LETTER

Early male maturity explains a negative correlation in reproductive success between hatchery-spawned salmon and their naturally spawning progeny

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Keywords
Captive propagation; domestication; early maturity; hatchery; parentage; selection; supportive breeding.

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Received
3 April 2012
Accepted
3 Jun 2012

Editor
Marc Mangel

doi: 10.1111/j.1755-263X.2012.00261.x

Abstract

Adaptation of plants or animals to captivity is a risk associated with any captive breeding program that has the intent of returning organisms to the wild. The risk is particularly acute for species that are captively bred and released on a large scale, as is the case for many species of fish. Several studies, particularly in salmonids, have reported rapid adaptation of populations to captivity, but the mechanisms of such adaptations are not always clear. We evaluated a large three-generation pedigree of an artificially supplemented salmon population, and found that the fish with the highest reproductive success in captivity produce early maturing male offspring that have lower than average reproductive success in the wild. In contrast to an earlier study of steelhead trout, we found little evidence that parental origin of the captive spawners influenced the subsequent reproductive success of their naturally spawning progeny.

Introduction

Captive propagation is a commonly used strategy to conserve plants and animals threatened in the wild (Snyder *et al.* 1996; Rakes *et al.* 1999). In some extreme cases, captive propagation is intended to be a long-term strategy for species preservation (Mallinson 1995). In this scenario, adaptation of the species to captivity may be an unavoidable outcome. Captive propagation is also used as a short-term strategy to supplement populations in their natural habitat while threats to viability are addressed (Ryman *et al.* 1995). In this case, adaptation to captivity is likely to be deleterious, because it will cause reduced fitness of the species in its natural habitat (Lynch & O'Hely 2001; Ford 2002; Araki *et al.* 2008; Frankham 2008).

Supplementation is a common strategy for the conservation of salmonid fishes. On the west coast of North America, ~2 billion juvenile salmon are released annually from hatcheries (Naish *et al.* 2008). Many of these releases are for fishery enhancement. However, after the listing of 28 evolutionarily significant units (ESUs; Waples 1991) of Pacific salmon under the Endangered Species Act, many salmon hatchery programs were classified as supplementation programs (Waples & Drake 2004; Naish *et al.* 2008). Supplementation programs capture adult salmon, breed them in captivity, and then release their juvenile offspring near wild spawning grounds. The offspring go to sea and return to spawn as adults in or near the stream in which they were released.

Some supplementation programs have been successful at increasing the abundance of salmon in the natural environment (e.g., Sharma *et al.* 2006), but numerous studies have suggested that supplementation can have deleterious impacts (reviewed by Waples & Drake

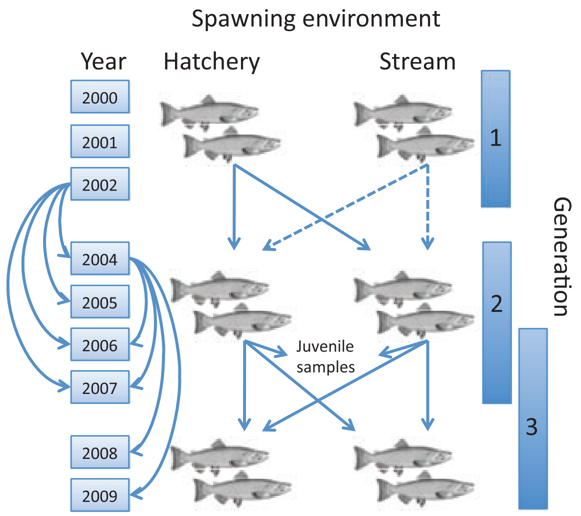

Figure 1 Illustration of the study design. Reproductive success (offspring per spawner) was measured in generations 1 and 2, by counting offspring in generations 2 and 3, respectively. Generation 3 was sampled at both the juvenile and adult life-stages, allowing two separate estimates of reproductive success of fish spawning in generation 2. Reproductive success based on generation 3 adults was calculated for spawners in 2004 and 2005 only. Spawners in the stream in generation 1 and their progeny (dashed lines) were not part of the analysis.

