Environmental Biology of Fishes **69:** 359–369, 2004.

Differential reproductive success of sympatric, naturally spawning hatchery and wild steelhead, *Oncorhynchus mykiss*

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Received 17 April 2003 Accepted 24 April 2003

Key words: assignment test, fitness, hatcheries, microsatellites, salmonidae, smolt production

Synopsis

Hatchery propagation of salmonids has been practiced in western North America for over a century. However, recent declines in wild salmon abundance and efforts to mitigate these declines through hatcheries have greatly increased the relative abundance of fish produced in hatcheries. The over-harvest of wild salmon by fishing mixed hatchery and wild stocks has been of concern for many years but genetic interactions between populations, such as hybridization, introgression and outbreeding depression, may also compromise the sustainability of wild populations. Our goal was to examine whether a newly established hatchery population of steelhead trout successfully reproduced in the wild and to compare their rate of reproductive success to that of sympatrically spawning native steelhead. We used eight microsatellite loci to create allele frequency profiles for baseline hatchery and wild populations and assigned the smolt (age 2) offspring of this parental generation to a population of origin. Adults originating from a generalized hatchery stock artificially selected for early return and spawning date were successful at reproducing in Forks Creek, Washington. Although hatchery females (N = 90 and 73 in the two consecutive years of the study) produced offspring that survived to emigrate as smolts, they produced only 4.4–7.0% the number produced per wild female (N = 11 and 10). This deficit in reproductive success implies that the proportion of hatchery genes in the mixed population may diminish since deliberate releases into the river have ceased. This hypothesis is being tested in a long-term study at Forks Creek.

Introduction

Salmonid fishes have a well-documented ability to home to their natal streams for reproduction (Quinn 1993). This homing limits gene flow among populations in different locations and allows the accumulation of differences in adaptive traits such as behaviour, morphology, physiology and disease resistance among populations (Ricker 1972, Taylor 1991). Selectively neutral genetic characters, such as polymorphic proteins and DNA microsatellite loci, do not directly reflect local adaptation, but can be used to infer whether populations are reproductively isolated from one another. Microsatellite DNA techniques have been applied to examine the relationships among many natural salmonid populations (e.g. Atlantic salmon, McConnell et al. 1995; Arctic char, Brunner et al. 1998; steelhead trout, Beacham et al. 1999); here we employed these techniques to differentiate between a native wild population and a transplanted hatchery population in one stream to compare the reproductive success of these forms under natural conditions.

Local, population-specific adaptations include changes in characteristics associated with reproductive success, such as adult body size and the seasonal patterns of migration and reproduction. The body size

of a female controls her capacity for egg production (number and size of eggs). The timing of spawning is also extremely important for reproductive success in salmonids, as the survival and growth of juveniles varies with the date when they emerge and begin feeding in spring (Brännäs 1995, Einum & Fleming 2000). Females that return early will have progeny that emerge earlier, and will be larger and have acquired a territory by the time later fry emerge (Chandler & Bjornn 1988). Eggs that have been deposited early, however, may be more susceptible to scour by high river flows (Cederholm[1]) and early fry may be vulnerable to predation (Brännäs 1995). The morphology and behaviour of males are shaped by the same processes of natural selection (e.g. migration, energetics and predator avoidance) but also by sexual selection for access to females on the spawning grounds (reviewed by Fleming 1996). Body size is a significant factor in these intrasexual competitive interactions. Populations evolve by culling individuals with inappropriate size, shape, breeding date or other traits, given the patterns of temperature, flow and biotic factors that characterize different rivers. Because body size and maturation timing are under partial genetic control (size in rainbow trout, Crandall & Gall 1993; timing in rainbow trout, Siitonen & Gall 1989; chinook salmon, Quinn et al. 2000; pink salmon, Smoker et al. 1998), these traits are passed on to subsequent generations.

It is widely accepted that these evolutionary processes confer a 'home court' advantage for salmon of the local population, relative to strays from other populations that might breed there (Quinn 1993). The survival advantages associated with such local adaptation are implied by the failure of virtually all transplants within the range of Pacific salmon to generate self-sustaining populations (Withler[2]), the higher survival rates of local compared to non-local salmon released from hatcheries (Reisenbichler 1988), and the evolution of local adaptations that confer survival advantages in transplanted populations (Quinn et al. 2001).

