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Reproductive success of captive-bred steelhead trout in the wild: Evaluation of three hatchery programs in the Hood River

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Abstract

Population supplementation programs that release captive-bred offspring into the wild to boost the size of endangered populations are now in place for many species. The use of hatcheries for supplementing salmonid populations has become particularly popular. However, whether such programs actually increase the size of wild populations remains unclear, and predictions that supplementation fish drag down the fitness of wild fish remains untested. To address these issues, we performed DNA-based parentage analyses on almost complete samples of anadromous steelhead (*Oncorhynchus mykiss*) in the Hood River in Oregon (U.S.A.). We found that steelhead from a supplementation hatchery (reared in a supplementation hatchery and then allowed to spawn naturally in the wild) had reproductive success indistinguishable from that of wild fish. In contrast, fish from a traditional hatchery (nonlocal origin, multiple generations in hatcheries) breeding in the same river showed significantly lower fitness than wild fish. Additionally, crosses between wild fish and supplementation fish were as reproductively successful as those between wild parents. Thus, there was no sign that supplementation fish drag down the fitness of wild fish by breeding with them for a single generation. On the other hand, crosses between hatchery fish of either type (traditional or supplementation) were less fit than expected, suggesting a possible interaction effect. These are the first data to show that a supplementation program using native brood stock can provide a single-generation boost to the size of a natural steelhead population without obvious short-term fitness costs. The long-term effects of population supplementation remain untested.

Introduction

Captive breeding and population supplementation have been applied to a variety of endangered animals from fish to mammals (Cuenco et al. 1993; Olney et al. 1994). Pacific salmon and steelhead (*Oncorhynchus* ssp.) are one of them, and many hatchery programs are dedicated to enhancing population sizes of these species. However, whether hatcheries should be used to supplement natural salmon populations is extremely controversial (e.g., National Research Council 1996; Waples 1999; Ruckelshaus et al. 2002). In a typical supplementation hatchery program, wild-born brood stock (parents of hatchery fish) are collected from a local river each generation, and large numbers of their offspring are released into the home stream just before they migrate to sea. Returning hatchery-born adults should then breed in the wild and boost the size of the natural population.

Despite the popularity of such programs, whether they actually work (boost the size of the wild population in subsequent generations) has never been tested adequately (Waples et al. 2006). Furthermore, there are reasons to worry that supplementation will drag down the fitness of natural populations. A large body of data suggest that salmon from traditional hatcheries (multiple generations in the hatchery, nonlocal origins) can decrease the viability of natural populations (Fleming & Peterson 2001; McGinnity et al. 2003; Myers et al. 2004; Berejikian & Ford 2004). Detrimental effects can include decreased effective population size (Wang & Ryman 2001) and increased genetic load owing to mutation accumulation and domestication selection (Lynch & O' Hely 2001; Ford 2002; Heath et al. 2003; Goodman 2005). Supplementation hatcheries, on the other hand, often use local, wild-born fish as brood stock each generation under the assumption that this tactic minimizes negative genetic effects of the hatchery. However, theoretical work shows that domestication selection and relaxed natural selection in the hatchery could have significant fitness consequences for the supplemented population, even if local, wild-born fish are used as brood stock each generation (Lynch & O' Hely 2001; Ford 2002; Goodman 2005). Thus, it is essential to test whether supplementation hatchery fish are as fit as wild fish when breeding in the wild.

To examine these issues, we estimated relative reproductive success (production of returning adult offspring) of anadromous steelhead (*Oncorhynchus mykiss*) in the Hood

River in Oregon (U.S.A.). Steelhead are an alternative life-history form of rainbow trout, which stay in freshwater throughout the life cycle. In this river system, a supplementation hatchery program for steelhead started in 1991, and since then almost every returning (pre-spawning) steelhead has had scale samples taken at a dam fish trap (over 35,000 fish). Using DNA samples from the scales, we performed microsatellite fingerprinting and parentage analyses to estimate the reproductive success of fish from the supplementation hatchery program (H_{supp}). The relative reproductive success of H_{supp} and wild fish in each breeding year was compared to that of fish from traditional hatchery programs (H_{trad}), which had been operated in this river before the supplementation program started. Our results provide the first evidence that a supplementation program using native brood stock can efficiently boost the natural population size without obvious short-term fitness costs.

