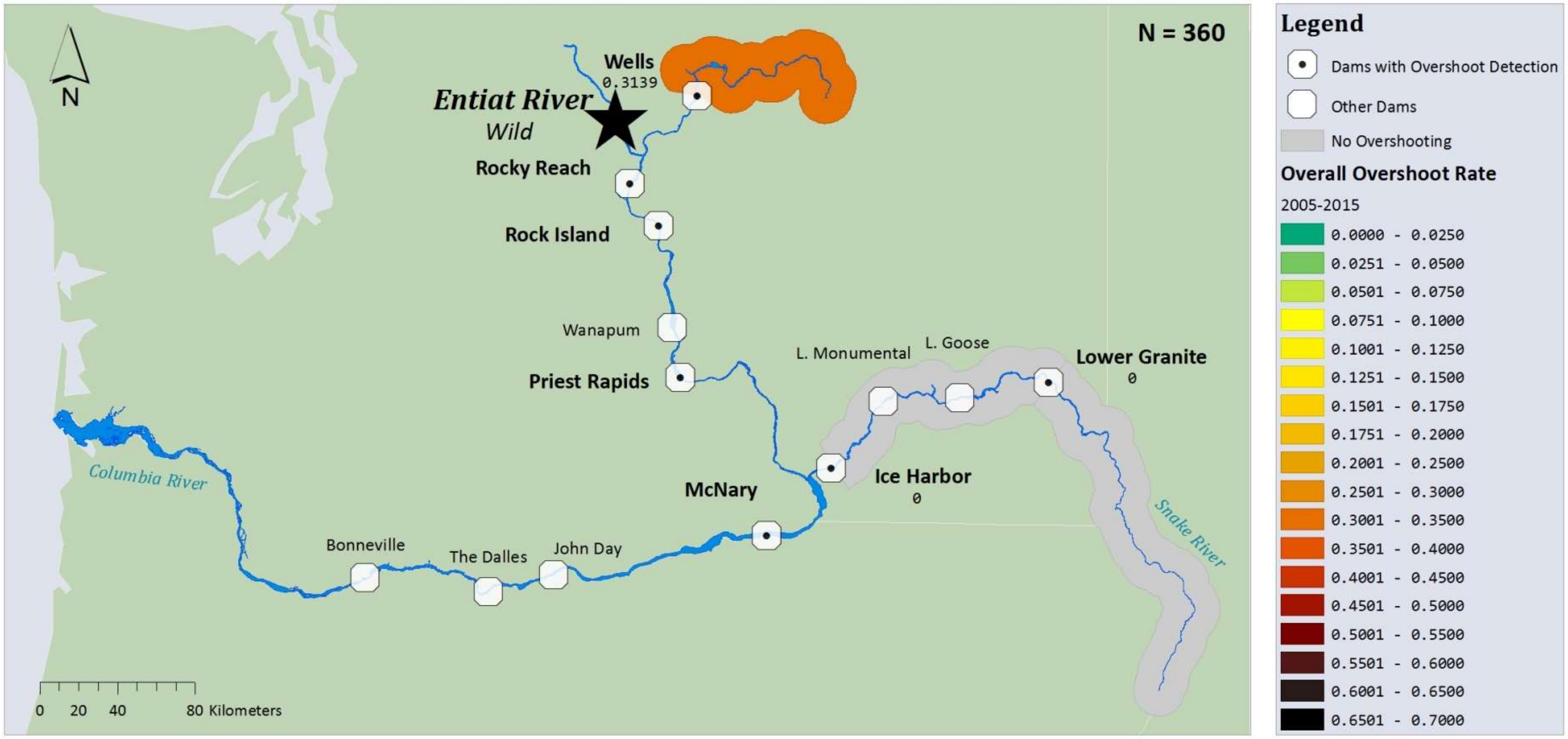

FIGURE F.13.—Map of overshooting by Entiat River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

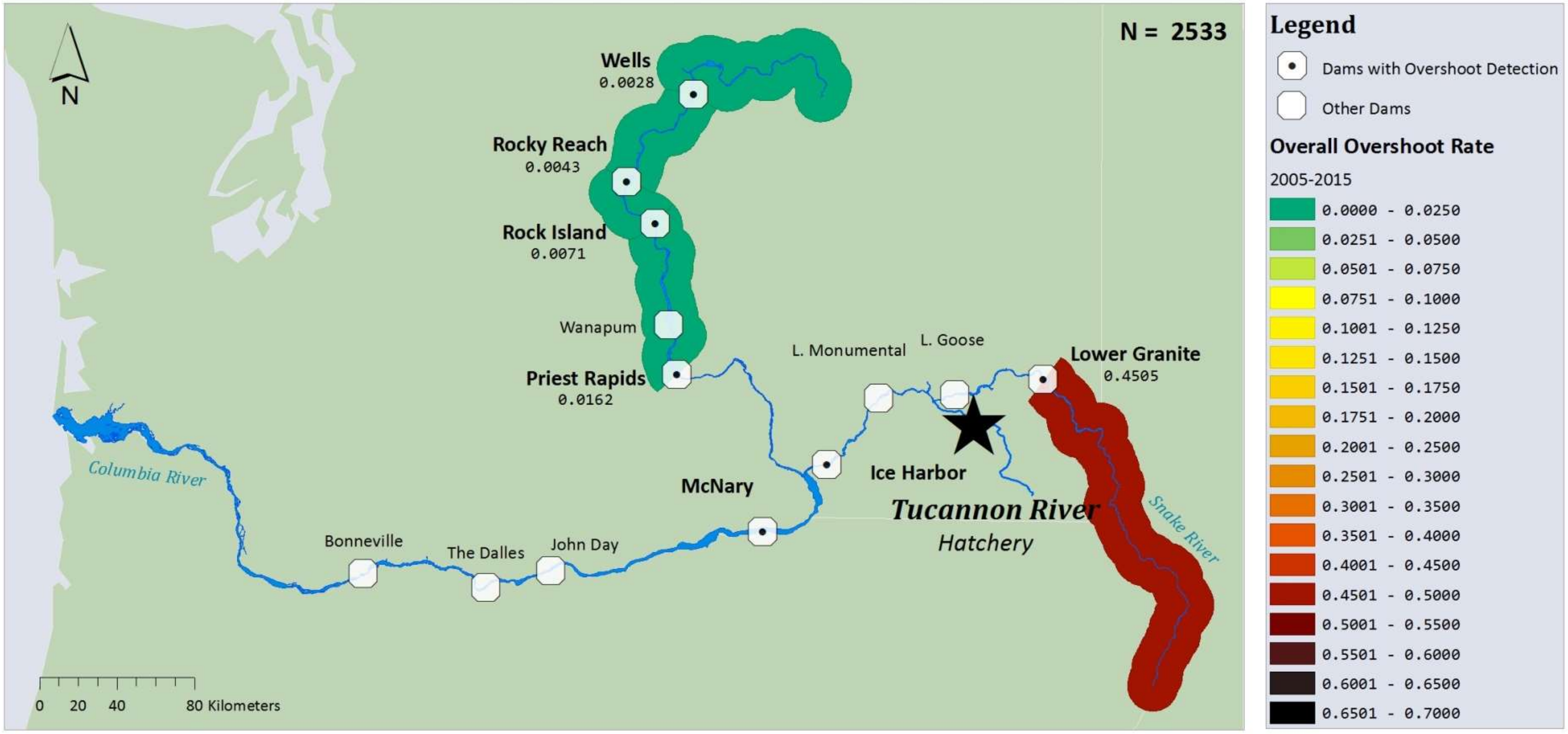

FIGURE F.14.—Map of overshooting by Tucannon River hatchery steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

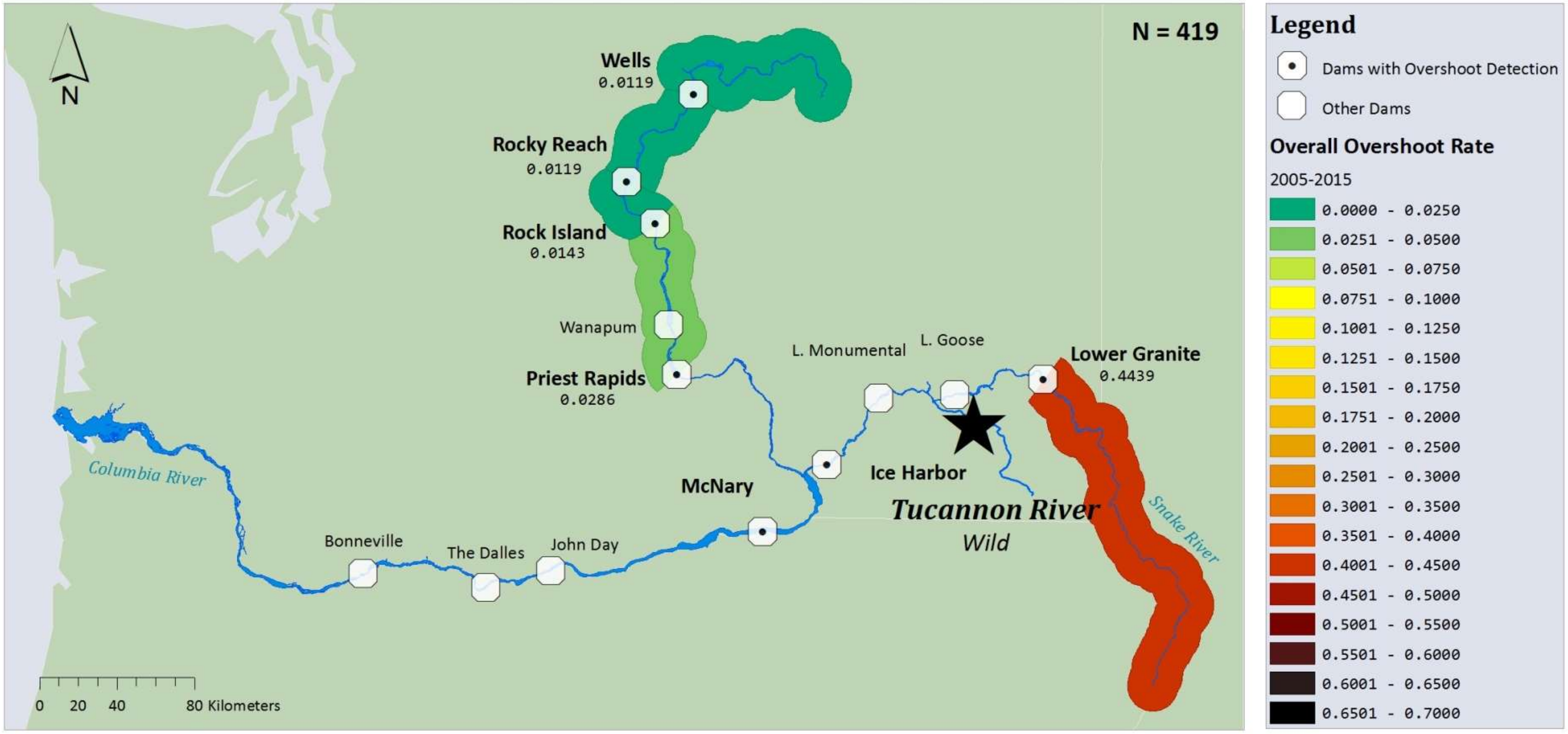

FIGURE F.15.—Map of overshooting by Tucannon River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

FIGURE F.16.—Map of overshooting by Clearwater River hatchery steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

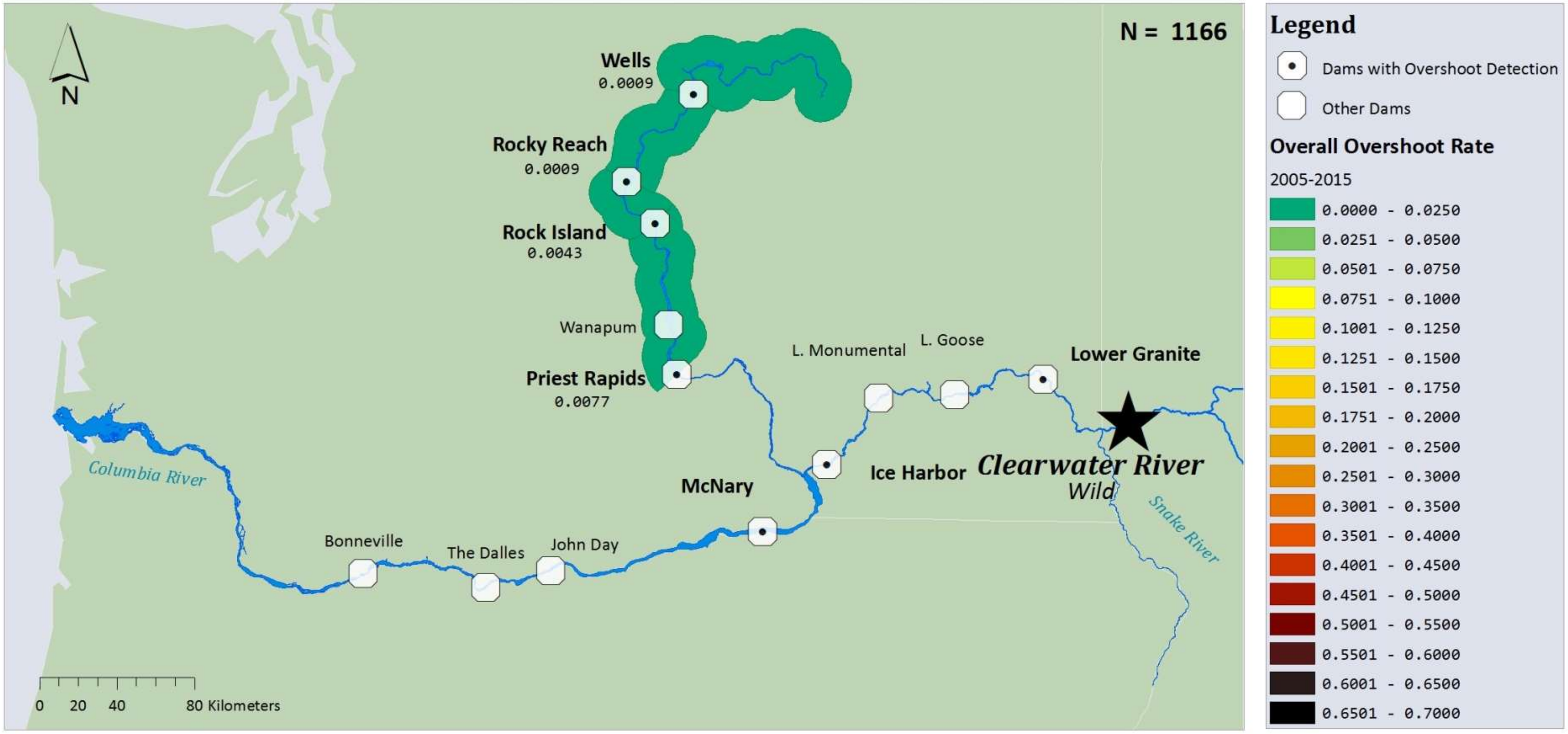

FIGURE F.17.—Map of overshooting by Clearwater River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

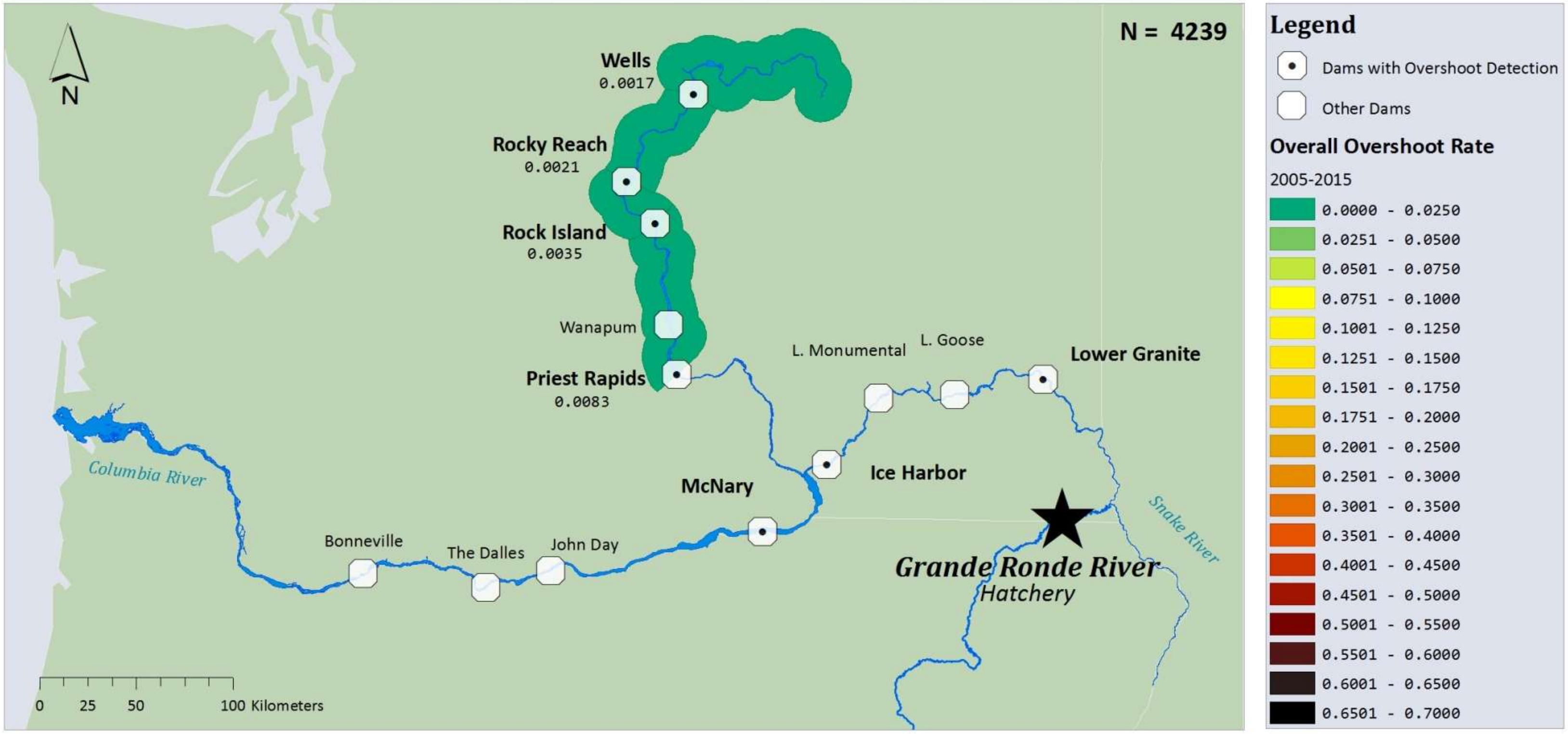

FIGURE F.18.—Map of overshooting by Grande Ronde River hatchery steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

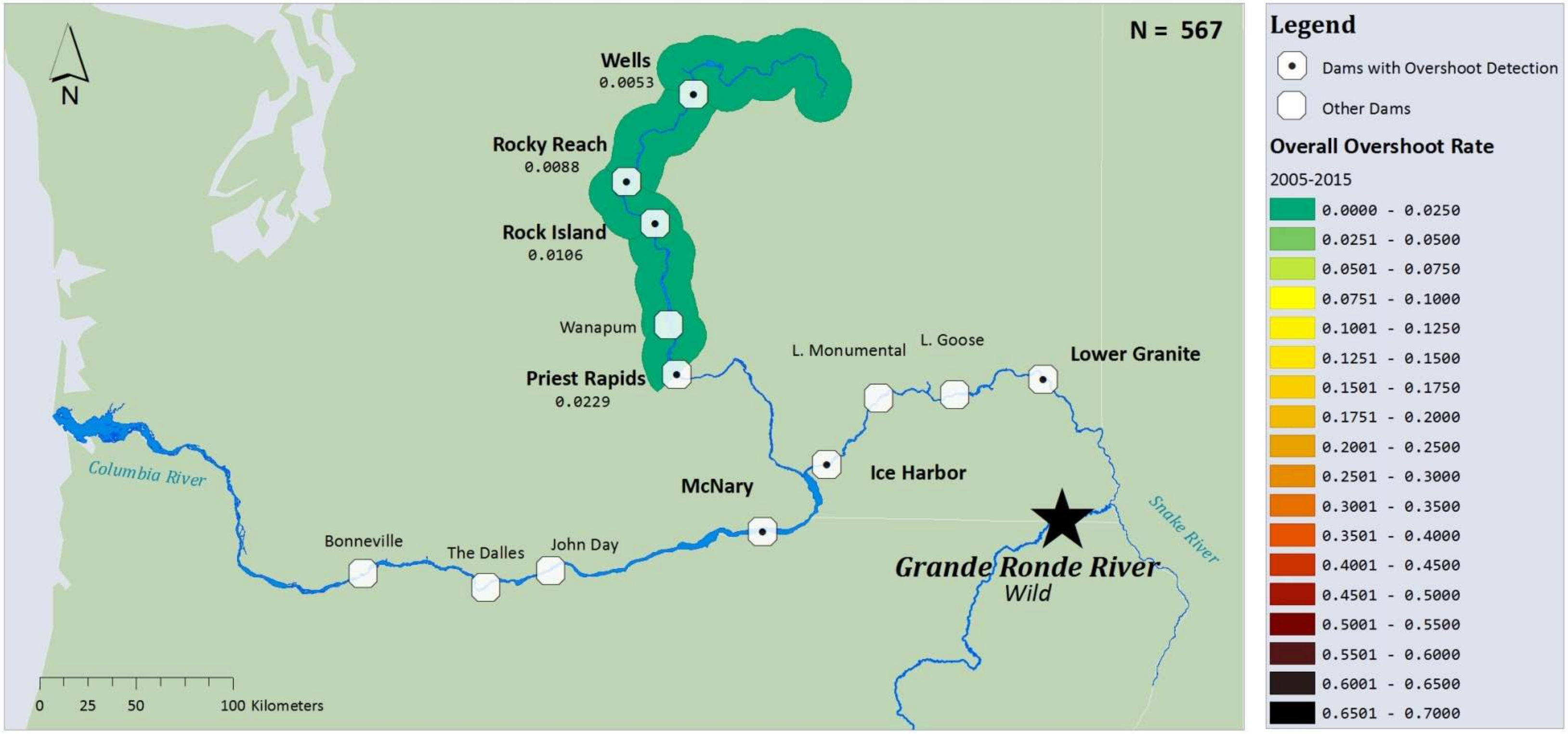

FIGURE F.19.—Map of overshooting by Grande Ronde River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

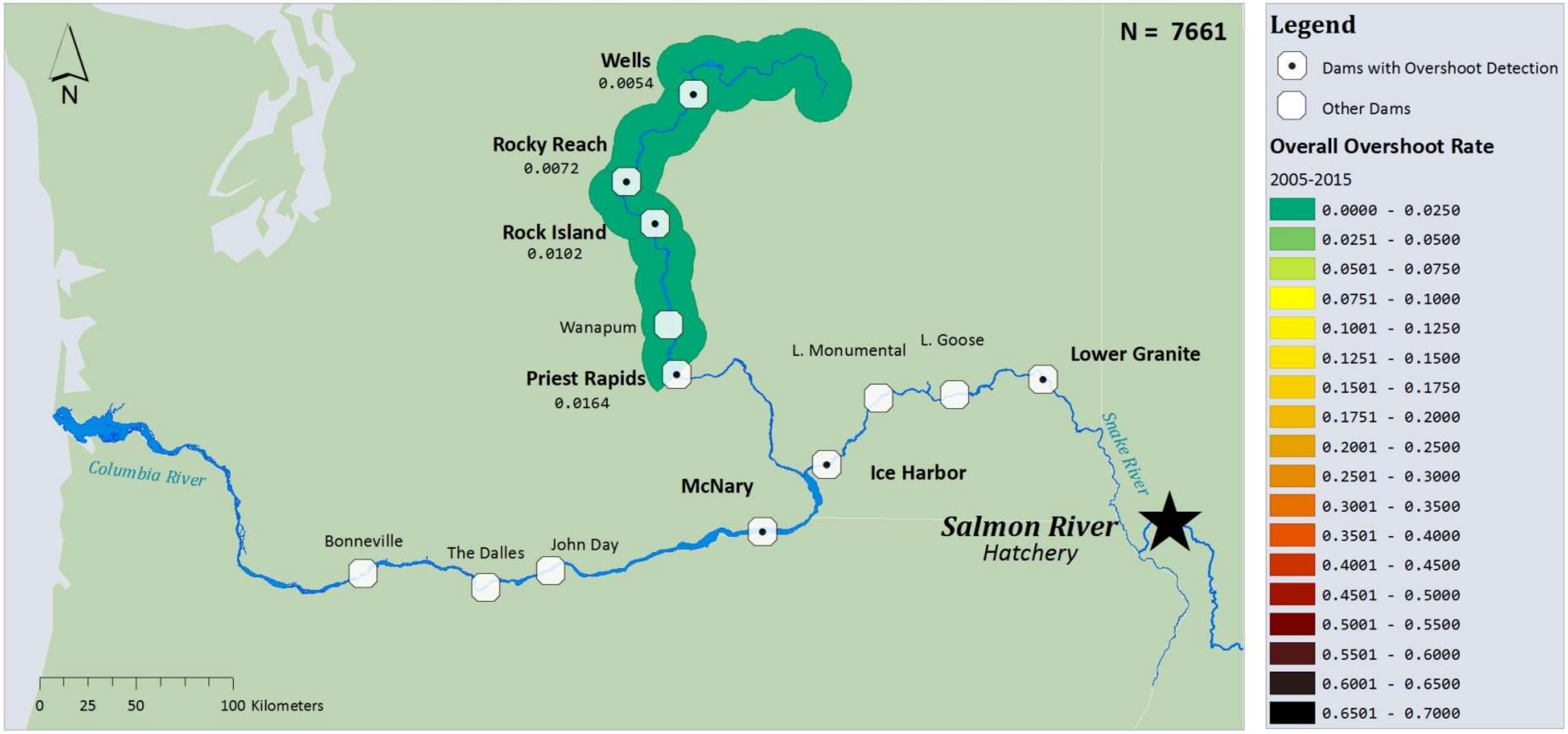

FIGURE F.20.—Map of overshooting by Salmon River hatchery steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

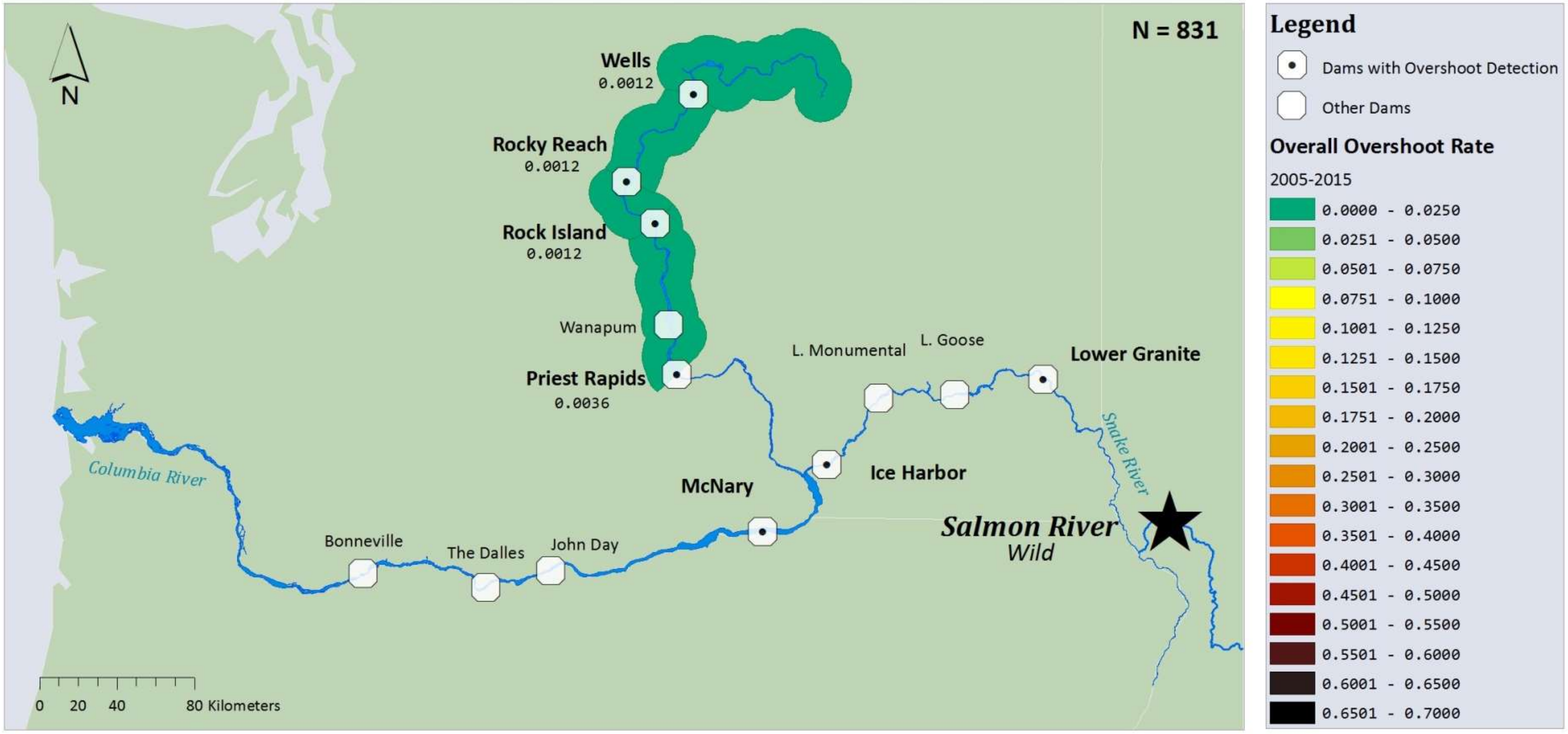

FIGURE F.21.—Map of overshooting by Salmon River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

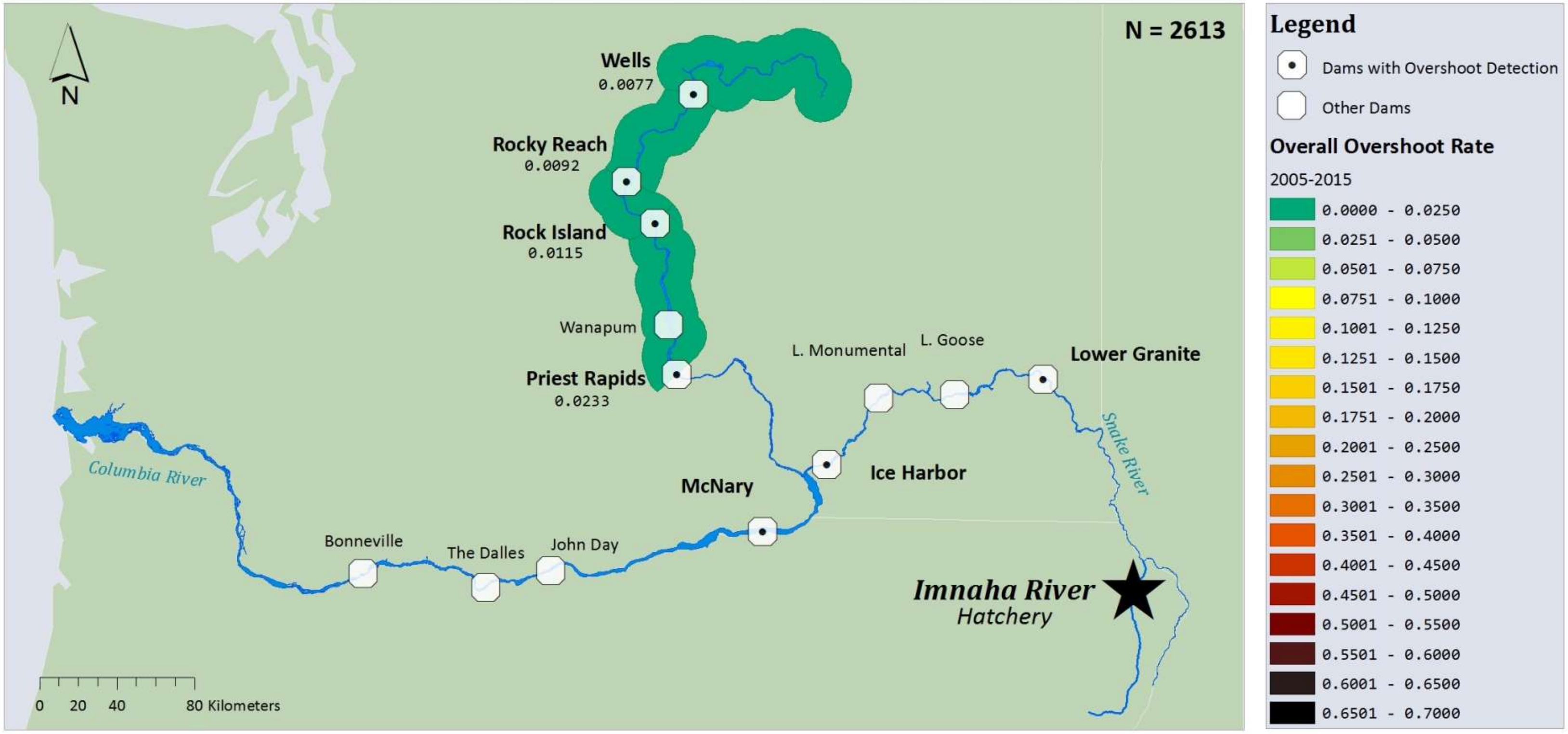

FIGURE F.22.—Map of overshooting by Imnaha River hatchery steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

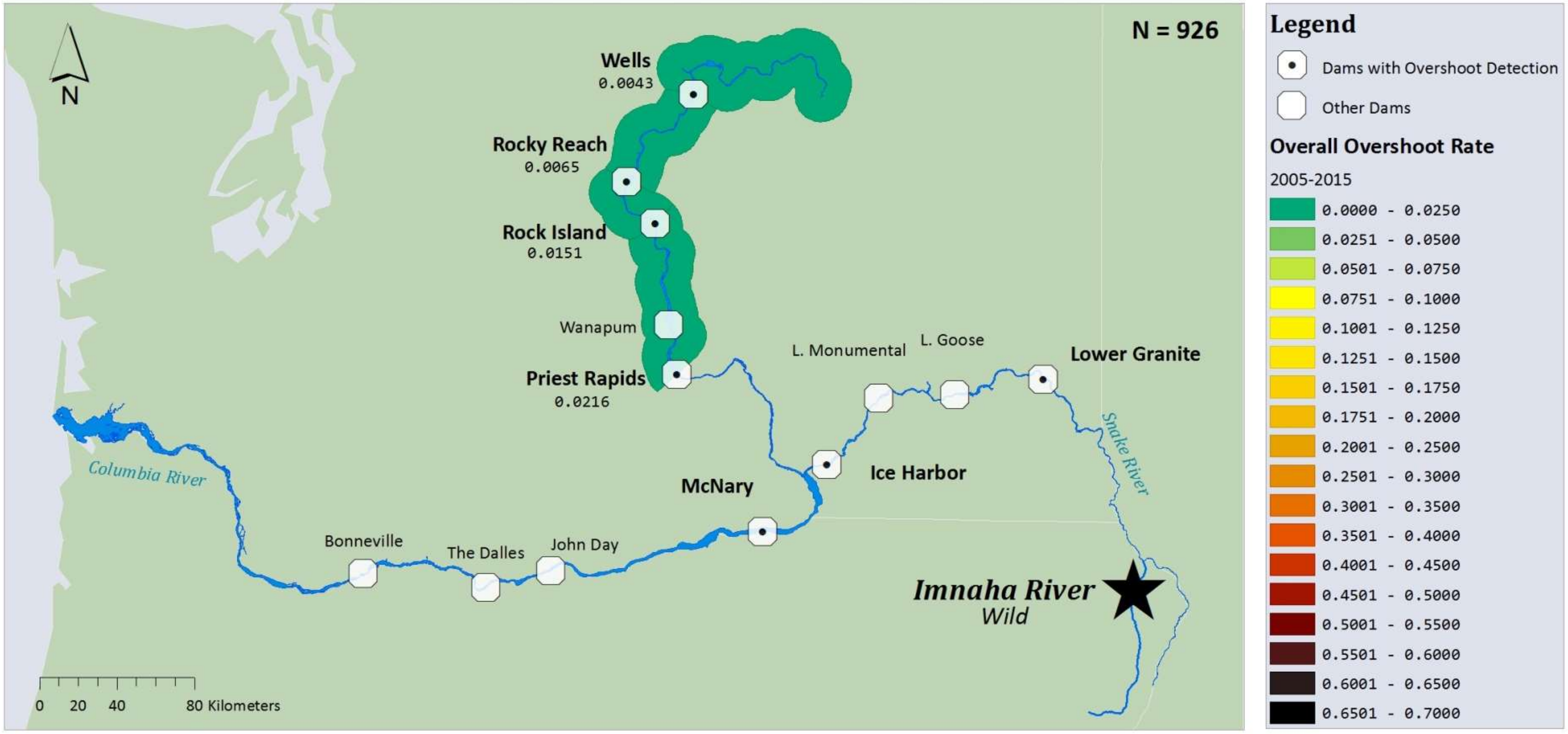

FIGURE F.23.—Map of overshooting by Imnaha River wild steelhead in the Columbia River basin. All fish from the run years 2005/2006 through 2014/2015 were pooled. Overshoot rates are the proportion of fish seen at the overshoot dam, or at any site above it, out of the total number of fish that were seen at Bonneville Dam (N). Proportions have not been corrected by detection probabilities at the dams.

