

Estimating the Ratio of Hatchery-Produced to Wild Adult Steelhead on the Spawning Grounds using Scale Pattern Analyses

M. B. DAUER, T. R. SEAMONS,* L. HAUSER, T. P. QUINN, AND K. A. NAISH

*School of Aquatic and Fishery Sciences, University of Washington,
Box 355020, Seattle, Washington 98195, USA*

Abstract.—Hatcheries produce Pacific salmon and trout *Oncorhynchus* spp. for many purposes, including fishery enhancement. The genetic integrity of wild populations spawning near such hatcheries may depend on the efficacy of their spatial or temporal separation from hatchery fish. We describe a simple, novel approach based on the examination of scales from an iteroparous species, steelhead *O. mykiss*, to evaluate whether the ratio of hatchery-produced adults to wild adults on the spawning grounds met recommended levels. In this river, migrating steelhead are diverted into the hatchery by a weir. Hatchery-produced fish are manually spawned and killed in the hatchery, whereas wild fish are passed over the weir and allowed to spawn naturally upstream from the hatchery. Therefore, in principle, all hatchery-produced adults should be captured at the hatchery on their first spawning migration. However, scales from 8.3% (58 of 699) of female and 2.6% (22 of 844) of male hatchery-produced steelhead adults showed evidence of previous spawning migrations. Although this frequency was lower than the incidence of repeat spawning by wild fish (males, 11.0%; females, 20.3%), these records nevertheless indicated significant reproductive opportunities in the wild for hatchery-produced fish. Combining these frequencies of repeat spawning with estimates of the survival and numbers of wild fish, we modeled the ratio of hatchery to wild fish on the spawning grounds using data from eight return years. This ratio exceeded the recommended levels under all reasonable scenarios modeled (14.7–89.6% hatchery fish). Combined with evidence of spatial and temporal overlap, our data suggest that unless changes are made to increase the capture efficiency of adults at Washington State’s Forks Creek Hatchery and similar hatcheries relying on segregated stocks, the risks of genetic introgression and ecological interactions with wild steelhead populations will remain high.

The goals of hatcheries vary from conservation to fishery enhancement (reviewed by Utter and Epifanio 2002), but hatcheries play a vital role in the management, population dynamics, and ecology of many fish species (Leber et al. 2005), especially salmonids (Naish et al. 2007). Production hatcheries, operated to supplement recreational, commercial, and tribal fisheries, may produce fish that differ genetically from wild populations if they use nonnative broodstock, maintain small effective population sizes, and if direct or inadvertent domestication selection occurs (Ryman and Laikre 1991; Utter 2001; Waples and Drake 2005). Concerns have increasingly been expressed regarding interactions between domesticated stocks and native populations (Chilcote 2003; Mobrand et al. 2005). When individuals from such hatcheries return to spawning grounds instead of the hatchery, they may compromise the future viability of the wild population by genetic effects from introgression (Allendorf and Waples 1996; Storfer 1999; Utter 2001) or by ecological interactions (Nicholas and

Van Dyke 1982; Chilcote et al. 1986; Kostow and Zhou 2006).

Mobrand et al. (2005) described many salmon hatchery practices in Washington State as operating in a manner inconsistent with scientific recommendations and in need of reform. They suggested that hatcheries adopt one of two management strategies to reduce genetic risks for wild populations (Chilcote et al. 1986; Mobrand et al. 2005). The “integrated” approach incorporates adults produced in both natural and hatchery environments in the broodstock, thus minimizing domestication selection by maximizing opportunities for natural selection in the wild. The alternative “segregated” approach should limit reproductive interactions between the two populations to 5% or less by spatial or temporal segregation (Chilcote et al. 1986; Mobrand et al. 2005). There is now an urgent need to test the effectiveness of these two approaches.

In Washington State, hatcheries attempting to enhance the fishery for steelhead *Oncorhynchus mykiss* have historically been operated under principles similar to those of segregated management. Many of these hatcheries of the winter-run or ocean-maturing steelhead use broodstock originally derived from the native population of Chambers Creek, Puget Sound, Washington (Crawford 1979; WDFW 1997). This stock has