Hatcheries have artificially propagated salmon and trout in Europe and North America for more than 100 years (Nielsen 1994), and recent work has expressed concern regarding their effects on wild populations (Ryman & Laikre 1991, Waples 1991, Utter 1998). Hatchery-produced juveniles may compete for food and space with native populations in streams (e.g. Nickelson et al. 1986, Nielsen 1994), but it is unclear what success hatchery salmon have when spawning in the wild, or what effects they have on the reproductive success of wild salmon. Hatchery fish spawning in the wild can be thought of as strays. Juveniles in hatcheries experience very different rearing conditions (e.g. feeding, use of space and predator avoidance) than do fish in streams, and this 'domestication selection' (Reisenbichler & Rubin 1999) produces differences in many behavioural traits (e.g. Berejikian 1995, Berejikian et al. 1996). This is also true for adults, who experience altered selective regimes when spawned in the hatchery (Waples 1991). Mate choice and spawning behaviour are not determined by the fish, but by the hatchery staff, who may accomplish domestication either purposely (e.g. shifting the timing of reproduction over generations by preferentially spawning early returning fish) or inadvertently, through selection of adults that would otherwise be culled by natural or sexual selection in the river.

Interactions between hatchery and wild fish are a pressing issue for salmonid conservation because hatchery production is such a large fraction of the total abundance in many areas. Light[3] estimated that approximately half of the adult steelhead trout, *Oncorhynchus mykiss*, in North America are of hatchery origin. Steelhead are an anadromous, iteroparous salmonid and spawning typically occurs during late winter and early spring (Busby et al.[4]), although dates differ among rivers. In Washington State, the great majority of hatchery steelhead are derived from a few stocks of complex ancestry. These stocks, notably one produced in the Chambers Creek Hatchery, have been selected to return and spawn earlier in the winter than wild populations (Crawford[5]).

[1] Cederholm, C.J. 1984. Clearwater River wild steelhead spawning timing. pp. 257–268 *In*: Proceedings of the Olympic Wild Fish Conference. Port Angeles, Washington.

[2] Withler, F.C. 1982. Transplanting Pacific salmon. Canadian Technical Report of Fisheries and Aquatic Sciences 1079, 27 pp.

[3] Light, J.T. 1989. The magnitude of artificial production of steelhead trout along the Pacific coast of North America, Fisheries Research Institute FRI-UW-8913, University of Washington, Seattle, 11 pp.

[4] Busby, P.J., T.C. Wainwright, G.J. Bryant, L. Lierhiemer, R.S. Waples, F.W. Waknitz & I.V. Lagomorsino. 1996. Status review of west coast steelhead from Washington, Idaho, Oregon and California. U.S. Dept. Commer., NOAA Tech. Memo. NMFS-NWFSC-27, 261 pp.

[5] Crawford, B.A. 1979. The origin and history of the trout brood stocks of the Washington Department of Game, Fisheries Research Report, Washington State Game Department, Olympia, 76 pp.

This project forms part of a growing literature comparing the fitness and reproductive success of wild and hatchery, and native and non-native populations, and investigating the consequences of allowing them to spawn in sympatry (steelhead, *O. mykiss*, Chilcote et al. 1986, Leider et al. 1990; coho salmon, *O. kisutch*, Fleming & Gross 1992; brown trout, *Salmo trutta*, Cagigas et al. 1999, Skaala et al. 1996; Atlantic salmon, *S. salar*, Mork 1991, Crozier 1993, Fleming et al. 1996, 2000, Crozier et al. 1997, Crozier 2000, Fleming & Petersson 2001). In Washington, as in many areas, hatcheries have been operating for many generations, making it difficult to study the genetic interactions between wild and hatchery fish. However, the initiation of steelhead production at the Forks Creek Hatchery, Washington provided a rare opportunity to investigate these interactions in the early years before the effects of introgression might occur. Here we present the initial results from our ongoing study designed to compare the reproductive success of hatchery and wild steelhead. We had three objectives at this stage of the project: (1) to characterize allele frequency profiles of the hatchery and wild populations before any interbreeding might occur and determine if they were different, (2) to determine whether hatchery steelhead successfully reproduced when permitted access to natural spawning grounds, and (3) to compare the reproductive success (in terms of smolts per female) of the hatchery and wild populations.