APPENDIX G.—Fallback rates to home

TABLE G.1.—Fallback rates to home of John Day wild steelhead. Fallback rates are adjusted by detection efficiencies in the home tributary. Fallback to home can occur along any pathway, including fish that overshoot further and then fallback to home. Rates not estimated either did not have sufficient numbers of fish, or did not have sufficient detection ability in the home tributary to estimate home efficiency. Parentheses contain ±2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
MCN → HOME	--	--	--	29.6% (±8.5%)	37.5% (±6.6%)	26.1% (±7.1%)	--	65.8% (±19.5%)	75.1% (±13.2%)	80.9% (±13.3%)	**52.5%**
ICH → HOME	--	--	--	17.5% (±11.0%)	16.1% (±9.2%)	7.0% (±7.6%)	--	0%	44.8% (±27.3%)	54.3% (±21.4%)	**23.3%**
LGR → HOME	--	--	--	0%	6.2% (±8.3%)	0%	--	0%	21.4% (38.3%)	0%	**4.6%**
PRA → HOME	--	--	--	--	--	42.9% (±36.7%)	--	--	--	--	**42.9%**

TABLE G.2.—Fallback rates to home of Umatilla steelhead. Fallback rates are adjusted by detection efficiencies in the home tributary. Fallback to home can occur along any pathway, including fish that overshoot further and then fallback to home. Rates not estimated either did not have sufficient numbers of fish, or did not have sufficient detection ability in the home tributary to estimate home efficiency. Parentheses contain ±2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
					Hatchery						
MCN → HOME	--	--	--	--	35.6% (±20.9%)	--	--	--	--	18.2% (±22.8%)	**26.9%**
					Wild						
MCN → HOME	--	--	--	--	--	--	--	--	72.4% (±16.3%)	77.5% (±15.9%)	**75.0%**
ICH → HOME	--	--	--	--	--	--	--	--	--	39.4% (±24.2%)	**39.4%**

TABLE G.3.—Fallback rates to home of Walla Walla steelhead. Fallback rates are adjusted by detection efficiencies in the home tributary. Fallback to home can occur along any pathway, including fish that overshoot further and then fallback to home. Rates not estimated either did not have sufficient numbers of fish, or did not have sufficient detection ability in the home tributary to estimate home efficiency. Parentheses contain ±2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
					Hatchery						
ICH → HOME	--	--	22.3% (±5.0%)	19.3% (±18.9%)	20.1% (±10.7%)	10.7% (±9.7%)	10.8% (±6.1%)	22.6% (±14.2%)	23.9% (±12.3%)	12.9% (±6.3%)	**17.8%**
LGR → HOME	--	--	--	0%	8.4% (±7.9%)	0%	7.3% (±8.1%)	--	23.0% (±18.5%)	2.3% (±4.5%)	**6.8%**
PRA → HOME	--	--	--	--	26.5% (±49.1%)	--	--	--	--	--	**26.5%**
					Wild						
ICH → HOME	--	--	--	--	53.3% (±32.5%)	39.5% (±20.2%)	58.1% (±23.0%)	28.5% (±17.0%)	38.6% (±26.6%)	41.0% (±20.6%)	**43.2%**
LGR → HOME	--	--	--	--	18.9% (±34.5%)	25.0% (±25.8%)	26.7% (±27.7%)	--	--	11.1% (±20.6%)	**20.4%**

TABLE G.4.—Fallback rates to home of upper Columbia steelhead. Fallback rates are adjusted by detection efficiencies in the home tributary. Fallback to home can occur along any pathway, including fish that overshoot further and then fallback to home. Rates not estimated either did not have sufficient numbers of fish, or did not have sufficient detection ability in the home tributary to estimate home efficiency. Parentheses contain ±2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
					Yakima, wild						
PRA → HOME	--	--	--	--	70.3% (±28.5%)	--	--	--	71.4% (±34.1%)	70.2% (±28.5%)	**70.6%**
					Wenatchee, hatchery						
RRE → HOME	--	--	--	--	--	--	31.4% (±7.0%)	29.4% (±6.3%)	13.7% (±9.5%)	30.6% (±18.9%)	**26.3%**
WEL → HOME	--	--	--	--	--	--	19.8% (±7.2%)	16.8% (±6.3%)	4.7% (±6.3%)	23.7% (±20.3%)	**16.2%**
					Entiat, wild						
WEL → HOME	--	--	--	--	56.4% (±19.1%)	58.7% (±26.7%)	67.0% (±21.9%)	60.2% (±30.5%)	93.4% (±12.6%)	59.2% (±20.1%)	**65.8%**

TABLE G.5.—Fallback rates to home of Snake River steelhead. Fallback rates are adjusted by detection efficiencies in the home tributary. Fallback to home can occur along any pathway, including fish that overshoot further and then fallback to home. Rates not estimated either did not have sufficient numbers of fish, or did not have sufficient detection ability in the home tributary to estimate home efficiency. Parentheses contain ±2 standard errors.

	Run Year										
	05/06	06/07	07/08	08/09	09/10	10/11	11/12	12/13	13/14	14/15	**Mean**
					Tucannon, hatchery						
LGR → HOME	--	28.0% (±27.0%)	13.0% (±23.7%)	--	22.9% (±5.0%)	22.8% (±7.8%)	31.4% (±12.0%)	40.1% (±17.8%)	69.3% (±14.6%)	34.8% (±13.9%)	**32.8%**
PRA → HOME	--	--	--	--	35.6% (±28.5%)	--	--	--	--	--	**35.6%**
					Tucannon, wild						
LGR → HOME	--	7.7% (±14.5%)	18.7% (±23.5%)	--	14.8% (±13.4%)	24.3% (±27.0%)	32.2% (±19.7%)	27.1% (±17.2%)	28.0% (±27.0%)	9.9% (±10.7%)	**20.3%**
					Imnaha, hatchery						
PRA → HOME	--	--	--	--	--	--	--	--	9.1% (±4.3%)	27.3% (±17.2%)	**18.2%**

Naturally, fallback to home rates drop as steelhead overshoot more dams further from their natal stream (Figure G.1). Steelhead that overshoot multiple dams must then fall back successfully through multiple dams to reach home, which compounds injury and mortality risks. Additionally, steelhead with poorer homing capabilities may tend to overshoot further distances, and may be inherently less likely to attempt to fall back. Distance between the overshoot dam and the mouth of the home tributary also shows an inverse relationship with fallback to home. Distance effects are inseparable from the number of dams overshot.

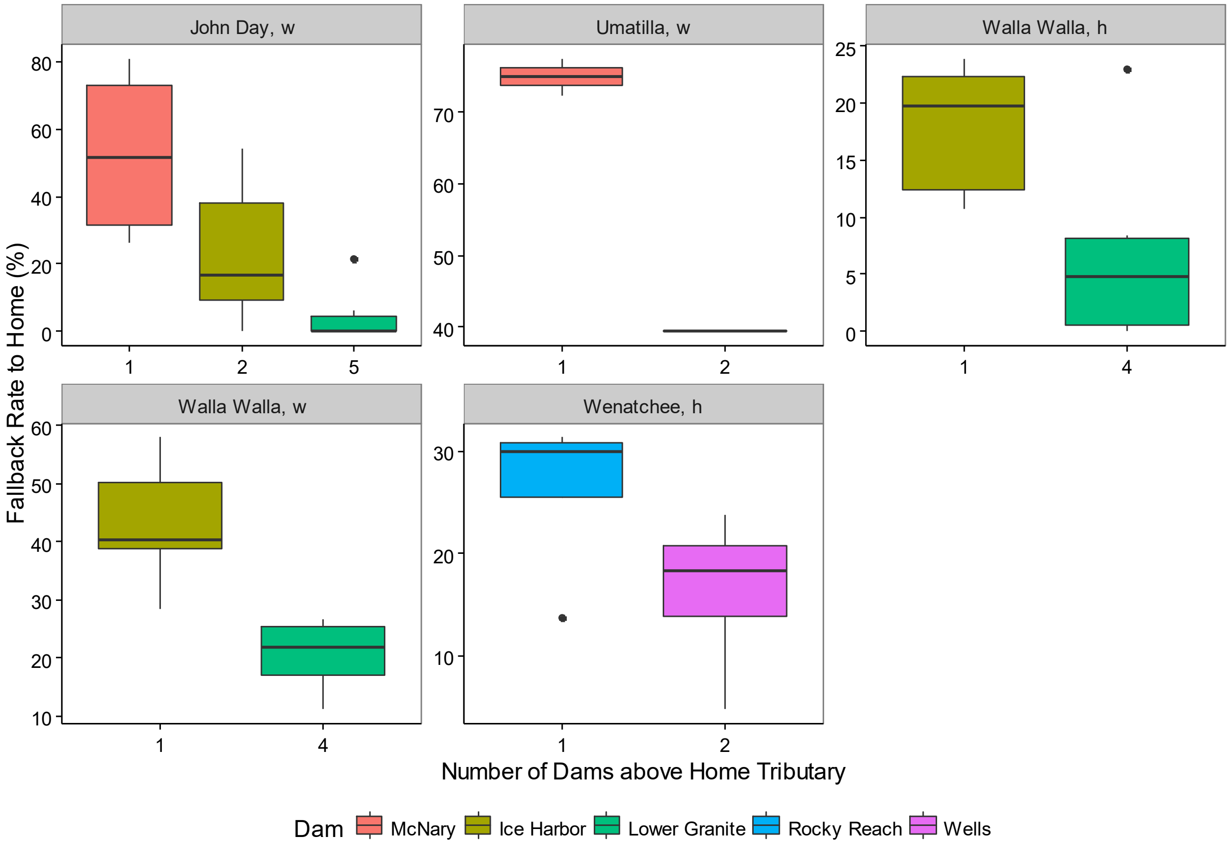

FIGURE G.1.—Fallback rates to home versus number of dams overshot. Fallback rates were adjusted by detection efficiencies in the home tributary. Fallback rates are along any path, and include fish that overshot further upstream and then fell back.

It is difficult to compare fallback in the Columbia and Snake rivers because of tremendous inter-population variation. However, fallback to home rates for populations that overshot in both rivers seem to indicate that fallback to home rates after overshooting Priest Rapids may be higher than fallback after overshooting Ice Harbor (Figure G.2). Unfortunately, neither population had samples larger than five overshoot Priest Rapids in more than one year.

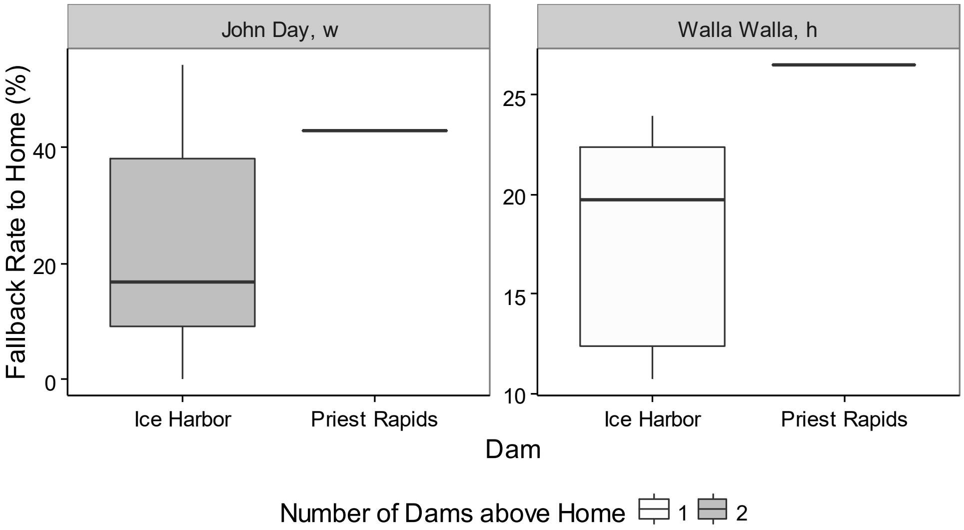

FIGURE G.2.—Fallback rates to home after overshooting Priest Rapids and Ice Harbor for populations that overshot in both the upper Columbia and Snake rivers. Fallback rates are adjusted by detection efficiencies in the home tributary. Fallback rates are along any path, and include fish that overshot further and then fell back.

APPENDIX H.—Alternative spawning sites

TABLE H.1.—Fates of John Day wild steelhead that overshot McNary Dam. Fallback to home estimates are adjusted by estimates of detection efficiencies at home. Years where detection efficiency at home was not estimable are not included. Percent of fish observed at up and downstream tributaries or hatcheries after overshooting is not adjusted by detection efficiencies. Primary up and downstream tributaries are the locations steelhead strayed to the most in that year.

			Alternative Site				
			Upstream		**Downstream**		
Run Year	# Overshot	**Fell back Home**	Observed	Primary Tributary	Observed	Primary Tributary	**Undetermined Loss**
2008/2009	112	29.6%	4.5%	Grande Ronde/Yakima	6.3%	Umatilla	59.7%
2009/2010	212	37.5%	6.1%	Grande Ronde	0.5%	Umatilla	55.9%
2010/2011	146	26.1%	2.1%	Grande Ronde	4.1%	Umatilla	67.7%
2012/2013	80	65.8%	6.3%	Grande Ronde	0%		28.0%
2013/2014	157	75.1%	3.2%	Grande Ronde/Walla Walla	4.5%	Umatilla	17.3%
2014/2015	131	80.9%	1.5%	Grande Ronde/Tucannon	1.5%	Umatilla	16.0%
All Years	**838**	**52.5%**	**3.9%**	**Grande Ronde**	**2.8%**	**Umatilla**	**40.8%**

TABLE H.2.—Fates of Umatilla hatchery steelhead that overshot McNary Dam. Fallback to home estimates are adjusted by estimates of detection efficiencies at home. Years where detection efficiency at home was not estimable are not included. Percent of fish observed at up and downstream tributaries or hatcheries after overshooting is not adjusted by detection efficiencies. Primary upstream tributaries are the locations steelhead strayed to the most in that year.

			Alternative Site			
			Upstream		**Downstream**	
Run Year	# Overshot	**Fell back Home**	Observed	Primary Tributary	Observed	**Undetermined Loss**
2009/2010	41	35.6%	2.4%	Walla Walla	0%	62.0%
2014/2015	11	18.2%	0%		0%	81.8%
All Years	**52**	**26.9%**	**1.2%**	**Walla Walla**	**0%**	**71.9%**

TABLE H.3.—Fates of Umatilla wild steelhead that overshot McNary Dam. Fallback to home estimates are adjusted by estimates of detection efficiencies at home. Years where detection efficiency at home was not estimable are not included. Percent of fish observed at up and downstream tributaries or hatcheries after overshooting is not adjusted by detection efficiencies. Primary upstream tributaries are the locations steelhead strayed to the most in that year.

			Alternative Site			
			Upstream		**Downstream**	
Run Year	# Overshot	**Fell back Home**	Observed	Primary Tributary	Observed	**Undetermined Loss**
2013/2014	29	72.4%	10.3%	Yakima	0%	17.3%
2014/2015	67	77.5%	6.0%	Tucannon	0%	16.5%
All Years	**96**	**75.0%**	**8.2%**	**Tucannon**	**0%**	**16.9%**

TABLE H.4.—Fates of Walla Walla hatchery steelhead that overshot Ice Harbor or Priest Rapids dams. Fallback to home estimates are adjusted by estimates of detection efficiencies at home. Years where detection efficiency at home was not estimable are not included. Percent of fish observed at up and downstream tributaries or hatcheries after overshooting is not adjusted by detection efficiencies. Primary upstream tributaries are the locations steelhead strayed to the most in that year.

			Alternative Site			
			Upstream		**Downstream**	
Run Year	# Overshot	**Fell back Home**	Observed	Primary Tributary	Observed	**Undetermined Loss**
2007/2008	10	22.3%	40.0%	Tucannon	0%	37.7%
2008/2009	187	19.3%	9.1%	Tucannon	0%	71.6%
2009/2010	249	20.1%	38.6%	Lyon's Ferry Hatchery	0%	41.3%
2010/2011	134	10.7%	6.0%	Tucannon	0%	83.3%
2011/2012	158	10.8%	29.7%	Tucannon	0%	59.5%
2012/2013	58	22.6%	37.9%	Tucannon	0%	39.5%
2013/2014	65	23.9%	4.6%	Tucannon	0%	71.5%
2014/2015	112	12.9%	13.4%	Tucannon	0%	73.7%
All Years	**973**	**17.8%**	**22.4%**	**Tucannon**	**0%**	**59.8%**

TABLE H.5.—Fates of Walla Walla wild steelhead that overshot Ice Harbor or Priest Rapids dams. Fallback to home estimates are adjusted by estimates of detection efficiencies at home. Years where detection efficiency at home was not estimable are not included. Percent of fish observed at up and downstream tributaries or hatcheries after overshooting is not adjusted by detection efficiencies. Primary upstream tributaries are the locations steelhead strayed to the most in that year.

			Alternative Site			
			Upstream		**Downstream**	
Run Year	# Overshot	**Fell back Home**	Observed	Primary Tributary	Observed	**Undetermined Loss**
2009/2010	18	53.3%	27.8%	Tucannon/Clearwater	0%	18.9%
2010/2011	40	39.5%	20.0%	Tucannon	0%	40.5%
2011/2012	47	58.1%	25.5%	Tucannon	0%	16.4%
2012/2013	30	28.5%	36.7%	Tucannon	0%	34.8%
2013/2014	13	38.6%	23.1%	Tucannon	0%	38.3%
2014/2015	22	41.0%	22.7%	Tucannon/Alpowa	0%	36.3%
All Years	**170**	**43.2%**	**26.0%**	**Tucannon**	**0%**	**30.9%**

TABLE H.6.—Fates of Yakima wild steelhead that overshot Priest Rapids Dam. Fallback to home estimates are adjusted by estimates of detection efficiencies at home. Years where detection efficiency at home was not estimable are not included. Percent of fish observed at up and downstream tributaries or hatcheries after overshooting is not adjusted by detection efficiencies. Primary upstream tributaries are the locations steelhead strayed to the most in that year.

			Alternative Site			
			Upstream		**Downstream**	
Run Year	# Overshot	**Fell back Home**	Observed	Primary Tributary	Observed	**Undetermined Loss**
2014/2015	11	70.2%	9.1%	Wenatchee	0%	20.7%
All Years	**11**	**70.2%**	**9.1%**	**Wenatchee**	**0%**	**20.7%**

TABLE H.7.—Fates of Wenatchee hatchery steelhead that overshot Rocky Reach Dam. Fallback to home estimates are adjusted by estimates of detection efficiencies at home. Years where detection efficiency at home was not estimable are not included. Percent of fish observed at up and downstream tributaries or hatcheries after overshooting is not adjusted by detection efficiencies. Primary upstream tributaries are the locations steelhead strayed to the most in that year.

			Alternative Site			
			Upstream		**Downstream**	
Run Year	# Overshot	**Fell back Home**	Observed	Primary Tributary	Observed	**Undetermined Loss**
2011/2012	230	31.4%	9.6%	Entiat	0%	59.0%
2012/2013	300	29.4%	7.7%	Methow	0%	62.9%
2013/2014	53	13.7%	22.6%	Methow	0%	63.7%
2014/2015	24	30.6%	20.8%	Methow/Entiat	0%	48.6%
All Years	**607**	**26.3%**	**15.2%**	**Methow**	**0%**	**58.5%**

TABLE H.8.—Fates of Entiat wild steelhead that overshot Wells Dam. Fallback to home estimates are adjusted by estimates of detection efficiencies at home. Years where detection efficiency at home was not estimable are not included. Percent of fish observed at up and downstream tributaries or hatcheries after overshooting is not adjusted by detection efficiencies. Primary upstream tributaries are the locations steelhead strayed to the most in that year.

			Alternative Site			
			Upstream		**Downstream**	
Run Year	# Overshot	**Fell back Home**	Observed	Primary Tributary	Observed	**Undetermined Loss**
2009/2010	27	56.4%	33.3%	Methow	0%	10.3%
2010/2011	14	58.7%	14.3%	Methow/Okanogan	0%	27.0%
2011/2012	18	67.0%	5.6%	Methow	0%	27.4%
2012/2013	10	60.2%	0%		0%	39.8%
2013/2014	15	93.4%	0%		0%	6.6%
2014/2015	24	59.2%	12.5%	Methow	0%	28.3%
All Years	**108**	**65.8%**	**10.9%**	**Methow**	**0%**	**23.2%**

TABLE H.9.—Fates of Tucannon hatchery steelhead that overshot Lower Granite or Priest Rapids dams. Fallback to home estimates are adjusted by estimates of detection efficiencies at home. Years where detection efficiency at home was not estimable are not included. Percent of fish observed at up and downstream tributaries or hatcheries after overshooting is not adjusted by detection efficiencies. Primary up and downstream tributaries are the locations steelhead strayed to the most in that year.

			Alternative Site				
			Upstream		**Downstream**		
Run Year	# Overshot	**Fell back Home**	Observed	Primary Tributary	Observed	Primary Tributary	**Undetermined Loss**
2006/2007	38	28.0%	2.6%	Asotin	0%		69.4%
2007/2008	261	13.0%	1.1%	Asotin	0%		85.9%
2009/2010	320	22.9%	15.3%	Clearwater	0%		61.8%
2010/2011	143	22.8%	8.4%	Asotin/Grande Ronde/Clearwater	0.7%	Almota	68.1%
2011/2012	65	31.4%	12.3%	Asotin	0%		56.3%
2012/2013	32	40.1%	12.5%	Clearwater	6.3%	Lyon's Ferry/Penawawa	41.2%
2013/2014	49	69.3%	6.1%	Grande Ronde	2.0%	Almota	22.5%
2014/2015	54	34.8%	20.4%	Asotin	0%		44.8%
All Years	**962**	**32.8%**	**9.8%**	**Asotin**	**1.1%**	**Almota**	**56.2%**

TABLE H.10.—Fates of Tucannon wild steelhead that overshot Lower Granite or Priest Rapids dams. Fallback to home estimates are adjusted by estimates of detection efficiencies at home. Years where detection efficiency at home was not estimable are not included. Percent of fish observed at up and downstream tributaries or hatcheries after overshooting is not adjusted by detection efficiencies. Primary upstream tributaries are the locations steelhead strayed to the most in that year.

			Alternative Site			
			Upstream		**Downstream**	
Run Year	# Overshot	**Fell back Home**	Observed	Primary Tributary	Observed	**Undetermined Loss**
2006/2007	13	7.7%	7.7%	Asotin	0%	84.6%
2007/2008	13	18.7%	15.4%	Asotin/Methow	0%	65.9%
2009/2010	27	14.8%	44.4%	Asotin	0%	40.8%
2010/2011	19	24.3%	26.3%	Alpowa	0%	49.4%
2011/2012	23	32.2%	30.4%	Asotin	0%	37.4%
2012/2013	26	27.1%	34.6%	Alpowa/Asotin	0%	38.3%
2013/2014	23	28.0%	34.8%	Alpowa	0%	37.2%
2014/2015	33	9.9%	39.4%	Asotin	0%	50.7%
All Years	**177**	**20.3%**	**29.1%**	**Asotin**	**0%**	**50.5%**

TABLE H.11.—Fates of Imnaha hatchery steelhead that overshot Priest Rapids Dam. Fallback to home estimates are adjusted by estimates of detection efficiencies at home. Years where detection efficiency at home was not estimable are not included. Percent of fish observed at up and downstream tributaries or hatcheries after overshooting is not adjusted by detection efficiencies. Primary upstream tributaries are the locations steelhead strayed to the most in that year.

			Alternative Site			
			Upstream		**Downstream**	
Run Year	# Overshot	**Fell back Home**	Observed	Primary Tributary	Observed	**Undetermined Loss**
2013/2014	12	19.5%	8.3%	Okanogan	0%	72.2%
2014/2015	10	50.0%	10.0%	Wenatchee	0%	40.0%
All Years	**22**	**34.8%**	**9.2%**	**Okanogan/Wenatchee**	**0%**	**56.1%**

APPENDIX I.—Influence of juvenile experiences by tributary

John Day.—John Day River steelhead in this study were all of natural origin. Since the John Day River is below dams where collection for barging occurs, all steelhead out-migrated in-river. Nearly all (94.2%) adult migrants reentered freshwater 1 or 2 years after ocean entry (Figure I.1). Run timing distributions were very similar between ocean age 1 and 2 steelhead (Figure I.2). In Chapter 2, I estimated that on average 53.3% (SE 2.4%) of John Day River steelhead that passed Bonneville Dam went on to overshoot McNary Dam.

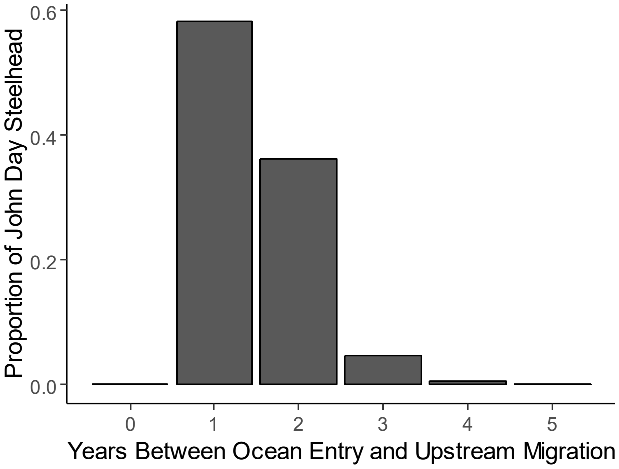

FIGURE I.1.—Ocean ages of PIT-tagged John Day River steelhead that migrated upstream 2005/2006 to 2014/2015.

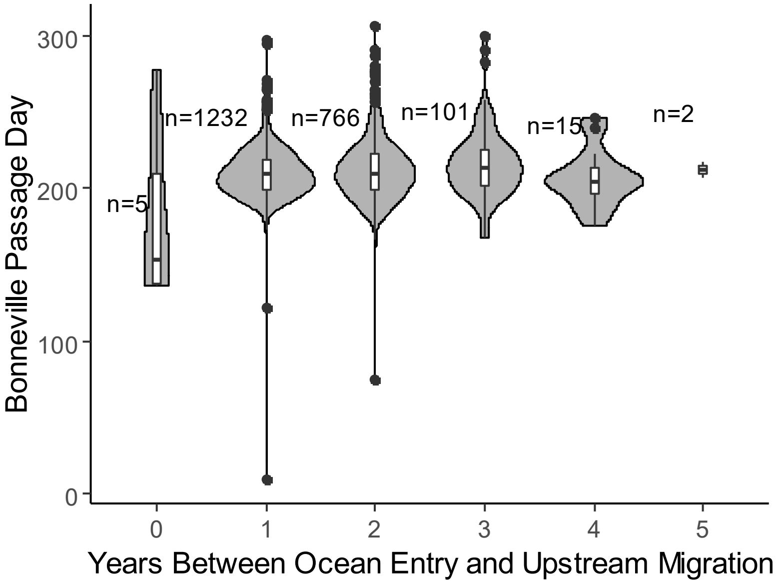

FIGURE I.2. Violin and box plots of overshoot timing (at McNary Dam) by John Day River steelhead of each ocean age. Bonneville passage day is the calendar day of the year. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value.

Within the John Day steelhead population, longer ocean residency significantly increased the probability of overshooting ($F_{1,2108} = 4.29$, $P = 0.019$). Steelhead that reentered freshwater two years after ocean entry displayed, on average, a 4 percentage point increase in overshooting relative to steelhead that reentered freshwater after only one year. However, a significant interaction between passage date and ocean age was also found (Table I.1, Figure I.3). Ocean age did not significantly affect the probability of moving directly to home ($F_{1,1524} = 2.32$, $P = 0.128$), falling back to home after overshooting ($F_{1,831} = 0.04$, $P = 0.851$), or the overall migration success ($F_{1,1524} = 0.10$, $P = 0.754$). An early migration stage was not modeled because dams between Bonneville and the John Day River did not possess adult PIT-tag arrays from 2005—2015.

TABLE I.1.—Final models of John Day River steelhead migratory behavior. Year was included as a blocking factor. Potential variables included Day and Ocean Age. AUC = area under the curve, Year = run year, Day = passage day, Ocean Age = number of years spent in ocean. P-value for variable entry was P = 0.05.

Migration Stage	**N**	**Final Model**	**AUC**
Go Directly Home	1531	~ Year + Day + Day^2 + Day^3	0.640
Overshoot	2121	~ Year + Day + Day^2 + Ocean Age + Day*Ocean Age + Day^2*Ocean Age	0.629
Fallback Home	838	~ Year	0.665
Overall Success	1531	~ Year	0.574

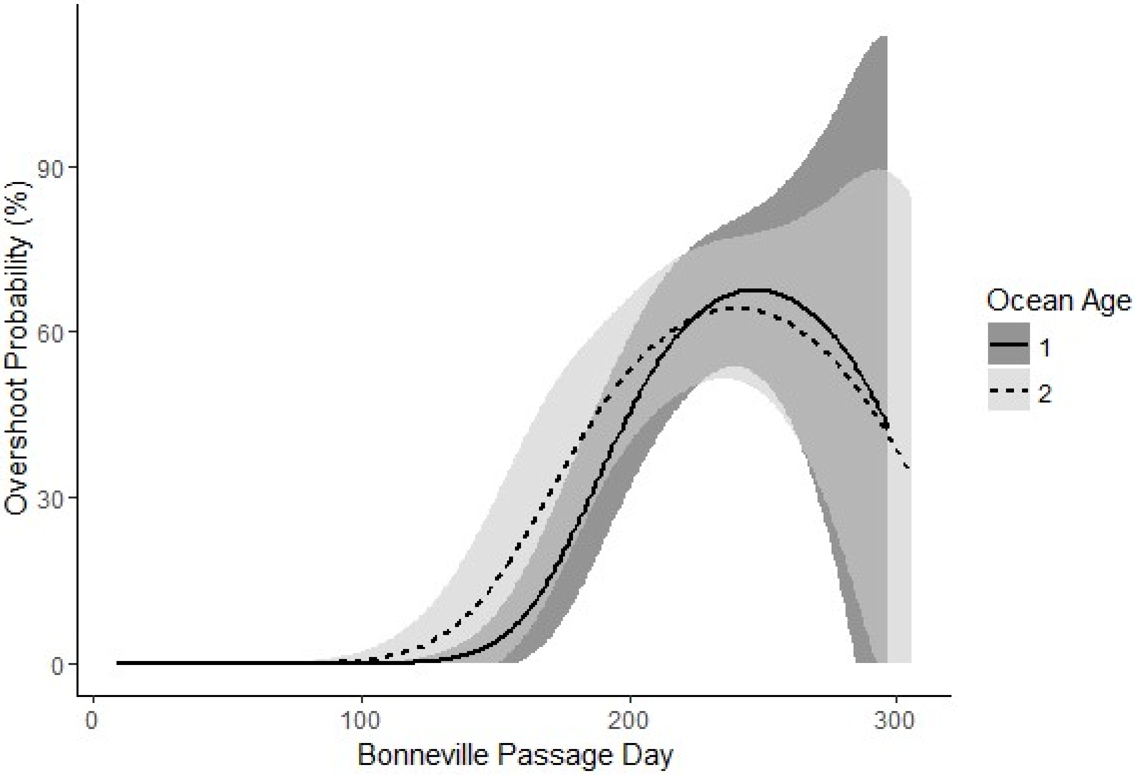

FIGURE I.3.—Predicted probability of overshooting McNary Dam, and 90% confidence interval, for John Day River steelhead that spent one or two years in the ocean. Baseline is steelhead that returned to freshwater in the run year 2014/2015. Bonneville Passage Day = Julian calendar day of the year of Bonneville Dam passage.