* Corresponding author: seamonst@u.washington.edu

Received February 11, 2008; accepted July 14, 2008
Published online January 15, 2009

undergone extensive domestication since the 1960s, mainly in the form of artificial selection for early return and spawning (November through February, compared with March through June for wild steelhead). This temporal segregation allowed managers to exploit hatchery stocks while offering some protection to native wild populations by permitting fishing to occur early in the season but closing it when most wild steelhead return. However, temporal separation in adult returns may not be sufficient to prevent spawning interactions because steelhead can successfully reproduce up to 4 months after they enter freshwater (Leider et al. 1984; Seamons et al. 2004). Salmonids may also be spatially segregated by trapping hatchery-produced adults at a weir or similar structure and allowing wild fish to pass upstream to spawn, using adipose fin clips to identify hatchery-produced fish. However, many factors may undermine the ability of a weir to capture all returning adults. Steelhead migrate during the period of most severe and unpredictable winter flooding in coastal rivers, allowing many, including hatchery-produced fish, to swim over or around weirs. In many cases there is suitable spawning habitat downstream from the weir where wild and hatchery fish can spawn.

One way to evaluate the efficacy of management programs where hatchery fish are known or allowed to spawn in the wild is to estimate the numbers of adults of each type (hatchery or wild) using a mark-recapture approach. Adults could be marked as they migrate upstream to spawn and then be either sampled on spawning grounds or, for steelhead, as they migrate downstream. Estimates of each group could then be compared with one another. This approach, however, would depend on permitting the very process that management seeks to prevent (i.e., natural reproduction by hatchery-produced fish). Another way would be to evaluate the reproductive success of hatchery fish spawning in the wild by DNA parentage analysis (e.g., Araki et al. 2007). While this method would not indicate how many hatchery fish were on the spawning grounds it would indicate how many hatchery fish successfully spawned. However, this approach can be costly and time-consuming, even in moderately sized populations, and its success depends on trapping a large fraction of the potential parents (Jones and Ardren 2003).

This paper reports a third alternative, an indirect approach to evaluating the management of hatchery fish on wild spawning grounds that is specific to iteroparous species. We took advantage of the fact that steelhead, unlike other Pacific salmon *Oncorhynchus* spp., are iteroparous, and a fraction of the population survives to spawn in multiple years. Individuals that

return to spawn in any given year are “marked” with a spawn check on their scales. Thus, the presence of fish with spawn checks indicated that they made spawning migrations in previous years. In a segregated system, some of the wild fish but none of the hatchery fish should spawn more than once (“repeat spawning”) because all hatchery fish should be intercepted and killed at the hatchery on their first spawning migration. The number of repeat spawners among the hatchery fish represents the minimum number of fish that had the opportunity to spawn in the wild in previous years for two reasons. First, postspawning survival to return is typically low in steelhead (Busby et al. 1996). Second, the probability of being captured at the hatchery upon return the second time is less than 100%. Given these conditions, we modeled the annual proportion of hatchery fish of the total number of fish spawning naturally using data from the Forks Creek Hatchery, a facility producing steelhead for fishery enhancement in Washington State. We then used the frequency of repeat spawners in a model akin to a mark-recapture approach to estimate the proportion of hatchery to wild fish on the spawning grounds and compared it with recommended proportions.

Methods

Site description and sampling.—Steelhead are naturally found throughout the Willapa River, Washington, and its tributaries. Estimates of the wild steelhead population in the entire Willapa River drainage range from 355 to 1,338 adult fish (Table 1; WDFW 2002). In Forks Creek, a tributary of the Willapa River, naturally spawning hatchery-produced steelhead tend to spawn between the weir at Forks Creek Hatchery and a diversion dam about 2 km upstream, whereas wild fish use the entire length of accessible creek (Mackey et al. 2001). The weir and the diversion dam are the only major artificial barriers to migration in the entire Willapa River watershed, and no other trapping occurs in the watershed; thus, there are no other obvious barriers to spatial overlap between hatchery and wild steelhead.

Steelhead propagation at Forks Creek Hatchery (46°33′29.09″N, 123°35′42.27″W) was initiated in 1994 with the planting of approximately 25,000 marked (adipose fin removed) steelhead smolts of Chambers Creek ancestry into Forks Creek. In subsequent years, hatchery-produced smolts were released directly into Forks Creek and also from acclimation sites downstream. These fish first returned as adults in the winter of 1995–1996 (hereafter referred to as return year [RY] 96). All hatchery and wild fish trapped by the hatchery weir from RY96 through RY03 were measured for fork length (FL) and weighed.

TABLE 1.—Number of hatchery and wild steelhead sampled, number and percent used for scale analyses, observed percentage of repeat spawners used in the analyses, and WDFW population estimates for the Willapa River.