Methods

Study populations

The Hood River basin is a sub-basin of the Columbia River in the Northwest United States. The river supports two populations of wild steelhead, a winter run and a summer run (see Kostow 2004 for details). Both runs breed in the spring, but in different forks of the river, and there is little or no hybridization between them. Interbreeding between steelhead and rainbow trout, on the other hand, is evident in another river system (Zimmerman & Reeves 2000), and is very likely in the Hood River (see Results).

We examined three different breeding years of fish populations from a supplementation program (H_{supp} populations Wi95, Wi96, Wi97) and from traditional hatchery programs (H_{trad} populations Wi91, Su95, Su96, Table 1). The Wi and Su stand for winter run and summer run, respectively, and the number that follows is the run year of parents (e.g., Wi91: winter-run steelhead returned in 1991-1992). The evaluation of the summer-run H_{supp} cannot be performed yet because its parental populations have returned only since 2001. An appreciable number of offspring reproduced by summer-run H_{supp} is expected to return after 2006.

Hatchery programs in the Hood River

The Hood River has been stocked for many years with winter-run and summer-run fish from traditional hatchery programs by the Oregon Department of Fish and Wildlife (ODFW). The brood stock of the traditional hatchery program in the Hood River for winter run is called Big Creek stock, whereas the summer-run brood stock is called Skamania stock. The Big Creek stock is a domesticated, out-of-basin, multigeneration hatchery stock founded in 1941 from collections in the lower Columbia River. The stock is maintained at an ODFW hatchery on Big Creek, a tributary to the Columbia River located 208 km downstream from the Hood River. The Skamania steelhead brood stock was founded in the 1950s from adults collected in Columbia River tributaries from Washington State, primarily from the Washougal River located at Columbia River kilometer 195. The brood stock program was maintained at the South Santiam Hatchery on the South Santiam River, a tributary of the Willamette River that enters the Columbia River at kilometer 170. It is noteworthy that unintentional selection for fecundity of this stock is reported by Crawford (1979). The winter H_{trad} stock was phased out of the Hood River in the early 1990s, while the summer H_{trad} stock was phased out in the late 1990s.

The supplementation program of steelhead in this river started in 1991 for the winter-run populations, and in 1997 for the summer-run populations. Substantial numbers of fish from these programs have been returning since 1995 (winter run) and 2001 (summer run). Details of this program are described in Olsen (2003). In summary, brood stock are collected from the Hood River (at the dam trap) each generation. They are spawned at the Parkdale Hatchery on the Middle Fork of the Hood River and released in the same year. Hatchery fish are reared to 1-year-old smolts. The smolts are acclimated in the Parkdale Hatchery and/or released directly into the Hood River. The number of returned adults from this program is counted at the dam trap, and only equal numbers of hatchery and wild spawners are allowed to pass upstream so that a predominance of hatchery spawners in the spawning grounds (and hence in the gene pool) is avoided.

Sample collection

Since 1991 almost every adult steelhead returning to spawn in the Hood River has been catalogued, measured, and had scale and fin-snip samples taken (for DNA analysis) at the Powerdale Dam fish trap by staff of ODFW (Table 1). This dam is located at the mouth of the Hood River (4.0 river miles). All fish approaching the dam are shunted into a trap and lifted into a building built specifically for the purpose of handling these fish. Steelhead spawn only above the dam, which is a complete barrier to all salmonids. After being measured and sampled, each fish was either recycled downstream (e.g., extra hatchery fish), taken as brood stock, or put above the dam to continue on to the spawning grounds. The size, run timing, age, gender, and disposition of every fish were recorded. The year in which each returning adult was born was determined via scale reading. Although there is a period when both runs return at the same time in a year (see Kostow 2004), they are usually quite distinguishable because they overlaps at the very end of winter-run (sexually matured) and at the very beginning of summer-run (premature). Our results from parentage analyses suggested that errors in distinguishing runs and sex are relatively minor and ignorable in our data (data not shown).

Microsatellite fingerprinting

Genotypes at 8 microsatellite loci (Omy1001, Omy1011, Omy1191, Omy77, One108, One2, Ssa407, and Str2, see Table 2) were identified for these samples. We followed a standard Chelex protocol for DNA extraction and amplification (see Nelson et al. 1998), with minor modifications (50-55 °C of annealing temperature). The genotype scoring was done on an ABI 3100 capillary electrophoresis system (Applied Biosystems, California). Ambiguous scorings for one mismatch between parental and offspring samples were checked twice and either corrected or reanalyzed to minimize scoring errors.