Umatilla.—Umatilla River steelhead included both natural and hatchery origin steelhead. All hatchery origin fish were marked at the Irrigon and Umatilla hatcheries, slightly downstream of the Umatilla River. Run timing of natural and hatchery origin steelhead was comparable (Figure I.4), with the hatchery stock delayed only slightly. In Chapter 2, I estimated that, on average, 31.1% (SE 5.6%) of hatchery and 43.6% (SE 5.1%) of natural origin Umatilla steelhead overshot McNary each year.

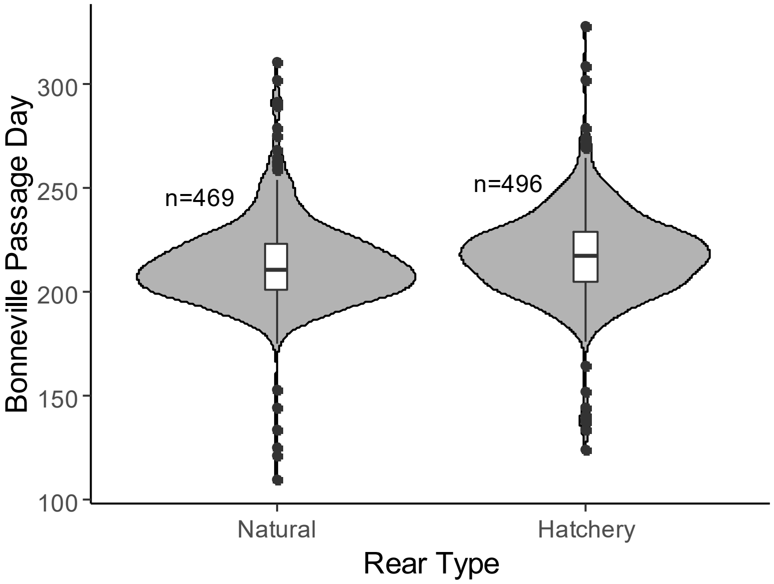

FIGURE I.4. Violin and box plots of overshoot timing (at McNary Dam) by Umatilla River steelhead of natural and hatchery rear types. Bonneville passage day is the calendar day of the year. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value.

Nearly all (97.6%) of Umatilla River steelhead reentered freshwater one or two years after their juvenile out-migration (Figure I.5). Run timing between ocean age 1 and 2 steelhead was similar (Figure I.6). Since the Umatilla River is below McNary, the last dam where fish are collected for barging, no Umatilla River steelhead were barged as juveniles.

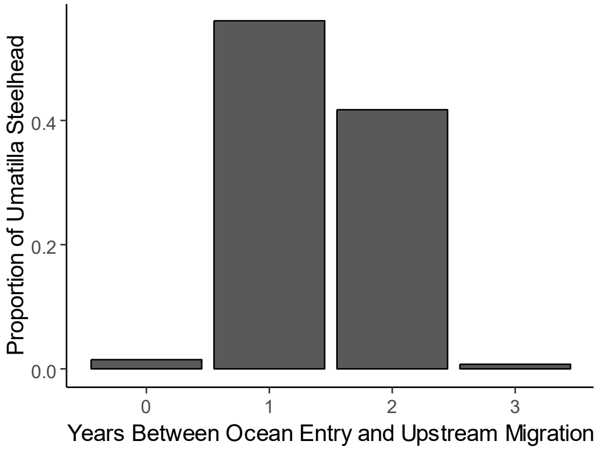

FIGURE I.5. Ocean ages of PIT-tagged Umatilla River steelhead that migrated upstream 2005/2006 to 2014/2015.

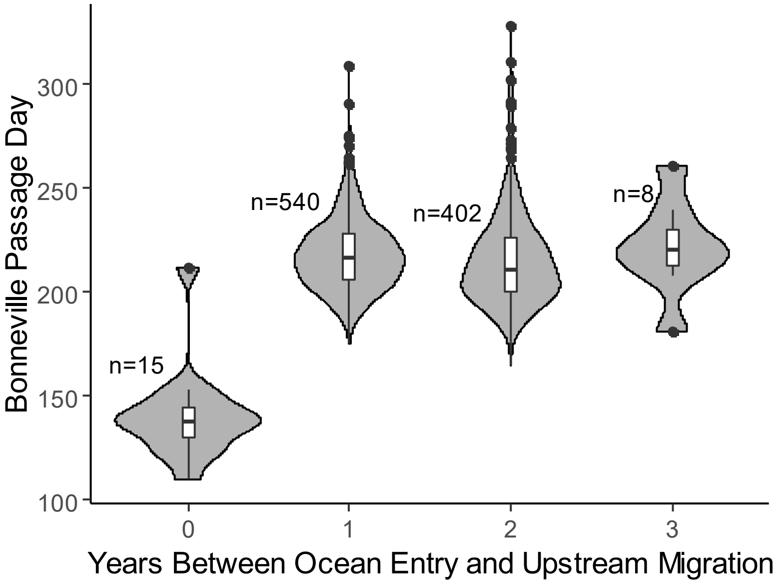

FIGURE I.6. Violin and box plots of Bonneville passage timing by Umatilla River steelhead of different ocean ages. Passage day is the calendar day of the year. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value.

Hatchery reared fish overshot at similar rates to naturally reared steelhead, but were less likely to return to home. Hatchery rearing significantly decreased the probability of moving directly to home ($F_{1,950}$ = 6.98, P = 0.004, Table H.2), falling back to home after overshooting ($F_{1,342}$ = 12.18, P = 0.0001), and moving along any route from Bonneville Dam to the Umatilla River ($F_{1,951}$ = 32.67, P < 0.0001). Hatchery rearing was associated with a 8 percentage point decline in returning directly to home, 26 percentage point decline in falling back to home, and 22 percentage point decline in successfully migrating from Bonneville to home along any pathway. In the fallback to home model, there was a significant interaction between rear type and overshoot timing, though wild steelhead were always more likely to fall back to home (Figure I.7). While hatchery steelhead were less likely to move directly to home, they were not significantly more or less likely to overshoot than natural origin fish ($F_{1,953} = 2.05$, $P = 0.153$). This suggests that movement rates between the two stocks are actually similar, but that harvest pressure on hatchery fish in the mainstem river after the summer overshooting period results in reduced movement to home in spring.

TABLE I.2.—Final models of Umatilla River steelhead migratory behavior. Year included as a blocking factor. Potential variables included Day, Rearing, and Ocean Age. AUC = area under the curve, Year = run year, Day = passage day, Rearing = hatchery/natural origin, Ocean Age = number of years spent in ocean. P-value for variable entry was P = 0.05.

Migration Stage	**N**	**Final Model**	**AUC**
Go Directly Home	965	~ Year + Day + Day^2 + Day^3 + Rearing + Ocean Age	0.706
Overshoot	965	~ Year + Ocean Age	0.565
Fallback Home	355	~ Year + Day + Day^2 + Rearing + Day*Rearing + Day^2*Rearing	0.810
Overall Success	965	~ Year + Day + Day^2 + Day^3 + Rearing	0.753

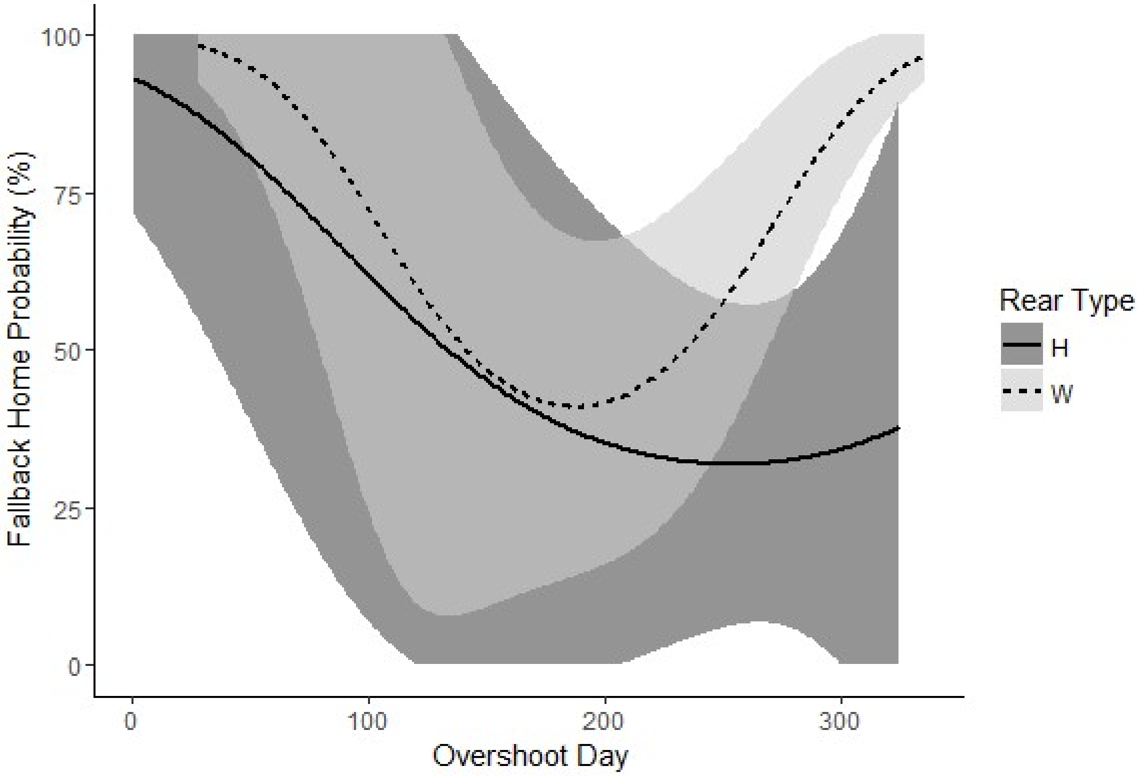

FIGURE I.7.—Predicted probability of falling back to home after overshooting McNary Dam, and 90% confidence interval, for hatchery (H) and natural (W) origin Umatilla River steelhead. Baseline is steelhead that returned to freshwater in the run year 2014/2015. Overshoot Day = Julian calendar day of the year of McNary Dam passage.

Ocean age produced smaller effects than hatchery rearing. Longer ocean residency led to reduced homing, but not enough to affect overall success. Increased ocean age significantly decreased migration directly to home ($F_{1,950} = 4.74$, $P = 0.015$) and increased the likelihood of overshooting ($F_{1,954} = 5.34$, $P = 0.011$). Umatilla River steelhead that remained in the ocean for two years had rates of direct migration to home 6 percentage points lower and overshooting rates 8 percentage points higher than steelhead that reentered freshwater after a single year in the ocean (Figure I.8). Ocean age did not significantly affect fallback to home ($F_{1,339} = 0.60$, $P = 0.440$) or overall success ($F_{1,950} = 2.18$, $P = 0.140$, Table H.2). An early migration stage was not modeled because dams between Bonneville and the Umatilla River did not possess adult PIT-tag arrays from 2005—2015.

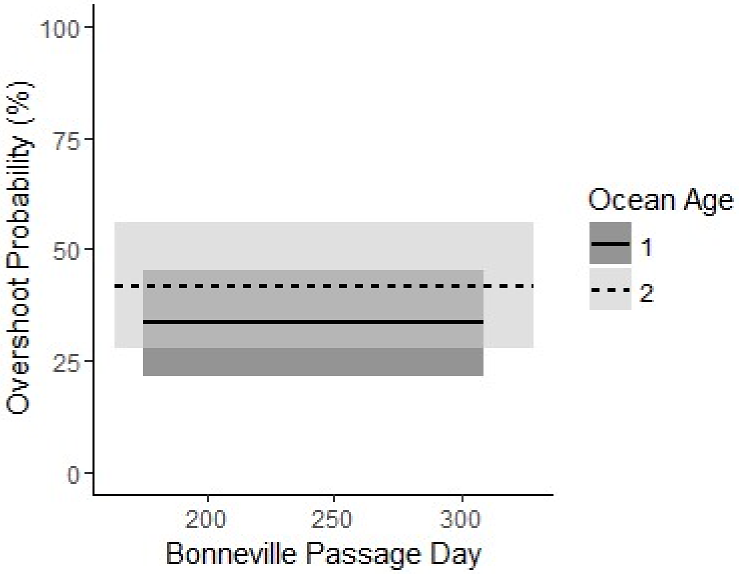

FIGURE I.8.—Predicted probability of overshooting McNary Dam, and 90% confidence interval, for Umatilla River steelhead. Baseline is steelhead that spent that returned to freshwater in the run year 2014/2015. Bonneville Passage Day = Julian calendar day of Bonneville Dam passage.

Walla Walla.—Walla Walla steelhead varied by rearing history and ocean ages. In Chapter 2, I estimated that, on average, 46.9% (SE 5.5%) of natural origin and 66.4% (SE 5.0%) of hatchery origin Walla Walla steelhead that pass McNary Dam go on to overshoot Ice Harbor Dam. In this Chapter, I further divided Walla Walla steelhead into three distinct rearing types: natural, endemic hatchery, and non-endemic hatchery. Hatchery stocks were reared at Lyon’s Ferry hatchery, which is located on the Snake River 108 rkm upstream of the Walla Walla River. While both hatchery stocks were raised at Lyon’s Ferry hatchery, the endemic stock is derived from wild Walla Walla steelhead while the non-endemic, or "Lyon's Ferry" stock, is derived from out-of-basin steelhead, primarily from the upper Columbia. The endemic stock is annually integrated with wild origin fish, and has run timings almost identical to the natural stock. In contrast, the segregated Lyon's Ferry stock generally runs over a month earlier (Figure I.9). Fin clipping was performed on the Lyon's Ferry stock, marking them as available for harvest by recreational fishing. Steelhead from the endemic hatchery stock were not marked, and were therefore not available to harvest.

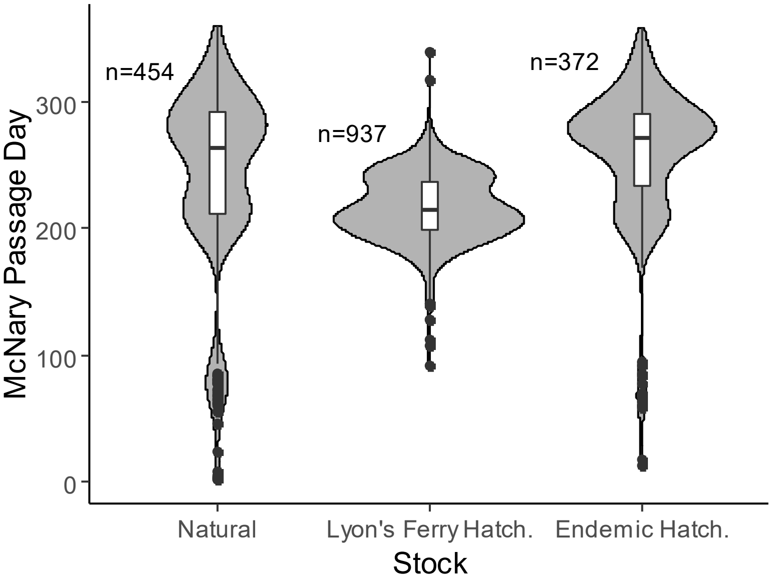

FIGURE I.9.—Violin and box plots of McNary Dam passage timing by Walla Walla River steelhead in each stock. Box plots show median values (vertical line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (circles). Violin plots show the probability density of data at each value. Passage day is the calendar day of the year.

Most (67.7%) of adult Walla Walla steelhead migrants returned to freshwater one year after ocean entry, while 30.1% returned after two years in the ocean (Figure I.10). Steelhead that spent two years in the ocean returned slightly earlier in the season than steelhead that returned after one year (Figure I.11). While collection for juvenile barging does occur at McNary dam, no PIT-tagged Walla Walla steelhead were identified as having been barged.

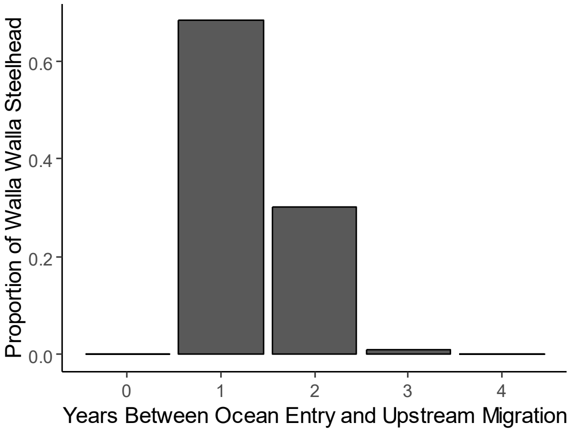

FIGURE I.10. Ocean ages of PIT-tagged Walla Walla River steelhead that migrated upstream 2005/2006 to 2014/2015.

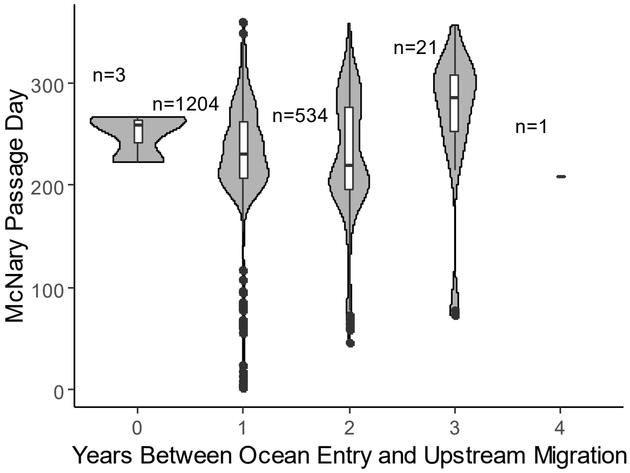

FIGURE I.11. Violin and box plots of run timing (at McNary Dam) by Walla Walla River steelhead of different ocean ages. Passage day is the calendar day of the year. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value.

Rearing history produced significant effects in each migration stage, including early migration ($F_{1,2188} = 8.08$, $P = 0.005$), movement directly to home ($F_{2,1736} = 41.07$, $P < 0.0001$), overshooting ($F_{2,1744} = 32.75$, $P < 0.0001$), falling back to home ($F_{2,1142} = 22.41$, $P < 0.0001$), and overall success ($F_{2,2181} = 199.21$, $P < 0.0001$). While both hatchery stocks performed poorer than natural origin steelhead, the endemic stock performed more similarly to natural origin steelhead than the Lyon's Ferry stock. The endemic hatchery stock may be expected to perform similarly to the natural origin stock, due to genetic and run timing similarities. Remaining differences between the endemic and natural origin stock may be due to differences in rearing history or harvest pressure.

TABLE I.3.—Final models of Walla Walla River steelhead migratory behavior. Year was included as a blocking factor. Potential variables included Day, Rearing, and Ocean Age. AUC = area under the curve, Year = run year, Day = passage day, Rearing = Lyon's Ferry hatchery/endemic hatchery/natural origin, Ocean Age = number of years spent in ocean. P-value for variable entry was $P = 0.05$.

Migration Stage	**N**	**Final Model**	**AUC**
Pass McNary	2199	~ Year + Rearing	0.579
Go Directly Home	1763	~ Year + Day + Day^2 + Day^3 + Day^4 + Day^5 + Day^6 + Day^7 + Rearing + Ocean Age + Year*Rearing + Day*Ocean Age + Day^2*Ocean Age + Day^3*Ocean Age + Day^4*Ocean Age + Day^5*Ocean Age + Day^6*Ocean Age + Day^7*Ocean Age	0.908
Overshoot	1763	~ Year + Day + Day^2 + Day^3 + Day^4 + Rearing + Day*Rearing + Day^2*Rearing + Day^3*Rearing + Day^4*Rearing	0.854
Fallback Home	1156	~ Year + Day + Day^2 + Rearing	0.758
Overall Success	2199	~ Year + Day + Day^2 + Rearing + Day*Rearing + Day^2*Rearing	0.800

During the early migration, both the endemic hatchery and Lyon’s Ferry steelhead were less likely to pass McNary Dam, by 6 percentage points. After passing McNary Dam, direct migration to home relative to the natural origin stock was 8 percentage points lower for the endemic hatchery stock and 19 percentage points lower for the Lyon’s Ferry hatchery stock. The endemic stock and natural origin stocks were equally likely to overshoot Ice Harbor Dam, while the Lyon’s Ferry stock was more likely to overshoot by 15 percentage points (Figure I.12). After overshooting, the likelihood of falling back to home compared to the natural stock was 15 percentage points lower for endemic hatchery and 21 percentage points lower for Lyon’s Ferry hatchery steelhead (Figure I.13). These individual stage effects amounted to a decrease in overall success of 16 percentage points for endemic hatchery steelhead and 44 percentage points for Lyon’s Ferry hatchery steelhead. Much of the differences in homing success, particularly for differences in fallback to home rates, may be due to harvest of hatchery steelhead in the mainstem river. However, not all hatchery stocks were fin clipped and open to harvest. The endemic Walla Walla fish were never fin clipped during the study period (personal communication, Joseph Bumgarner, WDFW). Despite not being available to harvest, the Walla Walla endemic stock still had fallback rates 16 percentage points lower on average compared to the naturally reared stock. Therefore, differences in fallback between hatchery and wild stocks cannot be explained by differential harvest pressure alone.

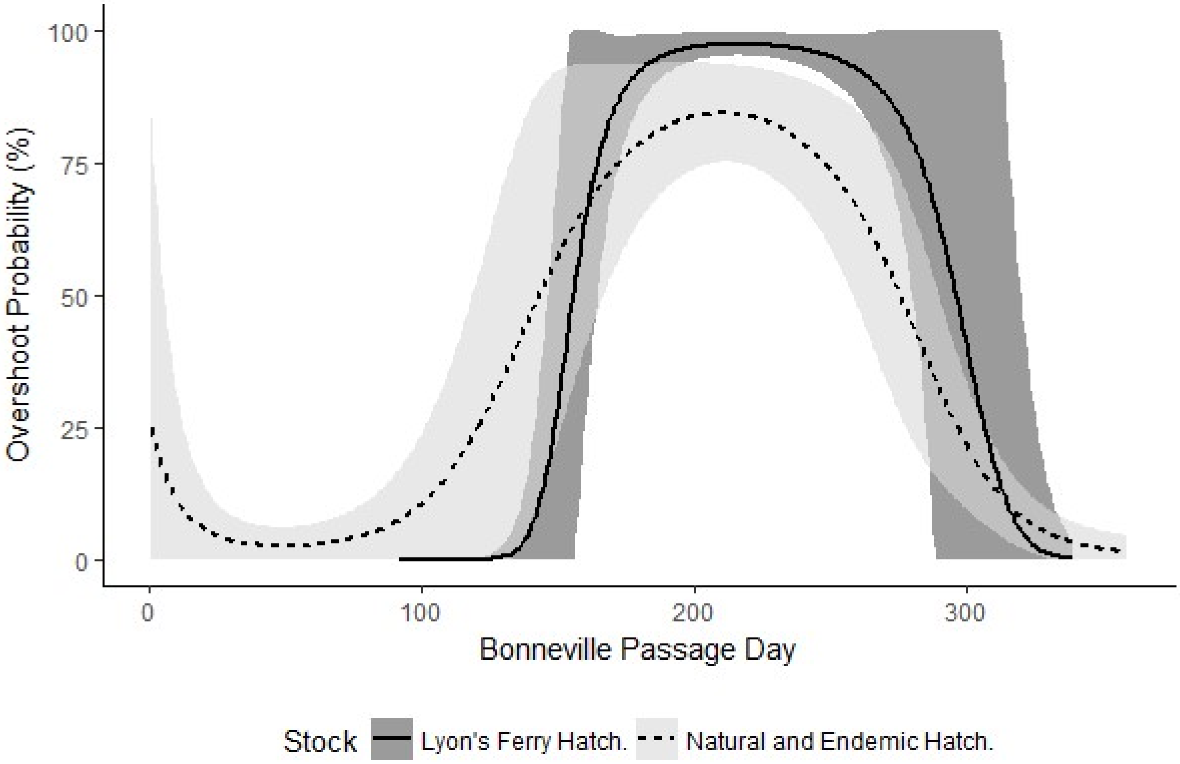

FIGURE I.12.—Predicted probability of overshooting Ice Harbor Dam after passing McNary Dam, and 90% confidence interval, for Walla Walla River steelhead. Baseline is steelhead that that returned to freshwater in the run year 2014/2015. Bonneville Passage Day = Julian calendar day of the year of Bonneville Dam passage.

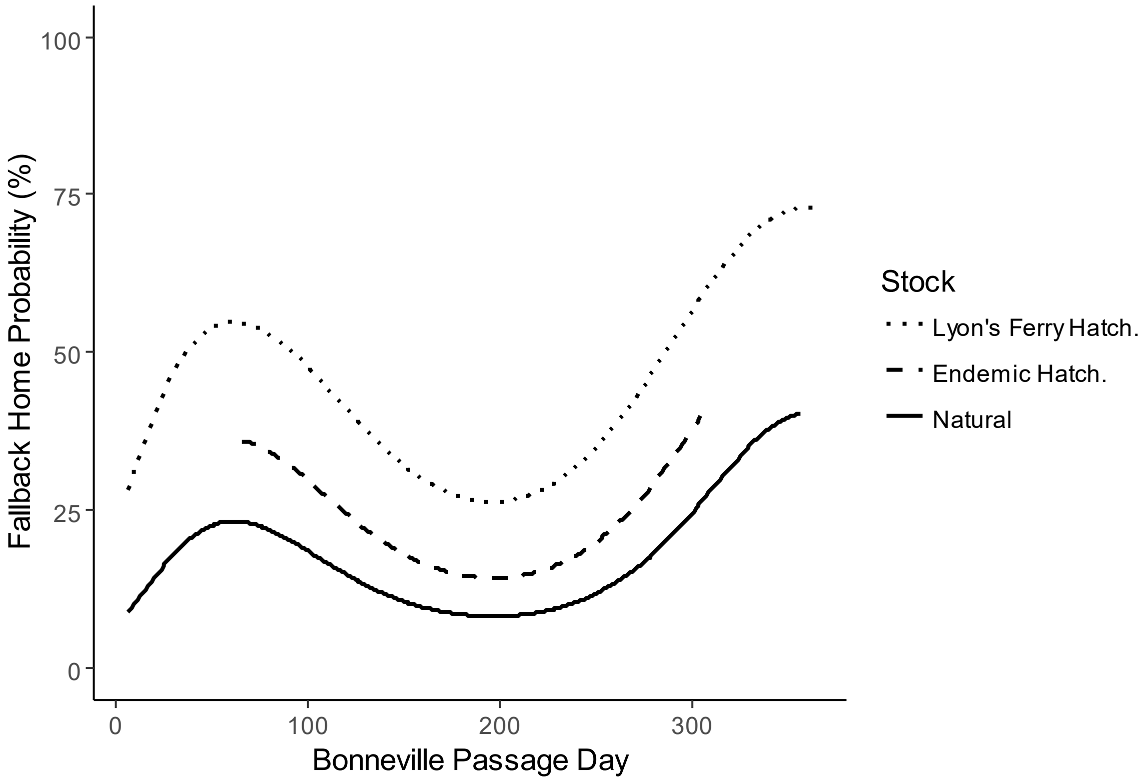

FIGURE I.13.—Predicted probability of falling back to home after overshooting Ice Harbor Dam for Walla Walla River steelhead. Baseline is steelhead that returned to freshwater in the run year 2014/2015 after spending one year in the ocean. Bonneville Passage Day = Julian calendar day of the year of Bonneville Dam passage.

Effects due to ocean age were slight and mostly insignificant. Only one significant effect of ocean residence time was found; longer ocean residency significantly decreased movement directly to home ($F_{1,1728} = 6.75$, $P = 0.005$). Walla Walla steelhead that reentered freshwater two years after ocean entry rather than one experienced a 4 percentage point decline in movement directly to home (Figure I.14). I did not find a significant effect on ocean age for early migration ($F_{1,2187} = 0.81$, $P = 0.367$), overshooting ($F_{1,1723} < 0.01$, $P = 0.978$), fallback to home ($F_{1,1139} = 1.48$, $P = 0.225$), or early success ($F_{1,2180} = 2.24$, $P = 0.135$).

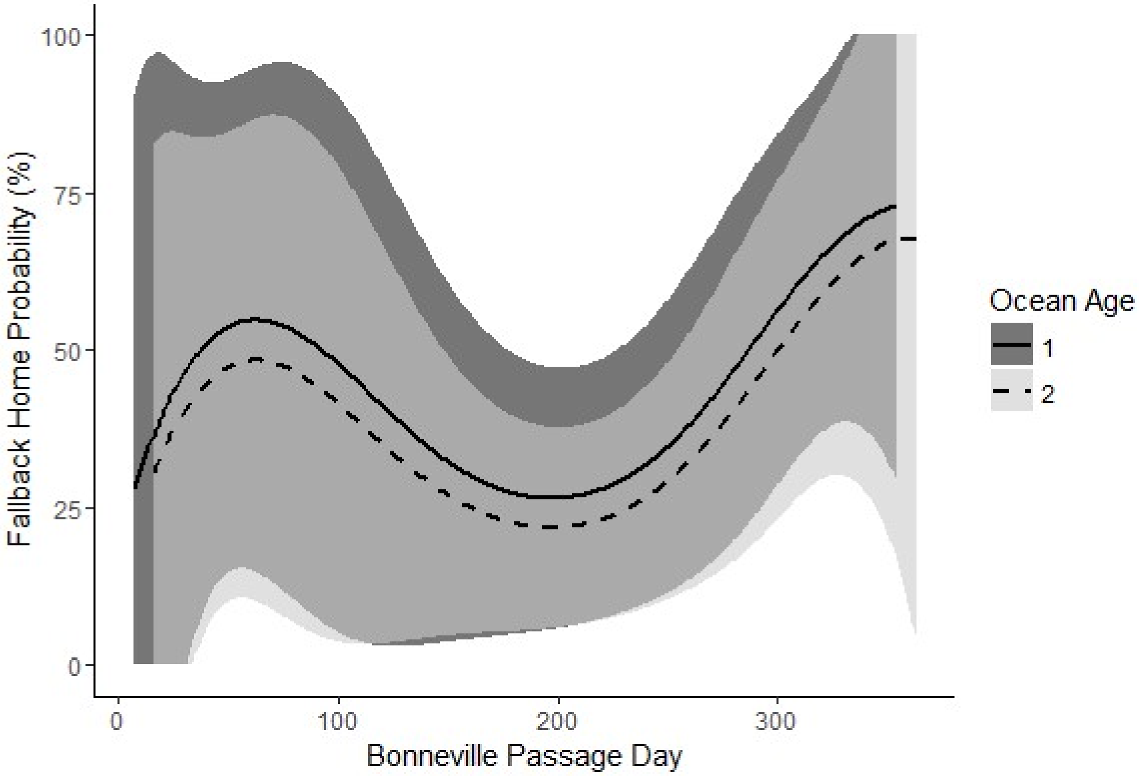

FIGURE I.14.—Predicted probability of falling back to home versus ocean age after overshooting Ice Harbor Dam, and 90% confidence interval, for Walla Walla River steelhead. Baseline is natural origin steelhead that returned to freshwater in the run year 2014/2015. Bonneville Passage Day = Julian calendar day of the year of Bonneville Dam passage.

Yakima.—Yakima River steelhead in this study were all of natural origin. All PIT-tagged Yakima River steelhead were found to have out-migrated as juveniles in-river. Most (90.4%) of Yakima River steelhead returned to freshwater 1 or 2 years after their juvenile out-migration (Figure I.15). Run timing among varied between the age classes, with older steelhead returning earlier (Figure I.16). The median McNary Dam passage date was 10 September for steelhead that spend one year in the ocean and 17 August for steelhead that spent two years.

In Chapter 2, I estimated that on average 16.3% (SE 2.2%) of Yakima River steelhead that passed McNary Dam went on to overshoot Priest Rapids Dam. Here, I found that ocean age did not significantly affect homing during any migration stage (Table H.4), including early migration ($F_{1,288} = 0.54$, $P = 0.464$), movement directly to home ($F_{1,229} = 2.16$, $P = 0.143$), overshooting ($F_{1,229} = 0.88$, $P = 0.348$), fallback to home ($F_{1,29} < 0.01$, $P = 0.949$), and overall success ($F_{1,288} = 1.70$, $P = 0.193$). The Yakima River possessed the smallest sample sizes of any tributary analyzed, likely resulting in limited inferential power.

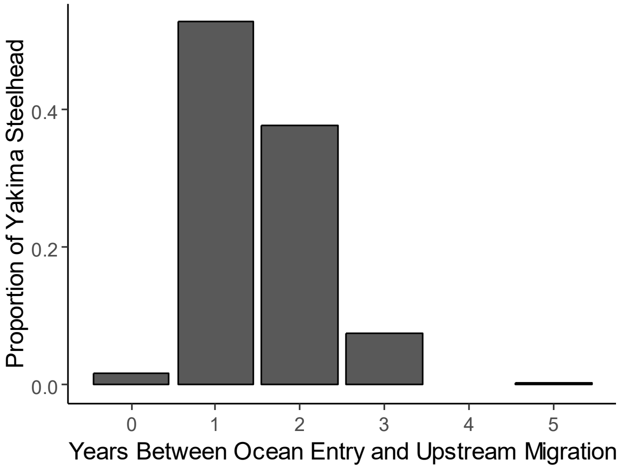

FIGURE I.15.—Ocean ages of PIT-tagged Yakima River steelhead that migrated upstream 2005/2006 to 2014/2015.

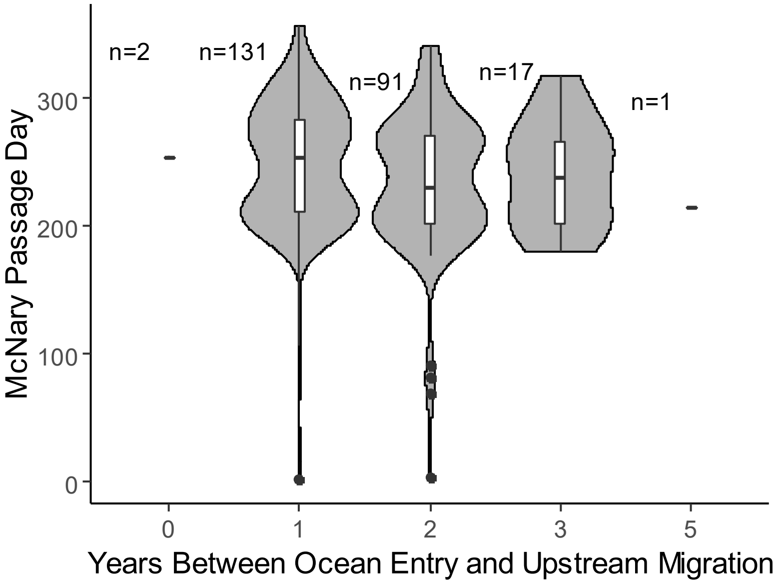

FIGURE I.16.—Violin and box plots of run timing (at McNary Dam) by Yakima River steelhead of different ocean ages. Passage day is the calendar day of the year. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value.