Population	Return year	Number sampled	Readable scales		Percent with spawn checks	Population estimate
			Number	Percent		
Hatchery	1996	192	142	74.0	10	
	1997	310	300	96.8	14	
	1998	45	44	97.8	5	
	1999	114	65	57.0	2	
	2000	174	79	45.4	6	
	2001	124	104	83.9	6	
	2002	347	284	81.8	10	
	2003	500	494	98.8	28	
	Total	1,806	1,512	83.7	81	
Wild	1996	23	18	78.3	5	460
	1997	22	20	90.9	2	355
	1998	60	59	98.3	9	414
	1999	12	12	100.0	2	721
	2000	22	21	95.5	1	1,059
	2001	48				1,228
	2002	45	42	93.3	4	1,338
	2003	45	29	64.4	7	738
	Total	277	201	72.6	30	

Scales were collected for age determination and spawning history, and fin tissue was collected for genetic analyses. In the first 2 years of the study (RY96 and RY97), adult hatchery fish in excess of broodstock needs were allowed to migrate upstream from the weir (167 and 189 fish, respectively). Identified by genetic data, one of these fish was sampled in a subsequent RY. This individual was excluded from analyses. Starting in RY98 all hatchery-produced fish were killed after capture. Naturally produced (unmarked) fish were always released alive after sampling.

The offspring of naturally spawning hatchery fish were visually indistinguishable from those of wild fish; therefore, unmarked adults of hatchery ancestry were identified using genetic methods. Briefly, all sampled individuals were genotyped at eight microsatellite loci. Individuals were assigned to either hatchery or wild ancestry by means of genetic assignment tests using genotypes from known hatchery and wild fish as genetic baseline data. Only unmarked fish whose genetic ancestry was inferred to be wild were used in further analysis. A more detailed description of our methods can be found in (Hauser et al. 2006).

Scales were prepared for analysis following Bernard and Myers (1996). Specifically, a scale from the preferred area from each fish was read using a microfiche reader fitted with a 15-mm lens on two independent occasions. Nomenclature for scale aging followed the convention of two numerals separated by a decimal point (N. Davis and J. T. Light, 1985 Fisheries Research Institute Report FRI-VW-8506). The first numeral represents the number of full years

spent in freshwater, and the one after the decimal represents the number of years spent in saltwater. An "S" denotes a year that included a freshwater spawning migration and takes the place of that year in the designation. Thus, mature fish with life histories of 1.1S1 and 1.3 would both have spent 1 year in freshwater and be 4 years old, but the former would have returned to freshwater during the third and fourth years whereas the latter would have returned only in its fourth year. An "X" was used in data analyses to represent a range of digits when individuals were pooled (e.g., X.2 would include fish of varied or uncertain freshwater ages but having 2 years at sea).

Scales were inspected for evidence of a previous freshwater spawning migration, or "spawn check" (Figure 1). These were identified as regions of resorption of saltwater circuli, indicated by rough or uneven circuli near the outer margin of the scale (Persson et al. 1995; N. Davis and J. T. Light, FRI report). This resorption at the outer margin of the scale occurs during periods of high calcium demand, such as sexual maturation and spawning or starvation (Persson et al. 1995). The modified region of the scale does not regenerate and new growth rings are deposited outside of the region; thus, the marks indicating these freshwater migrations are permanent.

Estimation of the ratio of hatchery to wild fish on wild spawning grounds.—To estimate the ratio of hatchery to wild fish, we used the numbers of repeat-spawning hatchery and wild fish in the wild as the basis for simple modeling exercises. Our methods were similar to mark-recapture methods in that fish were