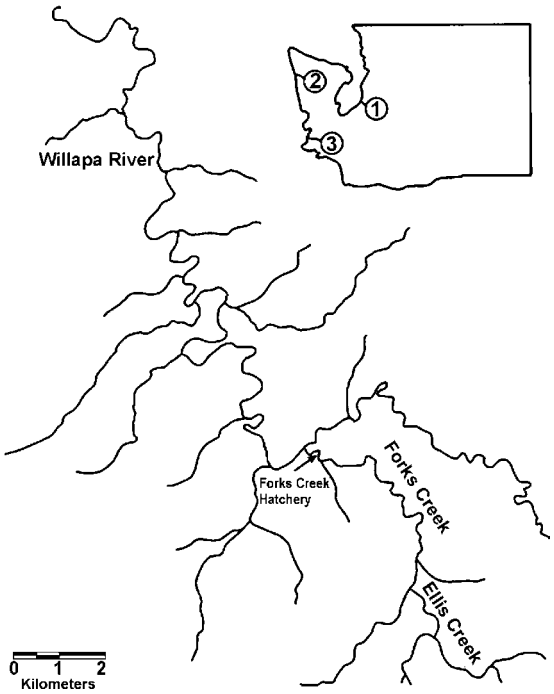

Figure 1. Location of Forks Creek Hatchery. Inset shows Washington State and the location of Chambers Creek Hatchery (1) from which the hatchery population was derived and Bogachiel Hatchery (2) from which the original hatchery smolts were taken for release in Forks Creek. Forks Creek Hatchery is designated by (3).

Methods

Study site

Forks Creek is a tributary of the Willapa River in southwest Washington (Figure 1). Forks Creek Hatchery is located ~250 m upstream of the confluence of Forks Creek and the Willapa River and has operated as a salmon hatchery since 1895. Prior to 1994, Forks Creek supported a small wild run of winter steelhead that spawns from approximately March through May (Mackey et al. 2001). In 1994, Forks Creek Hatchery received 25 000 smolts from the Bogachiel Hatchery, located to the north of the Willapa River along the west coast of Washington. This population was derived from a combination of native Bogachiel River steelhead and the Chambers Creek stock, a generalized hatchery stock artificially selected for early spawning (November to February; Ayerst 1977, Crawford[5], Mackey et al. 2001). These and all subsequent hatchery smolts were marked by the removal of their adipose fins. The first hatchery adults returned in the winter of 1995/1996 and we designated them as brood year ('BY') 1996. Returning salmon and steelhead are prevented from migrating upstream of the hatchery by a weir across the creek, allowing hatchery staff access to returning fish. Adult steelhead with an intact adipose fin (i.e. naturally produced) are placed upstream. Those missing an adipose fin are taken for spawning in the hatchery. In the first 2 years when hatchery adults returned, after the hatchery's capacity for steelhead eggs was met, excess hatchery fish were released upstream of the hatchery. This practice was then discontinued, and hatchery fish are no longer allowed upstream. Thus the wild population was exposed to a discrete, 2-year 'pulse' of hatchery influence.

Sampling

Our sampling in Forks Creek has been extensive. Since 1996, we have sampled all naturally produced smolts

trapped at the weir, as well as all adults, both hatchery and wild, trapped at the weir. We have also subsampled naturally produced juveniles in the stream and hatchery produced juveniles in the hatchery prior to their release. Examination of the length frequency distributions of juveniles, scales collected from adults, and the general life history of steelhead in this region lead us to conclude that virtually all smolts leave the river after 2 years of residence. Here we examine adults from BY1996 and BY1997, and their offspring: smolts collected in the spring of 1998 and 1999. The 55 wild and 362 hatchery adults which returned in 1996 and 1997, before any potential mixing of the hatchery and wild gene pools, provided our genetic baseline data.

Hatchery adults were sampled weekly at the hatchery from November to February. We recorded the date of spawning, sex, fork length, weight and took scale samples for age estimation and a fin clip for DNA analysis. Fecundity was also estimated for 65 hatchery females in 1996 and 1997 by obtaining the total mass of eggs, the mass of a sample of eggs, and the number of eggs in that sample. The best relationship, a linear one: fecundity $= 13.929 \times \text{length} - 4933.4$ ($r^2 = 0.414$), was used to estimate the potential egg deposition by naturally spawning females based on observed lengths.