TABLE I.4.—Final models of Yakima River steelhead migratory behavior. Year included as a blocking factor. Potential variables included Day and Ocean Age. AUC = area under the curve, Year = run year, Day = passage day, Ocean Age = number of years spent in ocean. P-value for variable entry was P = 0.05.

Migration Stage	**N**	**Final Model**	**AUC**
Pass McNary	302	~ Year + Day + Day^2 + Day^3	0.646
Go Directly Home	242	~ Year + Day + Day^2	0.821
Overshoot	242	~ Year + Day + Day^2	0.851
Fallback Home	40	~ Year	0.757
Overall Success	302	~ Year + Day + Day^2 + Day^3	0.644

Wenatchee.—The Wenatchee River population included natural and hatchery origin steelhead of varying ocean ages. No Wenatchee River steelhead were found to be barged as juveniles. Hatchery origin steelhead were all reared upstream of the Wenatchee River and transported downstream to the Wenatchee River basin for release. In Chapter 2, I estimated that, on average, 65.6% (SE 7.5%) of hatchery and 10.6% (SE 3.0%) of wild Wenatchee steelhead that passed Rock Island Dam continued upstream past the Wenatchee River to overshoot Rocky Reach Dam. However, from 2010/2011 to 2014/2015, annual overshoot estimates by hatchery fish declined from 82.4% (SE 3.8%) to 16.0% (SE 8.0%). During the study period, the Wenatchee hatchery program shifted from directly releasing all steelhead to acclimating juveniles overwinter within the basin. Therefore, for further analysis, Wenatchee hatchery steelhead were divided into three stocks: natural origin, acclimated hatchery, and direct release hatchery. These stocks had nearly identical run timing, despite differences in early rearing experience (Figure I.17).

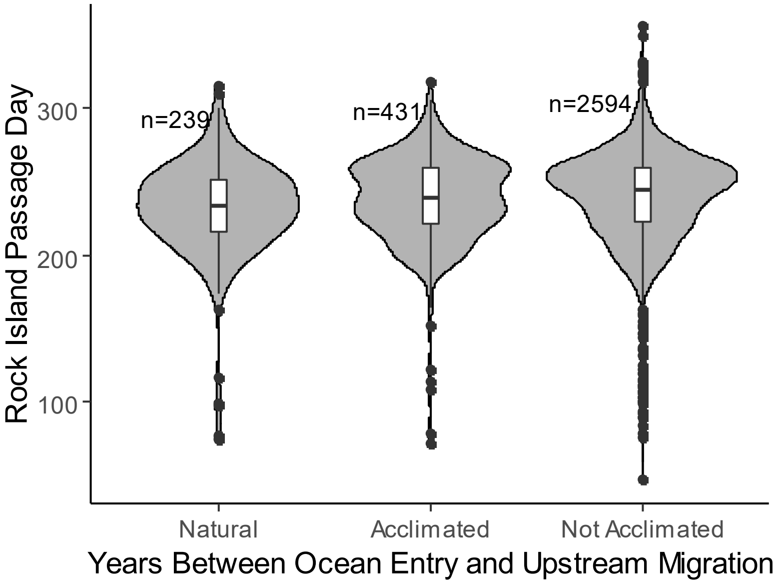

FIGURE I.17. Violin and box plots of run timing (at Rock Island Dam) by Wenatchee River steelhead of different rearing histories. Passage day is the calendar day of the year. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value. Natural = natural rearing, Acclimated = hatchery rearing with acclimation in the Wenatchee River basin, Not Acclimated = hatchery rearing with direct release into the Wenatchee River basin.

Almost all (97.4%) of Wenatchee River steelhead made their upstream migration one or two years after ocean entry (Figure I.18). The Wenatchee was the only stock out of the seven examined for which more steelhead returned after two years in the ocean rather than one. Steelhead with fewer ocean years returned home slightly later in the season than those that spent greater time in the ocean (Figure I.18). The median Rock Island passage date was 6 September for steelhead with only one ocean year and 22 August for steelhead with two ocean years.

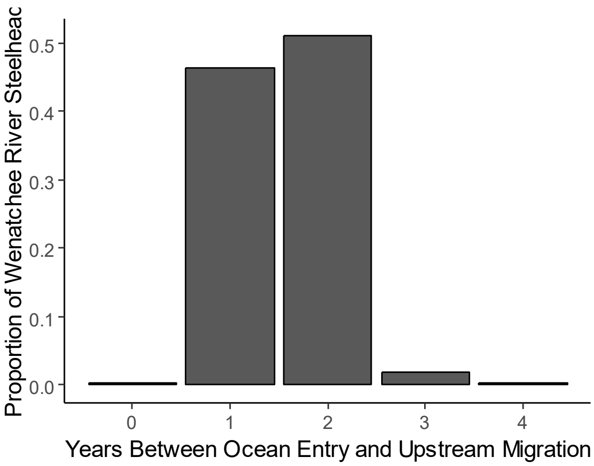

FIGURE I.18.—Ocean ages of PIT-tagged Wenatchee River steelhead that migrated upstream 2005/2006 to 2014/2015.

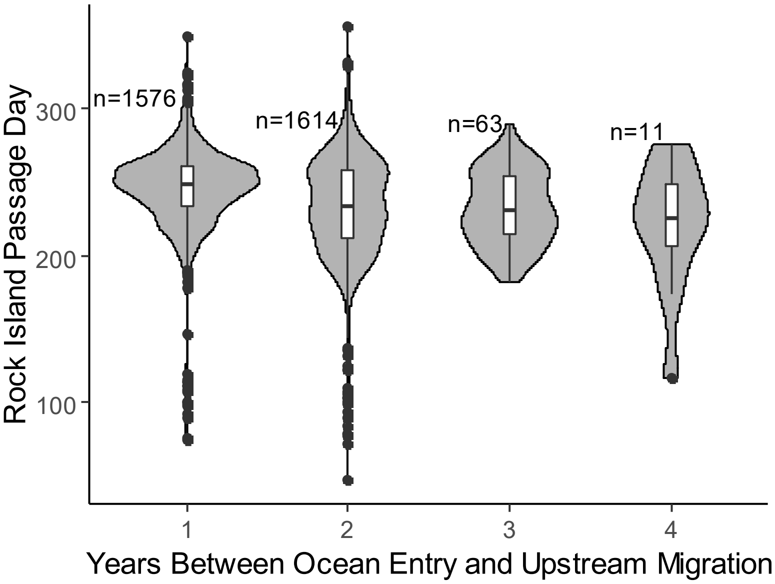

FIGURE I.19.—Violin and box plots of run timing (at Rock Island Dam) by Wenatchee River steelhead of different ocean ages. Passage day is the calendar day of the year. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value.

Hatchery rearing affected homing success during every period except the early migration (Table H.5). Hatchery-reared Wenatchee steelhead had similar success during the early migration compared to natural origin steelhead ($F_{1,4441} = 1.56$, $P = 0.212$). However, hatchery rearing had significant detrimental effects on homing for movement directly to home ($F_{1,2473} = 241.40$, $P < 0.0001$), overshooting ($F_{1,4441} = 194.34$, $P < 0.0001$), fallback to home ($F_{1,1607} = 22.03$, $P < 0.0001$), and overall success ($F_{1,3293} = 152.94$, $P < 0.0001$).

TABLE I.5.—Final models of Wenatchee River steelhead migratory behavior. Year included as a blocking factor. Potential variables included Day, Stock, and Ocean Age. AUC = area under the curve, Year = run year, Day = passage day, Stock = non-acclimated hatchery/acclimated hatchery/natural origin, Ocean Age = number of years spent in ocean. P-value for variable entry was P = 0.05.

Migration Stage	N	Final Model	AUC
Pass Rock Island	4455	~ Year + Day + Ocean Age + Day*Ocean Age	0.606
Go Directly Home	2495	~ Year + Day + Day^2 + Stock + Stock*Day + Stock*Day^2 + Year*Day + Year*Day^2	0.833
Overshoot	3018	~ Year + Day + Day^2 + Stock + Ocean Age + Year*Ocean Age + Day*Stock + Day^2*Stock + Year*Day + Year*Day^2	0.796
Fallback Home	1618	~ Year + Day + Day^2 + Day^3 + Stock	0.684
Overall Success	3303	~ Year + Day + Day^2 + Stock + Year*Stock	0.731

Acclimation had large effects on overshooting and movement directly to home, but not on fallback to home. Compared to naturally reared fish, migration directly to home was 71 percentage points lower for directly released steelhead, but only 41 percentage points lower for acclimated steelhead. On average, acclimating hatchery fish within the release basin was found to decrease overshooting in the Wenatchee hatchery population by 41 percentage points compared to directly releasing juveniles in spring (Figure I.20). Directly released hatchery steelhead had overshooting rates 65 percentage points higher than naturally reared fish, while acclimated juveniles had overshooting rates only 25 percentage points higher. These profound effects cannot be alternatively explained by run timing, because run timing was nearly identical among the three groups (Figure I.17).

Overshooting by acclimated steelhead has also decreased over time. In 2010/2011, acclimated steelhead overshot at a level approximately halfway between directly released and naturally reared steelhead (Figure I.20). Acclimated steelhead performance improved further in 2011/2012 and 2012/2013, and in the final two years of the study acclimated steelhead overshot at rates nearly as low as the naturally reared steelhead (Figure I.20). Acclimated steelhead released prior to 2011 were typically acclimated for shorter time periods (Hillman et al. 2016). Since 2011, all hatchery juveniles released in the Wenatchee River have been acclimated within basin over winter (Personal communication, Chris Moran, WDFW). The rise in the proportion of acclimated steelhead explains the steep decline in overshooting by Wenatchee river steelhead, as well as the corresponding increase in overall success through time (Figure I.21).

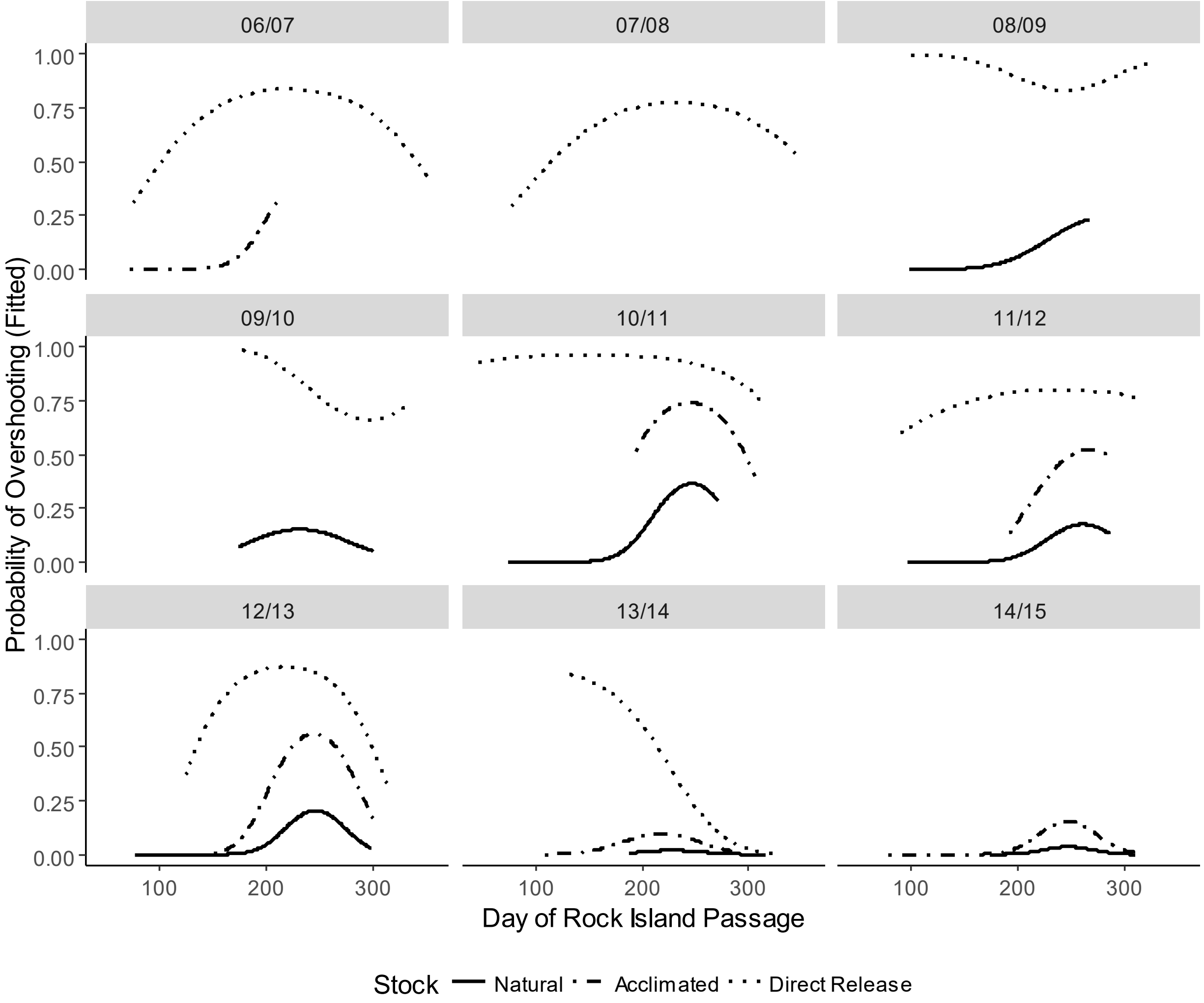

FIGURE I.20.—Estimated probabilities of overshooting by natural, acclimated hatchery, and directly released hatchery Wenatchee River steelhead after passing Rock Island Dam. Day of Rock Island Passage = Julian calendar day of the year of Rock Island Dam passage.

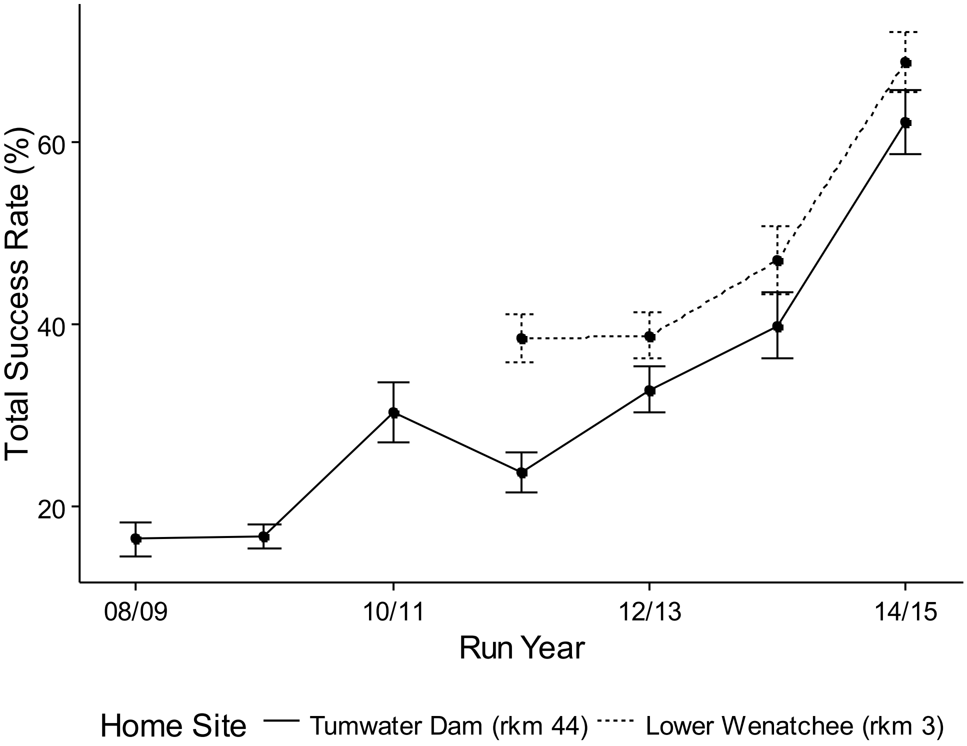

FIGURE I.21.—Annual total success rates of Wenatchee River hatchery steelhead from 2008/2009 to 2014/2015. Total success is the estimated movement rate from Bonneville Dam to the Wenatchee River. Success was measured at two sites, one near (3 rkm above) the tributary mouth, and one at rkm 44. Estimates of total success are adjusted by detection efficiencies. The lower Wenatchee PIT-tag array was not present until the 2011/2012 run year. Error bars represent ± 1 SE.

While acclimation greatly affected homing rates prior to overshooting, it did not affect the probability of falling back to home after overshooting. Both hatchery groups experienced lower fallback to home rates than the natural origin steelhead ($F_{1,1607} = 22.03$, $P < 0.0001$), but no significant difference between hatchery stocks was found (Figure I.22). Hatchery steelhead may be less likely to correct an overshoot and return downstream due to memory failure or attraction to upstream rearing areas. Alternatively, overshoot correction by hatchery steelhead may be diminished relative to natural origin steelhead because harvest of hatchery steelhead occurs in upstream overshoot areas.

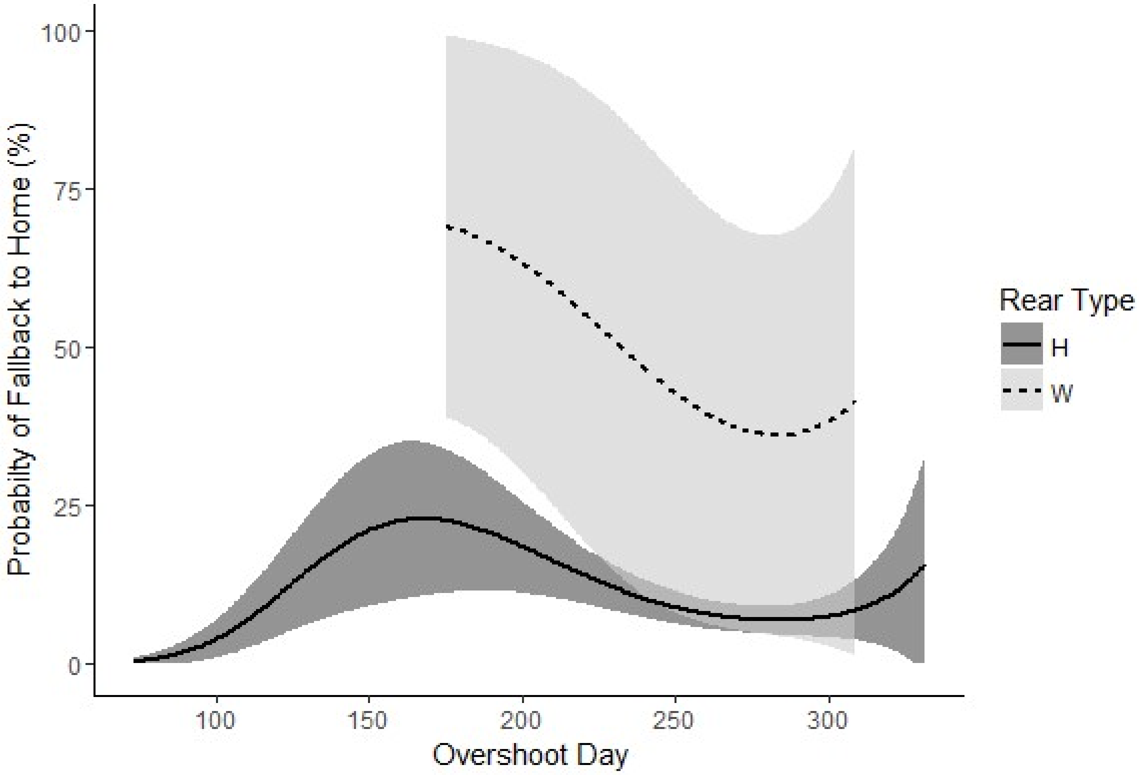

FIGURE I.22.—Predicted probability of falling back to home after overshooting Rocky Reach Dam for hatchery (H) and wild (W) rear types, and 90% confidence interval, for Wenatchee River steelhead. Baseline is steelhead that returned to freshwater in the run year 2009/2010 after spending one year in the ocean. Overshoot Day = Julian calendar day of the year of Rocky Reach Dam passage.

Effects due to ocean age were small. Steelhead that spent more time in the ocean were less likely to succeed during early migration ($F_{1,4442}$ = 6.63, P = 0.005) and less likely to overshoot ($F_{1,2984}$ = 4.17, P = 0.041). However, ocean residence time did not significantly affect movement directly to home ($F_{1,2458} = 0.93$, $P = 0.335$), fallback to home ($F_{1,1606} = 1.86$, $P = 0.172$), or overall success ($F_{1,3281} = 0.10$, $P = 0.756$). Wenatchee River steelhead that spent two years in the ocean before returning to freshwater had on average less likely to succeed during the early migration by 4 percentage points and less likely to overshoot Rocky Reach Dam by 4 percentage points compared to steelhead that spent a single year in the ocean. These effects were small relative to overall overshooting rates.

Entiat.—PIT-tagged Entiat River steelhead were entirely natural origin steelhead with juvenile detection histories only for in-river out-migrants. In Chapter 2, I estimated that, on average, 38.6% (SE 5.4%) of Entiat steelhead that passed Rocky Reach Dam continued upstream past the Entiat River to overshoot Wells Dam. Therefore, I examined the effect of ocean age on overshoot probability and homing success for Entiat fish. I found that 50.8% of Entiat River steelhead returned to the Columbia River after a single year in the ocean, and 43.1% returned after two years (Figure I.23). Run timing distributions of steelhead that spent one or two years in the ocean were very similar (Figure I.24).

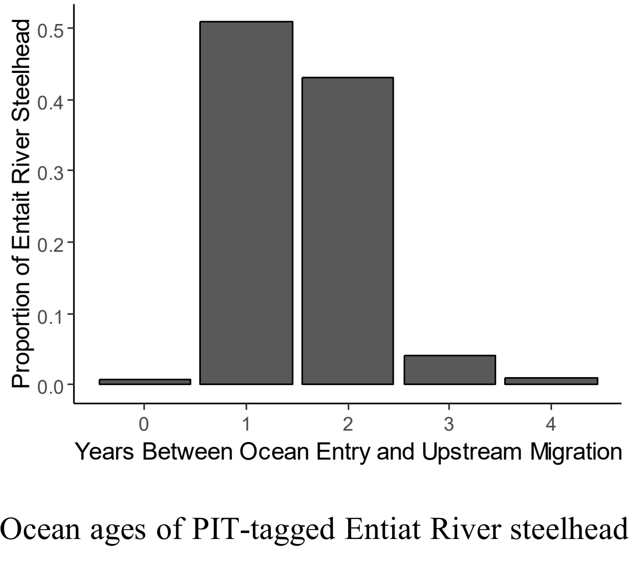

FIGURE I.23.—Ocean ages of PIT-tagged Entiat River steelhead that migrated upstream 2005/2006 to 2014/2015.

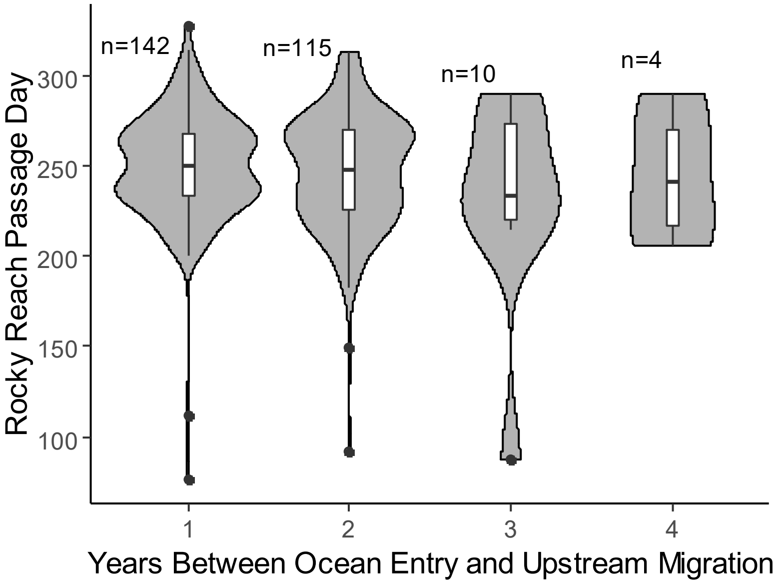

FIGURE I.24.—Violin and box plots of run timing (at Rocky Reach Dam) by Entiat River steelhead of different ocean ages. Passage day is the calendar day of the year. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value.

The largest effects due to ocean age, out of the seven tributaries investigated, were found here in the Entiat River population. Longer ocean residency was associated with decreased movement directly to home ($F_{1,257} = 5.02$, $P = 0.001$) and increased overshooting ($F_{1,258} = 5.09$, $P = 0.013$), though no significant effect was found on the probability of early migration success ($F_{1,350} = 0.23$, $P = 0.629$) or falling back to home after overshooting ($F_{1,104} = 0.01$, $P = 0.931$). After passing Rocky Reach Dam, Entiat River steelhead that spent two years in the ocean had migration rates directly to home 12 percentage points higher and overshooting rates 12 percentage points lower than steelhead that spent a single year in the ocean (Figure I.25). Despite negative effects on homing during these phases, ocean age did not significantly impact overall successful movement from Bonneville Dam to the Entiat River ($F_{1,347} = 1.19$, $P = 0.277$).

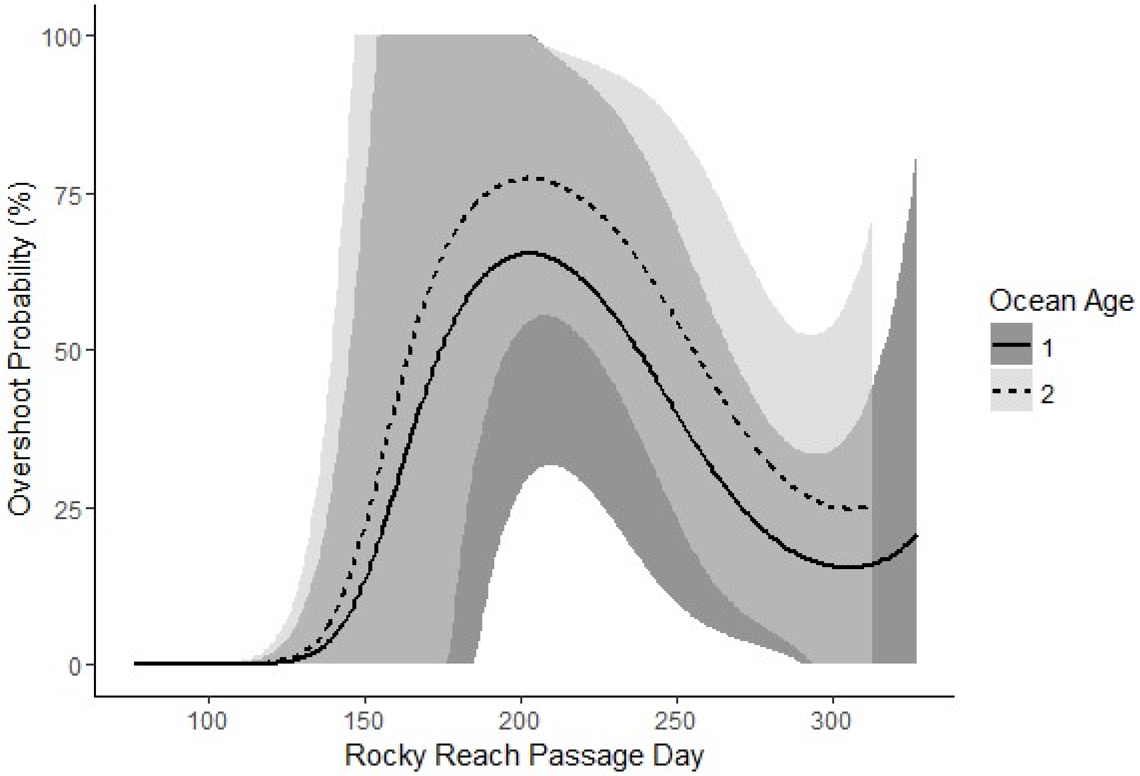

FIGURE I.25.—Predicted probability of overshooting Wells Dam after passing Rocky Reach Dam, and 90% confidence interval, for Entiat River steelhead. Baseline is steelhead that spent one or two years in the ocean and returned to freshwater in the run year 2014/2015. Rocky Reach Passage Day = Julian calendar day of the year of Rocky Reach Dam passage.

TABLE I.6.—Final models of Entiat River steelhead migratory behavior. Year included as a blocking factor. Potential variables included Day and Ocean Age. AUC = area under the curve, Year = run year, Day = passage day, Ocean Age = number of years spent in ocean. P-value for variable entry was P = 0.05.

Migration Stage	**N**	**Final Model**	**AUC**
Pass Rocky Reach	360	~ Year	0.601
Go Directly Home	269	~ Year + Day + Day^2 + Day^3 + Ocean Age	0.732
Overshoot	271	~ Year + Day + Day^2 + Day^3 + Ocean Age	0.730
Fallback Home	113	~ Year	0.631
Overall Success	356	~ Year	0.622

Tucannon.—Tucannon River steelhead varied by ocean age and barging and rearing histories. This was the only population out of the seven examined that included PIT-tagged steelhead that were barged during their out-migration. Out of a total of 2,926 Tucannon River steelhead, 515 were barged downriver as juveniles (Figure I.26). The in-river and transported Tucannon River steelhead have similar run timing, though the transported fish may be slightly delayed (Figure I.27). The median Ice Harbor passage date for steelhead that out-migrated in-river was 3 September, compared to 16 September for transported steelhead.

FIGURE I.26.—Juvenile transportation history of PIT-tagged Tucannon River steelhead that migrated upstream 2005/2006 to 2014/2015.

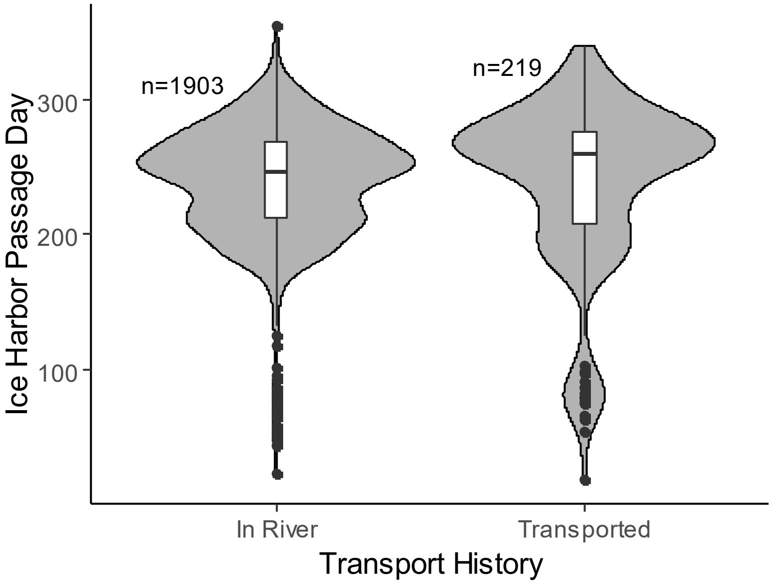

FIGURE I.27.—Violin and box plots of run timing (at Ice Harbor Dam) by Tucannon River steelhead with different juvenile transportation histories. Passage day is the calendar day of the year. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value.

In Chapter 2, I found that natural and hatchery origin Tucannon River steelhead overshot at similar rates. Annually, an average of 60.7% (SE 2.6%) of hatchery and 59.3% (SE 3.7%) of wild Tucannon steelhead that passed Ice Harbor Dam continued past the mouth of the Tucannon River and overshot Lower Granite Dam 73 rkm upstream. For further analysis, I divided Tucannon River hatchery steelhead endemic hatchery and non-endemic hatchery groups. Both hatchery stocks were reared at Lyon's Ferry hatchery, which is located on the Snake River 5 rkm downstream of the Tucannon River mouth. While both hatchery stocks were raised at Lyon's Ferry hatchery, the endemic stock is derived from wild Tucannon steelhead while the non-endemic, or "Lyon's Ferry" stock, is derived from out-of-basin steelhead, primarily from the upper Columbia. The Lyon's Ferry stock was subject to harvest pressures by recreational fishing in the Columbia River basin. In contrast, endemic hatchery steelhead were un-marked and unavailable for harvest. The endemic stock is annually integrated with wild origin fish, and has run timings almost identical to the natural stock. In contrast, the segregated Lyon's Ferry stock generally runs over a month earlier (Figure I.28). The median Ice Harbor passage date was 16 September and 18 September for natural and endemic stocks, respectively, while the median passage date for the Lyon's Ferry stock was 11 August.

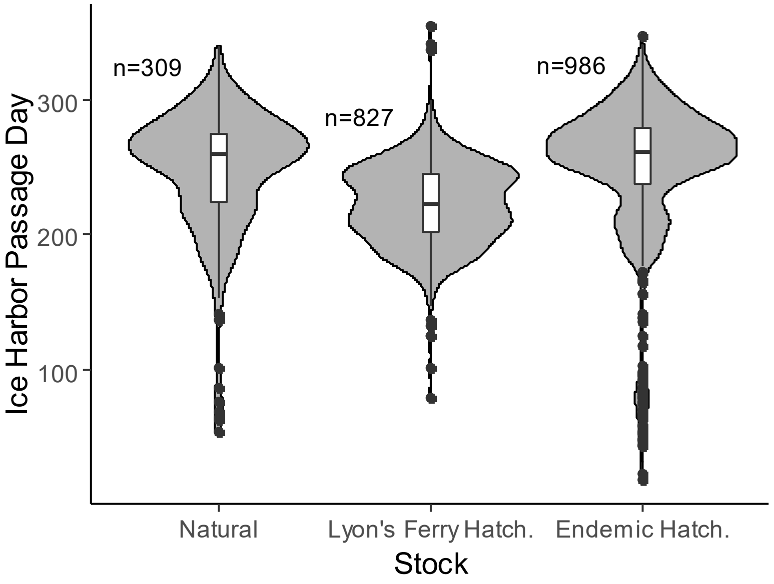

FIGURE I.28.—Violin and box plots of run timing (at Ice Harbor Dam) by Tucannon River steelhead of different stocks. Passage day is the calendar day of the year. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value.