Parentage analysis

We used an exclusion method to make parentage assignments (see Araki & Blouin 2005 for details). Putative parent-offspring pairs sharing at least 6 loci (some fish had missing data) and having no mismatching loci were assigned to parent-offspring pairs using the CERVUS program (Marshall et al. 1998). Because our preliminary analyses suggested some null alleles at Omy77 and Str2, homozygotes for Omy77 and Str2 were treated as heterozygotes for null alleles for conservative conclusions. For the Wi91, Wi95, Wi96, Wi97, Su95, and Su96, respectively, we used 999, 443, 571, 396, 643, and 1436 parental samples and 264, 1227, 976, 860, 198, and 569 unclipped offspring samples. For example, 264 of the unmarked adults that returned to the Hood River in the mid-1990s were identified, via scale reading, as having been born in 1992 and so were identified as the potential offspring of the sample of 999 adults that went upstream during the 1991-1992 run year. Total exclusionary powers were >0.9996 and >0.999991 for the first and the second parent, respectively.

Relative reproductive success and missing parents

For an unbiased estimate of the relative reproductive success (*RRS*) of hatchery fish to wild fish, we used

$$RRS = \frac{\hat{W}_{hat} - \left(\frac{N_{offspring} - N_{assigned}}{N_{parent}}\right)\left(\frac{\hat{b}}{1-\hat{b}}\right)}{\hat{W}_{wild} - \left(\frac{N_{offspring} - N_{assigned}}{N_{parent}}\right)\left(\frac{\hat{b}}{1-\hat{b}}\right)}$$

(Eqn. 14 in Araki & Blouin, 2005), where $\hat{W}_{hat}$ and $\hat{W}_{wild}$ are direct estimates of the absolute fitness (the ratio of a number of offspring assigned to a number of returned parents in each category) for hatchery-born and wild-born parents, $N_{offspring}$, $N_{assigned}$, and N_{parent} are the numbers of returned offspring ($N_{offspring}$), assigned offspring ($N_{offspring}$), and returned parents (N_{parent}), and $\hat{b}$ is the Type-B error rate, which is the rate at which non-parents are incorrectly assigned to offspring (see next section for details).

The proportion of offspring whose parents were sampled ($P_{sampled}$) was estimated using

$$P_{sampled} = \frac{1}{(1-\hat{a})(1-\hat{b})}\left(\frac{N_{assigned}}{N_{offspring}} - \hat{b}\right),$$

where $\hat{a}$ is the Type-A error rate, which is for failing to assign a true parent when that parent is in the sample (see next section). This equation can be obtained straightforwardly from Eqs. 15 in Araki and Blouin (2005).

If parents were not found in the putative run year that produced an offspring (estimated via scale aging), we searched the run year before and the year after. The number of matches found in plus or minus years was no more than the number of matches expected by chance alone given our empirical estimates of assignment error rates (i.e., result of Type-B error), so misread scales do not explain the large number of offspring that are missing parents.

We used a one-tailed permutation test for the hypothesis that hatchery fish have lower fitness than wild fish. In this test, numbers of offspring assigned to each parent are permutated 100,000 times (without replacement) and the probability of obtaining a value equal to or larger than the observed $\left(\hat{W}_{wild} - \hat{W}_{hat}\right)$ is evaluated (see Araki and Blouin 2005 for details). We had two reasons for using a one-tailed test. First, we had a clear, *a priori*, hypothesis that hatchery fish might have fitness that is lower than wild fish. Second, we wanted maximal power to detect lower fitness of hatchery fish because the biological consequences of failing to detect a real difference are far worse than of falsely concluding a difference exists. We calculated *p* values without adjustment for multiple comparisons because, again, we wanted to err on the side of detecting lower fitness of hatchery fish. Our conclusions did not change when we adjusted each *p* value for the number of independent tests of each hypothesis. For each type of hatchery fish, we also calculated Fisher's combined probability (Sokal & Rohlf 1995) from multiple independent tests of the hypothesis that hatchery fish have lower fitness than wild fish, where each run year is considered an independent test.

We evaluated the power of our tests by calculating the minimum effect size $\left(\hat{W}_{wild} - \hat{W}_{hat}\right)$ we could have detected with 80% and with 95% probability (Table 3, where effect size is presented as relative reproductive success, rather than as the minimum difference). The minimum difference was obtained from distributions of $\left(\hat{W}_{wild} - \hat{W}_{hat}\right)$ in the permutation tests.