Wild adults tended to return later in the year and were trapped on their way upstream at the hatchery weir and downstream at the smolt trap, located at the hatchery and operated from mid-late April to mid-June. Data taken from adult wild steelhead included date and direction of migration, sex, fork length, weight, a scale sample and a fin clip. Concern about the status of the wild population prevented us from sacrificing females for fecundity so we used the length–fecundity relationship from the hatchery fish to estimate the egg deposition by wild females.

Genetic analysis

Genomic DNA was extracted from fin clips stored in 95% ethanol by standard CTAB protocol (Fields et al. 1989) or by Qiagen kits. DNA was resuspended in 50–100 µl of TE solution (10 mM Tris, 1 mM EDTA in H_2O; pH 8.0) and stored at −20°C. Eight microsatellite loci were examined (Table 1). PCRs were carried out in 10 µl volumes (10 mM Tris–HCl (pH 8.3), 50 mM KCl, 1–2 mM $MgCl_2$ (see Table 1), 0.25 mM each dNTP, 1 U Taq DNA polymerase (Promega), 0.5 µM each primer and 100 ng DNA template) using an MJ Research PTC-200 thermocycler. Amplifications took place under the following conditions: (1) three cycles of 95°C for 1 min, X°C for 30 s, 70°C for 1 min; (2) 22 cycles of 95°C for 10 s, X°C for 30 s, 70°C for 1 min; (3) one cycle at 70°C for 45 min. X is an annealing temperature that varied among loci (see Table 1). Microsatellites were size fractionated using a 96-well capillary system Molecular Dynamics MegaBACE 1000 (Amersham Scientific). Electropherograms were analyzed using Genetic Profiler software version 1.1 (Molecular Dynamics).

Table 1. Microsatellite loci examined and PCR details. X is the PCR annealing temperature (°C), [$MgCl_2$] is the magnesium chloride concentration (mM), N_A is the number of alleles found in each population at that locus and H_E is the expected heterozygosity (%) for each population. All adults from 1996 and 1997 are included: 362 hatchery and 55 wild samples.

				Hatchery		Wild	
Locus	Reference	[$MgCl_2$]	X	N_A	H_E	N_A	H_E
Oki23	A. Spidle[a]	1	55	24	86.7	16	89.5
Omy77	Morris et al. (1996)	1	55	14	83	11	85.5
Omy1001UW	P. Bentzen[b]	1	55	21	87.7	16	90
Omy1011UW	P. Bentzen[b]	1	55	23	91.3	16	91.5
Omy1191UW	P. Bentzen[b]	1	65	26	93.3	26	94.9
Omy1212UW	P. Bentzen[b]	1	65	56	94	31	96.1
One108	Olsen et al. (2000)	1	55	26	91	16	91.4
Ssa85	O'Reilly et al. (1996)	2	60	24	82.6	15	85.6
Average				27	88.7	18	90.5

[a] A. Spidle, unpublished data. Genbank Accession # AF272822.
[b] P. Bentzen, unpublished data.

Data analysis

Heterozygosity, probability tests of Hardy–Weinberg equilibrium, tests of linkage disequilibrium, and genetic differentiation estimates among hatchery and wild populations were calculated using the GENEPOP (version 3.0) software package (Raymond & Rousset 1995). The program GENECLASS (Cornuet et al. 1999) was used both to self-classify the adult hatchery and wild samples to determine accuracy, and to assign smolts originating in the river from either hatchery- or wild-origin parents to a parental population of origin. GENECLASS uses a likelihood approach to calculate the probability of belonging to one of the baseline populations and is similar to Raanala & Mountain's (1997) method of identifying migrant individuals. We used the Bayesian likelihood algorithm option and the 'as is' procedure. A number of assignment tests were performed to (1) evaluate the extent of separation between the hatchery and wild populations, (2) determine the best baseline dataset, and (3) estimate the likelihood of misclassification of smolts. These tests included the following: 1996 and 1997 adults were self-assigned, true unknown test samples with genotypes not present in the baseline datasets were evaluated (1996 adults were assigned to 1997 and 1997 adults were assigned to 1996), and to improve the accuracy of determination we created a new baseline dataset by adjusting the sample size of the baseline hatchery population to match that of the baseline wild population. We did this by randomly selecting 55 hatchery adults from a pool of the 362 genotypes collected, and using these as the hatchery baseline samples. A list of 55 random numbers between 1 and 362 were generated in Microsoft Excel, and the DNA samples with the corresponding numbers were used. All 55 wild baseline samples were used. Multiple random samples showed consistent correct classification percentages, so we chose one random sample to use for the analyses. To estimate the likelihood of misclassification of smolts, we examined the log likelihood ratios (LLRs) of the correctly classified and misclassified individuals. Because we did not obtain 100% correct assignment of parents at an LLR of zero, we defined the ratio at which all baseline adults were correctly classified and used this ratio as a criterion for classifying smolts.