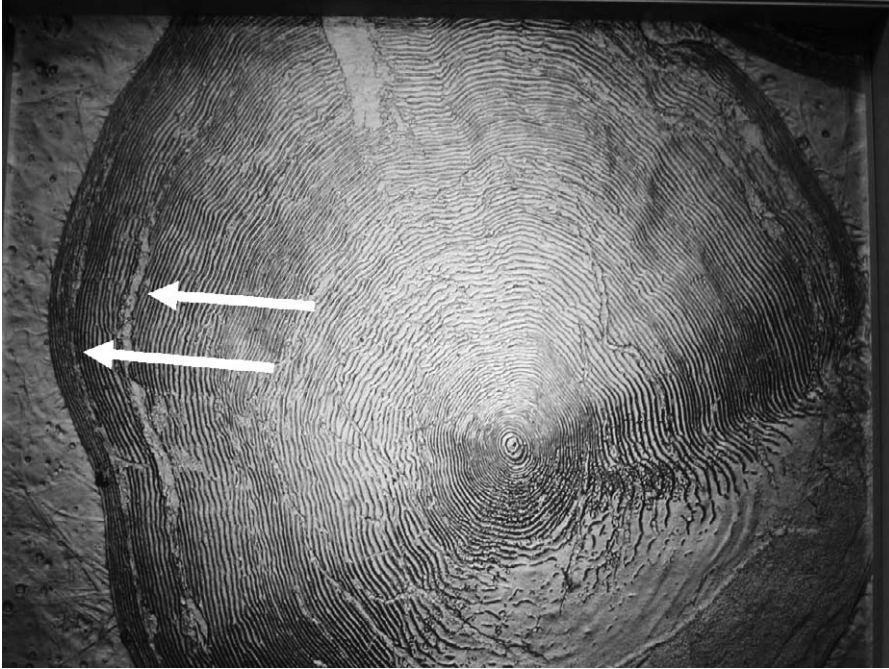


FIGURE 1.—An adult steelhead scale with two spawn checks (arrows) as viewed on a microfiche reader with a 15-mm lens. The total age of this fish is 2.1SS1 (see text).

marked at one point in time and recaptured later. However, because the number of unmarked individuals in any year (i.e., the spawning population) was completely independent of the number of unmarked individuals in any other year, normal mark–recapture methods could not be used (Pollock 1991). The number of individuals on their first spawning migration (i.e., acquiring a spawn check) in a given year was unknown, and sampling efficiency was probably different for hatchery and wild fish because of different river flow regimes during their migrations. Thus, we used a model incorporating survival between spawning migrations and sampling efficiency to examine the scenarios under which management recommendations may be met in this system.

The numbers of hatchery and wild fish were estimated as follows:

$$\hat{N}_t^{i,w} = N_{t-1}^{i,w}(S_i)(1 - P_i) + R(1 - P_i), \quad (1)$$

where i is either the hatchery (h) or wild population (w), $\hat{N}_t^{i,w}$ is the estimated number of fish of population i in the wild (and thus unsampled) in time t , $\hat{N}_{t-1}^{i,w}$ is the number of fish of population i unsampled and in the wild in time $t - 1$, S_i is the annual survival of repeat spawners, P_i is the probability of capture at the hatchery weir for population i , and R is the number

of first-time spawners in the population. Thus, the counts of repeat spawners are represented by the product $\hat{N}_{t-1}^{i,w}(S_i)(P_i)$ and the first-time spawners sampled at the hatchery by the product $R(P_i)$. For years in which fish were sampled with two spawn checks (i.e., they had made freshwater migrations in two previous years), the additional argument $N_{t-2}^{i,w}(S_i)(1 - P_i)$ was added to the right hand side of equation (1), which assumes that survival (S) is independent of age. For years in which not all fish sampled were aged (owing to either poor scale quality or lack of scales), we estimated the number of repeat spawners in the total sample from the counts found in the aged sample.

Equation (1) was used to examine the parameter values of survival (S_i) and the probability of capture (P_i) under which it would be reasonable to expect the number of naturally spawning hatchery adults to be less than 5% of the wild spawners (following the guideline of Mobrand et al. 2005). The analysis was conducted by computing the average proportion of hatchery fish in the wild while varying S_h and S_w between 1% and 15% and P_h between 1% and 100% and constraining the level of P_w to plausible values using Washington Department of Fish and Wildlife (WDFW) population estimates for the Willapa River, which includes Forks Creek (WDFW 2002). Specifically, P_w was determined for each analysis by minimizing the sum of squares of

TABLE 2.—Life history variation in hatchery and wild steelhead over 8 years of study. The totals include all fish for which scales were available.

Population	Freshwater age	Saltwater age and spawn history (%) ^a										Total	
				2		3			4				Unknown
		0 (FTS)	1 (FTS)	FTS	S1	FTS	1S1	S2	FTS	1SS1	2S1		
Hatchery (N = 1,543)	1		0.9	77.7	1.0	8.7	3.2		0.1	0.1	0.3		91.9
	2		0.1	0.5		0.1	0.0		0.1				0.7
	Unknown		0.1	3.6	0.1	1.0	0.6					2.1	7.4
	Total		1.0	81.9	1.0	9.7	3.8		0.1	0.1	0.3	2.1	
Wild (N = 207)	1			1.0									1.4
	2		2.4	44.4	1.0	6.3	5.8	0.5	0.5	1.4	0.5		62.8
	3		1.0	5.3			0.5						6.8
	4			0.5									0.5
	5	0.5											0.5
	Unknown			15.5		5.8	3.4			0.5	0.5	2.4	28.0
	Total	0.5	3.9	66.2	1.0	12.1	9.7	0.5	0.5	2.4	1.0	2.4	

^a FTS = first-time spawner; see Methods for an explanation of the other codes.

the residuals between predicted number of wild fish in the wild and WDFW population estimates for all years simultaneously using SOLVER (Microsoft Excel 2003).