Assignment error rate estimation

To estimate rates of type-A and -B errors we used an empirical method (Araki & Blouin 2005) based on known parent-offspring pairs of brood stock and their offspring from run years Wi93 and Wi94. In these samples, we had 79 and 43 brood stock (100% of the brood stock) and 280 and 176 offspring samples from these brood stock for Wi93 and Wi94, respectively. Estimated error rates were 15.6% (Type-A) and 1.75% (Type-B) for assigning male parents, and 5.70% (Type-A) and 1.97% (Type-B) for assigning female parents.

Correction for angling above the dam

Angling for hatchery steelhead trout was allowed above the dam in a limited area during 1993-1998. If hatchery fish were selectively taken before having the opportunity to spawn, then we would underestimate the fitness of hatchery fish that had a chance of spawning in the Hood River during those years. To correct for any angling effect on our estimates of relative fitness we used the ODFW upper-bound estimates of the harvest rate on hatchery fish in the Hood River of 5.0%, 20%, and 20% for Wi95, Wi96, and Wi97 and of 25% and 25% for the Su95 and Su96 run years, respectively (E.O., unpublished data). We assumed all harvest pressure fell on hatchery fish. Although angling may also cause higher mortalities in remained fish (e.g., by hooking), it has only a minor effect on our results because we calculated the ratio in which this effect is largely cancelled out (see equation above). These are liberal estimates of the harvest rate and so provide a likely upper bound on the relative fitness of hatchery fish, whereas estimates without correcting for angling provide a lower bound.

Results

We obtained genotype information for eight microsatellite loci in 4487 parental and 4094 offspring samples for total of six independent data sets (H_{trad}: Wi91, Su95, and Su96, H_{supp}: Wi95, Wi96, and Wi97). They represent 98.4% of all parents passed above the dam in these years and 96.7% of all offspring returned (Tables 1 & 2). These samples were subjected to parentage analyses, and we unambiguously assigned the paternity of 1630 offspring samples and the maternity of 2581 samples.

Although unbiased estimates of the relative reproductive success of the hatchery fish to the wild fish are shown with and without a correction for angling above the dam in Table 3 (see Methods), general conclusions are unchanged by this correction. Both of the H_{trad} stocks had significantly lower reproductive success than their natural-origin counterparts. The winter H_{trad} fish had 6-11% the fitness of wild fish in 1991. The relative reproductive success of summer H_{trad} was 31-45% that of wild fish in 1995 and 30-44% that of wild fish in 1996. These findings are consistent with many other studies that show that fish from traditional hatcheries have low fitness in the natural environment (Leider et al. 1990; McLean et al. 2003; McGinnity et al. 2003; Berejikian & Ford 2004; Salmon Recovery Science Review Panel 2004). On the other hand, estimates of the relative fitness of the winter-run H_{supp} were statistically indistinguishable from those of wild fish, with point estimates of 67-81% (females) that of wild fish in 1995, 93-133% that of wild fish in 1996, and 85-156% (females) that of wild fish in 1997 (Table 3).

Why the H_{supp} fish appeared to do slightly worse in 1995 than in 1996 or 1997 is not clear, although it may have something to do with 1995 being the first year in which H_{supp} returned to breed in appreciable number. In that first year the fish were almost all 3-year olds, rather than a mix of 3 and 4 -year olds as in subsequent years (owing to the overlap in generations). On the other hand, there were no obvious phenotypic differences between the 1995 versus the 1996 and 1997 fish, so at this point we can only speculate.

One caveat to the interpretation of these results is that even though we sampled almost 100% of all anadromous adults, we estimated that, on average, only 35% of offspring had both parents in the data set, 11% had a father only, and 31% had a mother only (Table 4). This is not caused by a technical error, because potential errors in the parentage assignment were taken into consideration (Araki & Blouin 2005). These results suggest that resident fish (nonanadromous) or precocious parr (presmolts) obtain a substantial number of opportunity for mating that result in anadromous offspring. The higher proportion of missing fathers than missing mothers is consistent with a hypothetical interaction between anadromous steelhead females and ‘sneaker’ resident males (Hendry et al. 2004). A high rate of interbreeding between different life-history forms in *O. mykiss* is also suggested in other river systems (Zimmerman & Reeves 2000), and it may be quite common in this species. Although interbreeding can have important demographic and evolutionary consequences at the whole-population level, we can only make conclusions about the anadromous component of reproduction in this study. Here we estimated the production of anadromous returning adults by anadromous adults of each type of fish when those fish breed in the wild. As long as anadromous hatchery and wild fish do not differ in the proportion of their offspring that are anadromous, our conclusions regarding the relative fitness of these two types of anadromous fish should be correct. The questions of whether hatchery fish tend to residualize (fail to outmigrate) in this system and whether any residents of hatchery-origin would have negative or positive ecological or genetic effects on the population are beyond the scope of this study.