2004). One issue of particular importance to salmon conservation is the loss of reproductive fitness of naturally spawning hatchery salmon, after as little as a single generation of hatchery spawning and rearing (reviewed by Araki *et al.* 2008). Several mechanisms could explain such rapid, heritable losses of reproductive success, including (1) domestication selection, (2) inbreeding depression due to small numbers of hatchery breeders, or (3) epigenetic effects related to the captive environment. Araki *et al.* (2008) concluded that domestication selection was plausible, but that such selection had to be quite strong in order to produce a rapid reduction in fitness.

Recently, Christie *et al.* (2011a) found direct evidence of strong domestication selection in steelhead trout (*Oncorhynchus mykiss*) in the form of a negative correlation between reproductive success in captivity in one generation and the reproductive success of that generation's progeny when they return to breed in the wild. Christie *et al.* (2011a) did not identify a mechanism for this negative correlation. Here, we explore the relationship between the reproductive success of salmon in captivity and the reproductive success of their progeny in the wild, and also find a negative correlation in fitness between generations. We find that the negative correlation is due largely to younger than normal sexual maturity of male fish released from the hatchery.

Methods

Study population—Our study population is the spring-run Chinook salmon (*O. tshawytscha*) that spawn in the Wenatchee River, Washington, and is described in detail by Williamson *et al.* (2010). Wild males spawn at 3–5 years of age, compared to 4–5 years for females. Some males, particularly when reared in the hatchery, mature at 2 years of age after an in-river migration that may (Zimmerman *et al.* 2003) or may not (Beckman & Larsen 2005; Larsen *et al.* 2010) reach salt water. Juveniles typically spend a year in freshwater before going to sea.

Since 1989, supplementation has been used to increase population abundance, and the hatchery program has produced ∼50%–80% of the individuals that spawn naturally in the river each year. Here, a hatchery fish refers to a fish whose parents spawned in the hatchery, and a natural fish refers to a fish whose parents spawned in the stream, regardless of their prior ancestry. In practice, hatchery fish are identified by an adipose fin clip that occurs prior to release. The hatchery fish that spawn in the wild in this population have about half the reproductive success of natural fish (Williamson *et al.* 2010). Here, we focus on understanding fitness variation within hatchery fish.

Sampling and genotyping—From 2004 to 2009, nearly all upstream migrating adult spring Chinook salmon were trapped and sampled at Tumwater Dam (river km 44), a barrier located downstream of the spawning areas. From every fish, we obtained a tissue sample for DNA analysis, and scales for age determination. Each fish was measured (fork length, nearest cm) and weighed (nearest g) and sexed. Samples from the broodstock fish used in 2000–2002 were obtained from the hatchery. Juvenile (age 1) samples were nonlethally collected from 2006 to 2009 in smolt traps located below the major spawning areas. See Williamson *et al.* (2010) for details.

Reproductive success—Our study encompassed three generations (Figure 1, Table S1), and focused on the relationship between reproductive success of captive fish in generation 1 and that of their naturally spawning progeny in generation 2. Generation 1 refers to the broodstock fish (both hatchery and natural) spawned in the hatchery in 2000–2002. Generation 2 are the hatchery fish that returned to spawn in 2004–2007, and are the progeny of generation 1. Most fish in generation 2 spawned in the river, but some were captured and used as broodstock. The fish in generation 3 are the offspring of generation 2, and were used only to estimate the reproductive success of generation 2. Generation 3 fish were sampled as both juveniles and adults, and the estimates of generation 2 reproductive success based on counts of their offspring at these two life-stages were treated separately. There were

473 spawners in generation 1, 10,545 in generation 2, 7,347 generation 3 juveniles, and 13,510 generation 3 adults (2,718 of which were also part of generation 2 due to overlapping generations), nearly all of which were analyzed as part of the study (Table S1).