Almost all (99.2%) Tucannon River steelhead returned to freshwater one or two years after entering the ocean (Figure I.29). Run timing was similar between fish with one and two years in the ocean (Figure I.30).

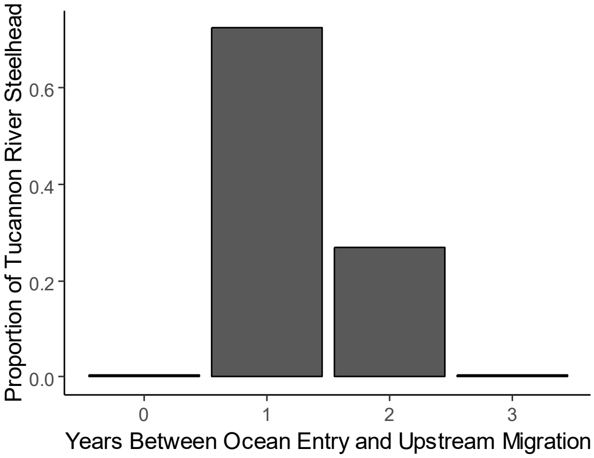

FIGURE I.29.—Ocean ages of PIT-tagged Tucannon River steelhead that migrated upstream 2005/2006 to 2014/2015.

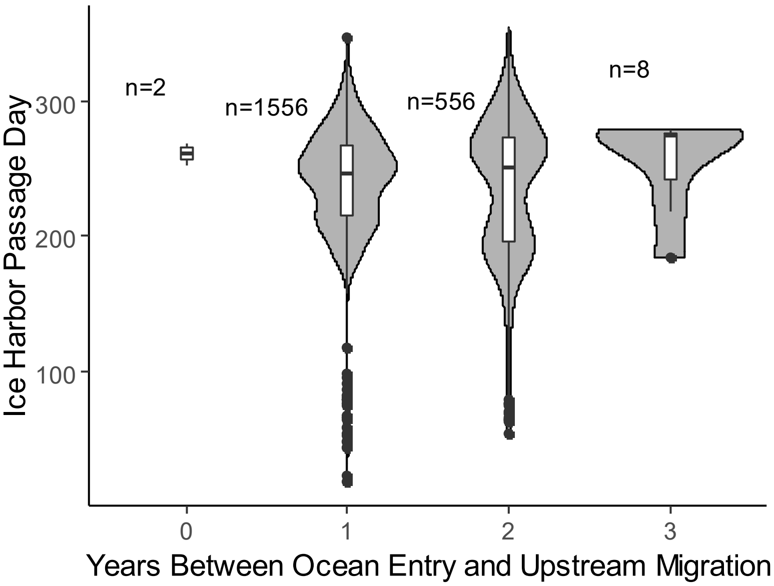

FIGURE I.30.—Violin and box plots of run timing (at Ice Harbor Dam) by Tucannon River steelhead of different ocean ages. Passage day is the calendar day of the year. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value.

Juvenile barging produced both negative and positive effects on homing success, though the net effect was negative. Juvenile barging significantly affected each stage of the adult migration except for fallback to home ($F_{1,1119} = 0.29$, $P = 0.593$). Significant detrimental effects on homing were found for early migration success ($F_{1,2915} = 215.55$, $P < 0.0001$) and overall success ($F_{1,2905} = 16.58$, $P < 0.0001$), while significant beneficial effects on homing were found for movement directly to home ($F_{1,2097} = 4.07$, $P < 0.022$) and overshooting ($F_{1,2107} = 9.24$, $P = 0.001$). The largest effect occurred during the early migration. Barged juveniles were less likely to move from Bonneville Dam to Ice Harbor Dam than fish that out-migrated in-river by 37 percentage points. An interaction between juvenile barging and run year was found for the early migration model (Table I.7). However, while the magnitude of the effect varied year to year, it was always worked in the same direction, to decrease the likelihood of successfully migrating up to Ice Harbor Dam (Figure I.31). Inspection of migration time between Bonneville and Ice Harbor reveals further differences between in-river and barged groups (Figure I.32). The median migration time taken to move from Bonneville Dam to Ice Harbor Dam, a distance of 304 rkm, was 18 days for steelhead that out-migrated in-river compared to 49 days for steelhead that were barged downriver. On average, in-river steelhead migrated upriver 2.7 times more quickly than the barged steelhead.

TABLE I.7.—Final models of Tucannon River steelhead migratory behavior. Year included as a blocking factor. Potential variables included Day, Barging, Stock, and Ocean Age. AUC = area under the curve, Year = run year, Day = passage day, Barging = transported/in-river juvenile migration, Stock = Lyon's Ferry hatchery/endemic hatchery/natural origin, Ocean Age = number of years spent in ocean. P-value for variable entry was $P = 0.05$.

Migration Stage	**N**	**Final Model**	**AUC**
Pass Ice Harbor	2926	~ Year + Barging + Year*Barging	0.666
Go Directly Home	2122	~ Year + Day + Day^{2} + Day^{3} + Day^{4} + Day^{5} + Day^{6} + Day^{7} + Barging + Day*Baring + Day^{2}*Barging + Day^{3}*Barging + Day^{4}*Barging + Day^{5}*Barging + Day^{6}*Barging + Day^{7}*Barging	0.716
Overshoot	2122	~ Year + Day + Day^{2} + Day^{3} + Barging + Stock + Day*Barging + Day^{2}*Barging + Day^{3}*Barging	0.713
Fallback Home	1133	~ Year + Day + Day^{2} + Stock	0.657
Overall Success	2926	~ Year + Barging + Stock + Year*Barging + Year*Stock	0.644

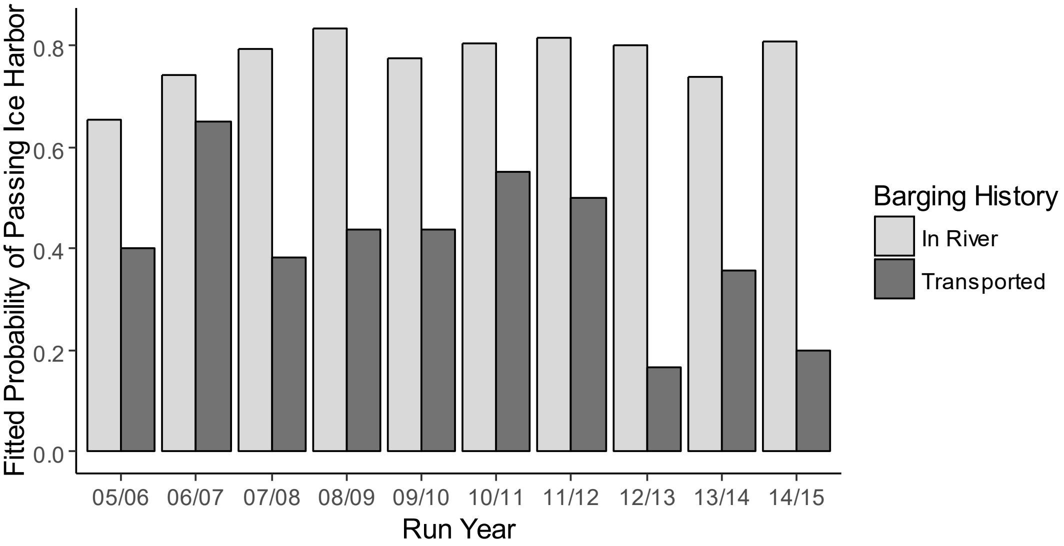

FIGURE I.31.—Estimated probability of moving from Bonneville Dam to Ice Harbor Dam for Tucannon River steelhead by year for barged and in-river migrants.

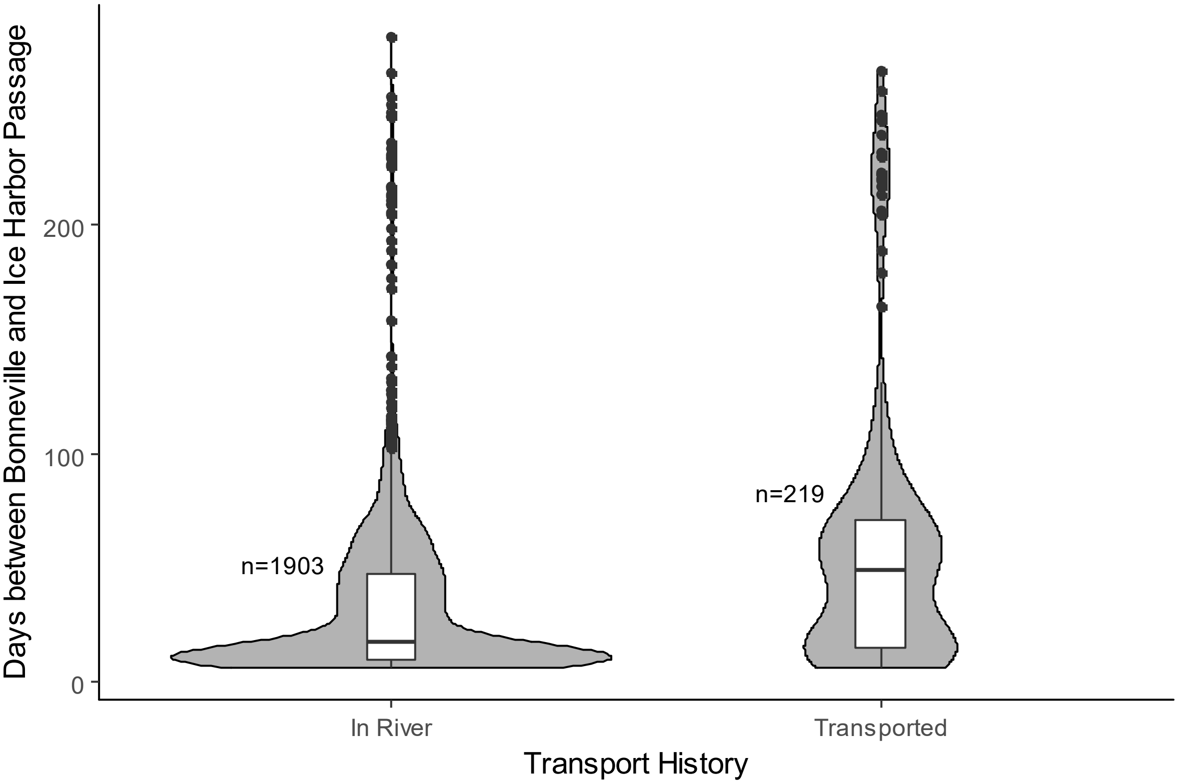

FIGURE I.32.—Violin and box plots of migration time by Tucannon River steelhead of different transport histories. Migration time is the number of days between Bonneville Dam passage at rkm 234 and Ice Harbor Dam passage at rkm 538. Box plots show median values (horizontal line), 25th and 75th percentiles (outer box), maximum values, excluding outliers (dashed line), and outliers (points). Violin plots show the probability density of data at each value.

If barged steelhead overcame the odds and passed Ice Harbor, they were actually more likely to home successfully than steelhead that out-migrated in-river. After passing Ice Harbor, previously barged steelhead had movement rates directly to home 6 percentage points higher and overshoot rates 12.16 lower than steelhead that out-migrated in-river. Barging was associated with positive effects during late migration, but, due to the large negative effect during the early migration, the net effect of juvenile barging was to reduce overall successful homing by 10 percentage points.

When hatchery stocks were pooled, hatchery rearing resulted in a significant beneficial effect on falling back to home ($F_{1,1121} = 8.11$, $P = 0.005$), but did not result in significant effects on homing during the early migration ($F_{1,2905} = 0.22$, $P = 0.642$), movement directly to home ($F_{1,2096} = 0.92$, $P = 0.337$), overshooting ($F_{1,2104} < 0.01$, $P = 0.977$), or overall success ($F_{1,2905} = 0.85$, $P = 0.355$). The two hatchery stocks produced different effects on overshooting and overall success. However, no significant difference in fallback to home was found between the two hatchery stocks. Hatchery rearing was associated with a 11 percentage point increase in fallback to home (Figure I.33).

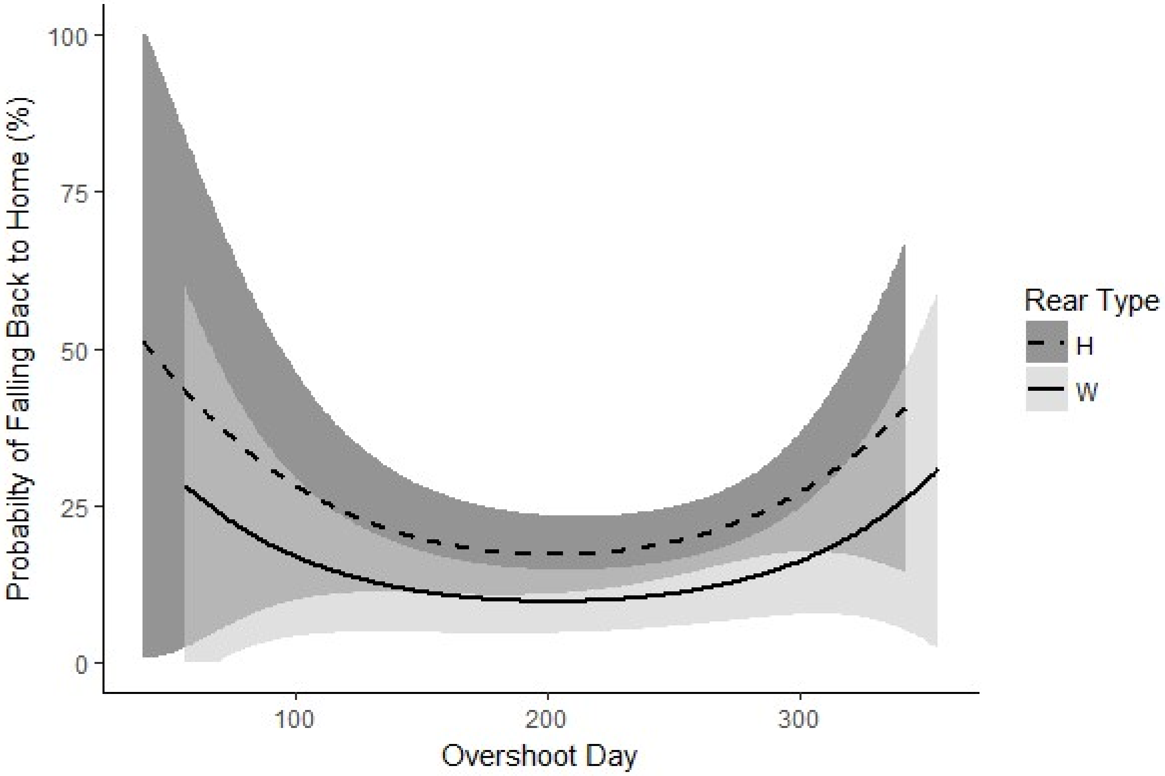

FIGURE I.33.—Predicted probability of falling back to home for each rear type after overshooting Lower Granite Dam, and 90% confidence interval, for Tucannon River steelhead. Baseline is steelhead that spent one year in the ocean and returned to freshwater in the run year 2009/2010. H = Hatchery, W = Wild, Overshoot Day = Julian calendar day of the year of Lower Granite Dam passage.

Unlike other tributaries, hatchery origin Tucannon River steelhead performed as well or better than the natural origin steelhead. Neither hatchery stock significantly differed from natural origin steelhead in early migration success or movement directly to home. However, the Lyon's Ferry hatchery steelhead were less likely to overshoot, by 7 percentage points, than the natural origin and endemic stocks (Figure I.34). Additionally, the endemic hatchery stock had successful homing rates between Bonneville Dam and the Tucannon River 5 percentage points higher than both the natural and Lyon's Ferry stocks. For unknown reasons, wild Tucannon River steelhead are drawn upstream in high numbers, and many are observed in upstream tributaries (Chapter 2).

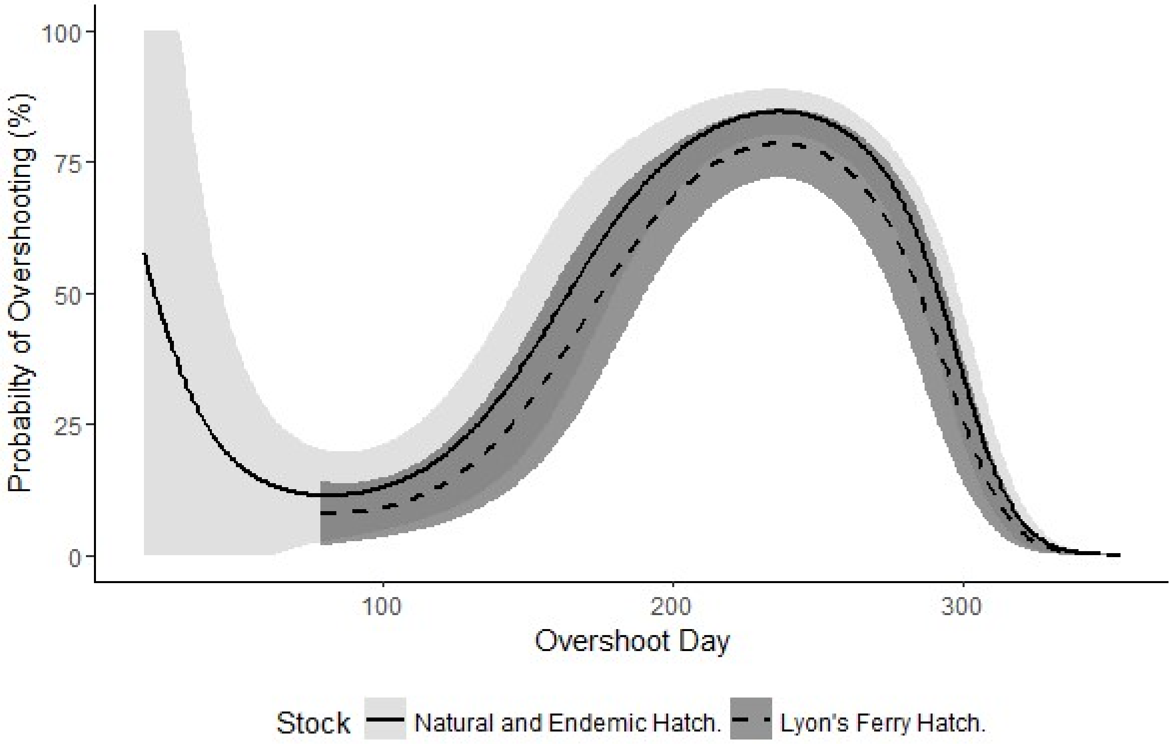

FIGURE I.34.—Predicted probability of overshooting Lower Granite Dam after passing Ice Harbor Dam, and 90% confidence interval, for Tucannon River steelhead. Baseline is steelhead that spent one year in the ocean and returned to freshwater in the run year 2009/2010. Overshoot Day = Julian calendar day of the year of Lower Granite Dam passage.

The effects of ocean age on homing success were highly insignificant during every period of the adult migration, including movement over Ice Harbor ($F_{1,2905} = 0.32$, $P = 0.570$), movement directly to home ($F_{1,2096} = 0.02$, $P = 0.873$), overshooting ($F_{1,2103} = 0.11$, $P = 0.734$), fallback to home ($F_{1,1120} = 0.14$, $P = 0.707$), and overall success ($F_{1,2895} = 0.04$, $P = 0.849$).

APPENDIX J.—Influence of adult experiences by tributary

John Day.—In Chapter 2, I estimated that on average 53.3% (SE 2.4%) of John Day River steelhead that passed Bonneville Dam went on to overshoot McNary Dam. In Chapter 3, I found that John Day River steelhead that spent greater time in the ocean were slightly more likely to overshoot. Here, I examined the influence of mainstem water temperature. Average water temperatures at McNary Dam ranged from 4.1 °C to 22.3 °C, with a median of 20.6 °C, when John Day River steelhead neared their home tributary. Shoreline orientations at John Day Dam were not measured because adult detectors were not installed at the dam until 2017.

Logistic regression did not find John Day River steelhead overshoot behavior to be significantly affected by water temperature in the mainstem river at a $P < 0.05$ level. Final models for both overshooting and movement directly to home included only the blocking factors for run year and ocean age (Table J.1). However, for the overshoot model, the first and second order temperature terms were nearly significant ($F_{2,2033} = 2.31$, $P = 0.100$). Overshoot probability appeared to increase with increasing temperature, until reaching a threshold temperature where overshoot probability decreased (Figure J.1). No evidence of an effect of mainstem temperature on movement directly to home was found ($F_{1,1456} = 0.13$, $P = 0.715$).

TABLE J.1.—Final models of John Day River steelhead migratory behavior. Year and Ocean Age included as blocking factors. Potential variables included water temperature at McNary Dam (Main. Temp.). AUC = area under the curve, Year = run year, Ocean Age = number of years spent in ocean. P-value for variable entry was P = 0.05.

Migration Stage	**N**	**Final Model**	**AUC**
Go Directly Home	1464	~ Year + Ocean Age	0.636
Overshoot	2046	~ Year + Ocean Age	0.597

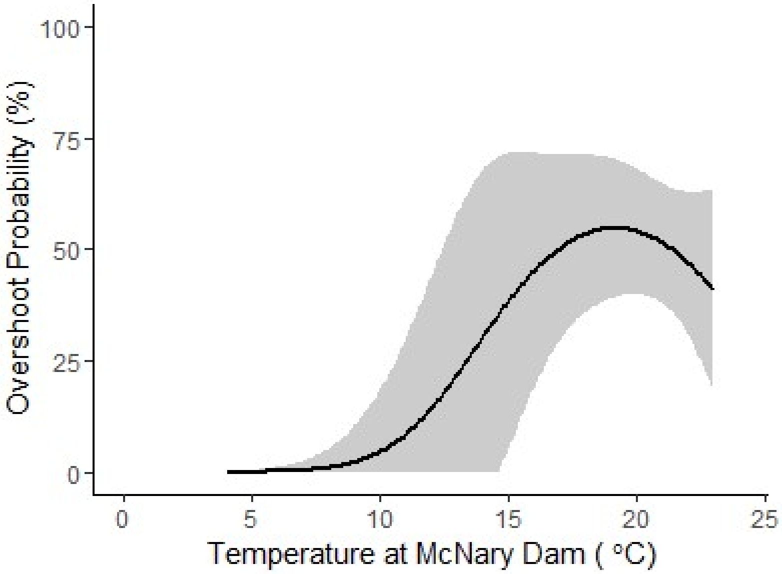

FIGURE J.1.—Predicted probability of overshooting McNary Dam, and 90% confidence interval, at different mainstem water temperatures for John Day River steelhead. Baseline is steelhead that spent one year in the ocean and returned to freshwater in the run year 2014/2015.

The lack of a significant effect of temperature was surprising because passage timing was found to be significant, and was therefore included as a blocking factor, in overshoot and direct homing models in Chapter 3. Passage timing was intended to account for seasonal environmental variation, including temperature. However, further analysis in this chapter found that water temperature was not significant enough to include in the final logistic model. Passage timing may therefore account for more variation than simply temperature differences.

Analysis of overshooting and movement directly to home using conditional inference trees found Bonneville passage day, mainstem temperature, and ocean age to produce significant splits (Figure J.2). John Day River steelhead that passed Bonneville Dam after 19 July were more likely to overshoot than those that arrived earlier. Among steelhead that passed Bonneville before July

19th, those that encountered higher mainstem water temperatures were more likely to overshoot. Within the high temperature group, overshooting was higher by steelhead that spent more time in the ocean. Movement directly to home was relatively unaffected by all splits. Instead the likelihood of not being observed overshooting or moving directly to home appeared to trade off with overshooting levels. Of the final 4 nodes, the only node not assigned to overshooting is early arriving steelhead that encountered lower water temperatures (Figure J.2). Steelhead that encounter lower mainstem temperatures may remain in the mainstem river below McNary Dam rather than overshooting. It is also possible that John Day River steelhead may enter alternative nearby tributaries.

In Chapter 2, I estimated the average annual fallback to home rate of John Day River steelhead to be 52.5% (SE 3.1%). In Chapter 3, ocean age was not found to significantly affect fallback to home. For John Day River steelhead that overshot McNary Dam, regression analysis found no significant positive relationships between fallback to home rates and flow during March ($F_{1,4} = 0.11$, $P = 0.378$) or spill during the months of January ($F_{1,4} = 0.35$, $P = 0.293$), February ($F_{1,4} = 0.01$, $P = 0.530$), or March ($F_{1,4} = 0.01$, $P = 0.465$). Since fallback rates were only able to be estimated in 6 years, inference using regression was limited.

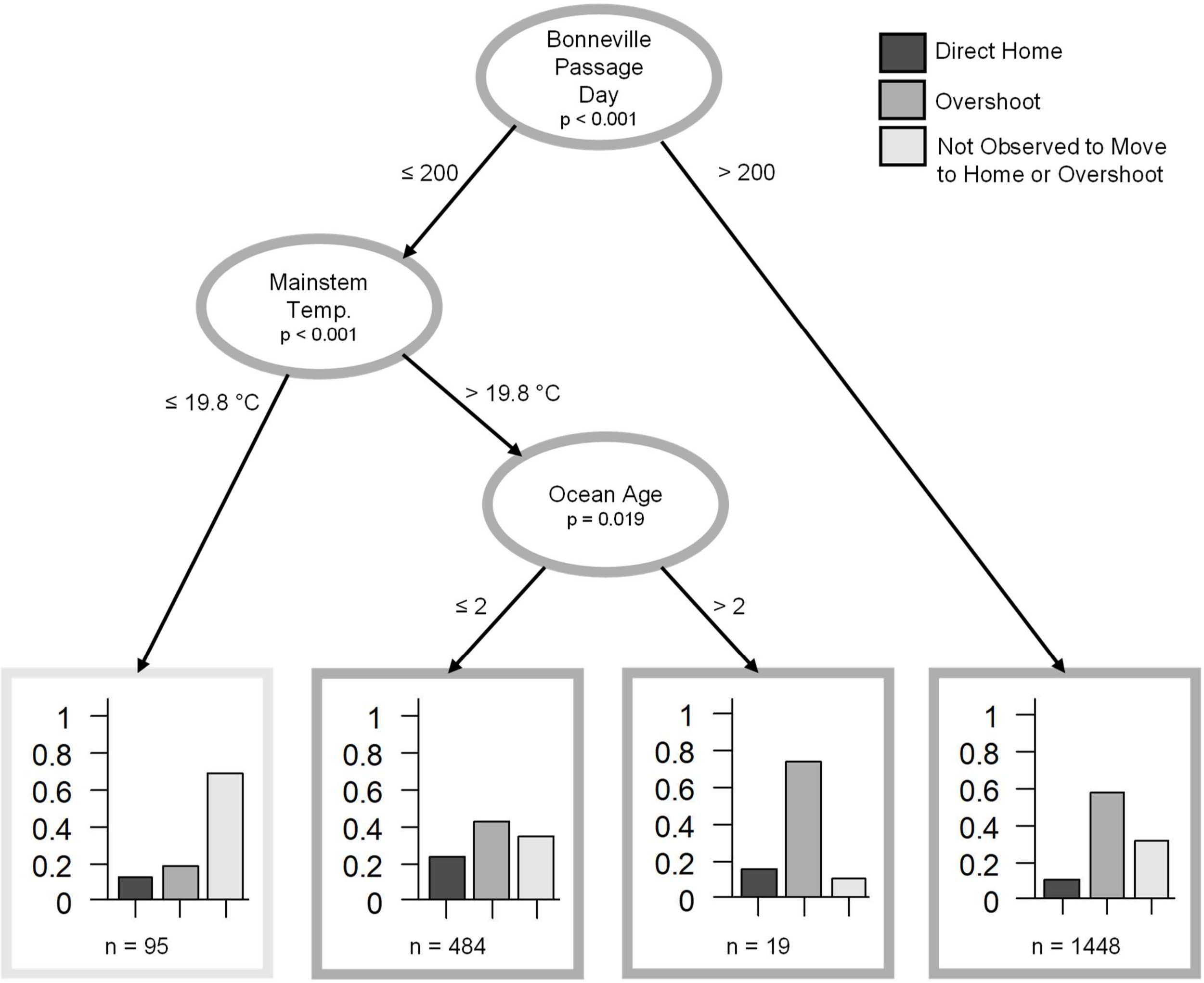

FIGURE J.2.—Conditional inference tree of adult John Day River steelhead migratory behavior between Bonneville and McNary dams. Direct Home = migrated to home without overshooting, Overshoot = overshot McNary Dam, Bonneville Passage Day = calendar day of Bonneville Dam passage, Mainstem Temp. = average temperature of McNary Dam tailwater as steelhead neared their home tributary, Ocean Age = ocean residency time in years.

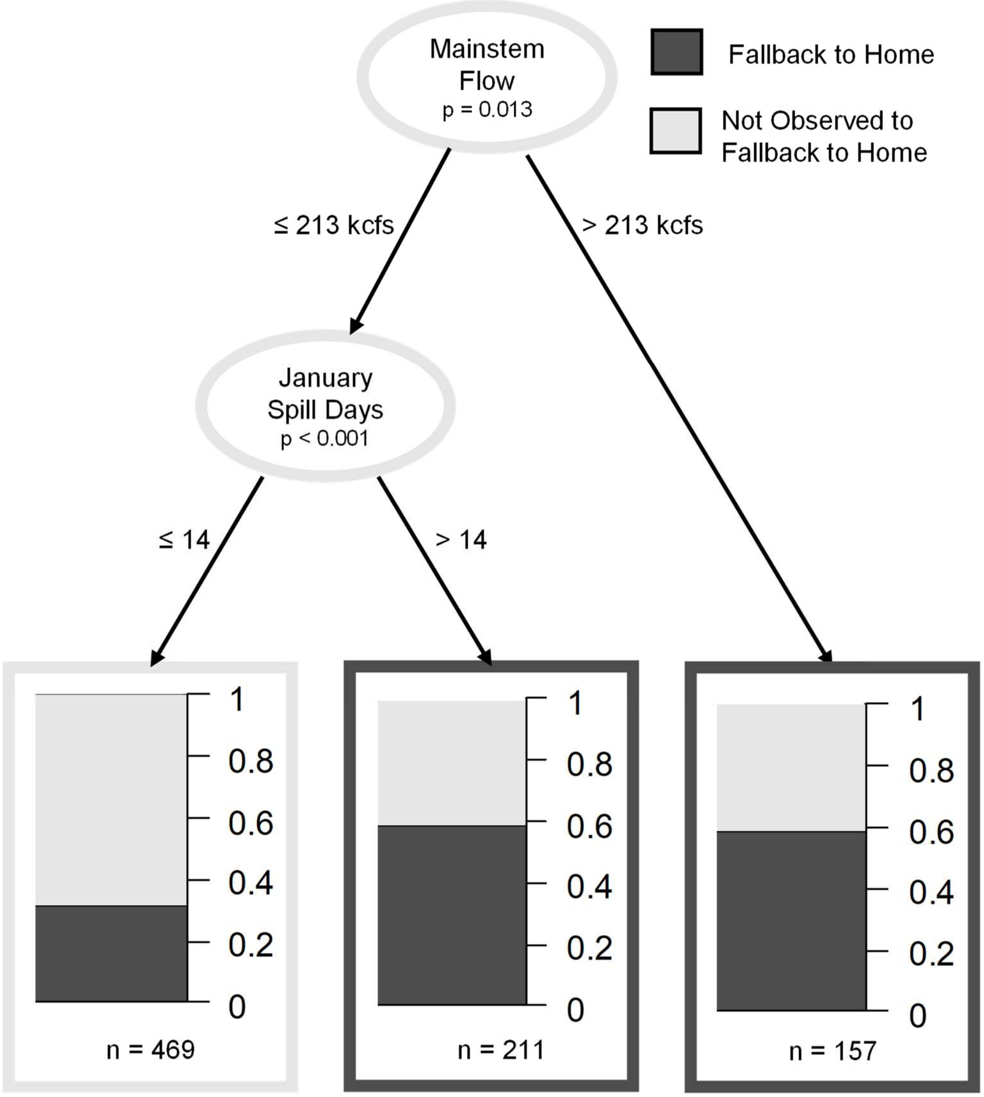

FIGURE J.3.—Conditional inference tree of adult John Day River steelhead migratory after overshooting McNary Dam. Fallback to Home = fell back downstream to home, Mainstem Flow = average flow at McNary Dam during March, January Spill Days = number of days in January during which any amount of water was spilled over McNary Dam.

Analysis of fallback to home with conditional inference trees found mainstem flow and January spill to produce significant splits (Figure J.3). More steelhead fell back to home in years with higher flow during March. Within the low flow group, greater spill in January was associated with higher fallback to home. Of the three final nodes, the only node not assigned to fallback to home was the low flow, low spill group.

Umatilla.—In Chapter 2, I estimated that, on average, 46.9% (SE 5.5%) of natural origin and 66.4% (SE 5.0%) of hatchery origin Walla Walla steelhead that pass McNary Dam go on to overshoot Ice Harbor Dam. In Chapter 3, I found that Umatilla River steelhead that spent and additional year in the ocean were more likely to overshoot, but that rear type did not have a significant effect. Here, I examined the influence of natal and mainstem water temperature.

As Umatilla River steelhead neared their home tributary, average water temperatures at McNary Dam ranged from 8.9 °C to 21.9 °C, with a median of 19.6 °C. In the same period, average water temperatures in the mainstem Umatilla River ranged from 4.1 °C to 23.9 °C, with a median of 17.2 °C. Water temperatures in the Umatilla River were generally lower than in the Columbia as Umatilla River steelhead arrived near home. The median temperature difference was -2.3 °C, with a range of -7.1 °C to 6.2 °C. Shoreline orientations at John Day Dam were not measured because adult detectors were not installed at the dam until 2017.

Logistic regression found a significant influence of water temperature on movement directly to home, but not on overshooting. The average difference in temperature between the McNary Dam outflow and Umatilla River significantly predicted the likelihood of moving directly to home ($F_{1,832} = 4.90$, $P = 0.027$). As natal temperature increased relative to mainstem water temperature, the probability of moving directly to home decreased (Figure J.4). Overshooting by Umatilla River steelhead was not found to be significantly influenced by temperature; the final overshoot model did not include any temperature factors (Table J.2).

TABLE J.2.—Final models of Umatilla River steelhead migratory behavior. Year, Rear Type, and Ocean Age included as blocking factors. Potential variables included water temperature at McNary Dam, water temperature in the Umatilla River, and water temperature difference between the Columbia and Umatilla rivers (Temp. Difference). AUC = area under the curve, Year = run year, Ocean Age = number of years spent in ocean, Rear Type = hatchery or natural rearing. P-value for variable entry was P = 0.05.