In the 'unknown' sample assignment tests, we assigned all smolts (366 from 1998 and 285 smolts from 1999) to a population of origin. Estimates of production for each population were determined by dividing the number of smolts assigned to that population by the number of females of that type that had ascended the creek to spawn in the parental year (i.e. two years before the smolts emigrated). After smolts were assigned to a population, we examined differences in date of emigration and size at emigration between the smolts produced by hatchery and wild parents with two-sample t-tests. We also assessed differences between the parent populations for these traits.

Results

Population genetics

Heterozygosities were high, ranging from 82.6% to 94.0% in the total hatchery parent population and 85.6–96.1% in the wild parent population (Table 1), 84.0–94.6% in the 1998 smolt population and 79.8–93.8% in the 1999 smolt sample (data not shown). Probability tests showed no significant departure from HWE in the wild adult population, however, with a sequential Bonferroni correction for multiple comparisons (Rice 1989), all loci in the hatchery population but one, Omy1001, significantly differed from Hardy–Weinberg proportions. The randomly generated hatchery sample used in the assignment test did not show a significant departure from Hardy–Weinberg proportions. Probability tests for genotypic linkage disequilibrium resulted in four significant values among 56 pairwise tests of eight microsatellite loci and two populations. These all occurred in the hatchery population (Omy77 × Oki23, Omy1011UW × Oki23, Ssa85 × One108, One108 × Oki23). Estimates of F_{ST} ranged from negative values to 0.013 and averaged 0.005 over all loci for the total combined adult sample (1996 and 1997, hatchery and wild). The random subsample of hatchery adults combined with the wild adults resulted in an F_{ST} estimate of 0.005.

Population assignment

Adult samples were used both for self-assignment and as unknowns. In the self-assignment tests, the individuals from the 1996 sample were correctly classified to their true populations, hatchery or wild, 86% of the time. The individuals from 1997 had a correct classification rate of 99%. When the 2 years were combined, correct classification was 85%. When classifying 1 year as true unknowns (genotypes not

found in the baseline file) to the other year as baseline data, 1996 as unknowns assigned to 1997 as baseline was 82% correct and 1997 as unknowns assigned to 1996 was 63% correct. In our created baseline data set (with the random sample from the hatchery population), self-assignment was 92% correct. Eight wild adults were incorrectly assigned to the hatchery population and one hatchery adult was incorrectly assigned to the wild population. In this, as in all of our assignment tests, there was a bias toward assigning wild fish to the hatchery population rather than the reverse, so the results will tend to over-estimate the productivity of hatchery females and underestimate the productivity of wild females.

Through self-assignment of our created baseline sample, we determined that the criterion for correct assignment of smolts was ±0.8 (Figure 2). Smolts from 1998 were assigned using the created baseline: 96 were assigned to the hatchery population and 269 to the wild population with an LLR of 0. With an LLR of ±0.8, we were unsure of the correct assignment of and therefore removed 42 hatchery-assigned smolts and 68 wild-assigned smolts (30% of the smolt sample). After this correction, 54 were assigned to the hatchery population and 201 to the wild population. Smolts from 1999 were assigned using the same created baseline dataset: 97 were assigned to the hatchery population and 188 were assigned to the wild population with an LLR of 0. With an LLR of ±0.8, 42 individuals were removed from the hatchery population and 23 individuals were removed from the wild population (23%), leaving 55 hatchery and 165 wild individuals. The possible range, then, for 1998 was 54–164 hatchery smolts and 201–311 wild smolts. The range in 1999 was 55–120 hatchery smolts and 162–230 wild smolts.

Because the assignment test results are the same regardless of the estimate used (fewer hatchery than wild smolts produced despite many times more hatchery females than wild females), we will use the LLR = 0 estimates. Hatchery females produced an average of 1.07 smolts per capita spawning in 1996 (smolt year 1998) and 1.33 smolts per capita spawning in 1997 (smolt year 1999). Wild females produced an average of 24.50 smolts per capita in 1996 and 18.80 in 1997.