For this analysis, we used counts of first-time spawners observed in the hatchery for the target return year as well as repeat spawners observed in the successive 2 years. Data from RY00 and RY01 were excluded from these analyses because no scales were collected from wild samples in RY01 and therefore there were no repeat spawners for the RY00 analysis or first-time spawners for the RY01 analysis (thus, no wild sample with which to compare). Data from RY03 were also excluded because there were no fish aged from RY04 or beyond.

Results

Scale Sampling and Life History Characterization

Scales were collected and analyzed for 1,543 hatchery and 207 wild individuals (86% of the hatchery and 75% of the wild adults captured). Of those, 1,512 (98%) scales from hatchery fish and 201 (97%) scales from wild fish were readable (i.e., provided age or life history information; Table 1). About 11% of all scales were read double-blind by an independent, highly experienced colleague (K. Myers, University of Washington, High Seas Salmon Program) as a measure of accuracy. Spawn check identification was consistent between readers; we estimated an error rate of approximately 1% for the data set.

Greater life history diversity was evident in the wild population. Total ages of fish returning to Forks Creek ranged from 2 to 6 years for hatchery fish and 3–7 years for the wild population. The most common life histories were 1.2 for hatchery fish and 2.2 for wild fish (Table 2). Steelhead smolts were released from the

hatchery at age 1 and the vast majority (99% of readable scales) reflected this age (age = 1.01 ± 0.087 years [mean ± SD]), though 11 individuals apparently spent a second year in freshwater before seaward migration. Wild fish, by comparison, almost always spent 2 years in freshwater before migrating to sea (87% of readable scales), but some spent a third year (9% of readable scales; age = 2.11 ± 0.437 years).

During the period studied (RY96–RY03), an average ± SD of 10 ± 8.26 hatchery fish returned each year with “spawn checks,” comprising 5.5% of the hatchery sample. Over this same period, an average of 4.3 ± 2.93 wild repeat spawners were detected per year, or 17.0% of the wild individuals sampled (Table 3). Repeat spawning was more common among females than males in both wild and hatchery populations. The most common repeat spawner life history was a first spawning migration after 2 years at sea and a repeat spawning the next year (X.1S1) for both hatchery and wild populations (3.8% and 9.7% of all fish sampled, respectively).

Estimated Ratio of Hatchery to Wild Fish in the River

For any value of wild adult survival (S_w), we used the estimated number of wild spawners in the entire

TABLE 3.—Hatchery and wild steelhead sampled at Forks Creek Hatchery on their first, second or third return migration, as indicated by spawn checks on adult scales.

Population	Sex	N	Freshwater migration (%)		
			1st	2nd	3rd
Hatchery	Male	844	97.4	2.6	0.0
	Female	699	91.7	8.2	0.1
Wild	Male	128	89.1	9.4	1.6
	Female	79	79.7	16.5	3.8

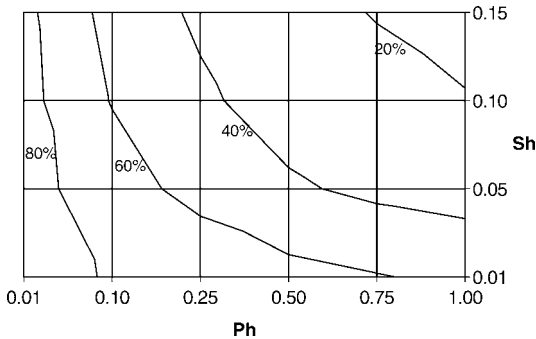


FIGURE 2.—Estimated percentage of hatchery steelhead in the wild at various levels of survival (S_h) and probabilities of capture at the weir for hatchery adults (P_h), assuming an average of 658 wild spawners and that the survival of wild fish (S_w) is 5%. The values for other levels of S_w were nearly identical and thus are not shown.