Migration Stage	**N**	**Final Model**	**AUC**
Go Directly Home	845	~ Year + Rear Type + Ocean Age + Temp. Difference	0.707
Overshoot	845	~ Year + Rear Type + Ocean Age + Year*Rear Type	0.636

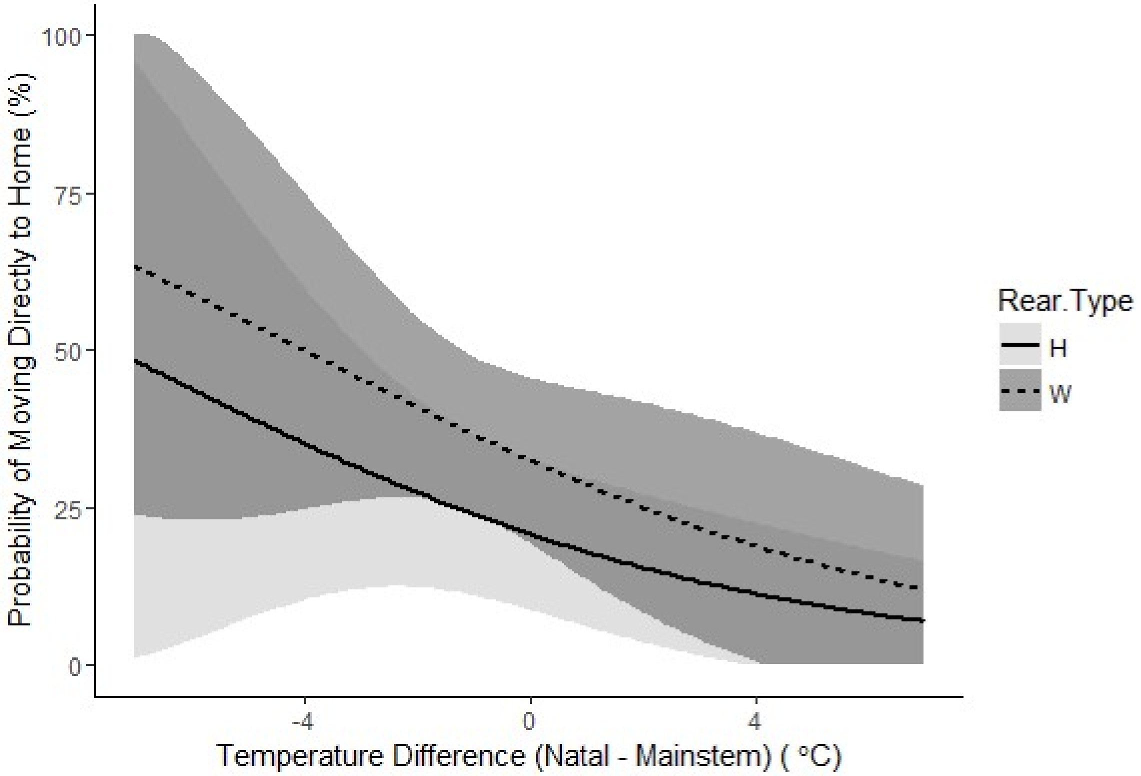

FIGURE J.4.—Predicted probability of moving directly to home after passing Bonneville Dam, and 90% confidence interval, given the temperature difference between the Umatilla River monitoring station and McNary Dam outflow for Umatilla River steelhead. Baseline is steelhead that spent one year in the ocean and returned to freshwater in the run year 2014/2015.

Analysis of overshooting and movement directly to home using conditional inference trees found only rear type to produce a significant split (Figure J.5). Compared to natural origin steelhead, hatchery steelhead were less likely to move directly to home and more likely to be assigned to the unobserved group. Hatchery Umatilla steelhead may either be straying to nearby tributaries, or experiencing increased harvest or mortality within the mainstem river below McNary Dam.

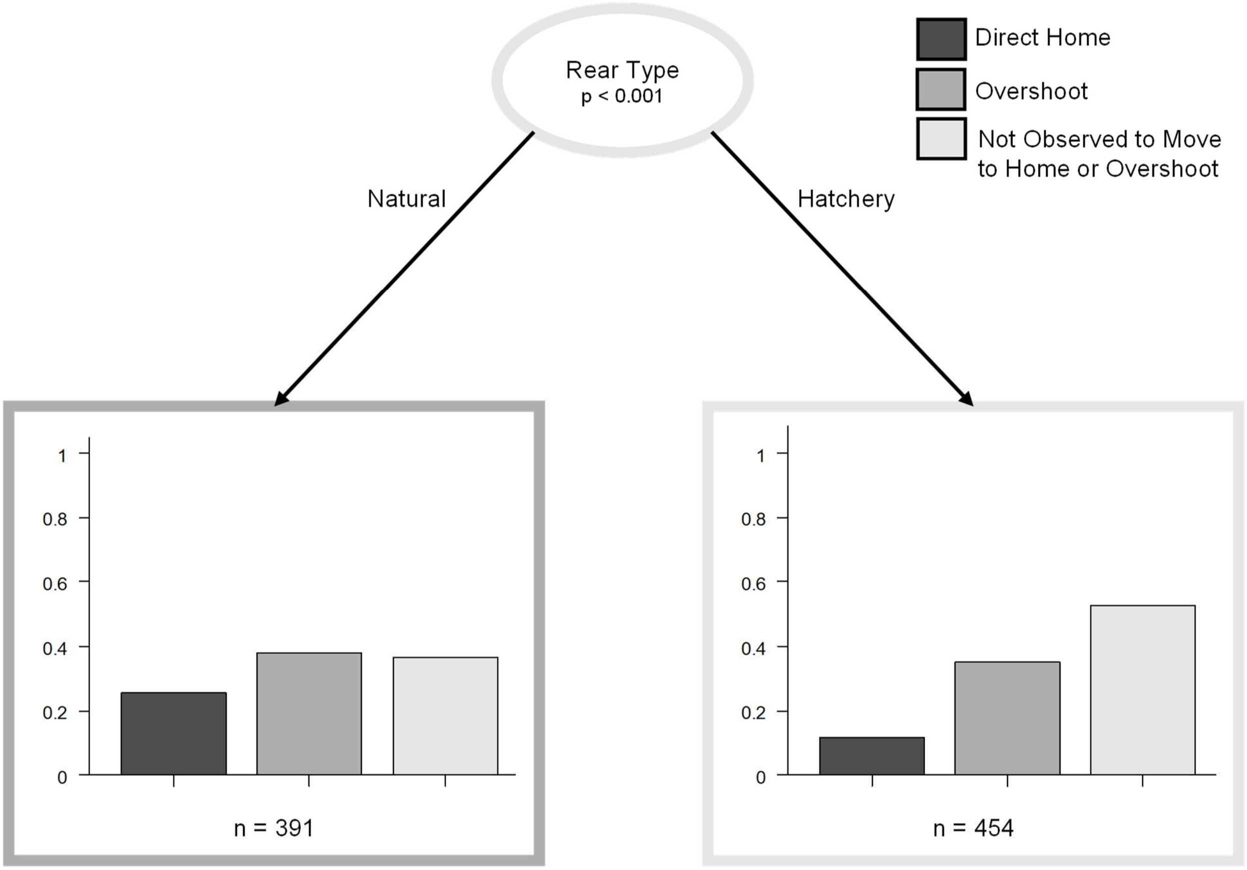

FIGURE J.5.—Conditional inference tree of adult Umatilla River steelhead migratory behavior between Bonneville and McNary dams. Direct Home = migrated to home without overshooting, Overshoot = overshot McNary Dam, Rear Type = rearing history (hatchery or wild).

In Chapter 2, I estimated the average annual fallback rates to home to be 26.9% (SE 8.7%) for hatchery and 75.0% (SE 2.6%) for wild Umatilla steelhead. However, due to difficulties with tributary arrays, fallback rates to home were only estimated for two years. In Chapter 3, I found hatchery steelhead to be less likely to fall back to home, by 26 percentage points on average. Ocean age did not significantly affect fallback. Here, for Umatilla River steelhead that overshot McNary Dam, regression analysis was not able to be performed because both the hatchery and natural stocks had only two years for which fallback to home rates were able to be estimated. Analysis of fallback to home with conditional inference trees found rear type and overshoot timing to produce significant splits (Figure J.6). Hatchery steelhead were much less likely to fallback than natural origin Umatilla steelhead. Within the naturally reared group, those that overshot later in the year, after 29 September, were more likely to fall back to home. This group may have experienced less thermal stress, because they did not overshoot during peak summer temperatures. Of the three final nodes, the only node assigned to fall back to home was naturally reared steelhead that overshot later in the year (Figure J.6).

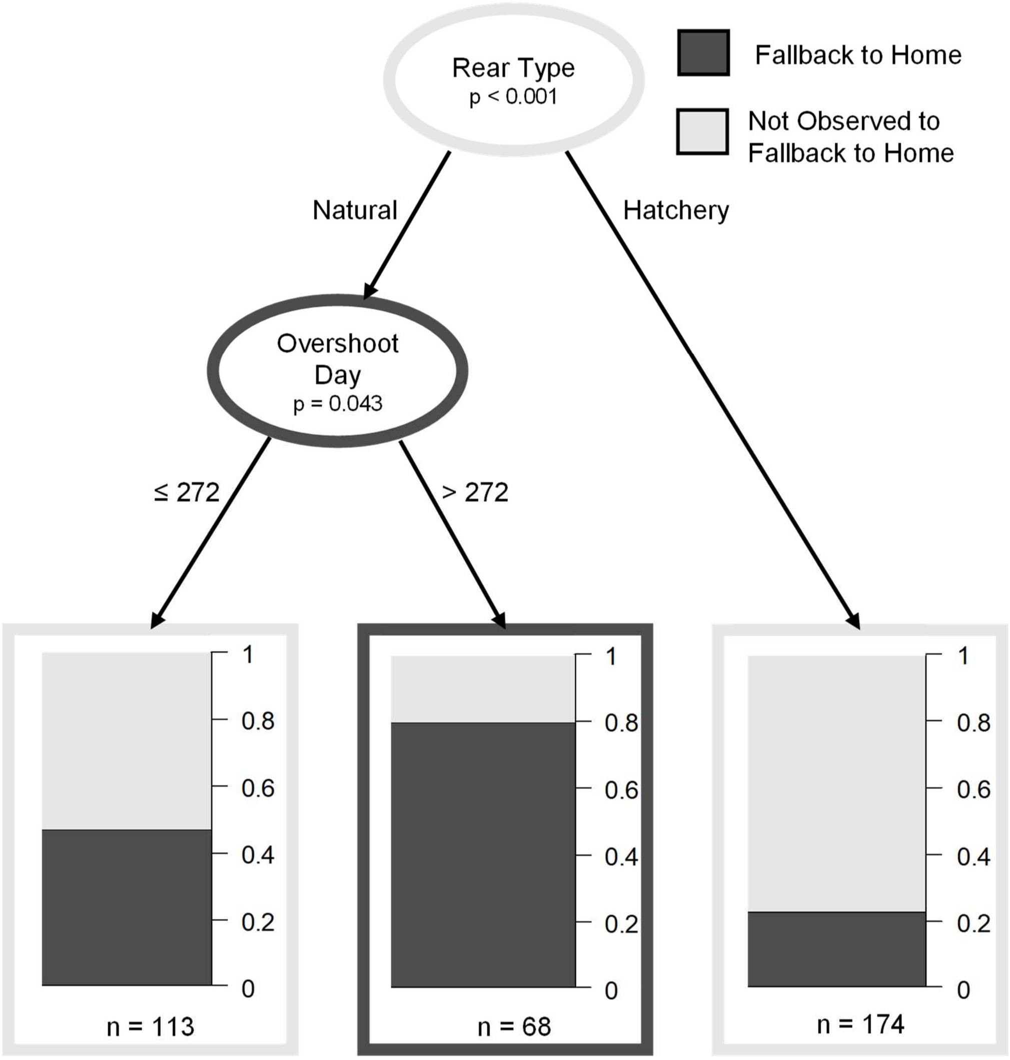

FIGURE J.6.—Conditional inference tree of adult Umatilla River steelhead migratory after overshooting McNary Dam. Fallback to Home = fell back downstream to home, Rear Type = rearing history (hatchery, natural), Overshoot Day = calendar day of overshoot at McNary Dam.

Walla Walla.—In Chapter 2, I estimated that, on average, 46.9% (SE 5.5%) of natural origin and 66.4% (SE 5.0%) of hatchery origin Walla Walla steelhead that pass McNary Dam go on to overshoot Ice Harbor Dam. In Chapter 3, I found that non-endemic Lyon's Ferry hatchery steelhead were more likely to overshoot, by 15 percentage points, than endemic hatchery and natural origin fish. Ocean age did not have a significant impact on overshooting. Here, I examined the influence of shoreline orientation, as well as water temperature in the mainstem and natal rivers.

As Walla Walla River steelhead neared their home tributary, average water temperatures at Ice Harbor Dam, where nearly all overshooting by Walla Walla steelhead occurred, ranged from 2.7 °C to 22.2 °C, with a median of 19.9 °C. In the same time frame, the median average water temperatures measured in the mainstem Walla Walla River, at rkm 53, was 19.0 °C, and average temperatures were as high as 23.24 °C. Water temperatures in the Walla Walla River were generally lower than in the Columbia, with a median temperature difference of -1.5 °C and a range of -11.5 °C to 4.8 °C. A strong positive relationship was found (r = 0.887) between water temperatures in the Walla Walla River and Snake River at Ice Harbor Dam (Figure J.7).

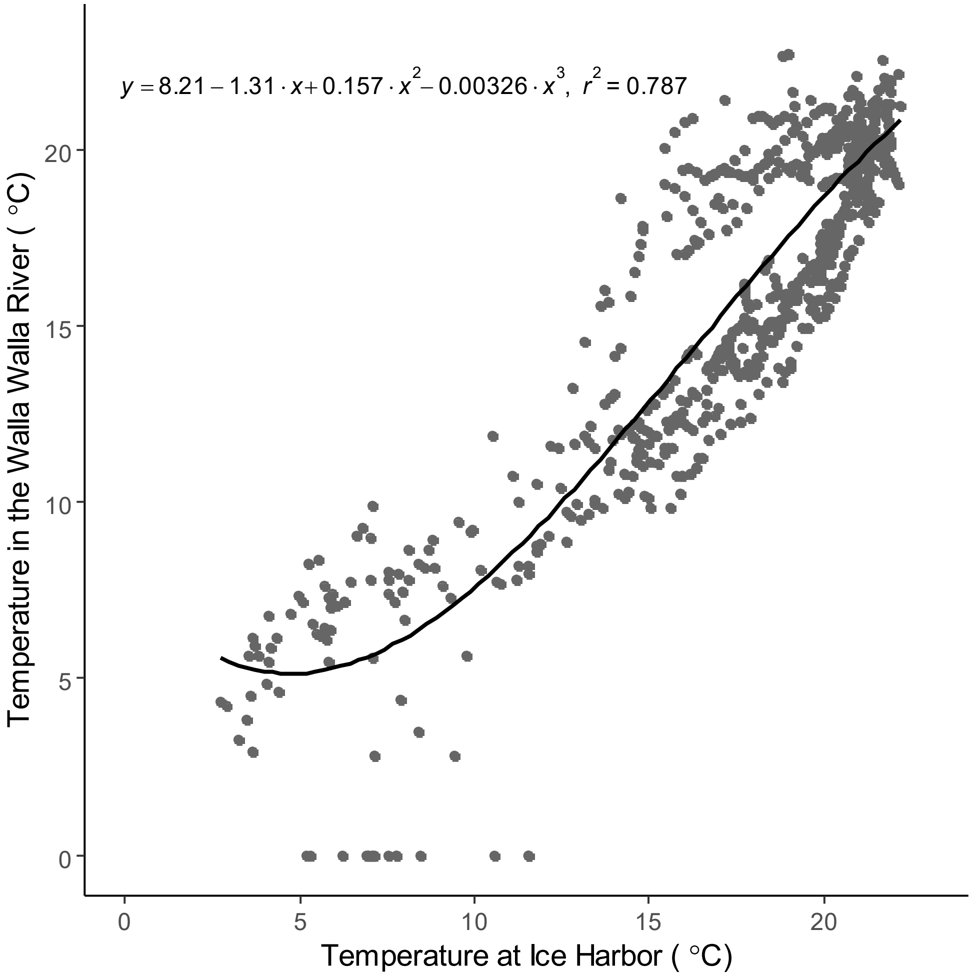

FIGURE J.7.—Relationship between water temperatures in the Walla Walla River and Ice Harbor Dam outflow (Natal – Mainstem) when Walla Walla River steelhead arrived near their natal tributary.

Most (76.6%) of Walla Walla steelhead were observed passing McNary Dam, located 39 rkm below the mouth of the Walla Walla River, in the southern ladder. Southern shoreline orientation corresponds with the entry of the Walla Walla River into the Columbia River.

At least one water temperature factor was included in final logistic models for both movement directly to home and overshooting (Table J.3). Increasing mainstem water temperature, as measured at Ice Harbor Dam, was significantly associated with decreasing probability of moving directly to home ($F_{2,1568} = 175.15$, $P < 0.0001$). Both mainstem water temperature and the natal-mainstem water temperature difference were significant in the final overshooting model. An interaction was also found between the temperature factors. The significance of the main effect of temperature on overshooting was $P < 0.0001$ ($F_{3,1546} = 116.38$) for mainstem temperature and $P = 0.0001$ ($F_{2,1546} = 9.07$) for the natal-mainstem water temperature difference. Within the observed temperature range, overshoot probability increased with increasing water temperature (Figure J.9). The predicted likelihood of overshooting increased most rapidly between 15 °C and 18 °C, and then leveled off at 20 °C (Figure J.9).

TABLE J.3.—Final models of Walla Walla River steelhead migratory behavior. Year, Stock, and Ocean Age included as blocking factors. Potential variables included water temperature at Ice Harbor Dam (Main Temp.), water temperature in the Walla Walla River, water temperature difference between the Snake and Walla Walla rivers (Temp. Diff.), and shoreline orientation at McNary Dam. AUC = area under the curve, Year = run year, Ocean Age = number of years spent in ocean, Stock = endemic hatchery, Lyon's Ferry hatchery, or natural stock. P-value for variable entry was P = 0.05.

Migration Stage	**N**	**Final Model**	**AUC**
Go Directly Home	1581	~ Year + Stock + Ocean Age + Main Temp. + Main Temp.^{2}	0.887
Overshoot	1581	~ Year + Stock + Ocean Age + Main Temp. + Temp. Diff. + Temp. Diff^2 + Main Temp.^{2} + Main Temp.^{3} + Year*Stock + Main Temp.*Temp. Diff. + Main Temp^2* Temp. Diff. + Main Temp.^{3}*Temp. Diff. + Main Temp.*Temp. Diff.^{2} + Main Temp.^{2}*Temp. Diff.^{2} + Main Temp.^{3}*Temp. Diff.^{2}	0.862

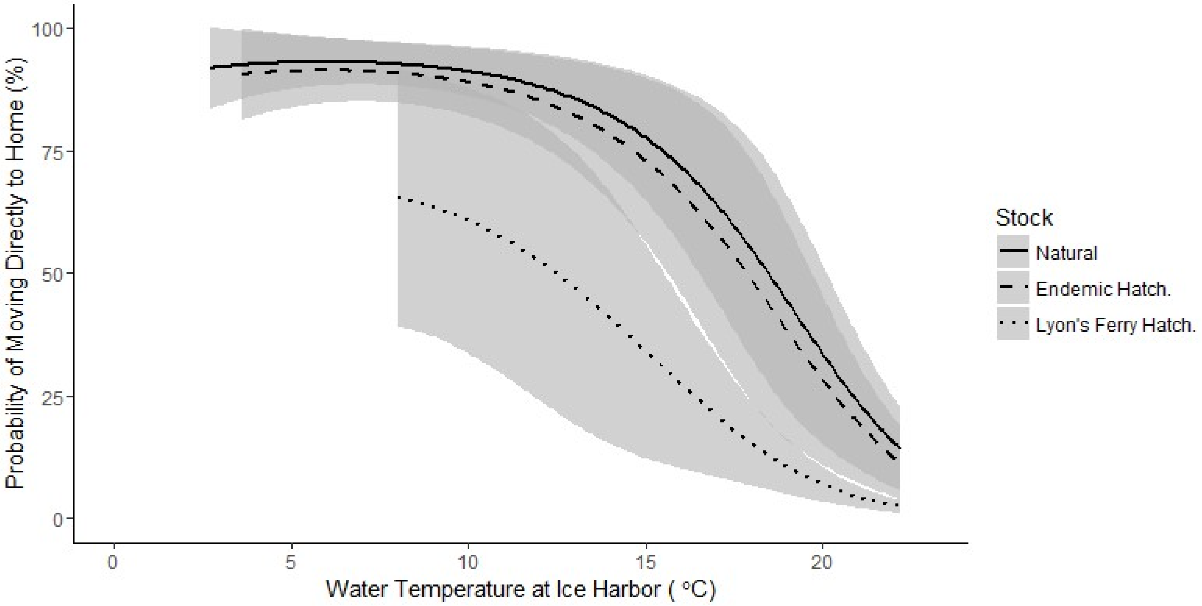

FIGURE J.8.—Predicted probability of moving directly to home after passing McNary Dam, and 90% confidence interval, at different mainstem water temperatures for Walla Walla River steelhead. Baseline is steelhead that spent one year in the ocean and returned to freshwater in the run year 2014/2015.

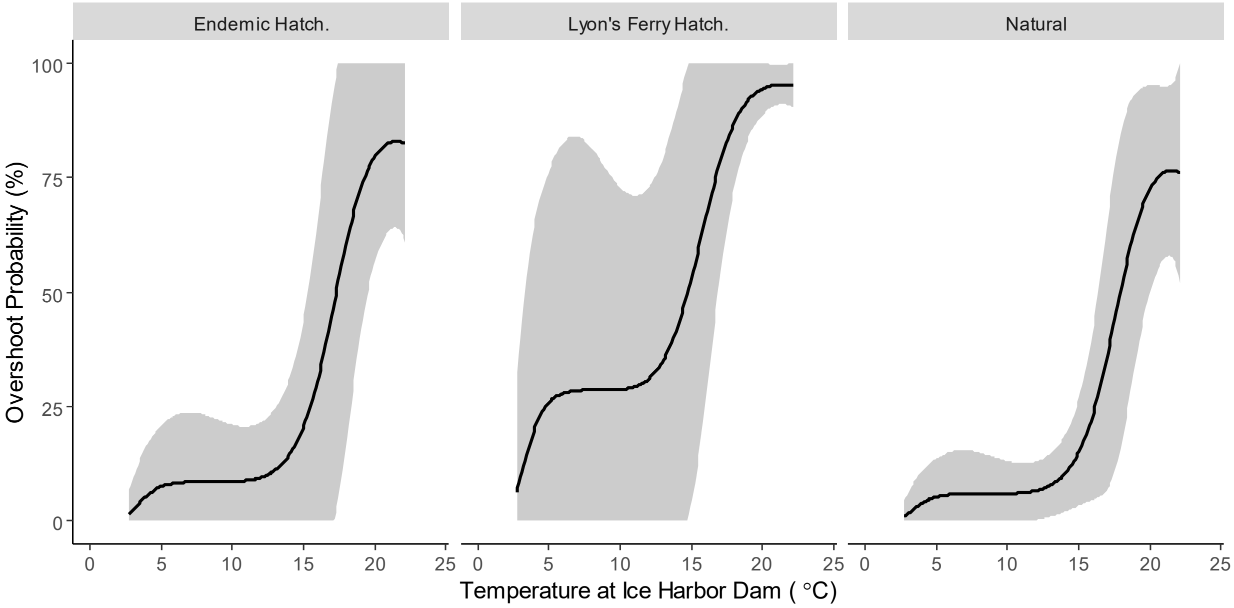

FIGURE J.9.—Predicted probability of overshooting after passing McNary Dam, and 90% confidence interval, at different mainstem water temperatures for Walla Walla River steelhead. Baseline is steelhead that spent one year in the ocean and returned to freshwater in the run year 2014/2015. Predicted values for steelhead from endemic hatchery, Lyon's Ferry hatchery, and natural origin stocks are plotted separately. Overshoot prediction used estimated temperature in the Walla Walla River based on the relationship with mainstem water temperature plotted in Figure J.7.

Shoreline orientation at McNary Dam was not significant enough to be included in the final model for overshooting ($F_{1,1545} = 1.84$, $P = 0.176$) or movement directly to home ($F_{1,1567} = 2.35$, $P = 0.125$). Though insignificant, the direction of the effect suggested higher homing rates for steelhead that were oriented to the southern shore, the same as the Walla Walla River, were more likely to directly home and less likely to overshoot.

Analysis of overshooting and movement directly to home using conditional inference trees found natal water temperature, mainstem water temperature, stock, and McNary passage date to produce significant splits (Figure J.10). Natal temperature produced the first split ($P < 0.0001$). Walla Walla steelhead that encountered higher natal water temperatures were most likely to overshoot, while steelhead that encountered lower natal water temperatures were more likely to move directly to home. Within the high natal temperature group, endemic hatchery and natural origin steelhead were less likely to overshoot and more likely to move directly to home. Lyon's Ferry hatchery steelhead were further divided by mainstem water temperatures. Within this group, lower water temperatures were associated with decreased overshooting and increased movement directly to home. The node with the highest overshooting rate (> 90%) encountered mainstem temperatures greater than 18.3 °C (Figure J.10).

Steelhead that encountered lower natal water temperatures (≤ 14.9 °C) were also further split within the overshooting tree by mainstem water temperature (Figure J.10). Higher mainstem water temperatures produced higher overshooting rates. The highest rates of movement directly to home belonged to steelhead that encountered natal temperatures less than 14.9 °C and mainstem temperatures less than 11.2 °C (Figure J.10).

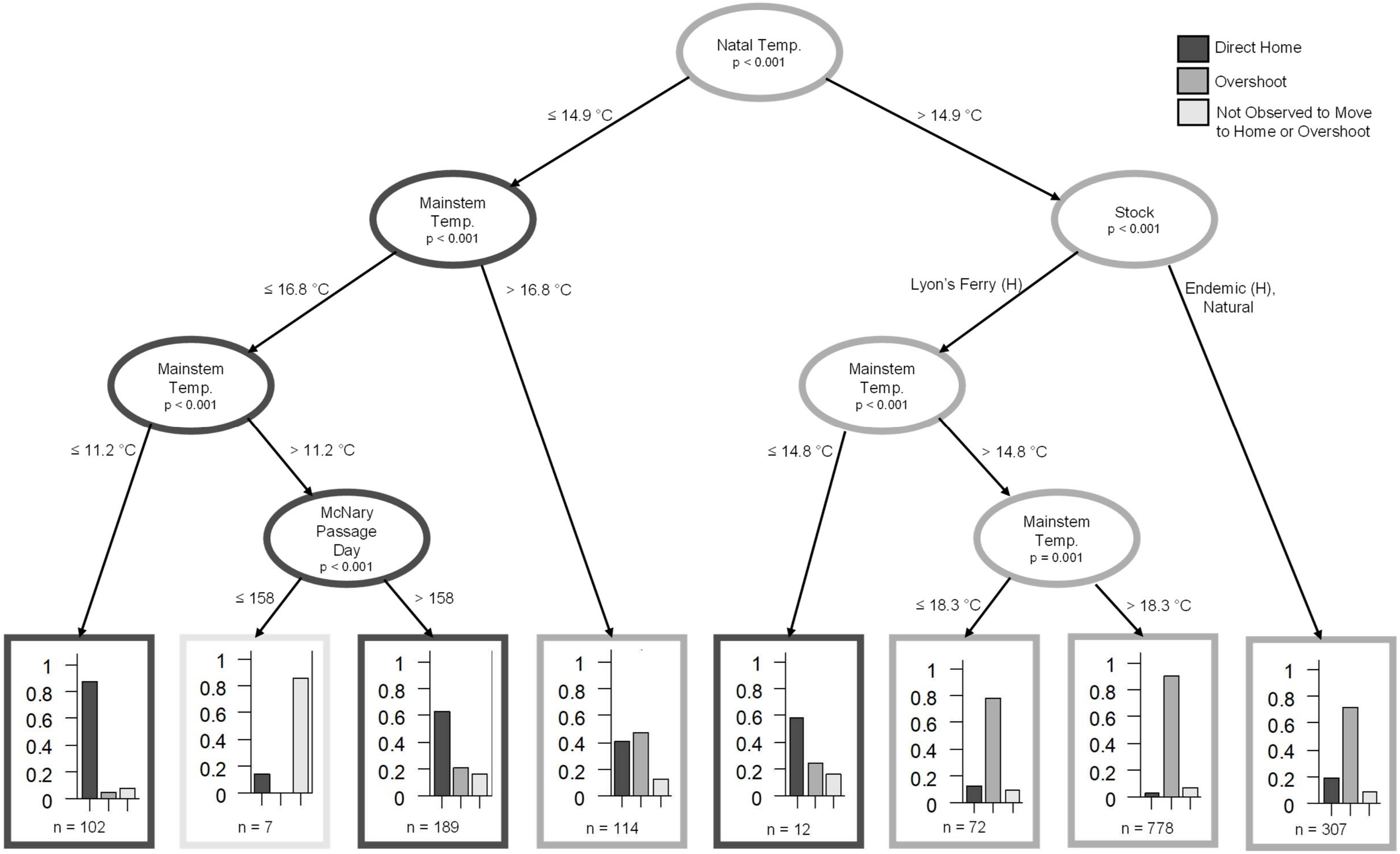

FIGURE J.10.—Conditional inference tree of Walla Walla steelhead behavior between McNary and Ice Harbor. Direct Home = migrated to home without overshooting, Overshoot = overshot Ice Harbor Dam, Natal Temp. = temperature at Walla Walla monitoring station, Mainstem Temp. = temperature of McNary Dam tailwater, McNary Passage Day = calendar day of McNary Dam passage, Stock = rearing history, natural, endemic hatchery, or Lyon's Ferry hatchery.

In Chapter 2, I estimated the average annual fallback rates to home to be 17.8% (SE 1.9%) for hatchery and 43.2% (SE 4.4%) for wild Walla Walla steelhead. In Chapter 3, I found that hatchery steelhead were less likely to fall back to home. Relative to natural origin Walla Walla steelhead, fallback rates to home were 15 percentage points lower for endemic hatchery and 21 percentage points lower for Lyon's Ferry hatchery steelhead. Ocean age did not significantly affect fallback to home. Here, I examined the influence of flow and spill on fallback to home in the natural and two hatchery stocks. I found a significant positive relationship between February spill and fallback to home in the endemic hatchery stock ($F_{1,5} = 9.60$, $P = 0.014$). Additionally, fallback to home by the Lyon's Ferry hatchery stock was positively associated with March spill ($F_{1,5} = 7.19$, $P = 0.021$). Spill and flow were not associated with increased fallback to home in the remaining months or stocks (Table J.4).

TABLE J.4.—One-tailed P-values testing for a positive association between estimated fallback rate and January, February, and March spill, as well as March flow at overshot dams for Walla Walla River steelhead. Values < 0.05 indicate a significant positive relationship (*) between fallback and spill or flow.

		One-tailed P-value			
Stock	DF	January Spill	February Spill	March Spill	March Flow
Natural	4	0.931	0.309	0.380	0.263
Endemic Hatchery	5	0.430	0.014*	0.693	0.793
Lyon's Ferry Hatchery	5	0.264	0.774	0.022*	0.148

Analysis of fallback to home by Walla Walla steelhead with conditional inference trees found only stock to produce significant splits (Figure J.11). Consistent with the results in Chapter 2, natural origin steelhead were the most likely to fall back, followed by endemic hatchery and then Lyon's Ferry hatchery fish. As noted in Chapter 2, no endemic hatchery steelhead released in the Walla Walla River had adipose fin clips. In contrast, Lyon's Ferry hatchery steelhead were adipose clipped and subject to harvest by fishermen.

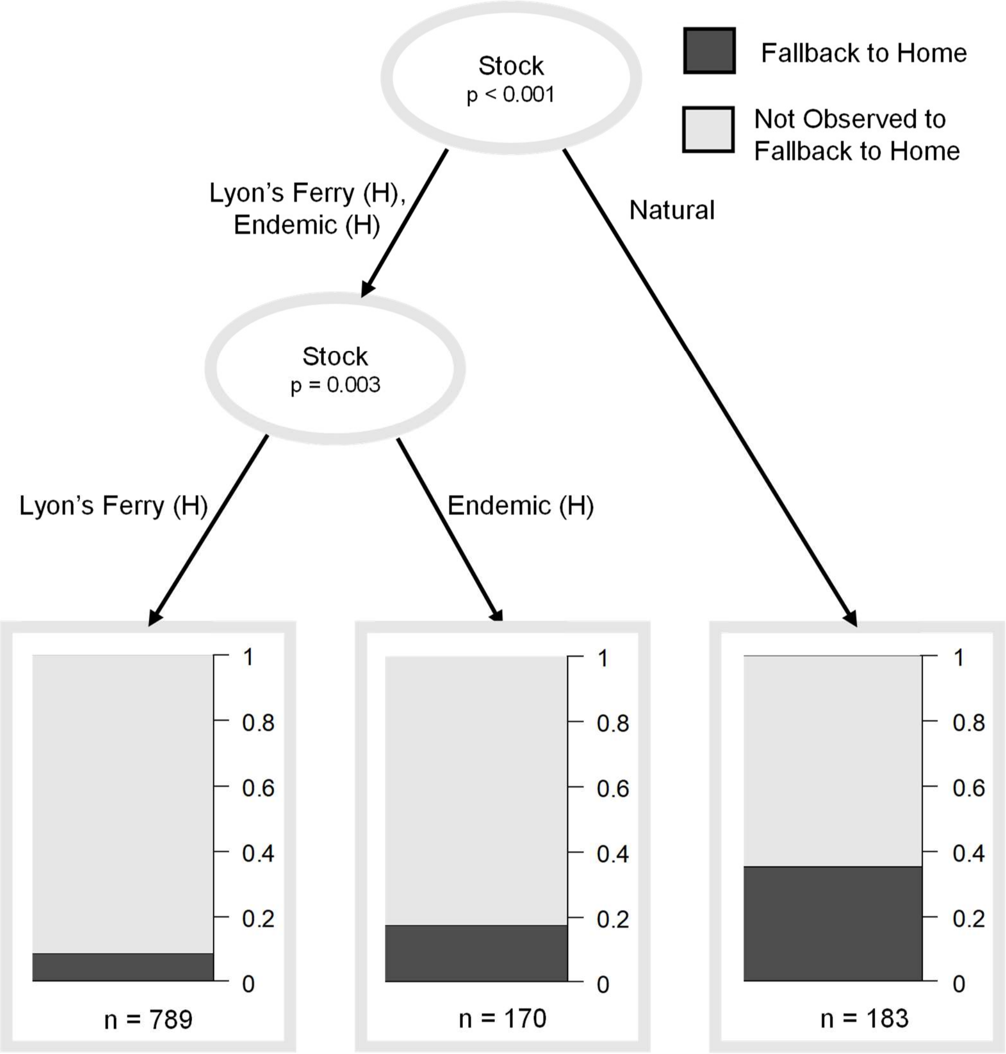

FIGURE J.11.—Conditional inference tree of adult Walla Walla River steelhead migratory behavior after overshooting Ice Harbor Dam. Fallback to Home = fell back downstream to home, Stock = rearing history (natural, endemic hatchery, Lyon's Ferry hatchery).