Another important question is whether H_{supp} fish impose a genetic load on the wild fish by mating with them. To test for evidence of such an effect we considered only the subset of offspring for which both parents were identified, and we assessed the fitness of different types of crosses. We compared the number of adult offspring produced per pair for wild females that crossed with either wild males or hatchery males (Table 5). The hypothesis being tested was that crosses involving hatchery males result in fewer offspring. We were most interested in paternal effects because maternal effects are more likely to contain a substantial nongenetic component from the different juvenile environments (Lynch & Walsh 1998), but we also analyzed data from the reciprocal crosses. Because there is no way to detect pairs that left no offspring, our analysis was confined to the subset of pairs that left one or more surviving offspring. By not counting the zero class we probably underestimated any fitness difference between mating types, making the test very conservative. Also, confining our analysis to the subset of offspring for which both parents were identified resulted in low sample sizes for some comparisons (Table 4). Nevertheless, the results are still informative and consistent with conclusions from the single-sex analysis above. Although there were no statistically significant effects of male type, point estimates of relative fitness were all < 1 for H_{trad} males (0.72-0.90), and were all > 1 for H_{supp} males (1.04-1.45; Table 5). Results for females were not significant and revealed no obvious trend. Most importantly, there was no evidence that mating with supplementation hatchery fish reduces the fitness of wild fish.

We did the same exercise for the number of adult offspring produced per pair for hatchery fish (in contrast to wild fish above) that crossed with either wild or hatchery fish, in order to see whether a difference between hatchery and wild fish depends on the type of fish with which they mate. The effect of fish type was stronger when mating with hatchery fish (Table 5). These results raise the possibility that there is an interaction effect such that [hatchery x hatchery] mating, including those between H_{supp} fish, are less fit than expected.

We estimated the number of returning adults produced per wild female taken into the hatchery and the number produced per wild female left in the river in each of winter run years 1992 to 1994. We examined those years because there were few or no hatchery fish on the winter-run spawning grounds, so we could estimate per-capita production by just wild females. From ODFW records we knew the number of females taken from the wild to be used as hatchery brood stock in each year was 28, 45, and 20 females in Wi92, Wi93, and Wi94, respectively. Not all females were successfully spawned in the hatchery, but we counted them all for conservative conclusions. We also knew the number of hatchery-born females that were from these brood stocks and that returned in subsequent years (152, 331, and 200 hatchery-born daughters returned from brood years 1993, 1994, and 1995). Thus, the per-capita productions of daughters by females taken for brood stock in these years were 5.4 (152/28), 7.4 (331/45), and 10.0 (200/20), respectively.

During those same run years 220, 212, and 83 wild females were passed above the dam. If one assumes that the 183, 136, and 188 unmarked, adult females that returned from those three brood years are all the daughters of anadromous wild females, then the per-capita production of daughters by wild fish is estimated as 0.83 (183/220), 0.64 (136/212) and 2.27 (188/83), respectively. These values would probably be overestimated because of the following reason: Our parentage analyses showed that we can usually find the mothers of only less than 70% of wild-born winter-run offspring (Table 4), and if one assumes that only 70% of returning offspring can be attributed to the anadromous wild females, their per-capita production of daughters would fall to 0.58, 0.45, and 1.59.

If one takes a conservative estimate of the fitness of H_{supp} daughters as 85% that of wild-born daughters (Table 3) and if all daughters had been passed upstream, then wild females taken into the hatchery would produce 7.8, 14.0, and 5.3 times as many wild-born grand-daughters as females left in the wild (e.g., [(5.4)(0.85)]/0.58 = 7.8 for Wi92, and so on). If one ignores possible contribution by resident fish and attributes all the unmarked returning daughters to anadromous females, then those ratios are 5.5, 9.8, and 3.7. So even by the most conservative estimates, females taken into the hatchery should have resulted in at least 3.7 to 9.8 times as many wild-born grand-daughters as females left in the wild.

Discussion

Wild and hatchery fish experience very different freshwater environments. Thus any fitness differences we observed could have a genetic or environmental origin, and a lack of difference could conceivably include environmental deviations that are the opposite of genetic effects. In the single-sex analysis we observed much lower relative fitness in H_{trad} than H_{supp} fish. Because these two types of fish experienced similar hatchery environments, it seems reasonable to conclude that most of that difference is indeed genetic. Phenotypic similarities of H_{supp} to H_{trad}, rather than to wild fish in the Hood River, support this conclusion (Kostow 2004). In the mated-pair analysis the fact that effects of fish type were stronger when the constant parent was a hatchery fish also suggests a genetic effect.