Willapa River obtained from WDFW (2002) to constrain the value of the probability of wild fish capture (P_w) to fall between 0.09 and 0.85. For example, if we assumed S_w to be 0.01, then P_w must have been 0.85 for the predicted number of wild fish in the wild to approximate abundance estimates (Table 1). We constrained repeat-spawner survival (as opposed to the proportion of repeat spawners observed in a given year) for both populations to between 1% and 15%, a wider range than the 6–10% reported for Washington State populations by Busby et al. (1996). Under all of the conditions modeled, the number of hatchery fish on the spawning grounds was in excess of 5% of wild spawners (Figure 2). The model was more sensitive to hatchery related parameters than to wild parameters, measured as the percent change in percent hatchery fish due to a change in P_i from 1% to 15% (mean \pm SD proportion of hatchery fish in the wild = $2.0 \pm 2.2\%$, versus $49 \pm 24.5\%$). The estimated percentage of hatchery-origin steelhead on the spawning grounds ranged from 14.7% to 89.6%. The cases predicting the fewest hatchery fish in the wild occurred when hatchery survival and probability of hatchery capture were both maximized ($S_h = 15\%$, $P_h = 100\%$; Figure 2). Not surprisingly, undersampling at the weir affected the calculated percent of hatchery fish in the wild. However, the analysis showed that for the proportion of hatchery fish on the spawning ground to fall below 5%, sampling efficiency of hatchery fish at the weir would have to be more than 25 times that of the wild fish ($P_h \gg P_w$).

Discussion

Interactions between hatchery fish in the wild and natural spawners may be detrimental to the wild

populations. Previous work on segregated steelhead systems has demonstrated the risk that numerically abundant hatchery-origin spawners may present to wild populations (Chilcote et al. 1986; Ryman and Laikre 1991; Kostow and Zhou 2006). Segregation is one of two strategies endorsed by the Hatchery Scientific Review Group in Washington State to minimize the negative effects of hatcheries on wild populations (Mobernd et al. 2005). Hatchery-origin adults from segregated hatcheries represent a divergent evolutionary pathway from wild stocks, and as such, reproduction between them should be minimized (Waples 1991; Campton 1995; Utter 2001).

Here we have presented a novel method of estimating the number of naturally spawning hatchery fish relative to the number of wild fish in a system that most closely resembles the segregated model. The use of scale patterns to estimate the relative abundance of hatchery fish in the wild demonstrated the difficulty that segregated steelhead hatcheries may experience when trying to adequately isolate hatchery and wild stocks. For each year in which samples were available, repeat-spawning adults were observed in the hatchery population even though all hatchery adults should have been killed at the hatchery on their first migration. Sensitivity analyses of our modified mark-recapture approach showed that hatchery fish exceeded suggested management goals under almost all scenarios examined. Under all plausible conditions for hatchery fish (i.e., survival less than 15%, and probability of capture less than 100%), the estimated numbers of hatchery fish on the spawning grounds were above the goals set to minimize the risk of introgression between hatchery and wild populations.

We used the number of wild spawners in the entire Willapa River estimated by WDFW (2002) to constrain the value of the probability of wild fish capture. Forks Creek is but one small component of the entire Willapa River system; thus, the number of wild fish spawning in Forks Creek should be less than that reported by WDFW for the Willapa River. If we were to use smaller estimates of wild steelhead abundance (i.e., that for Forks Creek alone) the ratio of hatchery to wild fish on the spawning grounds would be much higher than what we have presented. The fewest hatchery fish were predicted when survival of hatchery fish was highest. This was a result of the survival being coupled with a probability of capture. For any probability of capture, a lower survival meant that more fish made a spawning migration the previous year than were captured on their second migration. Our results also show that for the proportion of hatchery fish on the spawning ground to fall below the recommended 5% hatchery-to-wild proportion, the sampling efficiency of hatchery fish at

the weir would have to greatly exceed that of wild fish. This is unlikely because flows in the Willapa River were, on average, much higher during the spawning migration of hatchery fish (November through January) than during the migration of wild fish (February through May; USGS 2006). In addition, the hatchery-released steelhead smolts were from locations downstream from Forks Creek Hatchery. Returning adults from these smolts may have been more likely to return to their release site rather than to the hatchery. Further, actual numbers of adult wild and hatchery steelhead spawning in the wild were probably much higher than our estimates for two reasons. First, the weir was less than 100% efficient; so many adult fish were not sampled on both spawning migrations. Second, there was undoubtedly mortality between spawning events. However, due to a catch-and-kill recreational fishery on hatchery-produced steelhead and a fishery closure on wild or naturally produced (unmarked) steelhead, overall mortality for hatchery adults was probably higher than that of wild fish. Thus, we may have underestimated the number of naturally spawning hatchery fish more severely than the number of wild fish, further suggesting that the proportion of hatchery fish to wild fish on the spawning grounds is higher than what we have reported.