Wild and hatchery adults overlapped in size and migration date but wild fish tended to be larger and arrive later (Tables 2 and 3). Based on the length–fecundity relationship generated for the hatchery population (and assuming a similar relationship for the wild population), we estimated the mean fecundity to have been 4 547 eggs per wild female and 3 862 eggs each for hatchery females in 1996, and 4 607 eggs per wild female and 3 895 eggs each for hatchery females in

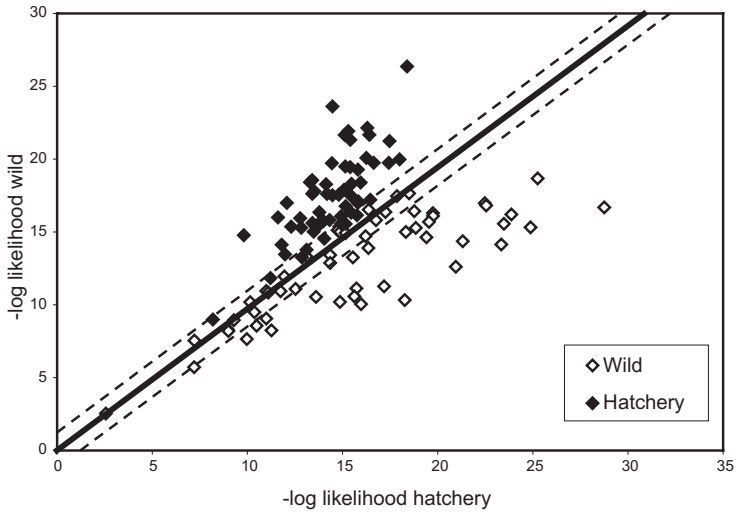

Figure 2. Separation of hatchery and wild populations based on microsatellite data. The negative log likelihood of an individual belonging to the wild population is plotted against the negative log likelihood of an individual belonging to the hatchery population, and the 1 : 1 line, along which an individual has an equal probability of being in either population, is a solid line. Each point is an individual; hatchery individuals are represented by black diamonds, and wild individuals are represented by white diamonds. These 110 fish include all wild fish from 1996 and 1997 and an equally sized random sample of the hatchery fish from those two years. The LLR lines, shown as dashed lines, indicate the cutoff criterion for 100% correct assignment.

Table 2. Mean fork length (mm) and estimated fecundity (# eggs per female) of hatchery- and wild-origin adult steelhead spawning naturally in 1996 and 1997 in Forks Creek.

	Females		Males	
	Wild	Hatchery	Wild	Hatchery
1996				
Mean length	681	632	686	629
Minimum length	623	440	459	406
Maximum length	756	762	910	760
Mean fecundity	4547	3862		
Total fecundity	50017	347580		
N	11	90	21	75
1997				
Mean length	685	634	619	649
Minimum length	590	530	450	433
Maximum length	780	772	810	724
Mean fecundity	4607	3895		
Total fecundity	46070	284335		
N	10	73	17	124

Table 3. Mean date naturally spawning steelhead in Forks Creek passed the weir in 1996 and 1997.

	Females		Males	
	Wild	Hatchery	Wild	Hatchery
1996	6 March	13 January	29 April	15 January
1997	23 April	31 January	20 May	30 January

1997. We then estimated the total egg production of each population in each year to have been 50 017 wild eggs and 347 580 hatchery eggs in 1996 (12.6% wild) and 46 070 wild eggs and 284 335 hatchery eggs in 1997 (13.9% wild). Because the wild females were somewhat longer than the hatchery fish, their total egg production was closer to that of hatchery fish than might be inferred from merely the total number of females (10.9% wild in 1996 and 12.0% in 1997).

The median emigration date of the hatchery and wild smolts was the same in 1998 and 1999 (Table 4). Hatchery smolts were longer by an average of 4 mm in 1998, but the same mean length as wild smolts in 1999 (2-sample t-test $p < 0.05$, Table 4).