There was a large range in the point estimates of relative fitness of H_{supp} fish (e.g. 0.67 to 1.26 without correction for angling), even though almost all estimates were not significantly different from 1.0. Therefore, power to detect a difference is an important issue because even a 10% reduction in fitness of H_{supp} fish relative to wild fish could have important consequences for the natural population if supplementation is continued over the long term (Lynch & O' Hely 2001). In our results of the permutation tests, statistical power was strongly affected by the number of offspring assigned (Table 3). Here we could have detected a significant difference between H_{supp} and wild fish with reasonable power (80%) if the true hatchery vs. wild RRS was less than around 0.85 (range 0.78 to 0.91, depending on year and parental gender; Table 3). Thus, if the true reproductive success of supplementation fish was up to 10-15% less than that of wild fish, we could easily have missed detecting such a difference in any given year. On the other hand, most of the point estimates were actually much closer to, or even greater than, 1.0. Furthermore, we have three years of data, and combining probabilities across these three data sets did not produce a significant result. Thus, it appears that any difference between H_{supp} fish and wild fish really is slight.

So was the Hood River supplementation hatchery program working? The answer depends on the goal of a supplementation program. In general, two goals can be defined for a supplementation program. A short-term goal is a single-generation boost to the size of a natural population, and a long-term goal is to establish a self-sustainable natural population. For the short-term goal, a key question is whether taking a wild fish into the hatchery resulted in more wild-born adults two generations later than if that fish had been allowed to spawn in the wild. Our conservative estimate of relative fitness for H_{supp} demonstrated that each wild female taken for brood stock should have generated approximately 4 to 10 times as many wild-born grand-daughters as a female allowed to spawn naturally. Of course this result would be obtained only if all the returning H_{supp} females had been allowed to pass upstream, which was not the case in the Hood River program (only equal numbers of hatchery and wild spawners were allowed upstream). Also, an assumption of a supplementation program is that the population is below carrying capacity. If that is not true, then no amount of adding extra breeders will help. Nevertheless, our data suggest that, all else being equal, the supplementation hatchery program in the Hood River should have increased the number of wild-born adults two generations later. Whether these results can be generalized to other supplementation programs remains to be studied.

To achieve the long-term goal, there are many other issues to consider rather than just the production of adults in a single generation (e.g., effective size, Wang & Ryman 2001; ecological issues, Weber & Fausch 2003). Most importantly, one must decide how long the supplementation program should continue. Many studies demonstrate that traditional hatcheries are incapable of maintaining self-sustainable natural populations (reviewed in Einum & Fleming 2003) and the cumulative fitness effects of selection in a supplementation hatchery should become important if continued for more than one generation (Lynch & O' Hely 2001; Ford 2002; Goodman 2005). Indeed, a recent meta-analysis suggests that hatchery fish initially lose fitness relative to wild fish at a rate in excess of 20%/generation for each generation the stock is run through a hatchery (Salmon Recovery Science Review Panel 2004). Our observation that H_{supp} x H_{supp} crosses produced fewer offspring than expected should also give one pause. Therefore, supplementation hatcheries should probably not be relied on as a permanent solution to dwindling natural populations (Salmon Recovery Science Review Panel 2004; Myers et al. 2004; Goodman 2005). But for the simple question of whether a supplementation program can give a single-generation demographic boost to a natural population of steelhead trout without obvious short-term genetic consequences, the answer in this case appears to be yes.

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2162.

Table 1. Number of parental steelhead passed above the Powerdale Dam (at the Hood River) and wild-born offspring returned in the subsequent years

Run year of the parent	Winter run			Summer run		
	No. of parents		No. of offspring	No. of parents		No. of offspring
	Wild-born	Hatchery-born		Wild-born	Hatchery-born	
1991-92	716*	292*	273*	-	-	-
1992-93	408	5	304	537	1,677	87
1993-94	382	2	212	240	1,108	128
1994-95	203	6	298	199	1,652	199
1995-96	276*	185*, †	1,237*	132*	518*	212*
1996-97	242*	283*, †	995*	182*	1,310*	615*
1997-98	226*	199*, †	901*	83	447	488
1998-99	299	220†	620	134	4	>270
1999-00	920	267†	>400	182	0	>211
2000-01	1,013	657†	>73	208	0	>45
2001-02	1,025	684†	>1	491	115†	>2
2002-03	725	413†	-	641	482†	-
2003-04	625	535†	-	241	189†	-
Total	7,060	3,748	5,314	2,871	7,502	2,257

Key to symbols: asterisk (*), number of samples used in this study; dagger (†), number of hatchery-born fish from the supplementation program. Run-year of the parents 1995-96 represents fish returned in 1995 (mostly summer-run) or 1996 (mostly winter-run), and they corresponds to Su95 and Wi95 in the text. The supplementation program started in 1991 for the winter-run and 1997 for the summer-run populations, and reasonable numbers of fish from this program are expected to return in 1995 and 2001, respectively. This data was updated 25 March 2005, and the number of offspring from Wi99 and Su98 or later are still growing.

Table 2. Characterization of microsatellite loci used for parentage analysis of Hood River hatchery and wild steelhead spawning in the 1991, 1995, 1996, 1997 run years.

		Wi91		Wi95		Wi96		Wi97		Su95		Su96	
		(n = 1,272)		(n = 1,681)		(n = 1,555)		(n = 1,256)		(n = 849)		(n = 2,040)	
Locus	Reference	alleles	H_e[a]	alleles	H_e	alleles	H_e	alleles	H_e	alleles	H_e	alleles	H_e
*Omy*1001	Spies et al. 2005	28	0.91	28	0.92	25	0.91	27	0.91	24	0.87	29	0.88
*Omy*1011	Spies et al. 2005	30	0.92	29	0.91	28	0.92	27	0.92	19	0.87	28	0.84
*Omy*77[b]	Morris et al. 1996	20	0.90	20	0.90	21	0.90	21	0.90	17	0.85	23	0.85
*One*108	Olsen et al. 2000	32	0.91	33	0.92	35	0.90	32	0.90	26	0.89	28	0.88
*One*2	Scribner et al. 1996	59	0.95	61	0.94	59	0.95	64	0.96	50	0.92	56	0.89
*Rt*191[c]	Spies et al. 2005	34	0.93	33	0.93	31	0.93	31	0.93	31	0.90	35	0.90
*Ssa*407	Cairney et al. 2000	25	0.91	27	0.90	28	0.91	26	0.91	24	0.90	28	0.88
*Str*2[b]	Estoup et al. 1998	45	0.96	45	0.96	45	0.96	44	0.96	41	0.92	47	0.92
Mean		34.1	0.92	34.5	0.92	34.0	0.92	34.0	0.92	29.0	0.89	34.3	0.88

For definitions of Wi91 – Su96, see the footnote of Table 1.

[a] H_e, expected heterozygosity.

[b] Because null alleles are likely to be present at this locus all homozygous genotypes were recoded as heterozygous possessing the detected allele and the null allele.

[c] Referenced as *Omy1191UW* in Spies et al. (2005).

Table 3. Relative reproductive success (RRS) of hatchery fish relative to wild fish returned in the same run year

Run year	Father				Mother			
	No. of offspring assigned[a]	RRS		Statistical Power[d] 80% / 95%	No. of offspring assigned[a]	RRS		Statistical Power[d] 80% / 95%
		without angling[b]	with angling[c]			without angling[b]	with angling[c]	
H_{trad}								
Wi91	107	0.056**	no angling	0.761 / 0.583	165	0.106**	no angling	0.777 / 0.618
Su95	49	0.308**	0.421*	0.613 / 0.400	78	0.333**	0.450*	0.656 / 0.458
Su96	268	0.296**	0.397**	0.759 / 0.620	352	0.280**	0.442**	0.821 / 0.696
Su95&Su96[e]		0.300**	0.405**			0.296**	0.444**	
H_{supp}								
Wi95	508	0.673*	0.710	0.823 / 0.695	792	0.771	0.805	0.883 / 0.783
Wi96	357	1.05	1.32	0.836 / 0.718	607	0.932	1.17	0.901 / 0.821
Wi97	185	0.846	1.18	0.787 / 0.628	481	1.26	1.56	0.873 / 0.768
Wi95-97[e]		0.865	1.06			0.984	1.18	

For definitions of Wi91 – Su96, see the footnote of Table 1.

[a] Number of offspring assigned to parents of that sex in that run and year (e.g., 49 offspring were assigned to male fish in Su95).