Our data suggested only that many hatchery fish had the opportunity to spawn in the wild, not that they actually did so. However, given what is known about steelhead life history it is likely that most of the fish spawned. Hatchery-produced steelhead have been observed jumping over the weir during periods of high river flow (R. Allan, WDFW, personal communication), and we have captured hatchery fish above the weir during surveys of Forks Creek. In addition, these hatchery fish have been observed to display normal spawning behaviors of steelhead (T. R. Seamons, personal observation). Finally, some fish in apparently postspawning or "spent" condition are trapped as they migrate downstream. Genetic risk due to hybridization between hatchery and wild fish may be minimal if there is adequate temporal or spatial segregation between these stocks. Mackey et al. (2001) found overlap in return timing between hatchery and wild fish in this population, and overlap in wild and hatchery steelhead timing has been documented elsewhere in Washington (Leider et al. 1984). Delayed spawning may provide an additional opportunity for reproductive interactions. Seamons et al. (2004) described successful spawning over a 4-month range in a population of wild steelhead in Snow Creek, Washington, and Leider et al. (1984) described a 6-month spawning interval for steelhead in the Kalama River, Washington. A similar range may occur in this hatchery population. We have captured

hatchery-produced adults in a downstream trap in Forks Creek as late as May 22, overlapping broadly with the timing of wild fish. However, little is known of the amount of actual interbreeding between hatchery and wild fish in this population.

Although our results pertain specifically to the Forks Creek Hatchery's steelhead program, the situation there is not unique (for example, see Leider et al. 1986). In all river systems with hatchery production, hatchery-produced fish will have opportunities to spawn naturally. Accordingly, managers may consider other methods of reducing the number of hatchery fish on the spawning grounds. Our method of examination of scales from steelhead in hatcheries may be a simple way to assess the extent to which hatchery steelhead have the opportunity for natural reproduction in such cases.

Acknowledgments

We thank G. Mackey, J. McLean, J. Cabarrus, D. Mai, and W. Atlas for data collection, K. Myers and N. Davis for help with scale reading and interpretation, and J. Cope and A. Punt for developing the model used in this paper. The hatchery staff, including G. Britter, R. Allan, K. Flowers, D. Shores, J. Allan, and M. Hash, was invaluable throughout the duration of this project. For financial support, we thank the Weyerhaeuser Foundation, the H. Mason Keeler Endowment, the Bonneville Power Administration, the National Science Foundation (grant DEB-9903914), and the Hatchery Science Reform Group in Washington State.

References

- Allendorf, F. W., and R. S. Waples. 1996. Conservation and genetics of salmonid fishes. Pages 238–280 in J. C. Avise and J. L. Hamrick, editors. Conservation genetics: case histories from nature. Chapman and Hill, New York.
- Araki, H., R. S. Waples, W. R. Ardren, B. Cooper, and M. S. Blouin. 2007. Effective population size of steelhead trout: influence of variance in reproductive success, hatchery programs, and genetic compensation between life history forms. *Molecular Ecology* 16:953–966.
- Bernard, R. L., and K. W. Myers. 1996. The performance of quantitative scale pattern analysis in the identification of hatchery and wild steelhead (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 53:1727–1735.
- Busby, P. J., and coauthors. 1996. Status review of West Coast steelhead from Washington, Idaho, Oregon, and California. NOAA Technical Memorandum NMFS-NWFSC-27.261.
- Campton, D. E. 1995. Genetic effects of hatchery fish on wild populations of Pacific salmon and steelhead: What do we really know? Pages 337–353 in Harold L. Schram, Jr. and Robert G. Piper, editors. Uses and effects of cultured fishes in aquatic ecosystems. American Fishery Society, Symposium 15, Bethesda, Maryland.