All individuals were genotyped at 11–15 polymorphic microsatellite loci as described in Williamson *et al.* (2010) and Table S2. The population was highly variable, with an average of 25 alleles per locus and average heterozygosity across loci of >0.75 (Williamson *et al.* 2010; Table S2).

The reproductive success of an individual spawner was defined as the number of offspring assigned to that spawner via parentage analysis. All parentage assignments were conducted using the Bayesian method in the FRANz computer package (Riester *et al.* 2009). The implementation is fast compared to other methods, and we have found that it produces very similar results to exclusion or likelihood methods (e.g, Gerber *et al.* 2003; Kalinowski *et al.* 2007) in our population. Assignments were performed separately for each group of annual spawners and their progeny (Table S3).

The reproductive success of each pair that spawned in captivity in generation 1 was calculated as the number of adult offspring in generation 2 that were assigned as progeny to that pair. Nearly all matings in the hatchery were between single pairs, thus producing full-sib families. The reproductive success of each full-sib family in generation 2 was calculated as the mean of the reproductive success of each family member. To control for different sample sizes of progeny and random variation among years, reproductive success was standardized by dividing the individual values by the annual means. The effect of generation 1 origin on generation 2 reproductive success was tested for male and female spawners separately using a two sample permutation test (″oneway˙test″ function in the ″coin″ library of the R package).

The relationship between fitness in generation 1 and generation 2 was examined graphically similar to Christie *et al.* (2011a). Males and females in generation 2 were analyzed separately. The average reproductive success of each family in generation 2 was plotted against that of their parents. Families of the same size in generation 2 were combined in order to reduce trends in variance across the x-axis. If, for example, there were 60 generation 2 individuals of family size 1, the average reproductive success of these 60 individuals was plotted. Confidence intervals were estimated by resampling the data 10,000 times for each family size and number of families of that size at random with respect to family membership. The axes of these plots are not entirely independent, because generation 1 reproductive success (x-axis) is used as the denominator to calculate the generation 2 family means (y-axis). Unlike normal regression methods, the resampling procedure takes this nonindependence into account by directly incorporating the sample sizes for each family in the same pattern as in the original data.

To complement the analysis of average reproductive success among generation 2 families, we also conducted an analysis evaluating factors influencing the fitness of individual generation 2 fish. To do this, we used a generalized linear model (GLM; negative binomial distribution with a log link; ″glm.nb″ in the MASS package in R) to evaluate the effects of spawner age, length, and parental (generation 1) reproductive success on individual reproductive success in generation 2.

Results

The number of adult offspring produced by generation 1 fish ranged from 1 to 98 (male offspring) or 1 to 57 (female offspring). For naturally spawning males in generation 2, there was a clear negative relationship between the reproductive success of their parents and their own offspring production (Figure 2). In other words, fish that had high reproductive success in captivity produced male offspring that tended to have low reproductive success in the wild. In contrast, no such relationship was apparent for females in the natural environment, or for either males or females that returned to spawn in the hatchery environment (Figure 2).

For males, the GLM results indicated a significant negative relationship between an individual's reproductive success in the wild and the reproductive success of its parents in captivity (Table 1). For females, the relationship was marginally significant only when reproductive success was measured as adults/spawner. No relationship between generation 2 and generation 1 reproductive success was found for either sex in the captive environment (Table 2). Length had a positive relationship with reproductive success in both environments for both sexes (Table 1, Table 2). For males, mean length and mean age among generation 2 families were highly correlated (Pearson's $r = 0.9959$, $t = 70.7$, $P < 2.2\text{e-}16$; Figure S1).

The origin (hatchery or natural) of broodstock fish in generation 1 had little effect on the reproductive success of their naturally spawning offspring. The only significant effect was a tendency for natural origin female broodstock to produce offspring that themselves produced more smolts when spawning naturally than offspring of hatchery origin broodstock (Table 3). No significant effect was detected when reproductive success was measured as adults per spawner, however, despite similar numbers of progeny sampled.