[b] Relative reproductive success of the hatchery fish relative to wild (e.g., hatchery-born male fish of the 1995 summer run produced an average of 0.308 offspring for each offspring produced by wild summer-run males in 1995). No angling harvest was adjusted. These estimates were calculated with the equation for *RRS* in Methods. The p values were calculated for each estimate by one-tailed permutation test of the hypothesis that hatchery fish have lower fitness than wild fish (** = $p < 0.01$, * = $p < 0.05$).

[c] Relative reproductive success of the hatchery fish relative to wild, adjusting angling harvest (see Methods). No angling was allowed above the dam for Wi91.

[d] Minimum effect size (displayed as RRS) detectable with 80% and 95% power. It was calculated from distributions of $\left(\hat{W}_{wild} - \hat{W}_{hat}\right)$ obtained from the permutation tests (not adjusted for angling harvest). For example, for Wi95 H_{supp} comparison using females, we had an 80% chance of detecting a hatchery to wild RRS of 0.883 or less.

[e] Data from multiple run years were averaged over Su95 and 96, and over Wi95-97, respectively, weighted by the number of parents identified in each run year. The p values were calculated based on Fisher's combined probability from multiple independent tests of the same hypothesis (i.e., for each run type, each run year provides an independent test of the hypothesis that hatchery fish have lower fitness than wild fish).

Table 4. Estimated proportion of offspring whose parents were sampled

Run Year	Both parents sampled (%)	Father only sampled (%)	Mother only sampled (%)	Neither parent sampled (%)
Su95	16.8	11.0	23.7	48.5
Su96	31.1	23.6	33.7	11.6
Wi91	42.0	5.7	25.6	26.7
Wi95	44.2	11.7	29.8	14.3
Wi96	38.2	7.5	28.6	25.7
Wi97	23.7	6.3	36.7	33.3
Average	35.2	10.8	30.9	23.1

For definitions of Wi91 – Su96, see the footnote of Table 1. These estimates were calculated with an equation for $P_{sampled}$ in Methods. Average values were weighted by the number of parental pair in each population.

Table 5. Relative reproductive success of the hatchery fish by different crosses ([Hatchery/Wild x Wild] and [Hatchery/Wild x Hatchery])

Run year	No. of parental pairs assigned[a]	No. of offspring assigned[b]	Relative reproductive success[c]	No. of parental pairs assigned[a]	No. of offspring assigned[b]	Relative reproductive success[c]
	[Hatchery/Wild male x Wild female]			[Hatchery/Wild female x Wild male]		
H_{trad}						
Wi91	72	106	0.72	60	100	0.72
Su95	6	11	0.90	6	14	1.08
Su96	30	48	0.85	22	53	0.91
Su95&96[d]			0.86			0.95
H_{supp}						
Wi95	76	296	1.04	46	233	0.87
Wi96	68	160	1.45	62	166	0.95
Wi97	30	59	1.17	47	95	1.12
Wi95-97[d]			1.22			0.98

	[Hatchery/Wild male x Hatchery female]			[Hatchery/Wild female x Hatchery male]		
H_{trad}						
Wi91	1	1	NA	5	7	0.00
Su95	13	19	0.56*	12	16	0.90
Su96	68	97	0.87	59	92	0.94
Su95&96[d]			0.82*			0.93
H_{supp}						
Wi95	34	86	0.63*	42	149	0.53**
Wi96	78	145	1.02	48	139	0.67**
Wi97	36	89	0.90	25	53	0.86
Wi95-97[d]			0.90			0.66**

For definitions of Wi91 – Su96, see the footnote of Table 1.

[a] Number of parental pairs of that type of cross that left at least one offspring returned to the dam.

[b] Number of offspring assigned to pairs of that type of cross.

[c] Relative reproductive success of hatchery fish relative to wild, holding sex of the cross constant (e.g., in the 1995 summer-run, hatchery males crossed to wild females produced 0.90 offspring for each offspring produced by wild males crossed to wild females. These estimates were obtained based on Eq. 14 in Araki & Blouin (2005). The *p* values were calculated by one-tailed randomization test with the null hypothesis that hatchery fish have lower fitness than wild fish. ** = $p < 0.01$, * = $p < 0.05$. Note that adjustments of angling harvest do not affect in this estimate, because this analysis was confined to the subset of pairs that left one or more surviving offspring.

[d] Data from multiple run years were averaged over Su95 and 96, and over Wi95-97, respectively, weighted by the number of parents identified in each run year. The p values were calculated based on Fisher's combined probability from multiple independent tests of the same hypothesis (i.e., for each run type, each run year provides an independent test of the hypothesis that hatchery fish have lower fitness than wild fish).