- Chilcote, M. W. 2003. Relationship between natural productivity and the frequency of wild fish in mixed spawning populations of wild and hatchery steelhead (*Oncorhynchus mykiss*). *Canadian Journal of Fisheries and Aquatic Sciences* 60:1057–1068.
- Chilcote, M. W., S. A. Leider, and J. J. Loch. 1986. Differential reproductive success of hatchery and wild summer-run steelhead under natural conditions. *Transactions of the American Fisheries Society* 115:726–735.
- Crawford, B. A. 1979. The origin and history of the trout brood stocks of the Washington Department of Game. Washington State Game Department, Fishery Research Report SH167.T86 C7, Olympia, Washington.
- Hauser, L., T. R. Seamons, M. Dauer, K. A. Naish, and T. P. Quinn. 2006. An empirical verification of population assignment methods by marking and parentage data: hatchery and wild steelhead (*Oncorhynchus mykiss*) in Forks Creek, Washington, USA. *Molecular Ecology* 15:3157–3173.
- Jones, A. G., and W. R. Ardren. 2003. Methods of parentage analysis in natural populations. *Molecular Ecology* 12:2511–2523.
- Kostow, K. E., and S. Zhou. 2006. The effect of an introduced summer steelhead hatchery stock on the productivity of a wild winter steelhead population. *Transactions of the American Fisheries Society* 135:825–841.
- Leber, K., S. Kitada, H. Blankenship, and T. Svasand. 2005. Stock enhancement and sea ranching. Blackwell Scientific Publications, Oxford, UK.
- Leider, S. A., M. W. Chilcote, and J. J. Loch. 1984. Spawning characteristics of sympatric populations of steelhead trout (*Salmo gairdneri*): evidence for partial reproductive isolation. *Canadian Journal of Fisheries and Aquatic Sciences* 41:1454–1462.
- Leider, S. A., M. W. Chilcote, and J. J. Loch. 1986. Comparative life history characteristics of hatchery and wild steelhead trout (*Salmo gairdneri*) of summer and winter races in the Kalama River, Washington. *Canadian Journal of Fisheries and Aquatic Sciences* 43:1398–1409.
- Mackey, G., J. E. McLean, and T. P. Quinn. 2001. Comparisons of run timing, spatial distribution, and length of wild and newly established hatchery populations of steelhead in Forks Creek, Washington. *North American Journal of Fisheries Management* 21:717–724.
- Mobrand, L. E., John Barr, Lee Blankenship, Donald E. Campton, Trevor T. P. Evelyn, Tom A. Flagg, Conrad V. W. Mahnken, Lisa W. Seeb, Paul R. Seidel, and William W. Smaker. 2005. Hatchery reform in Washington State: principles and emerging issues. *Fisheries* 30(6):11–23.
- Naish, K., Joseph E. Taylor, III, Philip S. Levin, Thomas P. Quinn, James R. Winton, Daniel Huppert, and Ray Hilborn. 2007. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. *Advances in Marine Biology* 53:61–194.
- Nicholas, J. W., and L. Van Dyke. 1982. Straying of adult coho salmon to and from a private hatchery at Yaquina Bay, Oregon Oregon Department of Fish and Wildlife, Report 82-10, Portland.
- Persson, P., Y. Takagi, and B. T. Bjornsson. 1995. Tartrate-resistant acid phosphatase as a marker for scale resorption in rainbow trout, *Oncorhynchus mykiss*: effects of estradiol-17-beta treatment and refeeding. *Fish Physiology and Biochemistry* 14:329–339.
- Pollock, K. H. 1991. Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. *Journal of the American Statistical Association* 86:225–238.
- Ryman, N., and L. Laikre. 1991. Effects of supportive breeding on the genetically effective population size. *Conservation Biology* 5:325–329.
- Seamons, T. R., P. Bentzen, and T. P. Quinn. 2004. The mating system of steelhead, *Oncorhynchus mykiss*, inferred by molecular analysis of parents and progeny. *Environmental Biology of Fishes* 69:333–344.
- Storfer, A. 1999. Gene flow and endangered species translocations: a topic revisited. *Biological Conservation* 87:173–180.
- USGS (U.S. Geological Survey). 2006. Daily mean flows of the Willapa River near Willapa, Washington. Available: <http://waterdata.usgs.gov>. (August 2006.)
- Utter, F. 2001. Patterns of subspecific anthropogenic introgression in two salmonid genera. *Reviews in Fish Biology and Fisheries* 10:265–279.
- Utter, F., and J. Epifanio. 2002. Marine aquaculture: genetic potentialities and pitfalls. *Reviews in Fish Biology and Fisheries* 12:59–77.
- Waples, R. S. 1991. Genetic interactions between hatchery and wild salmonids: lessons from the Pacific Northwest. *Canadian Journal of Fisheries and Aquatic Sciences* 48(Supplement 1):124–133.
- Waples, R. S., and J. Drake. 2005. Risk/benefit considerations for marine stock enhancement: a Pacific salmon perspective. Pages 260–306 in K. Leber, S. Kitada, H. Blankenship, and T. Svasand, editors. *Stock enhancement and sea ranching*. Blackwell Scientific Publications, Oxford, UK.
- WDFW (Washington Department of Fish and Wildlife). 1997. Policy of Washington Department of Fish and Wildlife and Western Washington Treaty Tribes concerning wild salmonids. WDFW, Olympia, Washington.
- WDFW (Washington Department of Fish and Wildlife). 2002. Salmonid stock inventory: Willapa winter steelhead. Available: <http://wdfw.wa.gov>. (August 2007.)