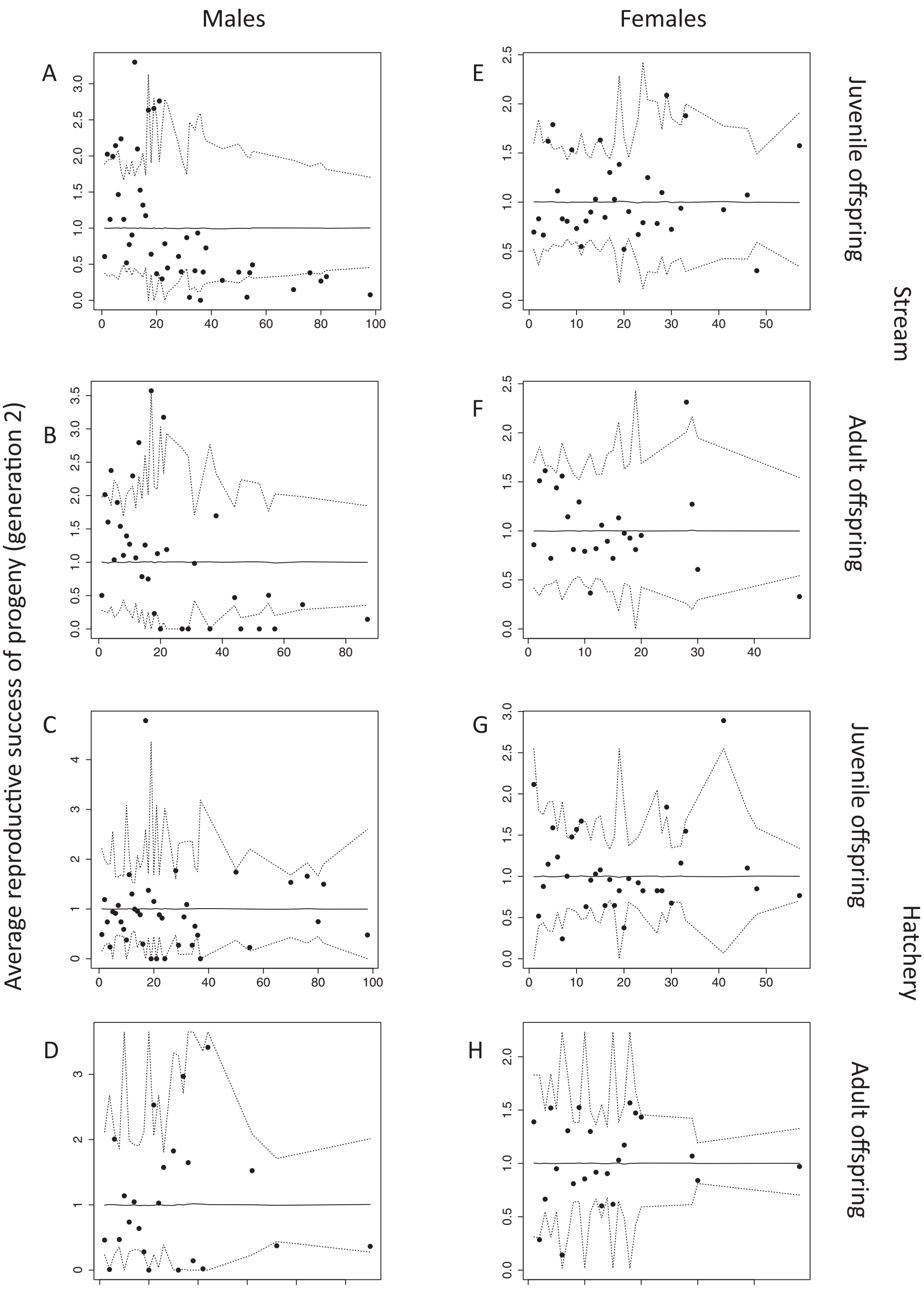

Figure 2 Plot of the relationship between parental reproductive success in captivity in generation 1 (x-axis) and average progeny reproductive success in nature in generation 2 (points, y-axis) for each family size in generation 1 for males (A-D) and females (E-H). Reproductive success was measured by counting smolts (A, E, C, G) or adults (B, F, D, H) in generation 3, either in the natural stream (A, B, E, F) or in the hatchery (C, D, G, H). Solid and dotted lines are the mean and 95% confidence intervals calculated by random resampling of the individual reproductive success data 10,000 times for each family size. The ragged shape of the confidence intervals is due to differences in the number of families of each size class.