Yakima.—In Chapter 2, I estimated that on average 16.3% (SE 2.2%) of Yakima River steelhead that passed McNary Dam went on to overshoot Priest Rapids Dam. In Chapter 3, I did not find a significant influence of ocean age on overshooting. Here, I investigated the influence of mainstem water temperature and shoreline orientation at McNary dam on overshooting and movement directly to home. Average water temperatures at Priest Rapids Dam ranged from 4.5 °C to 20.6 °C, with a median of 18.3 °C as Yakima River steelhead neared their home tributary. Most (67.9%) of Yakima River steelhead were observed passing McNary Dam, located 69 rkm below the mouth of the Yakima River, in the southern ladder. The southern ladder is on the opposite shoreline as the mouth of the Yakima River. Walla Walla River steelhead were also shown to favor the southern ladder at McNary Dam. The preference observed in Walla Walla River steelhead was stronger (76.6%), perhaps due to close proximity to the Walla Walla River, which is located on the southern shoreline.

Logistic regression found a significant influence of water temperature on movement directly to home and overshooting by Yakima River steelhead. Direct homing and overshoot models included mainstem temperature and an interaction between temperature and ocean age (Table J.5). Increasing water temperatures at Priest Rapids dam were associated with decreased movement directly to home (main effect: $F_{1,202} = 43.00$, $P < 0.0001$) and increased overshooting (main effect: $F_{1,202} = 51.65$, $P < 0.0001$). Significant interactions between temperature and ocean age were found, with ocean age 2 fish responding to changes in temperature at a lower threshold but with a more gradual slope than ocean age 1 fish (Figures J.12 and J.13).

TABLE J.5.—Final models of Yakima River steelhead migratory behavior. Year and Ocean Age included as blocking factors. Potential variables included water temperature at Priest Rapids Dam (Main Temp.) and shoreline orientation at McNary Dam. AUC = area under the curve, Year = run year, Ocean Age = number of years spent in ocean. P-value for variable entry was P = 0.05.

Migration Stage	**N**	**Final Model**	**AUC**
Go Directly Home	215	~ Year + Ocean Age + Main Temp. + Ocean Age*Main Temp.	0.815
Overshoot	215	~ Year + Ocean Age + Main Temp. + Ocean Age*Main Temp.	0.837

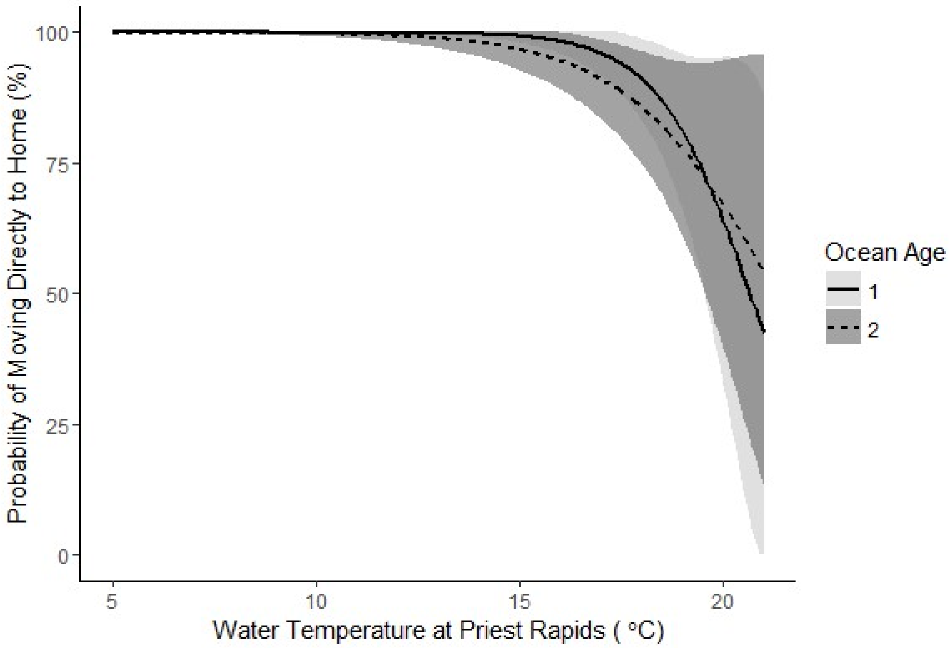

FIGURE J.12.—Predicted probability of moving directly to home after passing McNary Dam, and 90% confidence interval, at different mainstem water temperatures for Yakima River steelhead. Baseline is steelhead that spent one or two years in the ocean and returned to freshwater in the run year 2014/2015.

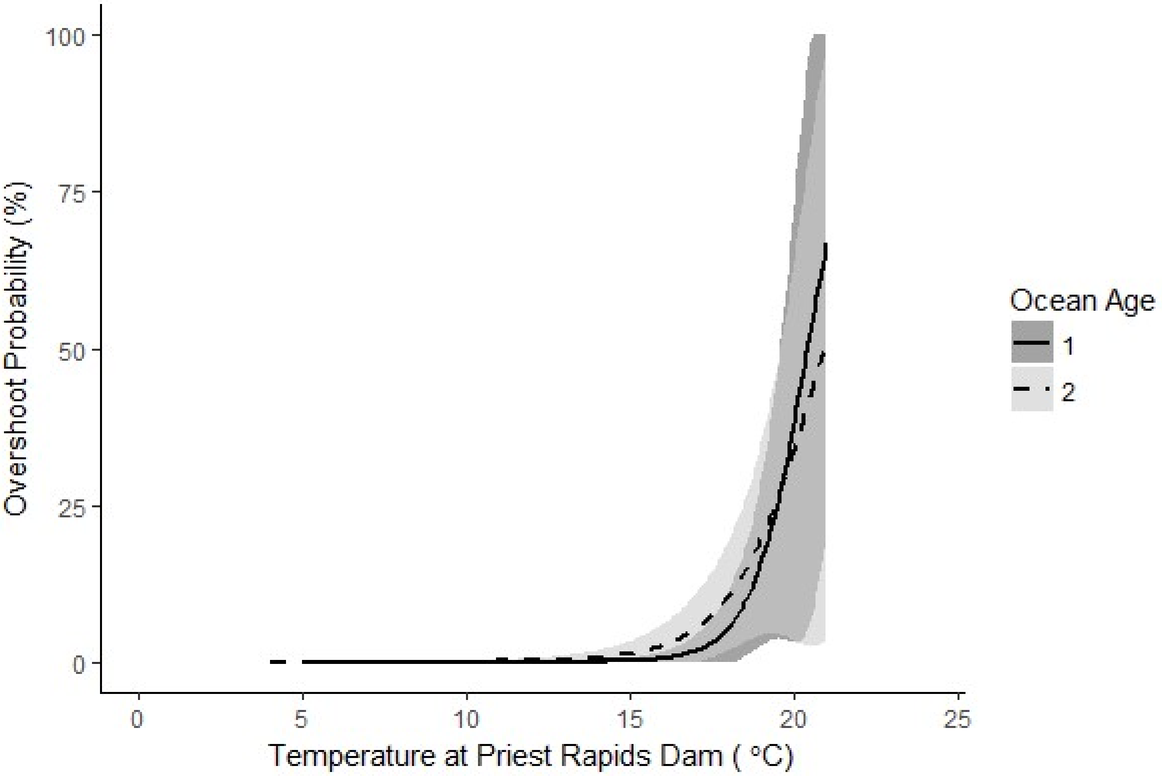

FIGURE J.13.—Predicted probability of overshooting after passing McNary Dam, and 90% confidence interval, at different mainstem water temperatures for Yakima River steelhead. Baseline is steelhead that spent one or two years in the ocean and returned to freshwater in the run year 2014/2015.

Shoreline orientation of steelhead at McNary Dam was not significant enough to be included in the final model for overshooting ($F_{1,201}$ = 2.70, P = 0.102) or movement directly to home ($F_{1,201}$ = 1.15, P = 0.285) for Yakima River steelhead. Though insignificant, the direction of the effect was opposite of hypothesized. Yakima River steelhead may have plenty of time to orient correctly after passing McNary Dam, as the Yakima River is 69 rkm upstream.

Analysis of overshooting and movement directly to home using conditional inference trees found mainstem water temperature and McNary passage date to produce significant splits (Figure

J.14). Yakima River steelhead that encountered higher mainstem water temperatures near their home tributary were more likely to overshoot and less likely to return directly to home. The highest rates of movement directly to home (> 90%) belonged to the group that encountered average mainstem temperatures less than 17.9 °C. Among steelhead that encountered mainstem temperatures between 17.9 °C and 18.6 °C, passing McNary Dam later in the year was associated with decreased overshooting. Of the final four nodes, the only node assigned to overshooting is the medium temperature group that passed McNary Dam before 30 July (Figure J.14).

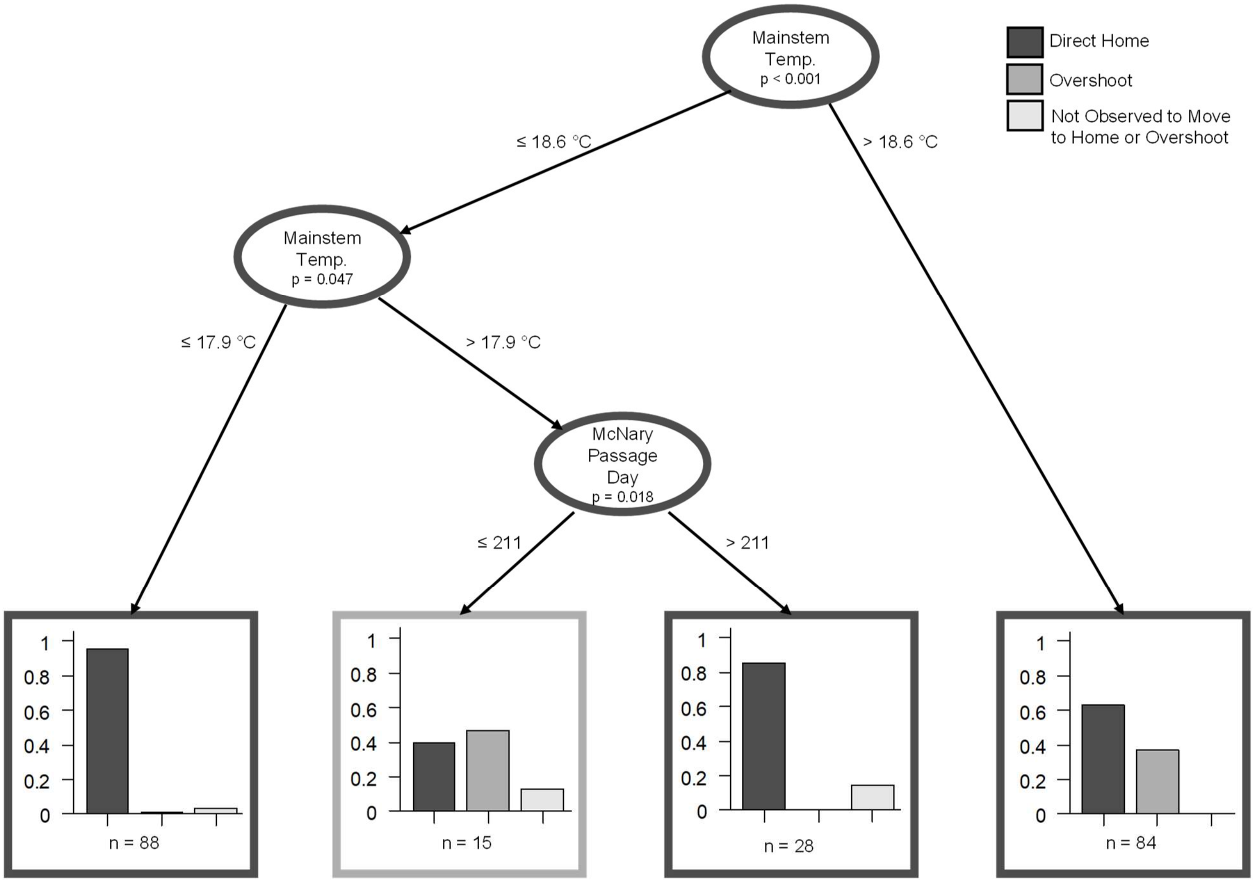

FIGURE J.14.—Conditional inference tree of adult Yakima River steelhead migratory behavior between McNary and Priest Rapids dams. Direct Home = migrated to home without overshooting, Overshoot = overshot Priest Rapids Dam, Mainstem Temp. = average temperature of Priest Rapids Dam tailwater as steelhead neared their home tributary, McNary Passage Day = calendar day of McNary Dam passage.

In Chapter 2, I estimated the average annual fallback rate to home to be 70.6% (SE 0.4%) for wild Yakima River steelhead. In Chapter 3, I did not find ocean age to significantly affect fallback to home. Here, I examined the influence of flow and spill on fallback to home. However, inference power was limited because I was only able to estimate fallback to home in 3 years. Additionally, within those three years there was virtually no variation in estimated fallback to home rate (range: 70.2%—71.4%). I did not find a significant positive relationship between fallback rate to home and flow during March ($F_{1,1} < 0.01$, $P = 0.407$) or spill during January ($F_{1,1} = 0.13$, $P = 0.609$), February ($F_{1,1} = 0.16$, $P = 0.760$), or March ($F_{1,1} = 2.21$, $P = 0.189$). Analysis of fallback to home using conditional inference trees did not result in any significant splits.

Wenatchee.—In Chapter 2, I estimated that, on average, 65.6% (SE 7.5%) of hatchery and 10.6% (SE 3.0%) of wild Wenatchee steelhead that passed Rock Island Dam continued upstream past the Wenatchee River to overshoot Rocky Reach Dam. However, from 2010/2011 to 2014/2015, annual overshoot estimates by hatchery fish declined from 82.4% (SE 3.8%) to 16.0% (SE 8.0%). In Chapter 3, I found that acclimation of Wenatchee hatchery steelhead within the release basin decreased overshooting by 41 percentage points compared to direct release. I also found a small effect of ocean age on overshooting; ocean age 2 fish were less likely to overshoot, by an average of 4 percentage points, than ocean age 1 fish. Here, I investigated the influence of water temperature in the Columbia River and shoreline orientation at Rock Island Dam on overshooting and movement directly to home.

As Wenatchee River steelhead neared their natal river, average water temperatures at Rocky Reach Dam ranged from 4.9 °C to 20.3 °C, with a median of 18.3 °C. Shoreline orientation at Rock Island Dam, 24 rkm below the Wenatchee River, indicated that most steelhead were aligned to the same shoreline as the mouth of the Wenatchee River. Wenatchee River steelhead passed primarily in the western ladder at Rock Island Dam. I found 74.8% to utilize the western ladder, 11.0% to utilize the middle ladder, and 14.2% to utilize the eastern ladder.

Logistic regression found a significant influence of shoreline orientation on movement directly to home ($F_{2,1594} = 28.47$, $P < 0.0001$) and overshooting ($F_{2,2075} = 24.97$, $P < 0.0001$) by Wenatchee River steelhead (Table J.6). Water temperature was also significant in the model for movement directly to home ($F_{2,1594} = 9.40$, $P < 0.0001$), but not in the model for overshooting ($F_{1,2074} = 2.73$, $P = 0.098$). Steelhead that passed in the eastern ladder, on the opposite shore of the natal river mouth, returned directly to home less and overshot more than steelhead that passed in the middle or western ladders (Figures J.15 and J.16). Orientation to the opposite shoreline may cause steelhead to miss the natal stream mouth and incoming water plume. Those that passed in the middle ladder experienced a smaller decline in probability of direct homing, after controlling for blocking factors, than those that passed in the eastern ladder (Figure J.17). Additionally, movement directly to home became less likely as water temperature of the Rocky Reach outflow increased (Figure J.17). This pattern is consistent with that found for other tributaries.

TABLE J.6.—Final models of Wenatchee River steelhead migratory behavior. Year, Stock, and Ocean Age included as blocking factors. Potential variables included water temperature at Rocky Reach Dam (Main Temp.) and shoreline orientation at Rock Island Dam (Shoreline). AUC = area under the curve, Year = run year, Stock = acclimated hatchery, non-acclimated hatchery, or natural stock, Ocean Age = number of years spent in ocean. P-value for variable entry was $P = 0.05$.

Migration Stage	**N**	**Final Model**	**AUC**
Go Directly Home	1626	~ Year + Stock + Ocean Age + Shoreline + Main Temp. + Main Temp.^{2} + Year*Main Temp. + Year*Main Temp.^{2}	0.878
Overshoot	2097	~ Year + Stock + Ocean Age + Shoreline + Year*Ocean Age	0.830

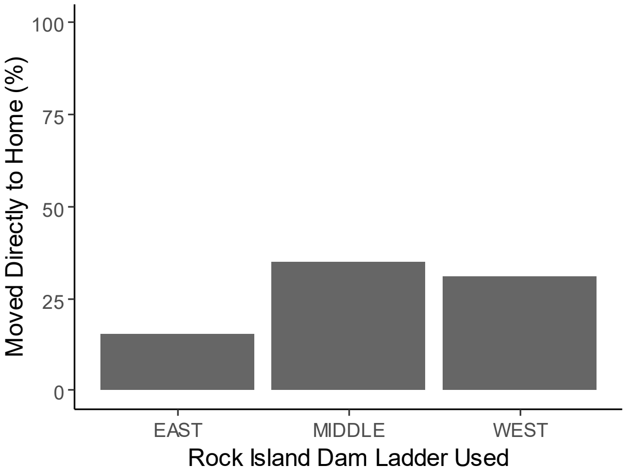

FIGURE J.15.—Percent of Wenatchee River steelhead observed to move directly to home after passing Rock Island Dam passage in either the west, middle, or east fish ladders. The west ladder is on the same side of the river as the mouth of the natal stream. Rock Island Dam is 24 rkm below the mouth of the Wenatchee River.

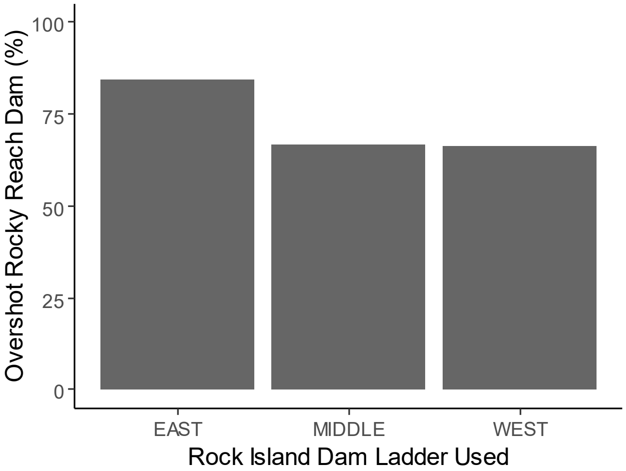

FIGURE J.16.—Percent of Wenatchee River steelhead observed to overshoot Rocky Reach Dam after passing Rock Island Dam passage in either the west, middle, or east fish ladders. The west ladder is on the same side of the river as the mouth of the natal stream. Rock Island Dam is 24 rkm below the mouth of the Wenatchee River.

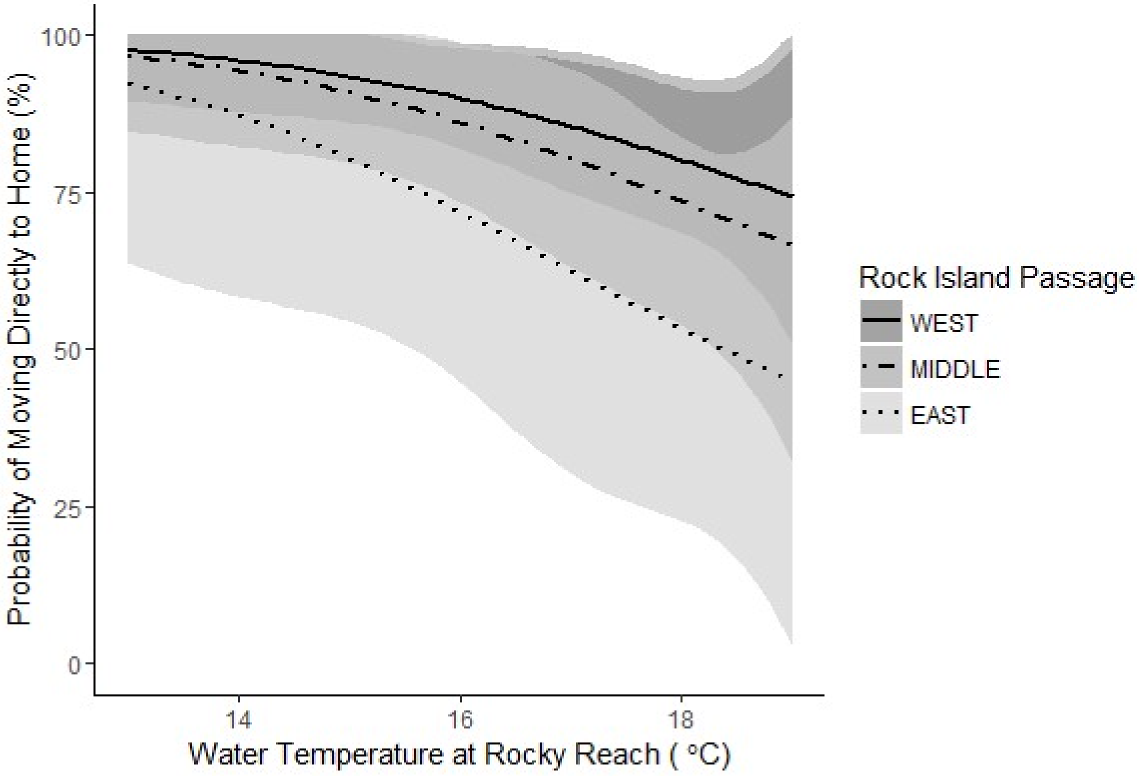

FIGURE J.17.—Predicted probability of moving directly to home after passing Rock Island Dam, and 90% confidence interval, at different mainstem water temperatures for natural origin Wenatchee River steelhead. Baseline is steelhead that spent two years in the ocean and returned to freshwater in the run year 2010/2011. Rock Island Dam passage occurred in the western, middle, or eastern dam ladder. The western ladder is on the same side of the river as the Wenatchee River.

Analysis of overshooting and movement directly to home using conditional inference trees found stock, shoreline orientation, Rock Island passage date, and mainstem water temperature to produce significant splits (Figure J.18). The first split occurred on stock ($P < 0.0001$), separating the non-acclimated hatchery steelhead from the acclimated hatchery and natural steelhead. Non-acclimated hatchery steelhead were predicted to overshoot, while the other group were predicted to return directly to home. This is consistent with the analysis performed in Chapter 3. Among the non-acclimated group, passage in the western ladder elevated the chances of returning directly to home and decreased the chances of overshooting slightly.

Acclimated hatchery and natural fish were further split by shoreline as well (Figure J.18). Those that passed in the middle or western ladders were predicted to return directly to home, while those that passed in the eastern ladder were predicted to overshoot. Among the steelhead aligned to the correct shoreline, naturally reared fish performed better than acclimated hatchery fish. In the other branch, acclimated hatchery and natural steelhead that passed in the eastern ladder were further split by Rock Island Passage Date and water temperature. Those that passed prior to 4 August were more likely to return directly to home and less likely to overshoot. The late-arrivers were predicted to overshoot at temperatures below 18.4 °C and return directly to home when temperatures exceeded 18.4 °C. These temperature results initially seem contrary to those found using logistic regression, however they are particular to a small group of steelhead in the conditional inference tree. It is likely that the earlier split on passage date also represented a response to temperature. Those that passed earlier, prior to peak temperatures, were more likely to return to home and less likely to overshoot. While overshooting generally was found to increase with temperature for steelhead from other tributaries, many demonstrated a decline in overshooting after reaching a high temperature threshold.

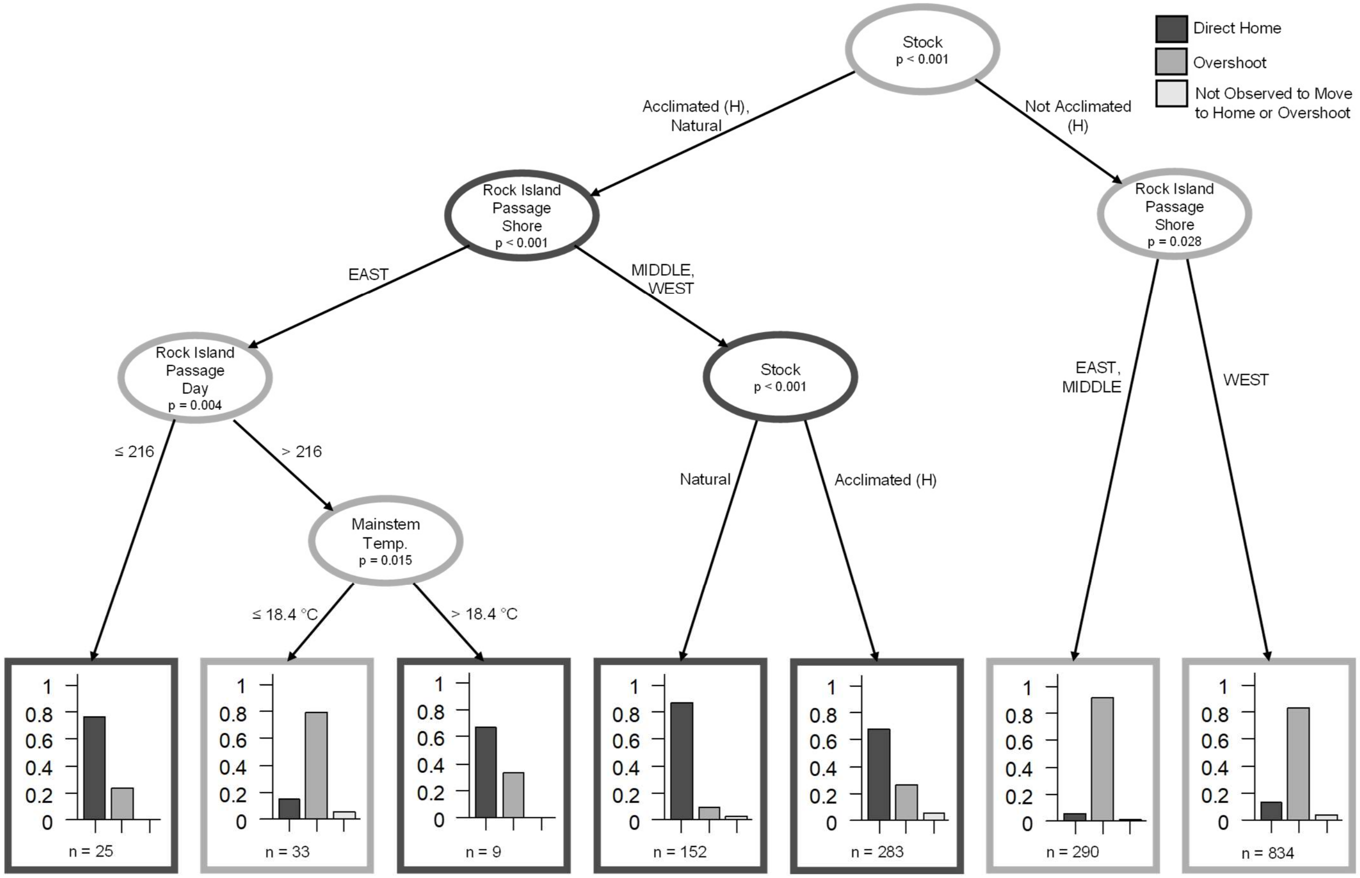

FIGURE J.18.—Conditional inference tree of Wenatchee steelhead behavior between Rock Island and Rocky Reach. Direct Home = migrated to home without overshooting, Overshoot = overshot Rocky Reach, Stock = rearing history (natural, acclimated hatchery, or non-acclimated hatchery), Rock Island Passage Shore = ladder used at Rock Island Dam, Rock Island Passage Day = calendar day of Rock Island passage, Mainstem Temp. = temperature of Rock Island Dam tailwater.

In Chapter 2, I estimated the average annual fallback rate to home to be 26.3% (SE 4.2%) for hatchery Wenatchee River steelhead. I was unable to estimate annual fallback by naturally reared steelhead due to low overshooting rates combined with small sample sizes of wild fish. In Chapter 3, I found that both acclimated and non-acclimated hatchery steelhead were less likely to fallback than naturally reared steelhead, by 40 percentage points. Ocean age was not found to significantly affect fallback to home. Here, I examined the influence of flow and spill on fallback to home. Regression analysis did not find a significant positive relationship between fallback rate to home by hatchery Wenatchee River steelhead and flow during March ($F_{1,2} = 0.05$, $P = 0.580$) or spill during January ($F_{1,2} = 0.1.898$, $P = 0.849$), February ($F_{1,2} < 0.01$, $P = 0.530$), or March ($F_{1,2} = 0.30$, $P = 0.320$). Like most other tributaries, while March flow was not significant at a $P < 0.05$ level, it was the most significant of the flow and spill factors tested.

Analysis of fallback to home using conditional inference trees found stock, mainstem flow, and ocean age to produce significant splits (Figure J.19). Natural origin steelhead fell back to home at much higher rates than hatchery origin steelhead. Consistent with the results of Chapter 2, acclimation did not affect fallback of hatchery fish. Hatchery steelhead that overshot in years with higher flow rates during March were more likely to fall back to home. Among the low flow group, steelhead that spent two years in the ocean were more likely to fall back to home than those that spent one year in the ocean.

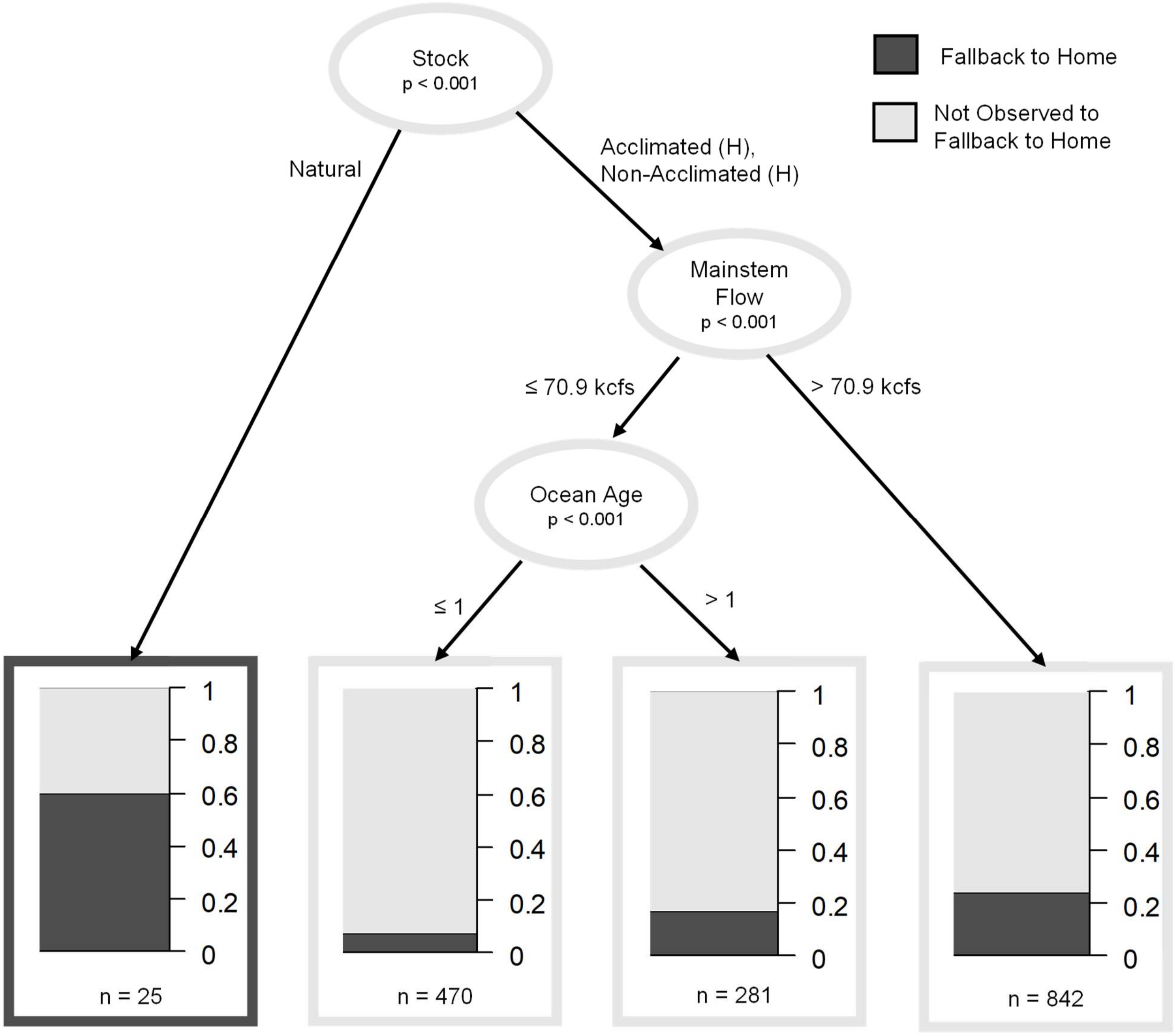

FIGURE J.19.—Conditional inference tree of adult Wenatchee River steelhead migratory after overshooting Rocky Reach Dam. Fallback to Home = fell back downstream to home, Stock = rearing history (natural, acclimated hatchery, non-acclimated hatchery), Mainstem Flow = average flow at Rocky Reach Dam during March, Ocean Age = ocean residency time in years.