Discussion

Assignment tests and population genetics

A test of individual assignment back to population of origin with our created baseline dataset indicated that 92% of the individual assignments were correct. Correct assignment to the hatchery population was 98%, and correct assignment to the wild population was 86%. Because the hatchery fish clustered more closely than the wild fish and the percentage of correct assignment was higher for this group, it was easier to determine if a fish originated from the hatchery than the wild population. The patterns of clustering indicated a higher degree of heterogeneity among the wild fish. Although the wild population is quite small (~30 fish return on average each year), its higher diversity may be due to reproductively successful strays either from other hatchery or wild populations, some form of inbreeding avoidance occurring in the population during spawning, or a higher long-term effective population size than the hatchery population as a result of a more constant population size, genetic contributions from mature male parr (Seamons et al., this issue) and a lack of artificial selection.

Table 4. Mean date of emigration and mean fork length (mm) at emigration from Forks Creek for hatchery and wild steelhead smolts, 1998 and 1999.

	Wild	Hatchery
1998		
Mean fork length	176.8	180.9
Mean emigration date	13 May	13 May
N	96	269
1999		
Mean fork length	163.3	163.2
Mean emigration date	21 May	21 May
N	97	188

The low F_{ST} value between the hatchery and wild populations (0.005) and the overlap of the two groups seen in Figure 2 can be explained by a number of features of the populations. The hatchery fish returning to Forks Creek may have clustered more closely than the wild fish due to the effects of repeated bottlenecks and small effective population size that can occur in hatcheries (Kincaid 1995, Verspoor 1988). The heterozygosities at the loci examined are high in both populations, and not very different between the two populations (Table 1). The number of alleles per locus was higher in the hatchery population because of the much higher (almost eight times) sample size. The wild adult population had allele frequencies consistent with Hardy–Weinberg proportions, but the adult hatchery population did not. This may reflect a number of population processes that have occurred extensively

in the history of the hatchery population but not in the wild population: non-random mating, high levels of random genetic drift from small effective population sizes, and domestication and artificial selection. All significant cases of linkage disequilibrium occurred in the hatchery population, which is also consistent with these processes acting differently on the two populations. Linkage disequilibrium can be generated by genetic drift and selection, both of which have occurred in the hatchery. Further, the rate at which linkage equilibrium re-establishes is slowed when the level of inbreeding is high, a process which may be maintaining linkage disequilibrium in the hatchery.

Smolt production

We obtained reasonable levels of correct assignment (cf. Beacham et al. 1999) and are confident in our ability to assign the offspring of naturally spawning wild and hatchery steelhead (the latter identified as adults by the absence of their adipose fins) to the correct population. However, because of the bias towards assigning to the hatchery population, reproductive success was underestimated for wild females and overestimated for hatchery females. Despite this bias, wild females outproduced hatchery females substantially in both years examined. Hatchery females produced an average of 1.07–1.33 smolts each and wild females produced an average of 18.80–24.50 smolts each.

Smolt production by steelhead varies among populations, and among years within a population. For example, estimates of smolts produced per female for Snow Creek, Washington range from 21.7 to 684 (T. Johnson, Washington Department of Fish and Wildlife, unpubl. data). Our results indicated that the production by wild fish was low but within the range observed for other populations, and the wild fish greatly outperformed the hatchery fish. A similar study on the Kalama River, Washington steelhead obtained comparable results: hatchery steelhead adults, although significantly outnumbering wild adults on the spawning grounds, produced fewer smolts per female than did wild spawners (hatchery steelhead had an average of 28% the reproductive success of wild steelhead to the smolt stage, Chilcote et al. 1986).

Why did wild steelhead outperform hatchery steelhead? In Forks Creek, differential reproductive success could be due to a number of differences between the populations but the most obvious are differential fecundity, the timing of reproduction by the parents, and domestication selection affecting adults or juveniles. The wild females were larger than the hatchery females in both years, and this may have resulted from the longer period of time spent at sea (i.e. the difference between arrival in January and April) or genetic factors. Using a relationship developed for the hatchery population, we estimated that on average each wild female would have produced 15% more eggs than each hatchery female. However, differences in number of smolts per female were 23-fold for females spawning in 1996 and 14-fold in 1997, so fecundity alone cannot explain the magnitude of the difference.