Table 1 Estimated coefficients from a generalized linear model (negative binomial, log link) of individual spawner reproductive success (measured as either juvenile progeny or adult progeny) in the natural environment as function of a fish's length and its parents' reproductive success when bred in captivity. Length and parental reproductive success were standardized by subtracting the mean and dividing by the standard deviation

	Fitness measured by juvenile counts		Fitness measured by adult counts	
Coefficient	Male spawners	Female spawners	Male spawners	Female spawners
Intercept	−0.272 (0.069)***	−0.023 (0.048)	−0.257 (0.096)**	0.001 (0.067)
Parental reproductive success	−0.425 (0.085)***	0.000 (0.048)	−0.321 (0.128)*	−0.151 (0.068)*
Length	0.384 (0.083)***	0.185 (0.046)***	0.344 (0.113)**	0.049 (0.067)

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 2 Estimated coefficients from a generalized linear model (negative binomial, log link) of individual spawner reproductive success (measured as either juvenile progeny or adult progeny) in the hatchery environment as function of a fish's length and its parents' reproductive success when bred in captivity. Length and family size were standardized by subtracting the mean and dividing by the standard deviation

	Fitness measured by juvenile counts		Fitness measured by adult counts	
	Male spawners	Female spawners	Male spawners	Female spawners
Intercept	−0.016 (0.070)	−0.024 (0.045)	−0.142 (0.146)	−0.023 (0.056)
Parental reproductive success	0.110 (0.069)	−0.048 (0.047)	0.245 (0.160)	−0.020 (0.056)
Length	0.227 (0.071)**	0.207 (0.046)***	0.717 (0.160)***	0.237 (0.056)***

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 3 Mean (sd, n) numbers of juvenile or adult progeny per parent for male and female spawners in generation 2 descended from either hatchery or natural origin broodstock parents in generation 1

		Effect of broodstock father origin on offspring reproductive success				Effect of broodstock mother origin on offspring reproductive success			
		Male spawners		Female spawners		Male spawners		Female spawners	
Life-stage of progeny	Spawning location	Natural origin	Hatchery origin	Natural origin	Hatchery origin	Natural origin	Hatchery origin	Natural origin	Hatchery origin
Juveniles	Stream	0.99 (1.95, 102)	1.47 (2.52, 141)	0.89 (1.18, 99)	1.00 (1.32, 136)	1.67 (2.43, 76)	1.00 (1.87, 153)*	1.21 (1.57, 76)	0.82 (1.04, 148)*
	Hatchery	0.69 (0.73, 31)	0.94 (0.98, 68)	1.02 (0.70, 32)	1.01 (0.68, 68)	0.75 (0.63, 32)	0.92 (1.03, 58)	1.06 (0.88, 36)	0.99 (0.66, 61)
Adults	Stream	1.12 (2.19, 99)	1.39 (2.47, 135)	0.95 (1.91, 79)	1.14 (1.53, 101)	1.28 (2.51, 72)	1.34 (2.85, 146)	1.24 (1.68, 62)	0.98 (1.36, 109)
	Hatchery	0.94 (1.12, 21)	0.88 (0.94, 39)	1.03 (0.45, 18)	0.98 (0.48, 34)	0.68 (0.80, 23)	1.14 (1.15, 32)	1.08 (0.58, 22)	0.98 (0.46, 28)

*$P < 0.05$.

