Factors influencing the relative fitness of hatchery and wild spring Chinook salmon (*Oncorhynchus tshawytscha*) in the Wenatchee River, Washington, USA

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Abstract: Understanding the relative fitness of naturally spawning hatchery fish compared with wild fish has become an important issue in the management and conservation of salmonids. We used a DNA-based parentage analysis to measure the relative reproductive success of hatchery- and natural-origin spring Chinook salmon (*Oncorhynchus tshawytscha*) in the natural environment. Size and age had a large influence on male fitness, with larger and older males producing more offspring than smaller or younger individuals. Size had a significant effect on female fitness, but the effect was smaller than on male fitness. For both sexes, run time had a smaller but still significant effect on fitness, with earlier returning fish favored. Spawning location within the river had a significant effect on fitness for both sexes. Hatchery-origin fish produced about half the juvenile progeny per parent when spawning naturally than did natural-origin fish. Hatchery fish tended to be younger and return to lower areas of the watershed than wild fish, which explained some of their lower fitness.

Résumé : Pour la gestion et la conservation des salmonidés, il est devenu important de comprendre la fitness relative des poissons d'élevage qui frayent naturellement par rapport à celle des poissons sauvages. Nous avons utilisé une analyse de filiation basée sur l'ADN pour mesurer le succès reproductif relatif de saumons chinook (*Oncorhynchus tshawytscha*) du printemps provenant d'élevages ou d'origine naturelle dans le milieu naturel. La taille et l'âge ont une forte influence sur la fitness des mâles, car les mâles plus grands et plus âgés produisent plus de descendants que les individus plus petits ou plus jeunes. La taille a un effet significatif sur la fitness des femelles, mais cet effet est moins important que sur la fitness des mâles. Chez les deux sexes, le moment de la montaison a un effet petit mais néanmoins significatif sur la fitness et les poissons qui reviennent tôt sont favorisés. Le site de fraie dans la rivière a un effet significatif sur la fitness des deux sexes. Lorsqu'ils frayent naturellement, les poissons d'élevage produisent environ la moitié de la descendance par parent que ne le font les poissons d'origine naturelle. Par comparaison aux poissons sauvages, les poissons d'élevage ont tendance à être plus jeunes et ils retournent à des sites plus en aval dans le bassin versant, ce qui explique en partie leur fitness réduite.

[Traduit par la Rédaction]

Introduction

Artificial propagation is a commonly used tool to conserve a wide variety of threatened species (Mallinson 1995). Hatchery propagation, in which fish are bred and reared for part of their lives in captivity before being released into the wild, is widely used to supplement wild salmon populations (Naish et al. 2007). For example, over 4 billion anadromous juvenile salmon are released annually into the North Pacific Ocean from hatcheries in North America and Asia (Beamish et al. 1997). Similar hatchery programs and large-scale closed-pen fish farming operations exist for Atlantic salmon (*Salmo salar*) in the North Atlantic Ocean and Baltic Sea. Hatcheries are increasingly intended to contribute to conserving natural salmonid populations, as well as to produce fish to mitigate for lost harvest opportunities (National Research Council 1996). In particular, supplementation projects, in which natural spawning by hatchery fish is intended to augment a natural population's abundance, have become common throughout the Pacific Northwest (Naish et al. 2007) and Europe (Fleming et al. 2000).

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A key biological uncertainty about the effects of hatchery production on natural populations is the degree to which hatchery-produced fish can reproduce in the natural environment (Reisenbichler and McIntyre 1977; Ford 2002; Araki et al. 2008). Evaluating relative reproductive success is therefore critical for determining if the considerable investment society has made in hatchery supplementation is actually contributing to the recovery of salmon populations (Mobrand et al. 2005). Accurately measuring the biological causes of variance in reproductive success is important not only for determining the benefits of conservation hatcheries, but also for evaluating the risks from fish that stray from "production" type hatcheries. The presence of large numbers of hatchery fish on spawning grounds can obscure the status of natural populations because their reproductive success is unknown (McClure et al. 2003) and may lead to reduced short- and long-term natural productivity because of genetic deterioration of the natural population as a result of interbreeding between naturally produced fish and hatchery fish (Lynch and O'Hely 2001; Ford 2002). By quantifying the reproductive success of hatchery fish relative to that of fish from the natural population, the viability of natural populations receiving hatchery fish can be more accurately evaluated.

Even when the relative reproductive success of hatchery-produced fish is quantified, the causes of fitness differences between hatchery and wild fish often remain unknown. Conceptually, there could be a wide variety of reasons why hatchery fish might have lower fitness than wild fish spawning in the same stream (Araki et al. 2008). Even in cases where hatchery fish have low fitness, the conservation implications are likely to vary depending on why the hatchery fish are less fit. For example, if reduced fitness is largely due to environmental effects such as release location, this would probably lead to fewer conservation concerns than if fitness reductions were due to genetic differences in behavior or physiology.

In a recent review, Araki et al. (2008) concluded that hatchery-produced steelhead (i.e., sea-run rainbow trout, *Oncorhynchus mykiss*) generally have lower reproductive success in the natural environment than wild steelhead. In contrast, they noted that few data are available on the relative reproductive success of hatchery and wild Chinook salmon (*Oncorhynchus tshawytscha*) despite the extensive use of hatchery supplementation for this species (Independent Scientific Advisory Board 2003, 2005; Araki et al. 2008). Recently, several papers have reported on studies of hatchery Chinook salmon breeding success in laboratory or semi-natural environments (Fritts et al. 2007; Pearsons et al. 2007; Schroder et al. 2008), but there are no published studies of the relative fitness of this species in the wild.

In this study, we assess the relative reproductive success of naturally spawning hatchery- and natural-origin spring run Chinook salmon in the Wenatchee River, Washington, USA, by employing a genetic pedigree analysis and determine the degree to which differences in reproductive success between hatchery and natural Chinook salmon can be explained by biological characteristics such as run timing, morphology, and spawning location.

Materials and methods

Study population

Our study population consists of the spring run Chinook salmon that spawn in the Wenatchee River, Washington (Fig. 1). The population is listed as "endangered" under the Endangered Species Act (Federal Register 70:37160). Starting in 1989, hatchery supplementation has been used in an attempt to increase population abundance, and in recent years the hatchery program has produced >50% of the individuals in the population that spawn naturally. The hatchery program's focus is primarily on the Chiwawa River, a major tributary of the Wenatchee River. Wild and hatchery-origin broodstock for the supplementation program are collected at a weir in the Chiwawa River, and the offspring of those fish are released back into the Chiwawa River as yearlings. Although juvenile fish are released only in the Chiwawa River, as adults they return to spawn in all of the major spawning areas throughout the watershed (Murdoch et al. 2008).

The population exhibits a "stream-type" life-history pattern (Healey 1991) in which adults return to fresh water in the spring several months prior to spawning, and juveniles migrate to the ocean during the spring 1 year following their emergence from the gravel (Healey 1983). In wild populations of Chinook salmon in the Columbia River, including the Wenatchee River, most anadromous males become sexually mature between ages three to five, and most females become mature at ages four or five (Myers et al. 1998). Another characteristic of stream-type Chinook salmon is that some male fish mature at 1 or 2 years of age without migrating to the sea (Rich 1920; Burck 1967; Mullan et al. 1992), but little is known about the reproductive success of these early maturing males.

Adult and juvenile trapping and sampling

In 2004 and 2005, beginning in early April and ending in early August, essentially all migrating spring Chinook salmon were trapped and sampled (scales, caudal fin clip) at Tumwater Dam, located at river kilometre (rkm) 43.7 on the Wenatchee River (Fig. 1, Table 1). Tumwater Dam is located below all of the major spring Chinook salmon spawning areas in the watershed, so we obtained samples from essentially all of the potential breeders, with the possible exception of those mature male parr that never migrated below Tumwater Dam and a very small number of adults that migrated after the trapping period ended. Biological data were collected from all adult salmon sampled (Table 1). Each fish was identified to gender, scanned for passive integrated transponder (PIT) tags (fish without a PIT tag had one inserted during sampling) and coded wire tags and the presence or absence of the adipose fin (indicating hatchery or wild origin; all hatchery fish released in the Wenatchee watershed have a clipped adipose fin). Fork and post orbital to hypural plate length were measured to the nearest centimetre and weight to the nearest 0.01 kg. Subsequent identification of PIT-tagged carcasses recovered on the spawning grounds permitted the comparison of carcass recovery distributions of individual hatchery- and naturally produced fish. Spawning location was based upon location of carcass recovery and linked back to fish identity at Tumwater Dam

Fig. 1. Map of the study area in Washington, USA. Major spring Chinook salmon spawning tributaries include the Chiwawa River, Nason Creek, White River, and Little Wenatchee River. Parents were sampled at Tumwater Dam, and progeny were sampled at White Trap, Nason Trap, Chiwawa Hatchery, and Lower Wenatchee Trap.

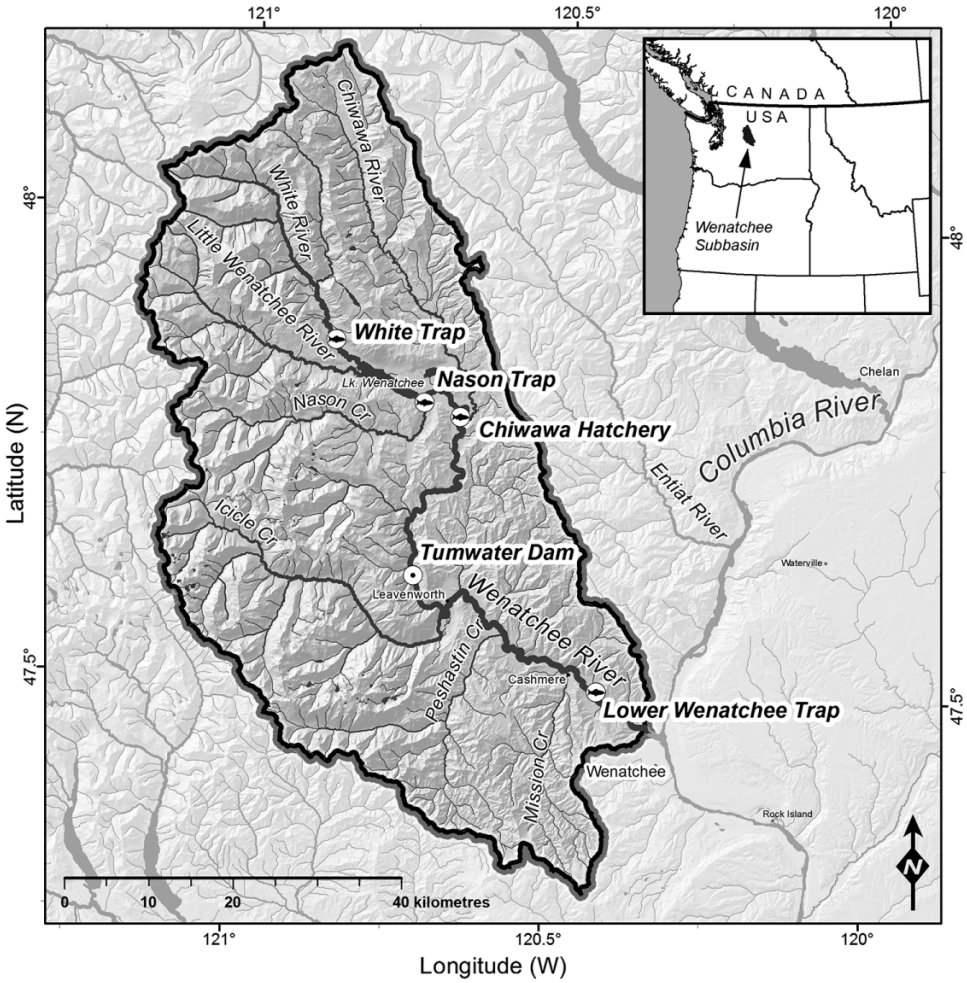


Table 1. Summary of 2004 and 2005 adult and juvenile Chinook salmon samples, stratified by year, origin, and life stage.

	Adults			Yearling juveniles			Subyearling juveniles	
Year	Origin	Males	Females	C	N	LW	C	N
2004	Hatchery	1502	270					
	Wild	437	376	744	203	647	576	447
	Unknown	18	13					
2005	Hatchery	1573	1724					
	Wild	235	238			889		
	Unknown	15	17					

Note: Trap locations are as follows: C, Chiwawa River; N, Nason Creek; LW, Lower Wenatchee River.

by PIT tag information. Spawning ground surveys of all potential spawning habitat were conducted twice a week throughout the entire spawning season (Murdoch et al. 2008). Carcass recovery location of each PIT-tagged fish was recorded using handheld GPS devices and converted to river kilometre using ArcView 9.2 (ESRI, Redlands, California).

Juvenile Chinook salmon samples (caudal fin clip) were taken from fish collected in rotary screw traps located on the lower Wenatchee River (rkm 9.6), Chiwawa River (rkm 1.0), and Nason Creek (rkm 0.8) (Fig. 1, Table 1). All rotary traps were located downstream from the majority of spawning habitat in each stream. The primary collection location was the lower Wenatchee River, which is below all spawning areas and operated from early February through August, although most yearling smolts were captured prior to 1 July. Depending on river discharge levels, one or two screw traps (1.5 m diameter) were operated, and trap efficiency ranged between 1% and 3%. Because of spring runoff, traps operated during 83% and 92% of the trapping period in 2006 and 2007, respectively. At tributary trap locations, yearling

(age 1) juveniles were sampled approximately daily from early March to late June. In addition, separate samples of subyearlings (age 0) juveniles produced by the 2004 spawners were collected weekly from late September to early November on the Chiwawa River and Nason Creek in 2005 (Table 1).

Microsatellite genotyping

Genomic DNA was extracted from fin clips according to the method of LaHood et al. (2008). All individuals were genotyped at 11 microsatellite loci: Ots3 (Banks et al. 1999); Ots104 (Nelson and Beacham 1999); Ots201b, Ots211, and Ots213 (Greig et al. 2003); Ots2M and Ots10M (Greig and Banks 1999); Ots519NWFSC (Naish and Park 2002); Oke4 (Olsen et al. 1998); Ogo4 (Olsen et al. 1998); and Ssa408 (Cairney et al. 2000). Microsatellite loci were amplified by polymerase chain reaction (PCR), and allele sizes were electrophoretically resolved and scored according to the method of Winans et al. (2004). For each fluorescent phosphoamidite-labeled primer set, the annealing temperature used was 48 °C (Ots3 and Ots104), 54 °C (Oke4, Ots10M, Ots213, and Ots519NWFSC), or 60 °C (Ogo4, Ots2M, Ots201b, Ots211, and Ssa408). Genotyping error rate per locus was determined by re-amplifying and re-scoring microsatellite loci for a subset of individuals and calculating the number of alleles mis-scored over the total number of alleles observed at each locus. Error rates varied among loci and were generally ~1%.

Parentage assignment

Parentage assignment methods and results are described in detail in a previous paper (Ford and Williamson 2009). Briefly, assignment of parentage was calculated using the likelihood methods of Meagher and Thompson (1986) and Gerber et al. (2000) as implemented in the program FAMOZ (Gerber et al. 2003). Individuals with missing data at more than one locus were excluded from the analysis. In addition, a small number (<2% of the samples) of summer run Chinook salmon, which are genetically distinct from the spring run population (Utter et al. 1995; Schwenke et al. 2006), were excluded from the analysis on the basis of their genotypes. Each individual in a sample of progeny was tested against all potential pairs of parents, and a log of odds score was calculated for each potential pair of parents and offspring as the log of the ratio of the probability of a parent pair – offspring relationship compared with the probability they were drawn randomly from the population. The analysis assumed a per locus genotyping error rate of 0.1%, which was lower than our estimated error rate. In evaluating simulated data, however, it produced more accurate results than an error rate of either 0% or 1.5%, similar to what has been reported previously (Sancristobal and Chevalet 1997; Gerber et al. 2000).

Ford and Williamson (2009) discovered a pattern of biased assignment failure, such that progeny of hatchery fish in this population were less likely to be assigned to the correct pair of parents than progeny of wild fish, because of higher levels of relatedness among the hatchery-origin fish. In situations where multiple parent pairs are compatible with some offspring, fractional assignment methods provide a statistically robust way to estimate selection gradients (e.g., Morgan and Conner 2001; Nielsen et al. 2001) and fitness differences between groups (Ford and Williamson 2009). In particular, Ford and Williamson (2009) found that both fractional assignment and assignment to the most likely parent pair without use of a statistical threshold for assignment produced unbiased estimates of relative fitness. For the fractional assignments, only the 20 most likely parent pairs for each offspring were included in the analysis rather than every possible combination of parents. The rationale for this was to make the calculations computationally tractable. The specific value of 20 was chosen because the likelihood value of the nth most likely parent pair declines rapidly with increasing n, and likelihoods were essentially zero by $n = 20$. As a point of comparison for the fractional assignment results, we also conducted analyses based solely on the single most likely pair of parents for each progeny (i.e., $n = 1$).

Relative fitness and selection analysis

The fitness of an individual spawner was defined as either the number of offspring assigned to that spawner (for the analyses using the single most likely pairs of parents) or the number of fractionally assigned offspring (for the analysis using the fractional assignments). For the fractional assignments only, the initial fitness values were standardized by the mean fitness values within sexes and years.

In addition to simply comparing the mean fitness estimates of wild and hatchery fish within sexes and years, we also simultaneously evaluated the effects of the following traits on fitness: weight, run time (day of year), age, origin (hatchery or natural), and spawning location. To facilitate comparisons among sexes, traits, and years and to identify which covariates had the largest effects on fitness, traits were standardized within each sex and year by subtracting the mean and dividing by the standard deviation. Weight was cube-root-transformed prior to standardization such that it was a more linear function of length, and run time was converted to ordinal days for ease of analysis and to permit comparison between years. For the relative fitness estimates based on the fractional assignments, linear regression models were used to test the significance of each covariate following Lande and Arnold (1983). For the ith parent, relative fitness can be written as

$$Y_i = B_0 + \sum B_j \cdot \mathrm{trait}_j + \varepsilon_i$$

where $\varepsilon_i \sim \mathrm{Normal}(0,\sigma)$, and traits refer to origin, age, weight, run timing, and (for some models) spawning location. For calculation of p values in the linear models only, the relative fitness values were transformed by raising to the 0.2 power to improve normality. All effect estimates and comparisons between hatchery and wild fitness, however, are reported using the untransformed relative fitness values (Lande and Arnold 1983). Because the relative fitness estimates based on the single most likely assignments are discrete variables, we used generalized linear models (GLMs) with a Poisson error distribution ("glm" in the statistical package R with log-link and treatment contrasts). This framework assumes that the offspring for the ith parent have an approximately Poisson distribution (u_i). Covariates are used to predict the natural log of the mean:

Table 2. Summary of genetic variation in the 2004 and 2005 hatchery and wild parents and their offspring.

			Parents (H_O/H_E)				Offspring (H_O/H_E)	
			2004		2005		2004	2005
Locus	Alleles	Exclusion probability	Hatchery (n = 1771)	Wild (n = 812)	Hatchery (n = 3294)	Wild (n = 473)	(n = 2524)	(n = 873)
Ogo4	18	0.824	0.82/0.81	0.78/0.82	0.82/0.83	0.84/0.82	0.79/0.81	0.81/0.83
Ots10M	7	0.361	0.51/0.54	0.53/0.55	0.56/0.53	0.56/0.55	0.54/0.54	0.53/0.55
Ots211	44	0.975	0.94/0.94	0.95/0.94	0.95/0.94	0.95/0.94	0.91/0.94	0.94/0.94
Ots213	36	0.952	0.94/0.91	0.90/0.91	0.93/0.90	0.91/0.91	0.89/0.90	0.91/0.91
Ots2M	16	0.392	0.56/0.54	0.53/0.56	0.58/0.55	0.52/0.55	0.53/0.55	0.57/0.58
Oke4	11	0.552	0.62/0.63	0.55/0.61	0.61/0.64	0.62/0.62	0.57/0.60	0.64/0.64
Ots104	67	0.984	0.96/0.95	0.93/0.95	0.95/0.95	0.93/0.95	0.94/0.95	0.94/0.95
Ots201b	36	0.970	0.95/0.93	0.92/0.93	0.93/0.93	0.92/0.93	0.91/0.93	0.87/0.94
Ots3	12	0.550	0.66/0.64	0.54/0.55	0.64/0.61	0.58/0.58	0.58/0.58	0.59/0.62
Ots519	12	0.614	0.66/0.70	0.72/0.70	0.65/0.67	0.66/0.68	0.71/0.70	0.68/0.69
Ssa408	27	0.938	0.86/0.89	0.87/0.91	0.88/0.90	0.86/0.89	0.86/0.90	0.88/0.91
Average	26	0.737	0.77/0.77	0.75/0.77	0.77/0.77	0.76/0.77	0.75/0.76	0.76/0.78
Cumulative	286	>0.999999						

Note: "Alleles" refers to the total number alleles in the combined samples. Exclusion probability was calculated using the formulas reported in Jamieson and Taylor (1997) as implemented in the FAMOZ program. It is the theoretical probability that a random pair of individuals drawn from a randomly mating population with the same allele frequencies as the observed parental population would be excluded as the parents of a randomly drawn offspring. H_O and H_E refer to observed and expected (under random mating) heterozygosity, respectively. The table includes all samples with data at five or more loci.

$$\log(u_i) = B_0 + \sum B_j \cdot \text{trait}_j$$

There are several differences between the GLM approach and standard regression approach. With GLMs, we assume that the relationship between covariates and relative fitness is linear in log space or exponential in normal space. The identity link function may be used in some cases to force the relationship to be linear in normal space; however, most ecological data sets (including this one) result in convergence problems because the mean of the Poisson should never be allowed to be negative. A second important difference in these approaches is that the linear regression model introduces one additional parameter (resulting in slightly more flexibility) because it explicitly estimates a residual error parameter. Hierarchical versions of GLMs can be modified to include residual error, but because significance testing and model selection are not straightforward for these models, we did not consider them here.

Results

Genetic variation

Across the 11 loci, both hatchery-origin and wild-origin adults and their offspring had high and approximately equal levels of variation (Table 2). The overall level of genetic differentiation among the four adult origin × year combinations was low (F_{ST} = 0.0039), but exact tests of differentiation among all pairs of populations defined by origin and sample year were highly significant (p < 0.00001 for all comparisons). The low level of differentiation is consistent with the high rates of gene flow between the hatchery and wild subgroups expected in this supplemented population. Expected two parent exclusion probabilities were very high: >0.999999 for both hatchery- and wild-origin parents. Genotypic frequencies at several loci were significantly (p < 0.0001) out of Hardy–Weinberg expectations, but the absolute differences between observed and expected heterozygosity at all loci were small (Table 2) and likely represent a combination of nonrandom mating and failure to detect all large alleles at these highly polymorphic loci. The parentage assignment methods used are robust to both of these phenomena.

Phenotypic differences between hatchery and wild fish

Hatchery and wild fish differed in several characteristics (Table 3). In particular, in 2004 most of the hatchery males were 2- and 3-year-olds, whereas most of the wild males were 4-year-olds. The large numbers of 2-year-old hatchery males in 2004 led to a highly male biased sex ratio for hatchery fish in that year. For some comparisons within age, sex, and year, hatchery and wild fish differed significantly in run timing and weight, but these comparisons were not consistent between years.

One notable difference between hatchery and wild fish of both sexes was carcass recovery location. Within both the Chiwawa River and Nason Creek (the two largest spawning tributaries), hatchery fish were recovered significantly lower in the watersheds than wild fish (Table 3). There were also areas, such as the Wenatchee River main stem, that had large numbers of hatchery carcass recoveries but few or no wild carcasses.

Fitness of hatchery and wild fish in the stream environment

The fitness distribution estimated from the fractional offspring assignments was highly skewed, with a mode near zero and a tail of larger fitness values (Fig. 2). Such a highly skewed fitness distribution is similar to what has

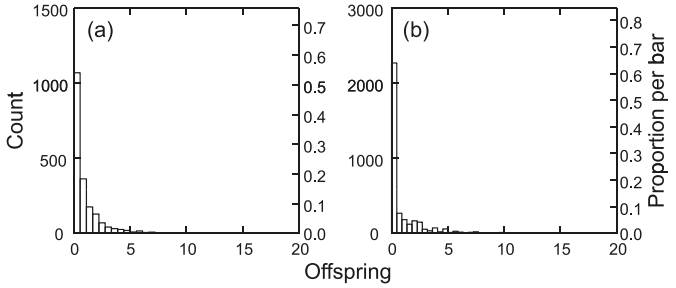
Table 3. Summary of trait variation in adult hatchery and wild spring Chinook salmon used in the parentage analysis.

		Males							Females						
		Hatchery			Wild				Hatchery			Wild			
	Age	*n*	Mean	SD	*n*	Mean	SD	*p*	*n*	Mean	SD	*n*	Mean	SD	*p*
Weight (kg)															
2004	2	626	0.12	0.11	—	—	—	—	—	—	—	—	—	—	—
	3	747	1.79	0.64	28	1.44	0.50	<0.001	3	3.27	0.46	0	—	—	—
	4	96	5.60	1.29	403	5.32	1.30	0.06	252	5.50	0.97	362	5.28	0.81	<0.001
	5	2	9.10	0.42	4	7.71	1.10	0.09	3	6.23	2.25	7	8.23	1.77	0.26
2005	2	290	0.10	0.031	—	—	—	—	—	—	—	—	—	—	—
	3	129	1.83	0.46	9	1.62	0.30	0.08	0	—	—	0	—	—	—
	4	1111	6.05	1.30	185	5.16	1.30	<0.001	1702	5.41	0.87	201	5.39	0.97	0.80
	5	6	8.10	2.20	39	9.23	1.93	0.28	8	7.23	1.41	44	7.99	1.31	0.19
Run timing (Julian days)															
2004	2	626	193.18	9.01	—	—	—	—	—	—	—	—	—	—	—
	3	747	179.61	9.21	28	178.71	12.42	0.71	3	185.30	2.89	0	—	—	—
	4	96	173.91	14.50	403	170.73	13.58	0.05	252	177.13	12.29	362	170.13	11.70	<0.001
	5	2	167.00	2.83	4	160.00	6.22	0.13	3	169.00	14.73	7	178.71	12.65	0.39
2005	2	290	191.22	12.66	—	—	—	—	—	—	—	—	—	—	—
	3	129	179.76	11.02	9	182.44	17.74	0.67	0	—	—	0	—	—	—
	4	1111	171.79	12.66	185	175.46	15.84	<0.001	1702	170.57	12.18	201	175.01	15.39	<0.001
	5	6	166.33	16.71	39	166.97	18.91	0.93	8	164.88	16.34	44	168.39	17.03	0.59
Location[a]															
Chiwawa River															
	3	25	19.35	11.54	2	20.48	3.18	0.75	0	—	—	0	—	—	—
	4	89	18.66	10.81	47	27.57	10.64	<0.001	194	20.26	11.86	63	29.54	11.20	<0.001
	5	0	—	—	3	28.77	12.93	—	0	—	—	8	28.83	8.77	—
Nason Creek															
	3	37	8.94	6.48	1	13.44	—	—	0	—	—	0	—	—	—
	4	54	6.73	5.64	48	13.60	7.09	<0.001	118	7.92	6.34	48	13.63	8.31	<0.001
	5	0	—	—	1	13.46	—	—	1	13.37	—	15	14.95	7.20	—
White River															
	3	0	—	—	0	—	—	—	0	—	—	0	—	—	—
	4	2	29.19	0.39	5	29.33	0.41	0.71	29	30.00	0.74	11	29.70	0.70	0.24
	5	0	—	—	0	—	—	—	0	—	—	0	—	—	—
Wenatchee River															
	3	3	83.61	2.71	0	—	—	—	0	—	—	0	—	—	—
	4	37	83.76	1.90	1	78.27	—	—	60	83.25	2.36	1	85.52	—	—
	5	0	—	—		—	—	—	0	—	—	1	84.27	—	—
Little Wenatchee River															
	3	0	—	—	0	—	—	—	0	—	—	0	—	—	—
	4	5	11.52	2.23	6	11.88	1.45	0.76	22	11.14	2.91	10	11.62	2.48	0.64
	5	0	—	—	0	—	—	—	0	—	—	0	—	—	—

Note: SD, standard deviation.

[a]Location refers to river kilometres from named river mouth. Data from 2004 and 2005 are combined.

Fig. 2. Histograms of estimated fitness (fractionally assigned offspring) for 2004 (*a*) and 2005 (*b*). Both absolute estimates (counts, left-hand axis) and the proportions per histogram category (proportion per bar, right-hand axis) are shown.



been observed for other salmonid species, including coho salmon (*Oncorhynchus kisutch*; Ford et al. 2006) and steelhead (Seamons et al. 2004; Araki et al. 2007*c*). The fitness distribution based on the most likely assignments appeared very similar (data not shown).

When progeny were counted as subyearlings (2004 brood year only), we found no significant difference in progeny per parent for hatchery- and natural-origin fish if the comparisons were made within age classes, although hatchery fish produced fewer sampled progeny/parent for all age classes except age 5 females (Table 4). When progeny were counted at the yearling stage, the 4-year-old (dominant) age class hatchery fish produced significantly fewer progeny per male and female parent than did 4-year-old wild fish in both 2004 and 2005. When all age classes were combined within each sex in either 2004 or 2005, hatchery males and females produced significantly fewer yearling progeny per parent compared with their wild counterparts.

In addition to wild origin, higher weight and earlier run timing were also associated with greater fitness (Fig. 3, Table 5). The effect of weight was more important than the effect of run timing and was larger for males than for females (Table 5). Hatchery origin still had a significant negative effect on fitness, after taking into account the effects of weight, run timing, and age (Table 5). A model that used progeny counts inversely weighted by daily trapping efficiency produced essentially identical results (data not shown).

We also investigated the effect of carcass recovery location, which was measured on the spawning grounds instead of at Tumwater Dam. Only ~10% of the fish sampled at the dam were recovered as carcasses, so we combined data from both years for this analysis. Because only the Chiwawa River and Nason Creek had large numbers of hatchery and wild spawners with a range of recovery locations, we limited our analysis to these two streams. Carcass recovery location had a significant effect on fitness, with fish that spawned higher upstream producing more progeny than fish spawning downstream (Fig. 4, Table 6). For both the linear and GLM fitness models, the hatchery-origin effect was reduced (becoming less negative) when recovery location was introduced as a covariate (Table 6). For females, the hatchery coefficient in the linear model becomes nonsignificant and very close to zero when spawning location is included as a covariate, although the hatchery effect remains significant (but reduced in magnitude) in the GLM.

Table 4. Mean progeny counts based on fractional assignments, and relative fitness of hatchery and wild fish for the 2004 and 2005 spawning years.

		2004												2005									
		Subyearling							Yearling					Yearling									
		Wild			Hatchery				Wild			Hatchery		Wild			Hatchery						
Sex	Age	n^a	Mean[b]	SD	n	Mean	SD	H/W[c]	Mean	SD		Mean	SD	H/W	n	Mean	SD	n	Mean	SD		H/W
Male	2	0	—	—	626	0.22	0.50	—	—	—		0.32	0.50	—	0	—	—	290	0.20	0.50		—
	3	28	1.06	2.03	740	0.72	1.32	0.68	0.84	1.19		0.70	1.01	0.83	9	2.03	2.32	129	0.74	1.34		0.36
	4	403	2.48	3.44	96	2.00	2.50	0.81	2.50	3.12		1.38	1.49	0.55*	185	2.04	3.29	1111	1.00	2.10		0.49**
	5	4	1.15	1.40	2	0.78	1.07	0.68	4.50	7.33		0.07	0.07	0.02	39	2.05	3.32	6	1.36	2.60		0.66
	All	435	2.38	3.37	1491	0.59	1.26	0.25**	2.42	3.17		0.58	0.92	0.24**	233	2.04	3.25	1536	0.83	1.86		0.40**
Female	4	362	1.04	1.37	252	0.89	1.14	0.86	1.24	1.37		0.69	0.10	0.55**	201	1.80	2.90	1702	0.88	1.70		0.49*
	5	7	0.32	0.35	3	0.69	0.58	2.15	0.54	0.47		0.38	0.34	0.70	44	1.97	2.34	8	1.72	2.53		0.78
	All	369	1.04	1.36	271	0.91	1.17	0.88	1.23	1.36		0.68	0.96	0.55**	245	1.83	2.80	1759	0.88	1.70		0.48**

Note: Parents with data missing at >1 locus were excluded from the analysis.

[a]*n* refers the parental sample size for the specific origin, sex, age and year class in questions. The parental sample sizes for the 2004 subyearlings and yearlings are identical, since it the same set of parents but two different samples of offspring.

[b]Mean and SD refer to the mean and standard deviation, respectively, of the number of progeny per parent for specific origin, sex, age, and year class in question.

[c]H/W is the ratio of mean progeny number between hatchery and wild fish for specific age, sex, and year classes. Significance of differences in mean progeny number between hatchery and wild fish were calculated using a *t* test with bootstrapped *p* values to account for non-normality and are indicated with asterisks: *, $p < 0.05$; **, $p < 0.01$.

Table 5. Effects of origin, age, run timing, and weight on male and female relative fitness.

	Fractional assignment (LM)[a]				Discrete assignment (GLM)[b]			
	2004		2005		2004		2005	
Effect	Male	Female	Male	Female	Male	Female	Male	Female
Intercept	0.94 (0.12)	1.20 (0.06)	1.74 (0.13)	1.82 (0.12)	–0.19 (0.08)	0.89 (0.03)	–0.15 (0.07)	–0.29 (0.08)
Weight	0.80 (0.09)	0.18 (0.05)	0.35 (0.07)	0.12 (0.04)	0.79 (0.06)	0.20 (0.03)	0.27 (0.04)	0.09 (0.03)
Origin (hatchery effect)	–0.79 (0.15)	–0.50 (0.1)	–0.96 (0.14)	–0.94 (0.13)	–0.62 (0.09)	–0.57 (0.06)	–0.66 (0.08)	–0.70 (0.08)
Run time	–0.15 (0.05)	–0.15 (0.05)	–0.08* (0.05)	–0.18 (0.04)	–0.09 (0.03)	–0.15 (0.03)	–0.07* (0.03)	–0.15 (0.03)
Age 3 effect[c]	0.95 (0.22)	—	0.63* (0.24)	—	0.80 (0.15)	—	0.39 (0.17)	—

Note: Age 2 males were excluded and ages 4 and 5 were combined for the analysis. Results from two parentage assignment methods and fitness models are presented: fractional assignment, using models with normal error, and the single most probable parent pair using generalized linear models (GLMs) with Poisson error. Standard deviations of covariate estimates are given in parentheses; coefficients with asterisks (*) represent nonstatistically significant results ($p > 0.05$). All other coefficients are significant (at least $p < 0.05$).

[a]Coefficients of the linear model (LM) based on fractional parentage assignment: progeny = intercept + return time + effect of hatchery origin + weight + effect of age 3 (males only) + ε (normal).

[b]Coefficients of Poisson generalized linear model (GLM) based on mostly likely parentage assignments: $\log(u_{\text{progeny}})$ = intercept + return time + effect of hatchery origin + weight + effect of age 3 (males only).

[c]The age 3 effect is the effect of being age 3 (instead of ages 4 or 5), independent from the effect of weight. It is only included in the analysis of males since all females were either age 4 or 5.

Fig. 3. Relationship among age, weight, and relative fitness for the combined 2004 and 2005 data for naturally spawning males (*a*) and females (*b*). Individual relative fitness was estimated as the fractionally assigned juvenile yearling progeny count for an individual divided by the mean counts per individual within sexes and years. Individuals of ages 3, 4, and 5 are indicated by solid circles, gray squares, and open circles, respectively. Density plots of weight (kg) and fitness are illustrated on the margins for ages 3 (black), 4 (gray), and 5 (open). The density plots are scaled to reflect distributions within age classes, and heights of the plots are not proportional to the relative abundance among age classes.

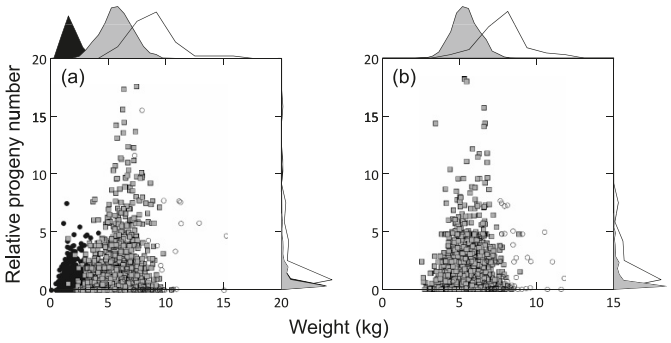


Fig. 4. Relationship between female and male carcass recovery location and relative fitness for the Nason Creek females (*a*) and males (*b*) and Chiwawa River females (*c*) and males (*d*) in 2004 and 2005 combined. Individual relative fitness for wild (open squares) and hatchery (solid circles) fish was estimated as the fractionally assigned yearling juvenile count for an individual divided by the mean counts per individual within sexes. Density plots of recovery location (stream kilometre) and fitness are illustrated on the margins for hatchery (filled) and wild (open) fish. The density plots are scaled to reflect distributions within origin classes, and heights of the plots are not proportional to the relative abundance among origin classes. Dashed and solid lines illustrate the linear relationship between spawning location and the standardized progeny counts for hatchery and wild fish, respectively.

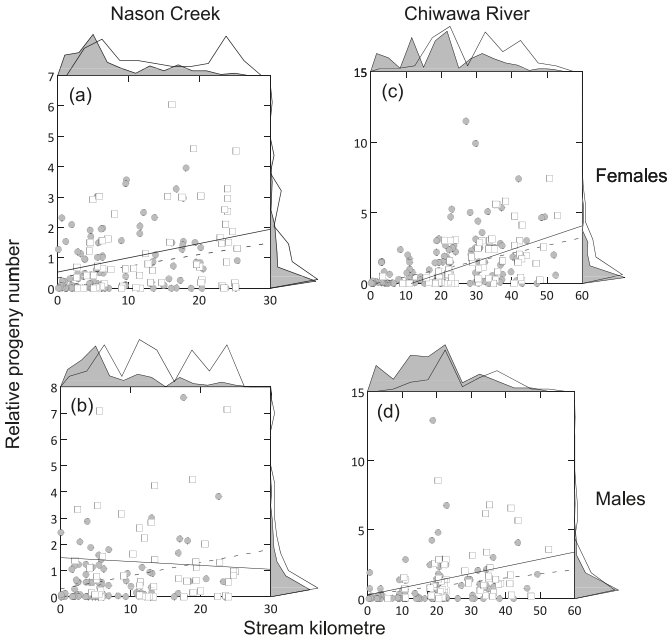


Table 6. Effects of origin, age, run timing, weight and spawning location on male and female relative fitness.

	Fractional assignment (LM)[a]				Discrete assignment (GLM)[b]			
	Male		Female		Male		Female	
Effect	Location	No location	Lococation	No location	Location	No location	Location	No location
Intercept	1.67 (0.24)	1.90 (0.24)	1.49 (0.19)	1.84 (0.20)	0.23 (0.10)	0.35 (0.10)	0.37 (0.07)	0.65 (0.06)
Weight	0.63 (0.16)	0.56 (0.16)	0.22* (0.10)	0.26 (0.11)	0.56 (0.07)	0.56 (0.07)	0.03* (0.04)	0.07 (0.04)
Origin (hatchery effect)	–0.47 (0.29)	–0.76 (0.29)	0.01* (0.22)	–0.49 (0.24)	–0.68 (0.12)	–0.79 (0.12)	–0.69 (0.10)	–0.95 (0.09)
Run time	0.19* (0.13)	0.09* (0.13)	0.10* (0.10)	–0.11* (0.11)	0.12 (0.05)	0.04* (0.05)	0.07* (0.05)	–0.03 (0.04)
Age 3 effect	0.44 (0.38)	0.30* (0.38)	—	—	0.81 (0.19)	0.75 (0.19)	—	—
Location	0.53 (0.13)	—	0.92 (0.10)	—	0.28 (0.05)	—	0.45 (0.05)	—

Note: Data are from 2004 and 2005 combined. For comparison, we included two models, one without the effect of location and one with location as a predictor. Age 2 males were excluded from the analysis and ages 4 and 5 were combined. The data used are the subset of all data for which location were available. Results from two parentage assignment methods and fitness models are presented: fractional assignment, using linear models (LM) with normal error, and the single most probable parent pair using generalized linear models (GLMs) with Poisson error. Standard deviations of covariate estimates are given in parentheses; coefficients with asterisks (*) represent nonstatistically significant results ($p > 0.05$). All other coefficients are significant (at least $p < 0.05$).

[a]Coefficients of the linear model based on fractional parentage assignment: progeny = intercept + return time + effect of hatchery origin + weight + effect of age 3 (males only) + ε (normal).

[b]Coefficients of Poisson GLM based on mostly likely parentage assignments: $\log(u_{\text{progeny}})$ = intercept + return time + effect of hatchery origin + weight + effect of age 3 (males only).

Discussion

Fitness distribution

Like previous studies of salmon fitness, the estimated offspring numbers per parent in our study were highly skewed. There are several potential causes of this skewed distribution. First, the number of offspring sampled was a small fraction of the total juvenile population, and if more progeny were sampled the fitness distribution would move to the right. Second, many of the adults in fact produced no progeny, because prespawn mortality in this population is as high as 50% (Murdoch et al. 2008). Finally, even among those fish that spawned, there appears to be a skewed distribution of progeny number, indicating a high variance in reproductive success.

Factors associated with low fitness of hatchery fish

Hatchery-origin adults in our study had less than half the mean fitness of their wild counterparts. This level of fitness reduction is similar to what has been observed in other species, particularly steelhead (e.g., Leider et al. 1990; Kostow et al. 2003; Araki et al. 2007*a*, 2007*b*). Like most steelhead hatchery programs, spring run Chinook salmon typically spend a full year rearing in the hatchery prior to release. If reduced fitness is correlated with hatchery residence time, then species that spend similar periods of time in hatchery rearing conditions might be expected to have similar reductions in fitness in the wild. However, a portion of the fitness differences we observed was explained by differences in spawning location, indicating that factors other then simply time spent in the hatchery can influence subsequent fitness.

For males, the relative fitness of hatchery fish was lower if all age classes were combined than if analyzed separately, because of the higher fraction of 3-year-old males among hatchery fish compared with wild fish. Hatchery fish have a tendency to mature at earlier ages than wild fish (Knudsen et al. 2006; Murdoch et al. 2008), but the difference is subtle and does not explain the differences in age structure we observed. Instead, these differences were due mostly to an increase in hatchery releases starting in 2003, and the 3-year-olds that returned to spawn in 2004 were in high abundance owing to this strong hatchery cohort (A.R. Murdoch, unpublished data). Neither weight nor run timing differed consistently between hatchery and wild fish, and neither of these traits explained the reduced fitness of hatchery fish.

Other than differences in age structure, carcass recovery location was the only measured trait that differed notably between hatchery- and wild-origin fish. Carcass recovery location also had a significant effect on fitness, such that fish that were recovered higher in the watershed had higher average fitness than those that were recovered lower in the watersheds. When spawning location was included as a predictor, the model coefficients associated with hatchery origin became less negative for both females and males and became nonsignificant for females in one of the two models. Overall, these results indicate that spawning location explains a portion but not all of the reduced fitness of hatchery fish in this study.

To our knowledge, this is the first direct estimate of the effect of general spawning location on fitness in a natural stream, although the result is consistent with previous indi-

rect observations, and there is a large literature on spawning site selection by salmon (reviewed by Quinn 2005). For example, Hoffnagle et al. (2008) found that hatchery Chinook salmon females were distributed lower in an Oregon watershed than wild females, and they hypothesized that this could have a deleterious effect on the fitness of the population. Schroder et al. (2008) found that small differences in spawning location within an artificial stream contributed to reduced fitness of hatchery spring Chinook salmon in the Yakima River.

The cause of the difference in spawning distribution in our study is probably due to the rearing methods and release location of the hatchery fish. Hatchery juveniles are initially reared in an offsite facility until 6–7 months of age, when they are transferred to a rearing pond near the mouth of the Chiwawa River. There, the fish are reared on a mixture of Chiwawa River and Wenatchee River water until they are released as smolts. Salmon are known to imprint on chemical cues in the water (Quinn and Fresh 1984; Quinn 1993). It is therefore not surprising that returning hatchery fish tend to spawn in the lower reaches of the Chiwawa River and areas nearby in Nason Creek and the Wenatchee River, since this is the area to which they imprinted as juveniles. Assuming that sufficient habitat capacity was available, releasing fish higher in the watershed might therefore result in improved fitness of the returning hatchery adults.

Our results do not directly address the mechanism by which spawning in the lower reaches of the Chiwawa River and Nason Creek leads to lower fitness, but there are two plausible factors. First, the density of spawners is higher in the lower reaches, owing to the large number of hatchery fish produced by the supplementation program. Second, the spawning and rearing habitat in the lower reaches are more impacted by roads and development (Upper Columbia Salmon Recovery Board 2007). Other aspects of the effect of spawning location remain to be explored. For example, relatively few wild fish but considerable hatchery fish spawned in the Wenatchee River proper, and this choice of spawning location may also contribute to the overall reduction in hatchery fish fitness.

One limitation of our study is that it does not directly estimate the genetic versus environmental components of differences between the hatchery and wild fish. In particular, the hatchery and wild spawners experienced different juvenile rearing environments, which could lead to environmentally induced differences in behavior or physiology that in turn lead to differences in fitness. The difference in spawning location between the two types of fish, for example, is probably due to differences in their early rearing environment. However, even after accounting for spawning location, hatchery fish remained less fit than wild fish (especially males), and some of those differences could be due to genetic effects or environmentally induced effects on traits we did not measure. For example, there have been studies that have found differences between hatchery fish in a variety of behavioral (e.g., Riddell and Swain 1991; Fleming and Gross 1992), morphological (e.g., Fleming and Gross 1989), and physiological traits (e.g., Hill et al. 2006).

We found larger effects of hatchery origin on fitness compared with some other recent studies of Chinook salmon in seminatural environments. In particular, Schroder et al. (2008) found that egg to fry survival for first generation hatchery females was 0.94 times that of wild females when measured in an artificial stream channel. There are several potential reasons for the greater differences in fitness in our study. First, the Wenatchee River supplementation program was started in 1989, and returning hatchery fish have comprised 36%–70% of the broodstock since 1994. The Yakima River program started in 1997 and uses only wild fish for broodstock, so the hatchery fish in the Wenatchee River have experienced more generations of domestication selection than the Yakima River fish. Second, we measured fitness over a longer period of the life cycle, allowing for more opportunities for differences in fitness between wild and hatchery fish to manifest. Third, a portion of the fitness differences we observed was due to large-scale differences in spawning location, which would not be able to be manifest in a spawning channel. Finally, the Wenatchee study was in a natural setting, compared with an artificial stream channel in the Yakima River. It is possible that the natural environment is less benign to hatchery-produced fish than the stream channel, leading to greater differences in fitness.

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References

Araki, H., Ardren, W.R., Olsen, E., Cooper, B., and Blouin, M.S. 2007*a*. Reproductive success of captive-bred steelhead trout in the wild: evaluation of three hatchery programs in the Hood River. Conserv. Biol. **21**(1): 181–190. doi:10.1111/j.1523-1739.2006.00564.x. PMID:17298524.

Araki, H., Cooper, B., and Blouin, M.S. 2007*b*. Genetic effects of captive breeding cause a rapid, cumulative fitness decline in the wild. Science (Washington, D.C.), **318**(5847): 100–103. doi:10.1126/science.1145621. PMID:17916734.

Araki, H., Waples, R.S., Ardren, W.R., Cooper, B., and Blouin, M.S. 2007*c*. Effective population size of steelhead trout: influence of variance in reproductive success, hatchery programs, and genetic compensation between life-history forms. Mol. Ecol. **16**(5): 953–966. doi:10.1111/j.1365-294X.2006.03206.x. PMID:17305853.

Araki, H., Berejikian, B.A., Ford, M.J., and Blouin, M.S. 2008. Fitness of hatchery-reared salmonids in the wild. Evol. Appl. **1**(2): 342–355. doi:10.1111/j.1752-4571.2008.00026.x.

Banks, M.A., Blouin, M.S., Baldwin, B.A., Rashbrook, V.K., Fitzgerald, H.A., Blankenship, S.M., and Hedgecock, D. 1999. Isolation and inheritance of novel microsatellites in chinook salmon. J. Hered. **90**(2): 281–288. doi:10.1093/jhered/90.2.281.

Beamish, R.J., Mahnken, C., and Neville, C.M. 1997. Hatchery and wild production of Pacific salmon in relation to large-scale, natural shifts in the productivity of the marine environment. ICES J. Mar. Sci. **54**(6): 1200–1215. doi:10.1016/S1054-3139(97)80027-6.

Burck, W.A. 1967. Mature stream-reared spring chinook salmon. Oregon Fish Commission Research Briefs, **13**: 128.

Cairney, M., Taggart, J.B., and Høyheim, B. 2000. Characterization of microsatellite and minisatellite loci in Atlantic salmon (*Salmo salar* L.) and cross-species amplification in other salmonids.

Mol. Ecol. **9**(12): 2175–2178. doi:10.1046/j.1365-294X.2000.105312.x. PMID:11123640.

Fleming, I.A., and Gross, M.R. 1989. Evolution of adult female life history and morphology in a Pacific salmon (coho: *Oncorhynchus kisutch*). Evolution, **43**(1): 141–157. doi:10.2307/2409170.

Fleming, I.A., and Gross, M.R. 1992. Reproductive behavior of hatchery and wild coho salmon (*Oncorhynchus kisutch*): does it differ? Aquaculture, **103**(2): 101–121. doi:10.1016/0044-8486(92)90405-A.

Fleming, I.A., Hindar, K., Mjolnerod, I.B., Jonsson, B., