

Estimates of Gene Flow for Puget Sound Hatchery Steelhead Programs

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Introduction

Hatchery programs can provide substantial economic, cultural, and conservation benefits, but potentially they can also pose risks to natural populations of salmon and steelhead. The Washington Department of Fish and Wildlife (Department or WDFW) operates segregated early winter steelhead hatchery programs in six Puget Sound watersheds for the purpose of providing recreational and tribal fishing opportunities. When Puget Sound steelhead were listed under the Endangered Species Act, the federal register notice (71 FR15666) concluded that “Potential harmful hatchery practices may pose ecological and genetic risks to natural populations and may represent a factor limiting the viability of the Puget Sound steelhead DPS into the foreseeable future.” The federal register notice also concluded that “the continued destruction and modification of steelhead habitat is the principal factor limiting the viability of the Puget Sound steelhead DPS into the foreseeable future.”

The Statewide Steelhead Management Plan (SSMP, 2008) directs the Department to operate harvest augmentation programs in a manner that is consistent with meeting the watershed-specific goals for the diversity, spatial structure, productivity, and abundance of natural origin stocks. The SSMP further states that the long-term goal for segregated harvest augmentation programs affecting natural origin stocks of importance for conservation and recovery is an average gene flow of less than 2% from the hatchery to the natural origin stock.

The Department and Puget Sound treaty tribes used four analyses to evaluate the potential genetic effects of the early winter steelhead programs on natural origin steelhead. The analyses are complementary in that they use multiple sources of information and address multiple questions.

- 1) Genetic Introgression. Introgression results from hybridization between hatchery and natural origin individuals. An analysis of genetic introgression (Warheit, 2014) as used to address the question “How have past early winter hatchery program practices affected the genetic characteristics of natural origin steelhead?” Since the analysis relied on tissue samples from collections of natural-origin steelhead, it provides a direct measure of the cumulative effects of the early winter hatchery program practices. However, it may also reflect the benefits of some practices that have now ended (e.g., off-station plants, recycling of returning adults, larger number of fish released).
- 2) Projected Genetic Introgression. A simple, heuristic model was developed to project how genetic introgression might change in the future based on the assumed parameter values and the model structure (Warheit, 2014).
- 3) Proportion Effective Hatchery Contribution. The proportion effective hatchery contribution (PEHC) is the proportion of natural spawners that are genetically derived from the early winter hatchery program and includes both hatchery-natural origin hybrids and pure natural-origin hatchery-lineage fish. The PEHC is calculated from an analysis of the genetic ancestry of tissue samples collected from natural-origin steelhead (Warheit 2014). Since the PEHC includes pure hatchery-lineage fish that have the potential to generate hybrid offspring, it addresses a broader question than would genetic introgression alone: “How may early winter hatchery program practices affect the potential for genetic introgression?” Like the analysis of introgression, PEHC relied on tissue samples collected from natural-origin steelhead and provides a direct measure of the effects of the early winter hatchery program.

- 4) **Gene Flow.** Whereas genetic introgression is a cumulative state, gene flow is the process that leads to genetic introgression. Gene flow may vary each year in response to hatchery program characteristics such as the number and location of fish released and the number of natural-origin spawners. To address the questions “What was the historical gene flow that led to the introgression results and what is the anticipated gene flow with the new proposed program?”, a potential range of gene flows from the early winter hatchery program into the natural origin populations re calculated on various assumptions of hatchery steelhead fitness, the overlap in spawn timing of hatchery and natural origin steelhead, and stray rates.

This report describes the methods and provides estimates of the potential range of gene flow.

Gene Flow Equation

Busack (2008) developed and provided the following motivation for the method used to estimate the potential range of gene flow. The potential risks due to gene flow depends on the domestication level of the stock used, the degree of non-locality of the stock used, the level of gene flow the population has already undergone (a stock that has already had a certain level of gene flow will be less impacted incrementally than one that has had less), and the level of gene flow. Gene flow depends on the relative abundance of hatchery and natural origin spawners on the spawning ground, their temporal and spatial overlap, and the relative success of the three types of matings (hatchery x hatchery [HxH], hatchery x natural [HxN], and natural x natural [NxN]). Fig. 1 shows the situation with regard to mating structure. There are three regions on the figure, each representing a different mating scenario. In region A, only hatchery-origin fish are present, so only HxH matings take place. In region C, only natural fish are present, so all matings are NxN. In region B, both types of spawners are present. Assuming fish mate at random and assuming single-pair mating, there will be p^2 HxH matings, $2p(1-p)$ HxN matings, and $(1-p)^2$ NxN matings, where p is the proportion of hatchery-origin fish present in region B. For example, if during the time the two runs overlap the proportion of hatchery-origin fish is 10%, the expected frequency of the three types of matings will be 1% HxH, 18% HxN, and 81% NxN.

The level of gene flow to be expected from the scenario depicted in Fig. 1 is:

$$Gene\ flow = \frac{b}{b + a(1 - q)(1 - o_N) + (1 - q)^2 o_N^2}, \text{ where}$$

$$a = o_N + q(o_H - o_N)$$

$$b = k_1(aq(1 - o_H) + q^2 o_H^2) + k_2 q(1 - q) o_N o_H$$

and k_1 and k_2 are the fitness of HxH and HxN matings relative to NxN, respectively; q is the proportion of hatchery fish among all spawners (regardless of overlap), o_h is the proportion of the hatchery spawners that are in the overlap region, and o_n is the proportion of the natural-origin spawners that are in the overlap region. For example, assume 1) there are 150 natural-origin spawners, and 20 hatchery-origin spawners present; 2) 10% of the natural-origin spawners overlap with 5% of the hatchery-origin

spawners; and 3) the fitness of HxH and HxN matings relative to NxN are 0.5 and 0.75, respectively. Here $q=20/170=0.118$, $o_H=0.05$, $o_N=0.1$, $k_1=0.5$, and $k_2=0.75$, so the gene flow is 6.4%

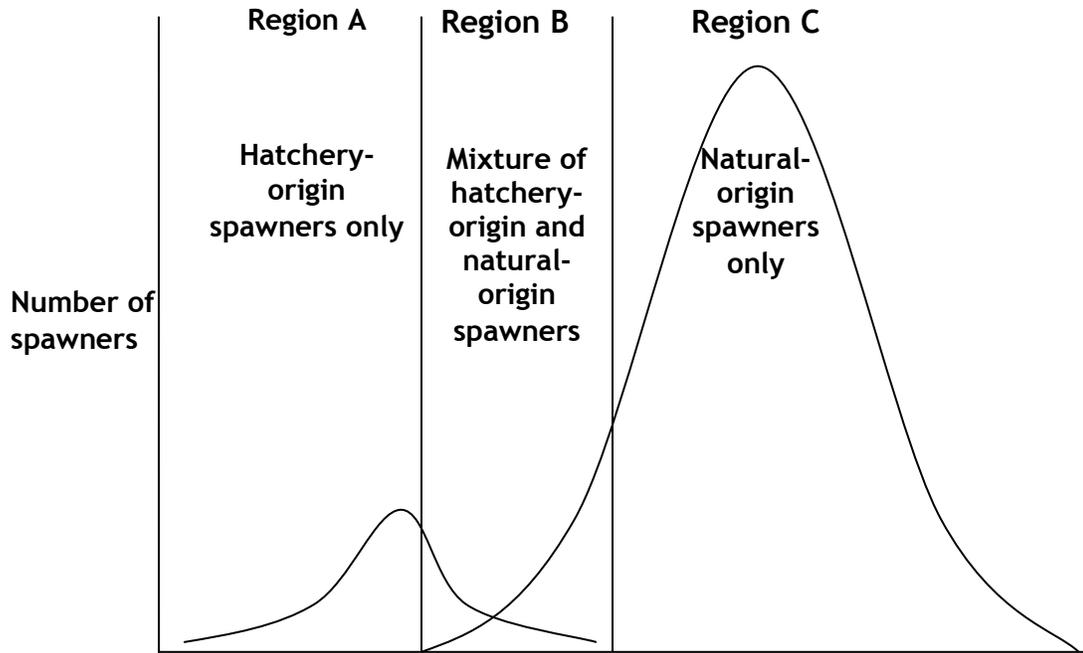


Figure 1. Schematic of temporal spawning overlap between early-run hatchery-origin winter steelhead and natural-origin winter steelhead. The shape, sizes, and placement of curves does not represent any particular real situation (reproduced from SSMP 2008).

Parameter Estimates

Parameter values for the gene flow equation were estimated from a variety of sources, whether from population-specific data or values reported in other studies, to cover the range of plausible values.

Spawn Timing Overlap of Natural-Origin Spawners (O_N). The spawn timing of Puget Sound populations of natural origin winter steelhead is difficult to estimate. This is primarily due to the difficulty of distinguishing natural and hatchery-origin spawners on the redds, but also reflects the challenging nature of counting redds in mid-winter.

The spawn-timing of natural-origin fish was estimated using two methods:

Method 1. The range of values from Scott and Gill (2008) to bracket the likely spawn timing.

Method 2. Population (or river) specific spawn-timing for winter steelhead estimated from redd surveys.

Method 1. Scott and Gill (2008) reviewed Washington state data for the spawn timing of natural origin winter steelhead and identified Snow Creek, a small stream that is a tributary to Discovery Bay and the Strait of Juan de Fuca, as having one of the strongest data sets. Prior to initiation of

research at Snow Creek, no hatchery-origin smolts had been released into Snow Creek, and, in the return years 1977-1978 and 1979-1980, any hatchery-origin strays from other watersheds were identified as they were passed upstream at the rack (Johnson et al. 1978; Johnson et al. 1980). Based on analysis of scale patterns, only one hatchery-origin steelhead is known to have been passed upstream during these two years. Redd surveys were conducted at approximately one week intervals with redds first observed on February 4, 1980, and the last new redds constructed were observed on May 24, 1978. Over the two years, the average date of redd construction was March 28 with a standard deviation of 18.1 days.

Scott and Gill (2008) also presented information on the spawn timing of winter steelhead for the Clearwater River, a tributary to the Queets River on the north Washington coast. Redd surveys were conducted in the mainstem of the Queets River and in tributaries on an irregular schedule in the years 1973 through 1980 (Cederholm 1984). Cederholm reported survey data for every year from 1973 through 1980, but 1978 was the only year with at least one survey in each of the months of January, February, and March. As in Snow Creek, no releases of hatchery-origin steelhead had occurred in the watershed in the years prior to the surveys. However, unlike Snow Creek, the incidence of hatchery-origin steelhead that may have strayed from other watersheds is not known. Cederholm found that redd construction appeared to occur earlier in the tributary streams than in the mainstem Clearwater River. The average date that a new redd was seen in the tributaries was March 27 versus April 21 in the mainstem of the Clearwater River; spawning was observed from January through June in both the tributaries and in the mainstem Clearwater River.

Snow Creek and mainstem Clearwater River data was used to parameterize a normal distribution and bracket the likely range of the spawn-timing of populations of winter steelhead in Puget Sound. The spawn timing overlap parameter was estimated by the probability that a natural origin fish spawned prior to the average date of spawning at Tokul Creek Hatchery plus three standard deviations (see discussion below). This resulted in estimates of O_N of 7.39% from the Snow Creek data and 0.69% from the mainstem Clearwater River data.

Sensitivity to the Normal distribution assumption, used to calculate O_N for both the Snow Creek and Clearwater River data, was evaluated by comparing a Normal to a Gamma distribution curve. The parameters (α and β) of an asymmetrical Gamma distribution function were calculated from the Normal μ and σ parameters: $\alpha = (\mu/\sigma)^2$ and $\beta = \sigma^2/\mu$ for the natural origin populations in Snow Creek and the Clearwater River. Using the normal curves, O_N was calculated as the probability of natural origin spawning prior to day 92 (the date by which 99.8% of the hatchery origin spawners would have spawned, i.e. the mean plus three standard deviations of the normal hatchery distribution). Given the results below and the sensitivity levels of gene flow to O_N (Figure 11), the Normal function was deemed sufficient.

Watershed	Normal			Gamma		
	Mean	StDev	$O_N = P(<92)$	alpha	beta	$O_N = P(<92)$
Snow Cr	118	18.1	7.4%	42.50	2.78	6.4%
Clearwater R	142	20.4	0.7%	48.45	2.93	3.1%

Method 2. O_N was estimated from river-specific observed redd data. Most WDFW steelhead redd surveys are not initiated until after March 15. However because some natural origin redds are constructed prior to March 15, a statistical probability function was used to fit the observed redd data post March 15 to estimate the proportion of natural origin redds created prior to March 15 (O_N) (Table 2). A statistical Gamma function, which allowed for asymmetrical spawn timing, was based on the date of redd observation described by the number of days prior to the end of the spawning season (Figures 2-10). In this case the zero point was at the end of the spawning season and the probability distribution was drawn to the left, a mirror image of how one is typically drawn.

Table 2. Estimates of O_N from river-specific redd data for Cases 3 and 6 (Tables 4-10).

River	O_N	Population(s)
Nooksack	6.21%	Nooksack River Winter
Skagit	4.96%	Aggregate of Skagit River Summer/Winter, and Nookachamps Creek Winter
Sauk	0.65%	Sauk River Summer/Winter
Stillaguamish	1.25%	Stillaguamish River Winter
Skykomish	1.96%	Snohomish/Skykomish River Winter
Pilchuck	1.88%	Pilchuck River Winter
Snoqualmie	2.10%	Snoqualmie River Winter
Green	1.28%	Green River Winter

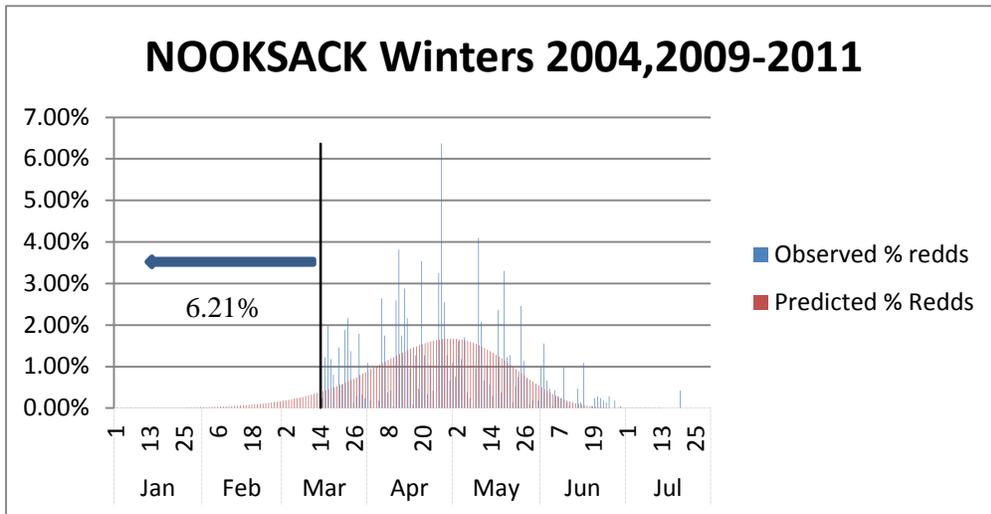


Figure 2. Nooksack River winter steelhead observed and predicted redd distribution. O_N was estimated as 6.21% of the area under the predicted curve to the left of March 15. The years represent available data.

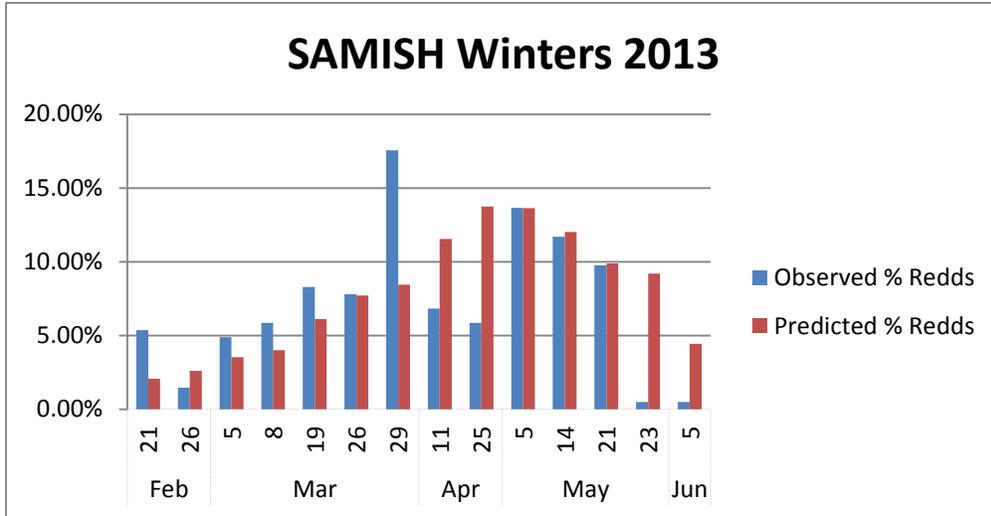


Figure 3. Samish River winter steelhead observed and predicted redd distribution. O_N was estimated as 11.22% of the area under the predicted curve to the left of March 15. 2013 represents the most recent year with the least influence from early winter hatchery steelhead smolt outplanting.

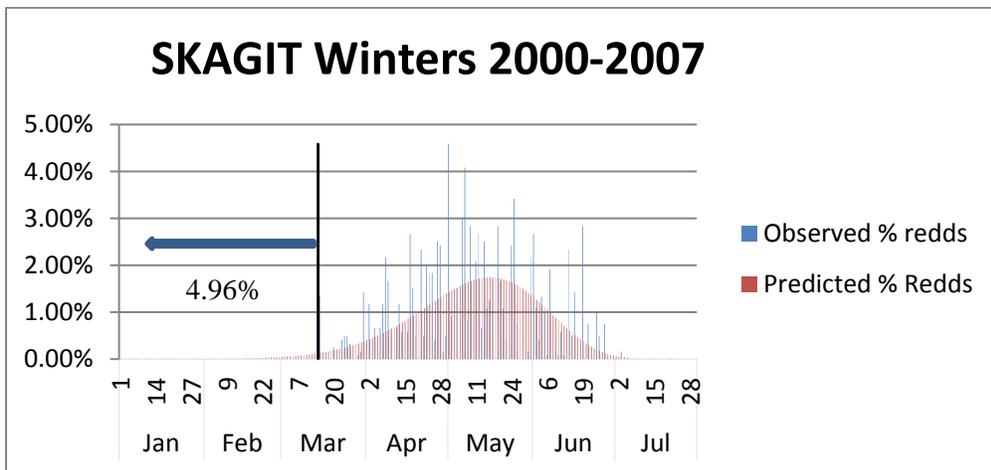


Figure 4. Skagit/Nookachamps winter steelhead observed and predicted redd distribution. O_N was estimated as 4.96% of the area under the predicted curve to the left of March 15.

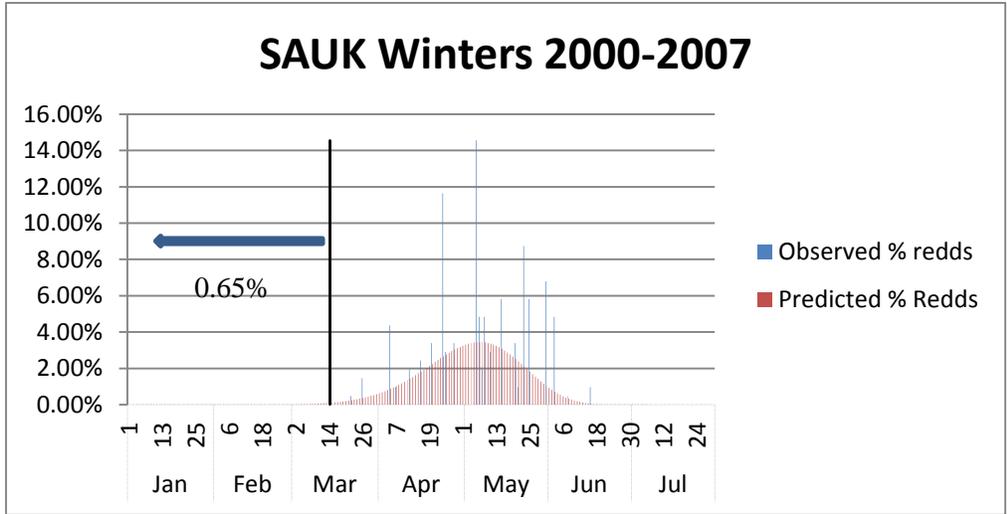


Figure 5. Sauk River winter steelhead observed and predicted redd distribution. O_N was estimated as 0.65% of the area under the predicted curve to the left of March 15.

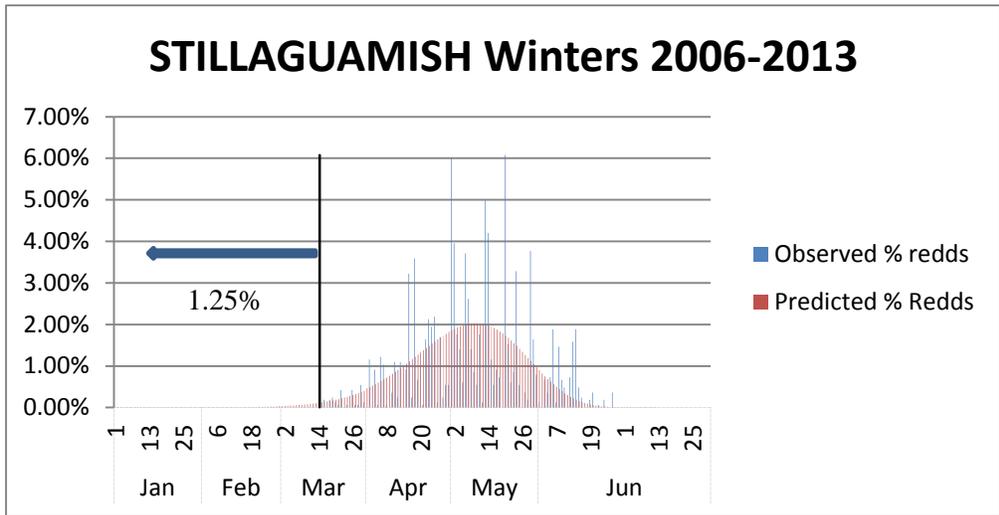


Figure 6. Stillaguamish River winter steelhead observed and predicted redd distribution. O_N was estimated as 1.25% of the area under the predicted curve to the left of March 15.

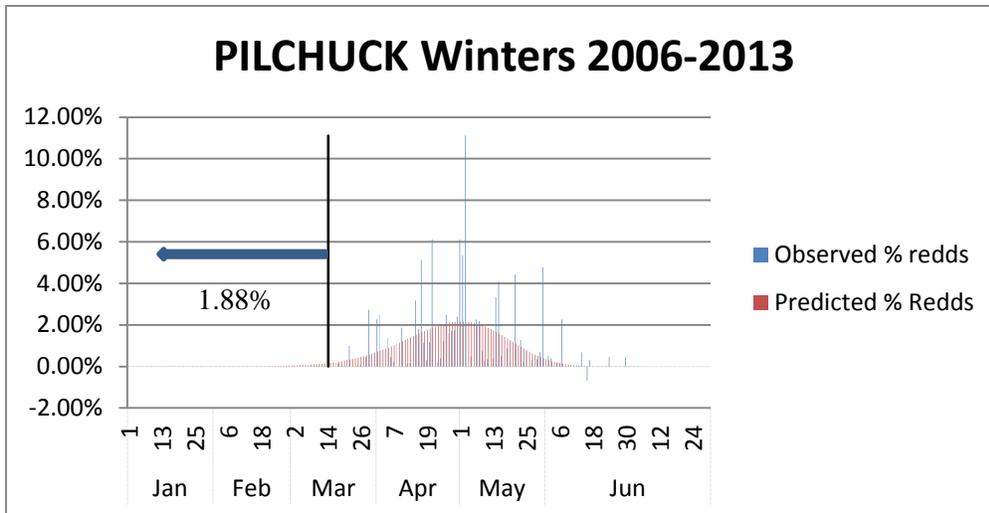


Figure 7. Pilchuck River winter steelhead observed and predicted redd distribution. O_N was estimated as 1.88% of the area under the predicted curve to the left of March 15.

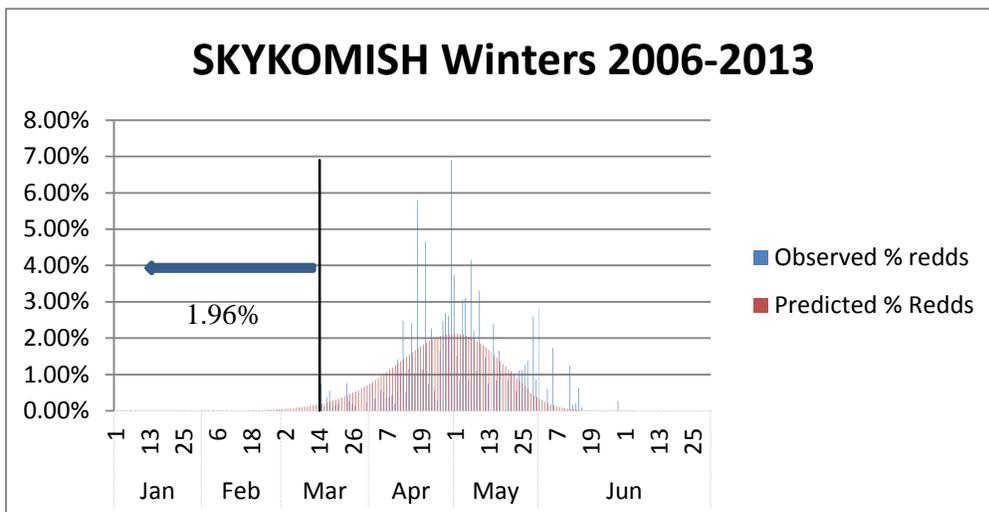


Figure 8. Snohmish/Skykomish River winter steelhead observed and predicted redd distribution. O_N was estimated as 1.96% of the area under the predicted curve to the left of March 15.

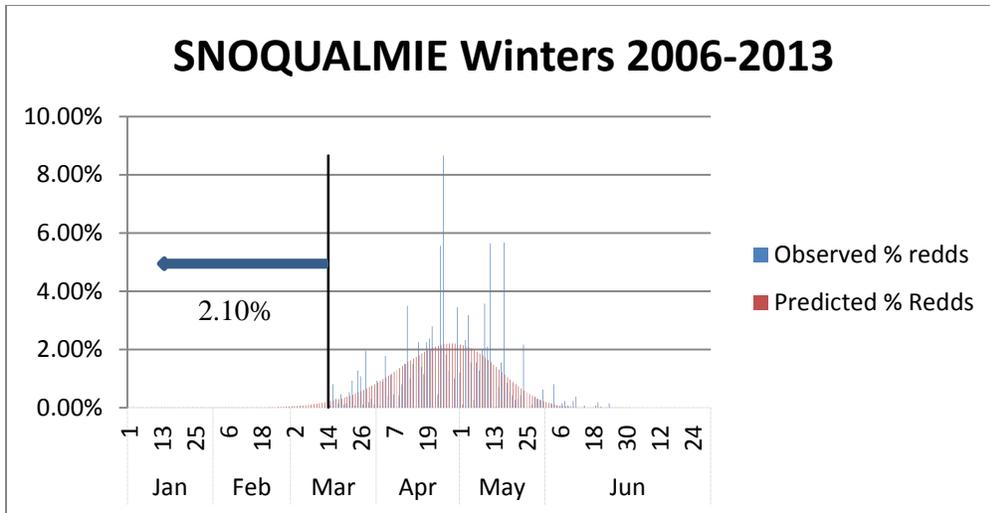


Figure 9. Snoqualmie River winter steelhead observed and predicted redd distribution. O_N was estimated as 2.10% of the area under the predicted curve to the left of March 15.

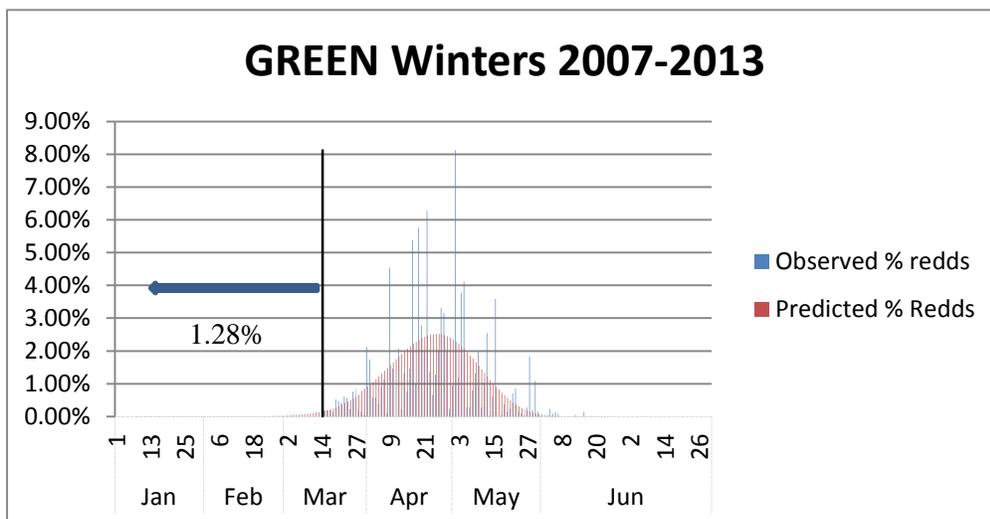


Figure 10. Green River winter steelhead observed and predicted redd distribution. O_N was estimated as 1.28% of the area under the predicted curve to the left of March 15.

Spawn Timing Overlap of Hatchery-Origin Spawners (O_H). The spawn timing of early winter hatchery steelhead was estimated using two methods:

- Method 1. Spawn timing at the Tokul Creek Hatchery.
- Method 2. River-specific entry timing of winter steelhead into the hatchery specific to that river system.

Method 1. Tokul Creek Hatchery was used to represent all Puget Sound early winter hatchery programs because of the long history of the program and because it was historically used as a source of eggs for early winter programs in other watersheds. The estimated date of mean spawning was January 14 with a standard deviation of 15.6 days. Using a normal distribution function parameterized with these values, the spawn timing overlap parameter was estimated as the probability that a hatchery fish spawned prior to the average date of spawning minus three standard deviations for the Snow Creek or mainstem Clearwater natural origin steelhead. This resulted in estimates of O_H of 11.53% for overlap with the Snow Creek natural origin steelhead and 1.09% with the mainstem Clearwater River natural origin steelhead.

Method 2. Since 2009, Puget Sound hatcheries have operated traps well into March to minimize the number of hatchery-origin fish in natural spawning areas. O_H was based on the assumption that early winter hatchery fish returning to the hatchery rack and early winter hatchery fish that stray to natural spawning grounds have similar maturation schedules. Since few natural origin winter steelhead spawn prior to January 31 (see discussion above), the percent of early winter hatchery fish returning to the rack after January 26 was used as the best available estimate of the proportion of early winter hatchery spawners that would spawn after January 31 into the overlap time period. The extra week of hatchery rack returns was used to provide a one week buffer for early winter hatchery fish that return to the rack but are not quite ripe.

Table 3. Estimates of O_H from hatchery specific data for the most recent three years for Cases 3 and 6 (Tables 4-10).

Hatchery	O_H
Kendall Creek	8.38%
Marblemount	13.74%
Whitehorse	18.41%
Reiter-Wallace	49.45%
Tokul	16.88%
Soos	11.36%

Relative Fitness of HxH Crosses (k_1). The early winter hatchery programs are operated with a segregated, nonlocal broodstock that has been domesticated over a period of more than 60 years. Unlike well run integrated hatchery programs, it is anticipated that the relative fitness will be low for fish produced from this type of program. A range of values (0.02 to 0.13) used for relative fitness was drawn from the empirical studies for steelhead programs that use nonlocal broodstock (Araki et al. 2008). These studies were not conducted with Puget Sound steelhead populations.

The co-managers are committed to continuing research and monitoring to refine estimates of fitness and overlap in spawning to better understand gene flow between early winter steelhead and natural-origin steelhead.

Relative Fitness of HxW Crosses (k_2). For this parameter, a value of 0.54 was used, which is halfway between the average value for HxH crosses (0.084) reported in Araki et al. (2008) and a relative fitness of 1.0.

Proportion of Total Natural Spawners of Hatchery-Origin (q). The proportion of total natural spawners of hatchery origin (q) was estimated from run reconstructions for each population of winter steelhead or river. The run reconstructions relied on the following data and assumptions:

- 1) The natural-origin spawners (NOS) were estimated from WDFW redd survey data and expanded the estimate by the proportion of spawning that occurred prior to the initiation of spawner surveys (see discussion above).
- 2) The hatchery-origin spawners in natural spawning areas (HOS) were estimated from the return of hatchery-origin fish to the hatchery expanded by assumed stray rates. The Hatchery Scientific Review Group has generally used stray rates of 10% or 20% for hatchery programs where juveniles are released on-station and the hatchery has adult collection facilities. To be conservative a stray rate of 20% or 30% was assumed for on-station releases. Given hatchery returns and predicted HOS, a total return rate from the on-station releases was applied to the off-station releases to calculate the off-station HOS. This method which assumed a stray rate of 20%-30% for on-station released fish, assumed a stray rate of 100% for off-station releases.

Gene Flow Estimates

Estimates of the potential range of gene flow are provided in tables 4-10. For each year, gene flow was calculated using the annual natural origin run size and hatchery return data. The No Offstation values are based on an average gene flow calculated the on-station hatchery releases only. This calculation represents the expected gene flow if there had only been the on-station releases. The last row in each table, is a reduction in gene flow based on a reduction of on-station release size and represents the expected gene flow adjusted by the change in release size in the 2014 submitted HGMP's.

Table 4. Estimated gene flow from the early winter hatchery program for the Nooksack River Winter steelhead population under six alternative cases. No estimates of Nooksack River Winter spawners are available prior to 2009-2010.

Spawn Year	Case 1 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.20		Case 2 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.20		Case 3 Natural: Nooksack Hatchery: Kendall Stray Rate = 0.20		Case 4 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.30		Case 5 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.30		Case 6 Natural: Nooksack Hatchery: Kendall Stray Rate = 0.30		
	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	
2001-2002	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
2002-2003	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
2003-2004	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
2004-2005	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
2005-2006	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
2006-2007	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
2007-2008	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
2008-2009	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
2009-2010	0.06%	0.13%	0.03%	0.15%	0.07%	0.19%	0.10%	0.22%	0.05%	0.26%	0.13%	0.33%	
2010-2011	0.10%	0.22%	0.05%	0.27%	0.13%	0.34%	0.17%	0.38%	0.09%	0.46%	0.22%	0.58%	
2011-2012	0.10%	0.22%	0.05%	0.27%	0.13%	0.34%	0.17%	0.38%	0.09%	0.46%	0.22%	0.58%	
Through 2011	0.08%	0.17%	0.04%	0.21%	0.10%	0.27%	0.13%	0.30%	0.07%	0.36%	0.17%	0.46%	
All Years	0.09%	0.19%	0.04%	0.23%	0.11%	0.29%	0.14%	0.33%	0.08%	0.40%	0.19%	0.50%	
No Offstation	0.09%	0.19%	0.04%	0.23%	0.11%	0.29%	0.14%	0.33%	0.08%	0.40%	0.19%	0.50%	
Release	150,000	0.10%	0.22%	0.05%	0.27%	0.13%	0.34%	0.17%	0.37%	0.09%	0.46%	0.22%	0.57%

Table 5. Estimated gene flow from the early winter hatchery program for Skagit River winter steelhead under six alternative cases.

Spawn Year	Case 1 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.20		Case 2 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.20		Case 3 Natural: Skagit Hatchery: Marblemount Stray Rate = 0.20		Case 4 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.30		Case 5 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.30		Case 6 Natural: Skagit Hatchery: Marblemount Stray Rate = 0.30	
	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13
2001-2002	2.07%	5.46%	1.28%	6.93%	2.78%	8.41%	2.35%	6.34%	1.50%	8.10%	3.10%	9.70%
2002-2003	0.26%	0.60%	0.14%	0.73%	0.47%	1.03%	0.31%	0.70%	0.16%	0.86%	0.54%	1.20%
2003-2004	0.32%	0.73%	0.17%	0.90%	0.57%	1.25%	0.40%	0.91%	0.21%	1.11%	0.68%	1.53%
2004-2005	0.55%	1.28%	0.29%	1.57%	0.92%	2.13%	0.66%	1.54%	0.36%	1.90%	1.07%	2.54%
2005-2006	0.65%	1.51%	0.35%	1.87%	1.06%	2.51%	0.77%	1.81%	0.42%	2.24%	1.22%	2.97%
2006-2007	0.58%	1.35%	0.31%	1.67%	0.96%	2.25%	0.70%	1.66%	0.38%	2.05%	1.14%	2.73%
2007-2008	0.30%	0.67%	0.16%	0.82%	0.52%	1.15%	0.36%	0.83%	0.19%	1.02%	0.63%	1.41%
2008-2009	0.31%	0.71%	0.16%	0.87%	0.55%	1.22%	0.39%	0.89%	0.21%	1.09%	0.67%	1.51%
2009-2010	0.19%	0.43%	0.10%	0.53%	0.35%	0.75%	0.26%	0.60%	0.14%	0.73%	0.47%	1.02%
2010-2011	0.12%	0.26%	0.06%	0.31%	0.21%	0.45%	0.16%	0.37%	0.09%	0.45%	0.30%	0.64%
2011-2012	0.10%	0.22%	0.05%	0.26%	0.18%	0.38%	0.14%	0.32%	0.07%	0.39%	0.26%	0.55%
Through 2011	0.54%	1.30%	0.30%	1.62%	0.84%	2.11%	0.64%	1.56%	0.36%	1.96%	0.98%	2.53%
All Years	0.50%	1.20%	0.28%	1.50%	0.78%	1.96%	0.59%	1.45%	0.34%	1.81%	0.92%	2.35%
No Offstation	0.08%	0.16%	0.04%	0.19%	0.14%	0.28%	0.13%	0.28%	0.07%	0.33%	0.23%	0.48%
Release	230,000	0.10%	0.22%	0.05%	0.26%	0.18%	0.38%	0.17%	0.37%	0.09%	0.45%	0.64%

Table 6. Estimated gene flow from the early winter hatchery program for the Stillaguamish River Winter steelhead population under six alternative cases.

Spawn Year	Case 1 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.20		Case 2 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.20		Case 3 Natural: Stillaguamish Hatchery: Whitehorse Stray Rate = 0.20		Case 4 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.30		Case 5 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.30		Case 6 Natural: Stillaguamish Hatchery: Whitehorse Stray Rate = 0.30	
	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13
	2001-2002	0.63%	1.47%	0.34%	1.82%	0.75%	2.28%	0.86%	2.05%	0.47%	2.54%	0.92%
2002-2003	0.04%	0.09%	0.02%	0.11%	0.09%	0.17%	0.06%	0.14%	0.03%	0.17%	0.13%	0.26%
2003-2004	0.13%	0.29%	0.07%	0.35%	0.25%	0.53%	0.19%	0.42%	0.10%	0.51%	0.33%	0.74%
2004-2005	0.41%	0.95%	0.22%	1.16%	0.57%	1.53%	0.56%	1.29%	0.30%	1.59%	0.69%	2.03%
2005-2006	0.20%	0.46%	0.11%	0.56%	0.35%	0.79%	0.31%	0.71%	0.16%	0.87%	0.48%	1.18%
2006-2007	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
2007-2008	0.16%	0.36%	0.08%	0.44%	0.30%	0.64%	0.25%	0.56%	0.13%	0.69%	0.41%	0.96%
2008-2009	0.20%	0.46%	0.11%	0.56%	0.35%	0.80%	0.31%	0.72%	0.17%	0.88%	0.48%	1.19%
2009-2010	0.16%	0.36%	0.08%	0.44%	0.30%	0.65%	0.25%	0.57%	0.13%	0.69%	0.41%	0.97%
2010-2011	0.18%	0.40%	0.09%	0.49%	0.32%	0.71%	0.27%	0.62%	0.14%	0.76%	0.43%	1.04%
2011-2012	0.18%	0.41%	0.09%	0.50%	0.33%	0.72%	0.31%	0.69%	0.16%	0.85%	0.47%	1.16%
Through 2011	0.21%	0.48%	0.11%	0.59%	0.33%	0.81%	0.31%	0.71%	0.16%	0.87%	0.43%	1.14%
All Years	0.21%	0.48%	0.11%	0.59%	0.33%	0.80%	0.31%	0.71%	0.16%	0.87%	0.43%	1.15%
No Offstation	0.14%	0.31%	0.07%	0.38%	0.26%	0.56%	0.24%	0.53%	0.13%	0.65%	0.38%	0.90%
Release	130,000	0.17%	0.37%	0.09%	0.44%	0.29%	0.64%	0.28%	0.62%	0.15%	0.75%	1.03%

Table 7. Estimated gene flow from the early winter hatchery program for the Snoqualmie River Winter steelhead population under six alternative cases.

Spawn Year	Case 1 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.20		Case 2 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.20		Case 3 Natural: Snoqualmie Hatchery: Tokul Creek Stray Rate = 0.20		Case 4 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.30		Case 5 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.30		Case 6 Natural: Snoqualmie Hatchery: Tokul Creek Stray Rate = 0.30		
	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	
	2001-2002	4.52%	14.12%	3.55%	18.32%	4.57%	20.10%	5.24%	16.91%	4.37%	21.93%	5.44%	23.87%
2002-2003	1.28%	3.16%	0.73%	3.95%	1.46%	4.79%	1.57%	3.98%	0.92%	5.01%	1.70%	5.95%	
2003-2004	1.67%	4.25%	0.99%	5.36%	1.78%	6.34%	2.14%	5.68%	1.33%	7.23%	2.17%	8.36%	
2004-2005	1.21%	2.96%	0.69%	3.71%	1.40%	4.52%	1.63%	4.13%	0.96%	5.21%	1.74%	6.17%	
2005-2006	1.07%	2.58%	0.60%	3.22%	1.29%	3.98%	1.44%	3.60%	0.84%	4.52%	1.59%	5.42%	
2006-2007	1.70%	4.36%	1.01%	5.50%	1.81%	6.49%	2.20%	5.86%	1.38%	7.46%	2.22%	8.60%	
2007-2008	2.86%	8.04%	1.92%	10.34%	2.82%	11.68%	3.54%	10.44%	2.54%	13.51%	3.49%	15.04%	
2008-2009	1.79%	4.62%	1.08%	5.85%	1.88%	6.86%	2.31%	6.23%	1.47%	7.95%	2.32%	9.13%	
2009-2010	1.29%	3.19%	0.74%	4.00%	1.47%	4.85%	1.67%	4.27%	1.00%	5.40%	1.78%	6.37%	
2010-2011	1.07%	2.59%	0.60%	3.22%	1.29%	3.99%	1.67%	4.27%	0.99%	5.39%	1.78%	6.36%	
2011-2012	1.05%	2.53%	0.59%	3.16%	1.27%	3.91%	1.64%	4.18%	0.97%	5.28%	1.76%	6.24%	
Through 2011	1.85%	4.99%	1.19%	6.35%	1.98%	7.36%	2.34%	6.54%	1.58%	8.36%	2.42%	9.53%	
All Years	1.77%	4.76%	1.14%	6.06%	1.91%	7.05%	2.28%	6.32%	1.52%	8.08%	2.36%	9.23%	
No Offstation	0.86%	1.97%	0.48%	2.41%	1.10%	3.07%	1.36%	3.26%	0.80%	4.03%	1.52%	4.88%	
Release	74,000	0.48%	1.07%	0.26%	1.29%	0.72%	1.75%	0.78%	1.79%	0.43%	2.19%	1.02%	2.80%

Table 8. Estimated gene flow from the early winter hatchery program for the Pilchuck River Winter steelhead population under six alternative cases.

Spawn Year	Case 1 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.20		Case 2 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.20		Case 3 Natural: Pilchuck Hatchery: Reiter- Wallace Stray Rate = 0.20		Case 4 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.30		Case 5 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.30		Case 6 Natural: Pilchuck Hatchery: Reiter- Wallace Stray Rate = 0.30	
	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13
2001-2002												
2002-2003	0.12%	0.28%	0.06%	0.33%	0.46%	0.67%	0.14%	0.32%	0.07%	0.38%	0.49%	0.74%
2003-2004	0.12%	0.26%	0.06%	0.31%	0.44%	0.63%	0.13%	0.30%	0.07%	0.36%	0.48%	0.70%
2004-2005	0.21%	0.48%	0.11%	0.58%	0.62%	1.02%	0.24%	0.54%	0.12%	0.65%	0.66%	1.12%
2005-2006	0.16%	0.37%	0.08%	0.44%	0.54%	0.83%	0.19%	0.42%	0.10%	0.50%	0.58%	0.92%
2006-2007	0.04%	0.09%	0.02%	0.10%	0.19%	0.25%	0.04%	0.10%	0.02%	0.12%	0.22%	0.28%
2007-2008							0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
2008-2009	0.49%	1.14%	0.25%	1.36%	0.89%	1.95%	0.55%	1.29%	0.29%	1.53%	0.93%	2.13%
2009-2010	0.36%	0.83%	0.19%	1.00%	0.79%	1.54%	0.41%	0.94%	0.21%	1.12%	0.83%	1.69%
2010-2011	0.29%	0.67%	0.15%	0.80%	0.72%	1.31%	0.33%	0.76%	0.17%	0.91%	0.76%	1.44%
2011-2012	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Through 2011	0.23%	0.51%	0.12%	0.62%	0.58%	1.03%	0.23%	0.52%	0.12%	0.62%	0.55%	1.00%
All Years	0.20%	0.46%	0.10%	0.55%	0.52%	0.91%	0.20%	0.47%	0.11%	0.56%	0.49%	0.90%
No Offstation	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Release	256,000	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%

Table 9. Estimated gene flow from the early winter hatchery program for the Snohomish/Skykomish River Winter steelhead population under six alternative cases.

Spawn Year	Case 1 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.20		Case 2 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.20		Case 3 Natural: Skykomish Hatchery: Reiter-Wallace Stray Rate = 0.20		Case 4 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.30		Case 5 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.30		Case 6 Natural: Skykomish ¹ Hatchery: Reiter-Wallace Stray Rate = 0.30		
	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	
	2001-2002	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
2002-2003	0.12%	0.28%	0.06%	0.34%	0.47%	0.69%	0.16%	0.37%	0.08%	0.45%	0.56%	0.85%	
2003-2004	0.17%	0.38%	0.09%	0.46%	0.57%	0.87%	0.23%	0.52%	0.12%	0.63%	0.68%	1.12%	
2004-2005	0.15%	0.33%	0.08%	0.40%	0.52%	0.78%	0.20%	0.46%	0.11%	0.56%	0.64%	1.02%	
2005-2006	0.09%	0.20%	0.05%	0.24%	0.37%	0.52%	0.13%	0.28%	0.07%	0.35%	0.48%	0.70%	
2006-2007													
2007-2008													
2008-2009													
2009-2010	0.36%	0.82%	0.19%	1.01%	0.86%	1.61%	0.52%	1.20%	0.28%	1.48%	1.02%	2.17%	
2010-2011	0.23%	0.53%	0.12%	0.65%	0.69%	1.14%	0.35%	0.80%	0.19%	0.99%	0.85%	1.58%	
2011-2012	0.77%	1.81%	0.42%	2.24%	1.21%	3.03%	1.23%	3.01%	0.70%	3.77%	1.54%	4.70%	
Through 2011	0.16%	0.36%	0.08%	0.44%	0.50%	0.80%	0.23%	0.52%	0.12%	0.64%	0.60%	1.06%	
All Years	0.24%	0.54%	0.13%	0.67%	0.59%	1.08%	0.35%	0.83%	0.19%	1.03%	0.72%	1.52%	
No Offstation	0.17%	0.38%	0.09%	0.46%	0.43%	0.77%	0.28%	0.64%	0.15%	0.79%	0.59%	1.19%	
Release	256,000	0.25%	0.57%	0.14%	0.69%	0.56%	1.08%	0.40%	0.95%	0.23%	1.16%	0.74%	1.66%

Table 10. Estimated gene flow from the early winter hatchery program for the Green River Winter steelhead population under six alternative cases.

Spawn Year	Case 1 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.20		Case 2 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.20		Case 3 Natural: Green Hatchery: Soos Creek Stray Rate = 0.20		Case 4 Natural: Snow Creek Hatchery: Tokul Creek Stray Rate = 0.30		Case 5 Natural: Clearwater R. Hatchery: Tokul Creek Stray Rate = 0.30		Case 6 Natural: Green Hatchery: Soos Creek Stray Rate = 0.30		
	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	K ₁ = 0.02	K ₁ = 0.13	
	2001-2002	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA
2002-2003	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	NA	
2003-2004	0.24%	0.54%	0.13%	0.66%	0.32%	0.87%	0.28%	0.65%	0.15%	0.79%	0.37%	1.03%	
2004-2005	1.37%	3.42%	0.79%	4.29%	1.24%	4.96%	1.57%	3.98%	0.93%	5.01%	1.39%	5.74%	
2005-2006	0.26%	0.60%	0.14%	0.73%	0.35%	0.95%	0.32%	0.73%	0.17%	0.89%	0.41%	1.15%	
2006-2007	3.21%	9.23%	2.23%	11.91%	2.78%	13.13%	3.55%	10.48%	2.55%	13.56%	3.13%	14.87%	
2007-2008	5.52%	18.01%	4.70%	23.34%	5.43%	25.16%	6.08%	20.21%	5.39%	26.13%	6.17%	28.06%	
2008-2009	4.55%	14.24%	3.59%	18.49%	4.24%	20.08%	5.03%	16.10%	4.13%	20.90%	4.81%	22.61%	
2009-2010	7.48%	25.56%	7.19%	32.70%	8.09%	34.85%	8.27%	28.45%	8.25%	36.15%	9.22%	38.37%	
2010-2011	3.77%	11.27%	2.76%	14.59%	3.36%	15.97%	4.17%	12.76%	3.17%	16.55%	3.79%	18.04%	
2011-2012	0.52%	1.21%	0.28%	1.49%	0.59%	1.85%	0.69%	1.62%	0.37%	2.00%	0.73%	2.43%	
Through 2011	3.30%	10.36%	2.69%	13.34%	3.23%	14.50%	3.66%	11.67%	3.09%	15.00%	3.66%	16.23%	
All Years	2.99%	9.34%	2.42%	12.02%	2.93%	13.09%	3.33%	10.55%	2.79%	13.55%	3.34%	14.70%	
No Offstation	0.23%	0.53%	0.12%	0.65%	0.29%	0.83%	0.39%	0.90%	0.21%	1.10%	0.44%	1.37%	
Release	70,000	0.41%	0.96%	0.22%	1.18%	0.46%	1.45%	0.66%	1.60%	0.37%	1.99%	0.67%	2.37%

Sensitivity to Input Assumptions

The gene flow equation demonstrates different levels of sensitivity to the different input parameters. To explore that sensitivity a baseline geneflow (Table 11) was calculated using the average input value over all the watersheds and all the cases considered. Variation in geneflow from that baseline was calculated by varying each parameter in isolation, keeping all others the same (Figure 11). The parameters were systematically each reduced by 50% and increased by 50%.

Table 11. Input parameter values used in sensitivity analysis.

Input Parameter	Average value over watersheds and cases	Parameter value at a 50% increase	Parameter value at a 50% decrease
O(n)	3.63%	5.44%	1.81%
O(h)	12.19%	18.29%	6.10%
K1	0.07	0.11	0.04
K2	0.54	0.81	0.27
On Station pHOS	5.05%	7.58%	2.53%

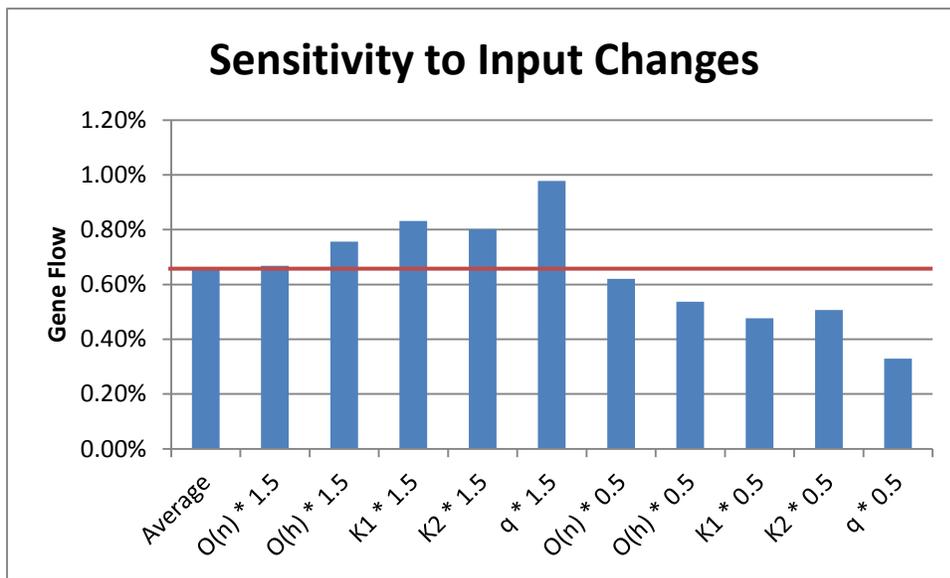


Figure 11. Gene flow values when varying each parameter in isolation by a 50% increase and a 50% decrease over the input value averaged over all watersheds and all cases. The average line demonstrates the comparison.

Calculation of Future PEHC

The calculation of future PEHC was done as follows:

$$1. PEHC_{future} = \frac{PEHC_{past} * \frac{HOS_{future}}{HOS_{past}}}{PEHC_{past} * \frac{HOS_{future}}{HOS_{past}} + (1 - PEHC_{past})}$$

where,

$$2. HOS_{past} = \frac{1}{11} \sum_{i=2001/02}^{2011/12} (HOS_i^{On-Stn} + HOS_i^{Off-Stn})$$

$$3. HOS_{future} = \left(\frac{1}{11} \sum_{i=2001/02}^{2011/12} HOS_i^{On-Stn} \right) * \left(\frac{Release_{future}^{On-Stn}}{\frac{1}{11} \sum_{i=2001/02}^{2011/12} Release_i^{On-Stn}} \right)$$

$$4. HOS_i^{On-Stn} = HatcheryReturn_i^{On-Stn} * \frac{1 - HomingRate}{HomingRate}$$

$$5. HOS_i^{Off-Stn} = Release_{i-2}^{Off-Stn} ReturnRate_i$$

$$6. ReturnRate_i = \frac{HatcheryReturn_i^{On-Stn} / HomingRate}{Release_{i-2}^{On-Stn}}$$

For

$Release_i^{On-Stn}$ = on station release in year i ,

$Release_i^{Off-Stn}$ = off station release in year i ,

$HatcheryReturn_i^{On-Stn}$ = Hatchery origin fish from the on-station release in year i that returned to the hatchery 2 years later,

$HomingRate$ = 0.8 or 0.7, assumed, and

$PEHC_{past}$ = proportion effective hatchery contribution as measured by genetic analysis (Warheit 2014).

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