Discussion

Selective differences between captive and natural environments have been hypothesized as a mechanism leading to low fitness of captively propagated organisms when they are released into the wild (Frankham *et al.* 1986; Ford 2002; Araki *et al.* 2008). The negative relationship we found between the number of offspring produced by individuals bred in captivity and the subsequent reproductive success of these offspring in the wild provides support for this hypothesis. A similar negative intergenerational fitness relationship was recently reported in steelhead trout (Christie *et al.* 2011a), suggesting that such effects may not be unusual in salmonid fishes.

A novel contribution of our study is the finding of a mechanism explaining why broodstock fish with the greatest reproductive success in captivity tended to produce offspring with poor reproductive success in the wild. The broodstock fish in generation 1 that produced the largest numbers of male offspring also tended to produce younger, smaller offspring, which had relatively low reproductive success in the wild (Figure 3). Size and age have been previously demonstrated to be a good

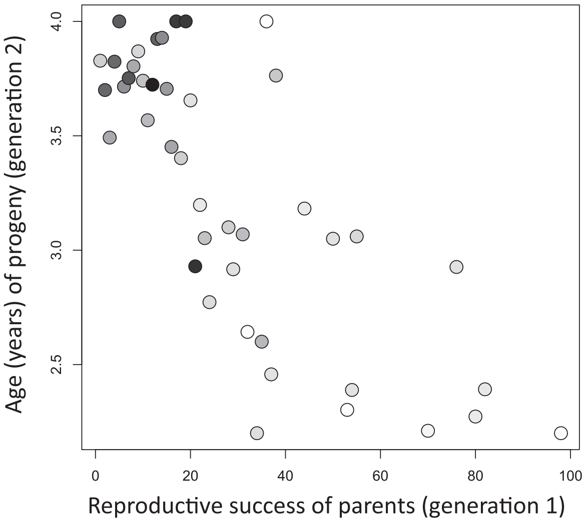

Figure 3 Plot of the relationship between parental broodstock reproductive success in captivity in generation 1 and the average age of their male progeny in generation 2. The shading of the points indicates average relative reproductive success (scaled from 0 to 1) of spawners in generation 2 in the natural stream: darker shades indicate higher relative reproductive success.

predictor of reproductive success in salmon (e.g., Seamons *et al.* 2007; Ford *et al.* 2008; Williamson *et al.* 2010; Berntson *et al.* 2011), and our results continue to support this conclusion (Table 2, Figure S1).

Our results also suggest that early male maturity could be an important mechanism leading to reduced reproductive success of hatchery salmon. Hatchery rearing has been shown to increase rates of early male maturity in Chinook salmon populations (Larsen *et al.* 2004; Larsen *et al.* 2006; Larsen *et al.* 2010). Early male maturity also occurs in wild populations, but is much less common (Larsen *et al.* 2010). If there are genotypes in salmon populations that do not lead to early maturity in the wild but do lead to early maturity in a hatchery setting, supplementation would select against these genotypes due to the poor reproductive success of their offspring in the wild. Age of male maturity has in fact been shown to be heritable in Chinook salmon (Hard *et al.* 1985; Hankin *et al.* 1993; Heath *et al.* 1994; Heath *et al.* 2002; Hard 2004), including our study population (Table S4), suggesting that such a mechanism may in fact be plausible. Increasing the frequency of young males on natural spawning grounds may also change patterns of sexual selection (Berejikian *et al.* 2010), which could be an additional source of genetic change attributable to supplementation. Hatchery practices that reduce the incidence of early male maturity (e.g., Tipping & Byrne 1996; Larson *et al.* 2006) might therefore also have the beneficial effect of decreasing the strength of selection caused by hatchery supplementation.

Offspring number has been shown to be a poor indicator of fitness when offspring vary in quality, in which case grandoffspring may be a better indicator of long-term fitness (Smith & Fretwell 1974; Messina & Fox 2001). In the natural stream, the number of grandoffspring produced by the generation 1 spawners was roughly constant with respect to generation 1 offspring numbers (Figure 4 panels A and B). In other words, the larger families may have low reproductive success on a per capita basis, but the total reproductive output of such families is similar to that of smaller families with higher per capita reproductive success. In contrast, when generation 2 hatchery fish returned to spawn in the same environment as their parents, there was a positive relationship between generation 1 offspring and grandoffspring numbers (Figure 4 panels C,D). Additional work examining tradeoffs between offspring number and offspring quality in the wild component of the population will be needed to further evaluate these patterns.

Greater inbreeding due to a higher probability of mating with a sibling could potentially also cause lower reproductive success in larger families (Christie *et al.* 2011a). There was no indication that inbreeding depression played a role in our results, however, as very few of the inferred matings involved full or half-siblings (Table S5).

The finding of a negative intergeneration fitness correlation primarily in males is a notable difference between our results and a prior study in steelhead trout, which found a negative relationship in both sexes (Christie *et al.* 2011a). A possible explanation for the difference between the two studies is a difference in life-history patterns between Chinook salmon and steelhead. Steelhead exhibit a great deal of life-history diversity, including both anadromous and resident forms, iteroparity and semelparity, and variation in both freshwater and saltwater residence time (Quinn 2005). However, steelhead that go to sea exhibit little variation between the sexes in seawater residence time compared to Chinook salmon (Busby *et al.* 1996). Unlike Chinook salmon, steelhead do not typically have a life-history pattern in which some males spend a year less at sea than the shortest sea-residence time for females (Berejikian *et al.* 2012). Early maturity would therefore not be expected to produce sex-specific results in steelhead if only anadromous fish are studied.

Steelhead males are more likely than females to mature as parr without ever going to sea, however (Seamons *et al.* 2004; Araki *et al.* 2007). Mature parr are difficult to sample comprehensively, but if they could be sampled and counted, it is possible that sex-specific differences in

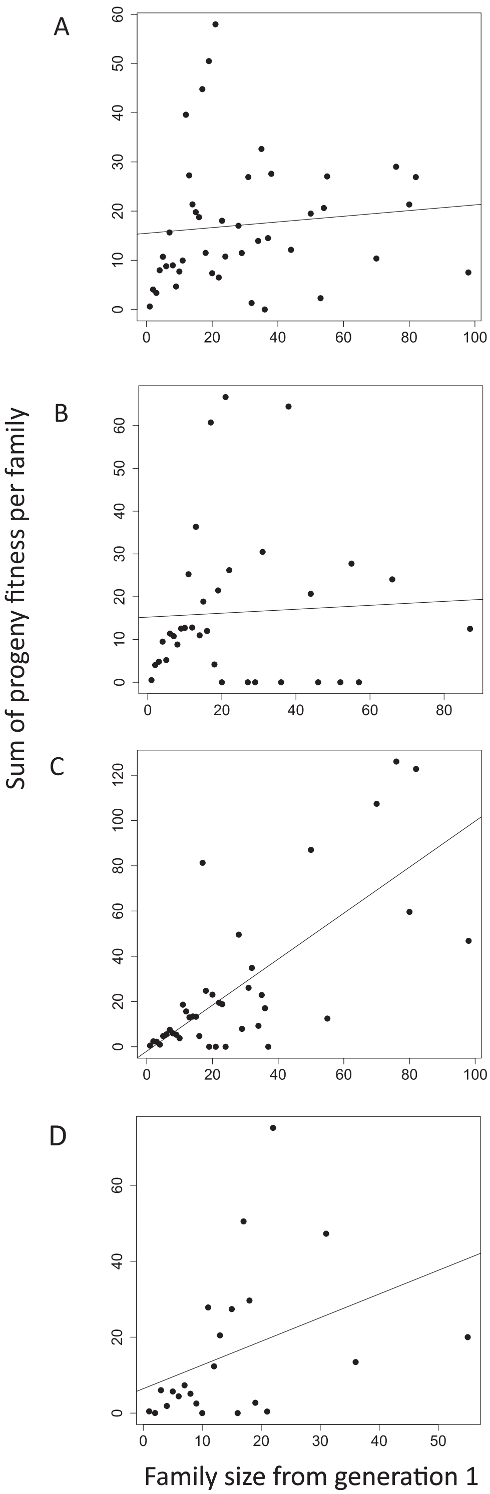

Figure 4 Plot of the relationship between number of offspring produced by spawners in captivity in generation 1 (x-axis) and the average sum of the those offspring's progeny produced in nature in generation 2 (y-axis) for each family size in generation 1 measured by counting smolts (A, C) or adults (B, D) in generation 3 in the natural stream (A, B) or in the hatchery (C, D). *P*-values associated with the linear regression lines in each plot are 0.5, 0.77, <0.001, and 0.06, for the plots A, B, C, and D, respectively.

fitness correlations between generations would also be observed in steelhead. Christie *et al.* (2011b) used grandparentage analysis to infer that hatchery origin mature parr had very low reproductive success, perhaps indicating that early male maturity is also a partial cause of domestication of hatchery steelhead.

We also examined the effect of parental origin (hatchery or wild) on offspring fitness, similar to earlier studies of steelhead (Araki *et al.* 2007) and coho salmon (*O. kisutch*; Theriault *et al.* 2011). In the steelhead study, the fitness of hatchery steelhead with two wild parents was significantly higher than that of hatchery steelhead with one wild and one hatchery parent. In contrast, and similar to the coho salmon study, we found little evidence that the use of wild origin fish as broodstock influenced the reproductive success of their progeny. This observation appears consistent with the observed high rates of exchange between the hatchery and natural environments in our study population (Ford *et al.* 2011).

One argument against domestication selection as a mechanism for genetic change in salmon hatcheries has been the observation that survival rates in captivity often exceed 90% (Waples & Drake 2004). The lack of high mortality has been equated with a lack of selection, or with only ″relaxed″ selection (e.g., Cuenco *et al.* 1993). Reisenbichler *et al.* (2004) demonstrated that differential mortality after release could be substantial, and therefore potentially a strong source of selection. Our results provide another example of how selection on reproductive success after release could potentially lead to rapid genetic change of supplemented populations despite low levels of mortality while in captivity.

Our results support concerns that altered age structure is a major pathway by which captive breeding changes salmon populations (Hankin *et al.* 2009). Our findings also suggest that it is essential to consider environment-by-genotype interactions when evaluating selection in captivity, because the life-history traits expressed by fish in captivity may differ from those expressed by the same genotypes in the wild. Particularly in highly fecund organisms, an altered life-history pattern in a captive population may be important early warning that genetic change is occurring.

Acknowledgments

This work was funded primarily by the Bonneville Power Administration (project 2003–039) and the Chelan County Public Utility District. Mark Christie, Krista Nichols, Barry Berejikian, Donald Larson, Brian Beckman, Jeff Hard, Robin Waples, and two anonymous reviewers provided valuable input on an earlier version of this manuscript.

Supporting Information

Additional Supporting Information may be found in the online version of this article, including Supplementary Methods and References.

Table S1: Summary of samples used in the study. The generations are indicated by colored boxes: green, blue, and pink for generations 1, 2, and 3, respectively. Samples were not collected in 2003, or from the stream prior to 2004. Unboxed samples were collected but not included in this study.

Table S2: Microsatellite loci used for parentage analysis.

Table S3: Summary of parentage assignments for brood years 2000–2007.

Table S4: Estimated broad sense heritability of male maturity age for the 2001 and 2002 hatchery brood years.

Table S5: Summary of generation 2 (2004-2007) matings by origin.

Figure S1: Plots illustrating the relationships between the reproductive success (juvenile offspring/spawner) of naturally spawning male salmon and their length, age and reproductive success of their captively bred parents.

Figure S2: Plots illustrating the relationships between the reproductive success (juvenile offspring/spawner) of naturally spawning female salmon and their length, age, and reproductive success of their captively bred parents.

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