Entiat.—In Chapter 2, I estimated that, on average, 38.6% (SE 5.4%) of Entiat steelhead that passed Rocky Reach Dam continued upstream past the Entiat River to overshoot Wells Dam. In Chapter 3, I found that ocean age significantly affected the probability of overshooting and moving directly to home. Ocean age 2 steelhead were more likely to overshoot and less likely to move directly to home, by 12 percentage points, than ocean age 1 steelhead. Here, I investigated the effects of mainstem water temperature on overshoot behavior. Average water temperatures at Wells Dam ranged from 6.1 °C to 20.0 °C, with a median of 18.5 °C, when Entiat River steelhead neared their home tributary (Figure J.20). Only one fish ladder was present at Rocky Reach Dam. All Entiat River steelhead therefore passed Rocky Reach Dam on the western shore, the same shore as the mouth of the Entiat River 15 rkm upstream.

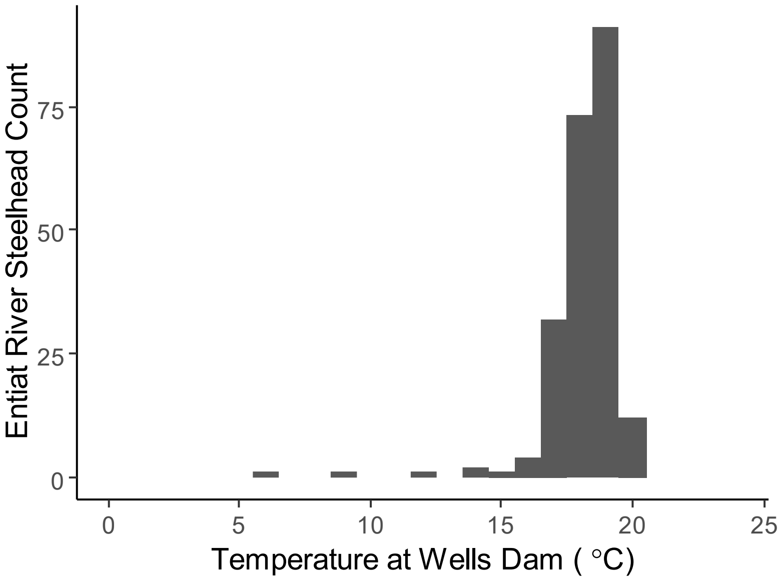

FIGURE J.20.—Histogram of water temperatures in the Columbia River when Entiat River steelhead arrived near their natal tributary.

Logistic regression found a significant influence of water temperature in the Wells Dam outflow on movement directly to home ($F_{3,207} = 2.96$, $P = 0.033$) and overshooting ($F_{3,207} = 2.83$, $P = 0.040$) by Entiat River steelhead. First, second, and third order terms for temperature were included in both final models (Table J.7). While movement directly to home generally decreased with increasing temperature, the relationship was not monotonic (Figure J.21). The model fitted an unusual increase in movement directly to home between 16 °C and 18 °C, followed by a decline. As you can see from Figure J.20, this pattern was not due to scarce data within this temperature interval. The model predictions for overshooting followed a similar, though opposite pattern (Figure J.22). While the model predictions between 16 °C and 18 °C were odd compared to the pattern observed in other tributaries, the general relationship of increased overshooting with increasing temperature was still demonstrated for Entiat River steelhead.

TABLE J.7.—Final models of Entiat River steelhead migratory behavior. Year and Ocean Age included as blocking factors. Potential variables included water temperature at Wells Dam (Main Temp.). AUC = area under the curve, Year = run year, Ocean Age = number of years spent in ocean. P-value for variable entry was P = 0.05.

Migration Stage	**N**	**Final Model**	**AUC**
Go Directly Home	218	~ Year + Stock + Ocean Age + Main Temp. + Main Temp.^{2} + Main Temp.^{3}	0.691
Overshoot	218	~ Year + Stock + Ocean Age + Main Temp. + Main Temp.^{2} + Main Temp.^{3}	0.670

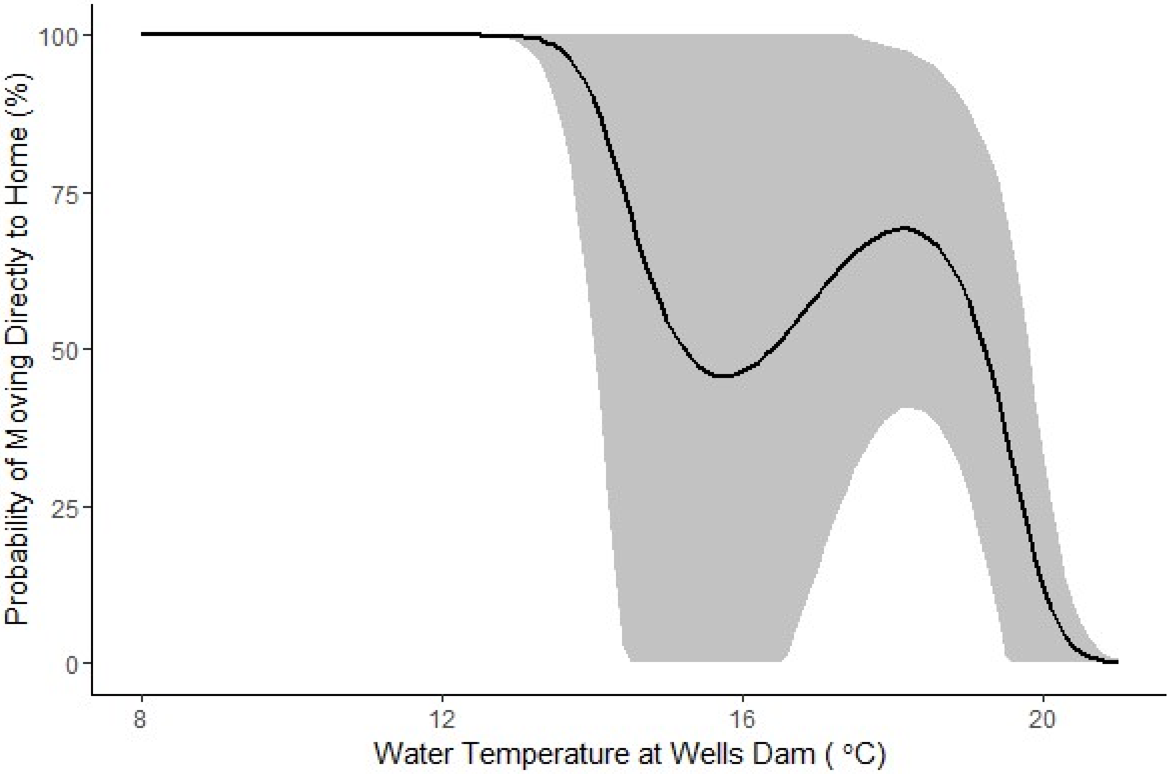

FIGURE J.21.—Predicted probability of moving directly to home after passing Rocky Reach Dam, and 90% confidence interval, at different mainstem water temperatures for Entiat River steelhead. Baseline is steelhead that spent one year in the ocean and returned to freshwater in the run year 2014/2015.

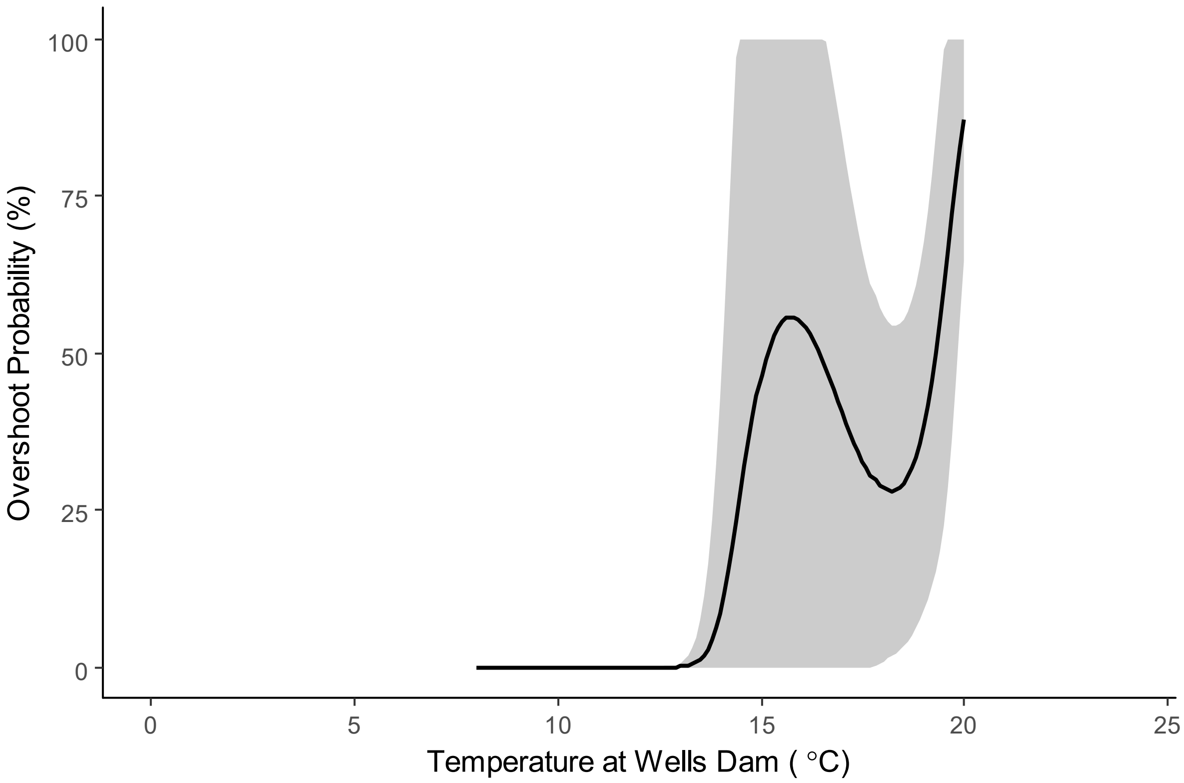

FIGURE J.22.—Predicted probability of overshooting after passing Rocky Reach Dam, and 90% confidence interval, at different mainstem water temperatures for Entiat River steelhead. Baseline is steelhead that spent one year in the ocean and returned to freshwater in the run year 2014/2015.

In Chapter 2, I estimated the average annual fallback rate to home to be 65.8% (SE 6.3%) for wild Entiat River steelhead. In Chapter 3, ocean age was not found to significantly affect fallback to home. Here, I examined the influence of flow and spill on fallback to home. Regression analysis did not find a significant positive relationship between fallback rate to home and flow during March ($F_{1,4} = 0.62$, $P = 0.284$) or spill during January ($F_{1,4} = 3.85$, $P = 0.061$), February ($F_{1,4} = 1.01$, $P = 0.814$), or March ($F_{1,4} = 0.97$, $P = 0.191$). While not quite significant at a $P < 0.05$ level, spill during January did appear to be positively related to fallback to home rate. Like Yakima

River steelhead, which also had a limited sample size and relatively high fallback rates to home, analysis of fallback to home using conditional inference trees did not result in any significant splits for Entiat River steelhead.

Tucannon.—I estimated overshoot rates by hatchery and wild Tucannon River steelhead in Chapter 2. Annually, an average of 60.7% (SE 2.6%) of hatchery and 59.3% (SE 3.7%) of wild Tucannon steelhead that passed Ice Harbor Dam continued past the mouth of the Tucannon River and overshot Lower Granite Dam 73 rkm upstream. In Chapter 3, I found that Lyon's Ferry hatchery steelhead were less likely to overshoot, by 7 percentage points, than endemic hatchery and natural origin steelhead. Additionally, I found that Tucannon River steelhead barged as juveniles had movement rates directly to home 6 percentage points higher and overshoot rates 12 percentage points lower than steelhead that out-migrated in-river. Ocean age did not significantly affect overshooting. Here, I investigated the influence of mainstem and natal water temperature on direct homing and overshooting.

As Tucannon River steelhead neared their home tributary, average water temperatures at Lower Granite Dam ranged from 3.0 °C to 20.0 °C, with a median of 18.3 °C. In the same time frame, average water temperatures measured in the mainstem Tucannon River, at rkm 41, ranged from 0.7 °C to 20.2 °C, with a median of 14.5 °C. Water temperatures at the Tucannon River monitoring station were generally lower than at Lower Granite Dam, with a median temperature difference of -2.9 °C and a range of -8.5 °C to 1.4 °C. Shoreline orientations at Lower Monumental Dam were not measured for Tucannon River steelhead, because the dam lacked adult detectors until 2014.

Logistic regression found a significant influence of mainstem water temperature on movement directly to home ($F_{2,2033} = 70.82$, $P < 0.0001$) and overshooting ($F_{4,2054} = 31.89$, $P <$

0.0001) by Tucannon River steelhead. Temperature in the Tucannon River was also included in the model for direct homing ($F_{2,2033} = 3.72$, $P = 0.024$). The percent of steelhead observed to move directly to home declined with increasing mainstem water temperature (Figure J.23) and natal river water temperature (Figure J.24). Overshoot probabilities rose with increasing temperatures at Lower Granite Dam, until falling off around 18 °C (Figure J.25).

TABLE J.8.—Final models of Tucannon River steelhead migratory behavior. Year, Stock, Barging, and Ocean Age included as blocking factors. Potential variables included water temperature at Lower Granite Dam (Main Temp.), water temperature in the Tucannon River (Natal Temp.), and water temperature difference between the Tucannon and Snake rivers. AUC = area under the curve, Year = run year, Stock = endemic hatchery, Lyon’s Ferry hatchery, or natural stock, Barging = barged or in-river out-migration, Ocean Age = number of years spent in ocean. P-value for variable entry was P = 0.05.

Migration Stage	**N**	**Final Model**	**AUC**
Go Directly Home	2073	~ Year + Stock + Barging + Ocean Age + Main Temp. + Main Temp.^{2} + Natal Temp. + Natal Temp.^{2} + Barging*Natal Temp. + Baring*Natal Temp.^{2} + Year*Natal Temp. + Year*Natal Temp.^{2} + Stock*Ocean Age	0.735
Overshoot	2073	~ Year + Stock + Barging + Ocean Age + Main Temp. + Main Temp.^{2} + Main Temp.^{3} + Main Temp.^{4} + Barging*Ocean Age	0.697

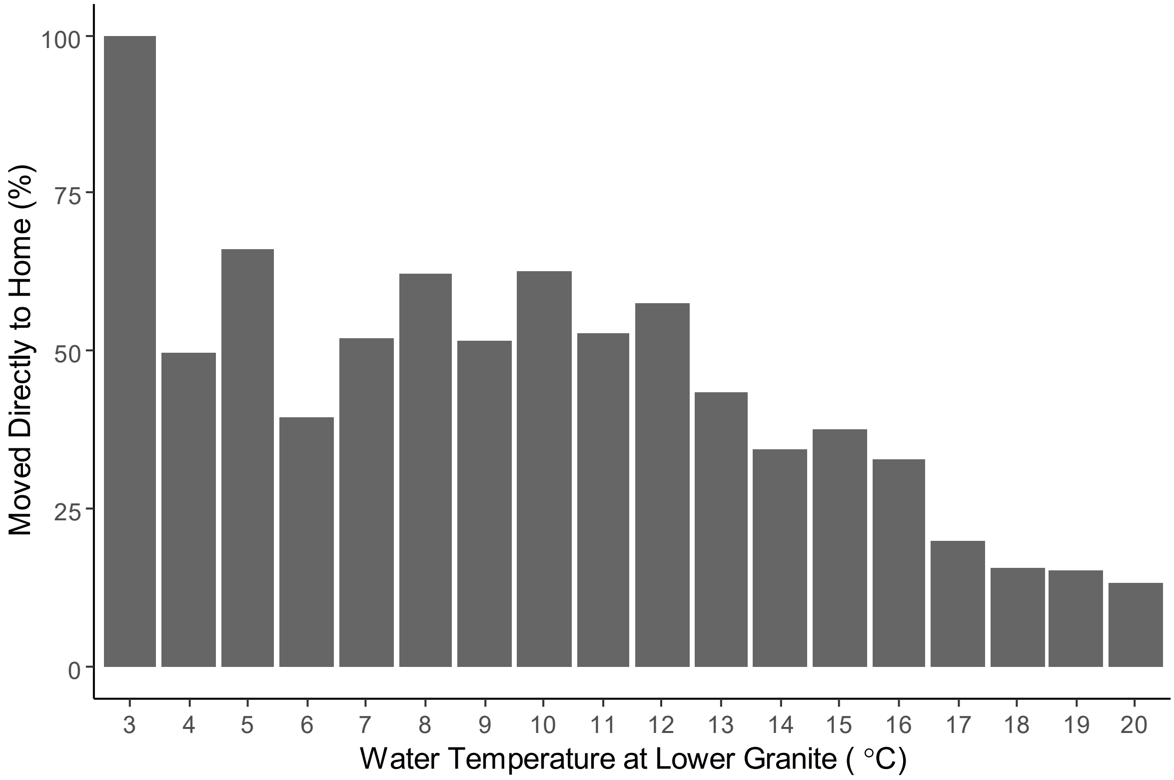

FIGURE J.23.—Percent of Tucannon River steelhead observed to move directly to home from 2005—2015 after passing Ice Harbor Dam versus water temperature in the mainstem river.

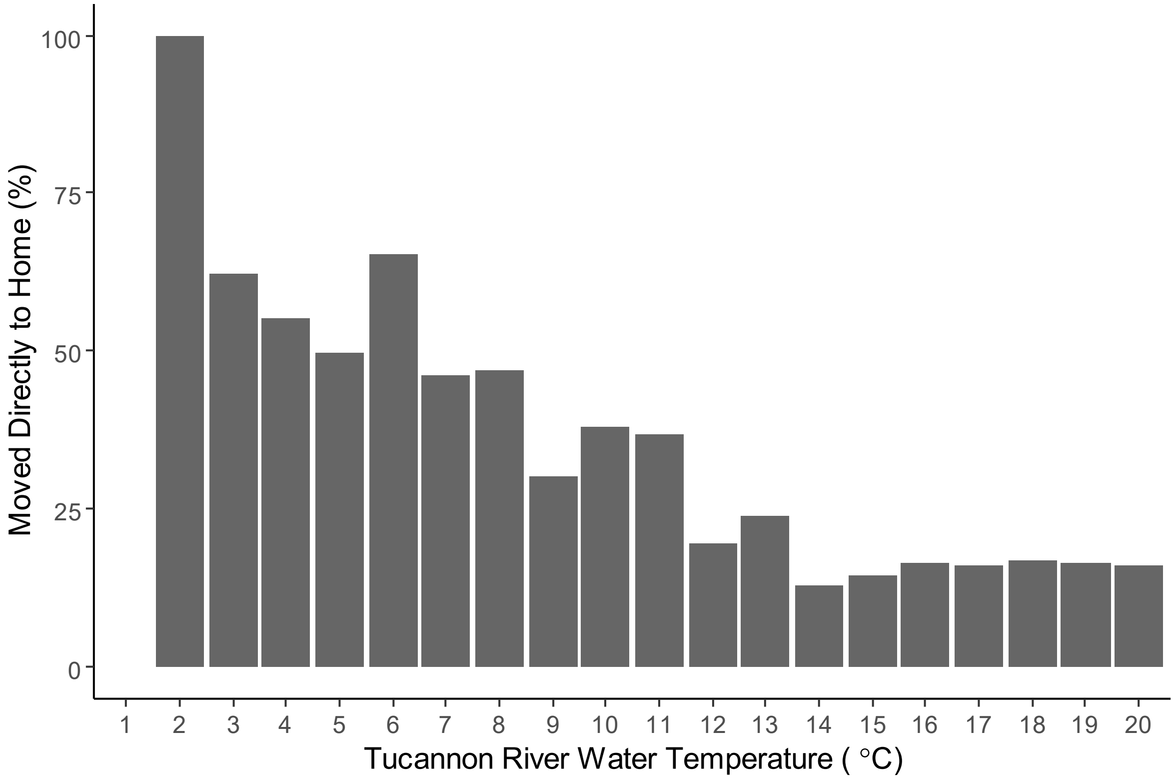

FIGURE J.24.—Percent of Tucannon River steelhead observed to move directly to home from 2005—2015 after passing Ice Harbor Dam versus water temperature in the Tucannon River.

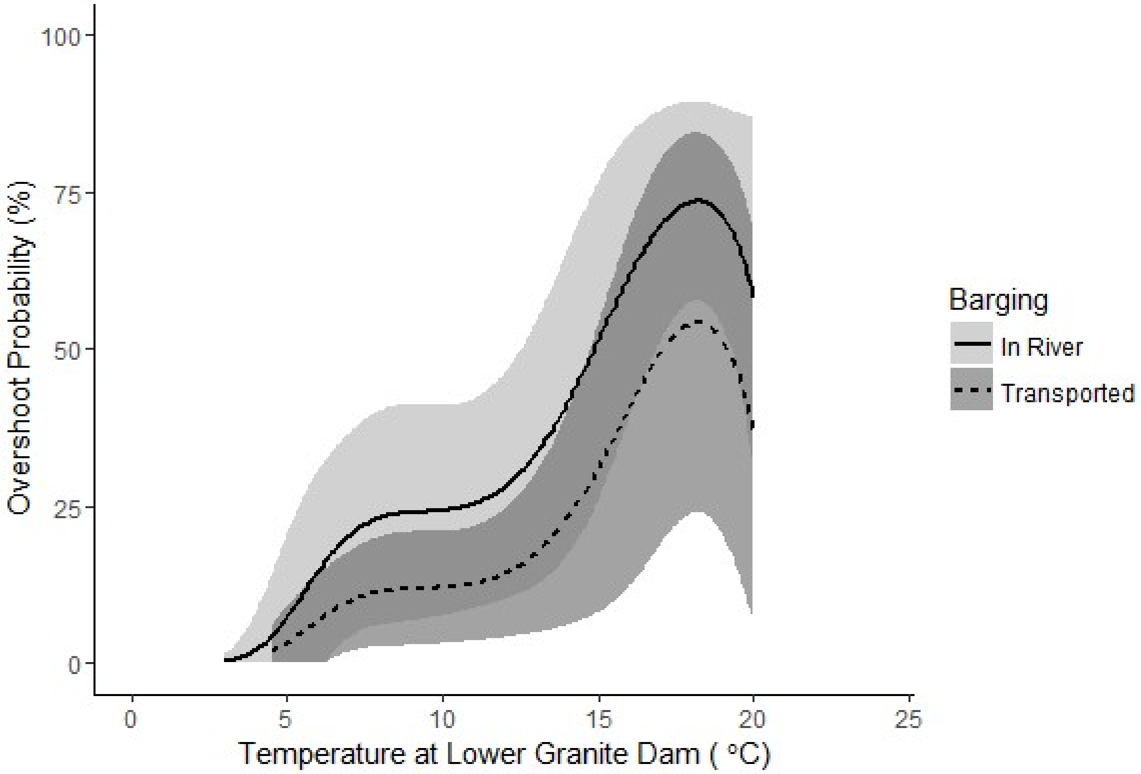

FIGURE J.25.—Predicted probability of overshooting after passing Ice Harbor Dam, and 90% confidence interval, at different mainstem water temperatures for Tucannon River steelhead. Baseline is natural origin steelhead that spent one year in the ocean and returned to freshwater in the run year 2014/2015. In River = in-river out-migration as a juvenile, Transported = barged downriver as a juvenile.

Analysis of overshooting and movement directly to home using conditional inference trees found mainstem temperature, stock, natal temperature, Ice Harbor passage day, and barging to produce significant splits (Figure J.26). The first split occurred on mainstem temperature ($P < 0.0001$), with steelhead exposed to average temperatures greater than 16.5 °C predicted to overshoot, and steelhead exposed to average temperatures less than 16.5 °C predicted to return directly to home. Among the low temperature group, a second split on mainstem temperature, at

13.7 °C, divided steelhead into a lower temperature group predicted to move directly to home and a medium temperature group predicted to overshoot. The medium temperature group was further split by temperature in the Tucannon River, with the higher natal temperature group being more likely to be unobserved, either at home or overshooting, than the lower natal temperature group.

Within the high mainstem temperature group created by the first split, steelhead were further split by stock, barging, and Ice Harbor passage date (Figure J.26). Consistent with the results of Chapter 3, Lyon’s Ferry hatchery steelhead were less likely to overshoot than endemic hatchery and natural origin steelhead. Additionally, within the Lyon’s Ferry group, steelhead transported as juveniles were more likely to return directly to home and less likely to overshoot. Within the endemic hatchery and natural origin steelhead group, those that passed Ice Harbor between 24 August and 13 September, the period of peak water temperatures, were more likely to overshoot and less likely to return directly to home than those that passed earlier or later (Figure J.26).

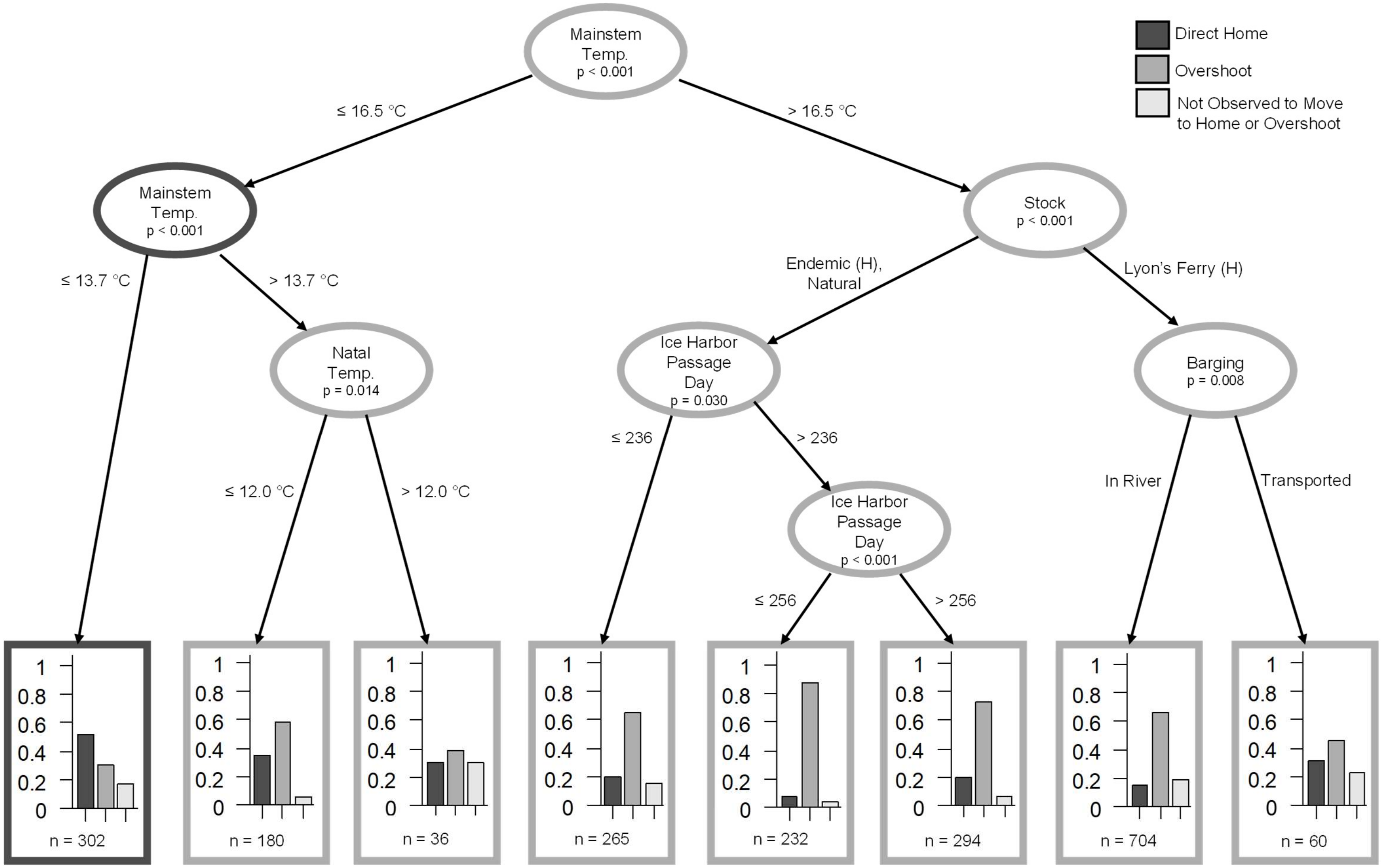

FIGURE J.26.—Conditional inference tree of Tucannon steelhead behavior between Ice Harbor and Lower Granite. Direct Home = migrated home without overshooting, Overshoot = overshot Lower Granite, Mainstem Temp. = temperature of Lower Granite tailwater, Stock = rearing history (natural, endemic hatchery, or Lyon's Ferry hatchery), Natal Temp. = temperature at Tucannon monitoring station, Barging = juvenile out-migration history, Ice Harbor Passage Day = calendar day of Ice Harbor passage.

In Chapter 2, I estimated the average annual fallback rate to home to be 32.8% (SE 6.0%) for hatchery and 20.3% (SE 3.2%) for wild Tucannon River steelhead. In Chapter 3, I found hatchery steelhead to be more likely to fall back to home, by 11 percentage points, than natural origin Tucannon River steelhead. Ocean age and barging history were not found to affect fallback to home. Here, I examined the influence of flow and spill on fallback to home. Fallback to home by wild Tucannon River steelhead was not found to be significantly associated with March flow or spill during January, February, or March (Table J.9). Fallback to home by hatchery Tucannon River steelhead, however, was found to be positively associated with the number of spill days in March ($F_{1,6} = 4.03$, $P = 0.046$).

TABLE J.9.—One-tailed P-values testing for a positive association between estimated fallback rate and January, February, and March spill, as well as March flow at overshot dams for Tucannon River steelhead. Values < 0.05 indicate a significant positive relationship (*) between fallback and spill or flow.

		One-tailed P-value			
Stock	DF	January Spill	February Spill	March Spill	March Flow
Wild	6	0.132	0.571	0.253	0.129
Hatchery	6	0.567	0.710	0.046*	0.169

Analysis of fallback to home using conditional inference trees found March spill and stock to produce significant splits (Figure J.27). Steelhead that overshot during run years where water was spilled over Lower Granite Dam for more than 8 days in March were predicted to fall back to home, while those that overshot in years with 8 or fewer spill days in March were not predicted to fall back to home. However, within the high spill group, natural origin steelhead responded much less strongly than endemic hatchery steelhead. Greater spill may affect wild Tucannon River steelhead less strongly, due to the strong tendency to stray to upstream tributaries observed in Chapter 2.

At Lower Granite, more than 8 days of spill during March only occurred in 2014. In this year, all PIT-tagged Tucannon River steelhead were either of natural or endemic hatchery origin. No steelhead derived from the Lyon's Ferry hatchery stock were represented in 2014. Therefore, it is possible high levels of spill could be serving as a surrogate for hatchery stock origin. However, this seems unlikely because the two Tucannon River hatchery stocks were found to have nearly identical rates of fallback to home in Chapter 3.

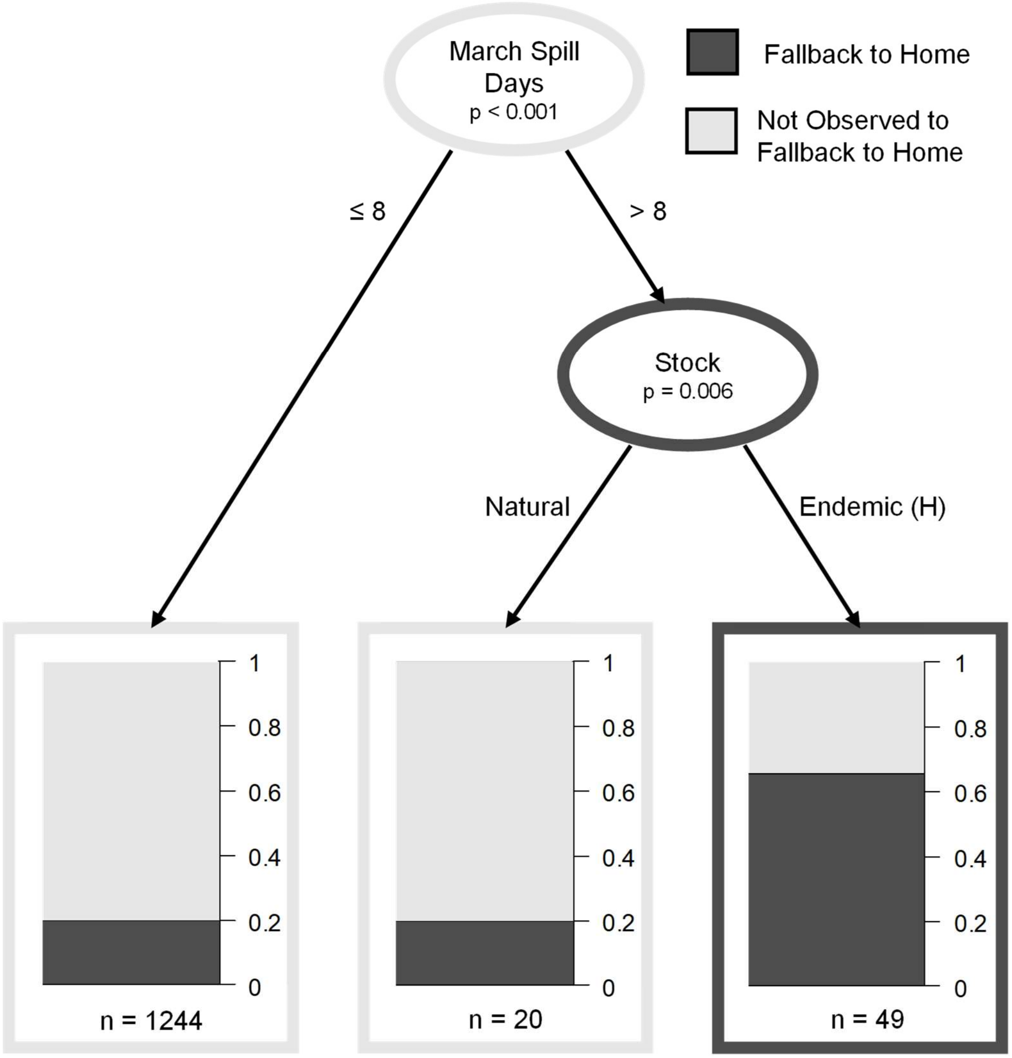

FIGURE J.27.—Conditional inference tree of adult Tucannon River steelhead migratory after overshooting Lower Granite Dam. Fallback to Home = fell back downstream to home, March Spill Days = number of days during March during which any amount of water was spilled over Lower Granite Dam, Stock = rearing history (natural, endemic hatchery, Lyon's Ferry hatchery).