In Washington State, steelhead management policy has included the temporal segregation of hatchery and wild fish through an advancement of the spawn timing of hatchery fish. This temporal separation was originally achieved with the Chambers Creek stock, which was later taken to many hatcheries throughout the state. Such early spawning, leading to early emergence of fry, lengthens the growing period and enables the juveniles to achieve smolt transformation after 1 year, rather than 2 years as is typical of wild populations. The strategy of early spawning may work well for hatchery fish returning to hatcheries to spawn, but it may reduce their fitness under natural conditions. Forks Creek is subject to floods and scour during the early months of the year, and this may explain why few wild steelhead spawn there before March (Mackey et al. 2001). Hatchery steelhead return to Forks Creek mainly in December and January, at the time of coldest temperatures and highest discharge, which might lead to gravel scour, fine sediment transport, and embryo mortality. Cederholm[1] hypothesized that in western Washington, steelhead seldom spawn before February in order to avoid high flows that may decrease their reproductive success. In Forks Creek, the wild fish follow this strategy, and the difference in spawn timing may be one reason why wild steelhead produced many more smolts than hatchery steelhead.

If the progeny of hatchery females survived the incubation period, they would emerge much earlier than those of wild fish (estimated peak dates of 21 April as opposed to 16 June, Mackey et al. 2001). If space and food are limited, there should be an advantage for the early (hatchery) fish (Brännäs 1995, Einum & Fleming 2000). In general, the density of steelhead (and their primary interspecific competitors, coho salmon and cutthroat trout) is low in Forks Creek, as indicated by sampling of juveniles in the creek and counts of smolts

leaving the creek (Quinn & McLean, unpubl. data). Thus early emergence of hatchery steelhead may not provide a substantial advantage in acquiring territories, and cold water may reduce the size advantage associated with early emergence. Unfortunately, our data do not allow us to separate patterns of mortality during the incubation stage from those in the river.

In addition to differences related to egg production and the timing of breeding and emergence, genetic differences between wild and hatchery adults or juveniles resulting from hatchery propagation may have contributed to the differential reproductive success. The hatchery fish are originally from a distant location and have undergone generations of selection for success in hatchery environments. Evidence indicates that hatchery steelhead derived from a wild population may differ from wild fish in predator avoidance (Berejikian 1995) and agonistic behaviour (Berejikian et al. 1996) of juveniles after several generations. Studies have also indicated that the reproductive behaviour of hatchery adults differs from that of wild conspecifics, and this too may have contributed to the lower productivity of hatchery fish (Jonsson et al. 1991, Fleming et al. 1996). In contrast, the wild population should be adapted for local in-stream conditions that affect fitness (e.g. redd site selection, nest preparation, etc.) and has not experienced artificial or domestication selection.

Which factor (fecundity, timing of reproduction, juvenile or adult behaviour) had the most influence on the differential reproductive success of these two groups? Population-level comparisons between groups such as these that differ in many characteristics make it difficult to determine the most important causes of unequal production. Investigation into the reproductive success of individual adults (e.g. wild and hatchery fish with the same timing and size) will be needed to disentangle the interactions among these factors.

Hybridization between hatchery and wild steelhead is perhaps the most critical issue facing the wild population in Forks Creek. Reproductive success through the smolt stage of the hatchery fish is so much lower than that of the wild fish that hybridization (if it commonly occurs and if the productivity of hybrids is intermediate between the pure forms) has the potential to extirpate the wild population. Unique locally adapted gene complexes may be lost, and a potentially severe reduction in abundance might result. If the reproductive rate does not meet replacement at the adult stage, the population will decline. The number of smolts produced by wild females was comparatively low, suggesting that the population is not very productive and hence vulnerable to a reduction in productivity.

When hatchery fish outnumber wild fish on the spawning grounds, which was the case in the two years of our study, the two gene pools might mix despite differences in average timing (Mackey et al. 2001). Repeated releases of hatchery fish over many years (the pattern that has prevailed in most situations where hatchery and wild salmon are produced in the same river), will exaggerate this problem. In Forks Creek, hatchery steelhead are no longer deliberately released upstream of the hatchery, and this may prevent the negative effects of repeated releases. This situation is unique in that we have sampled the first generation of hatchery releases, and we will be able to monitor what happens in the future.

Acknowledgements

We thank the many people involved in sample collection, especially the Forks Creek Hatchery staff and Greg Mackey. Long Live the Kings assisted with the trapping operation, and we particularly thank Brodie Smith and Larry Sienko for help in that regard. We thank two anonymous reviewers for valuable comments on the manuscript. This work was made possible by financial support from the Weyerhaeuser Company Foundation, the National Science foundation (Grant DEB-9903914) and the Hatchery Science Reform Group in Washington State.

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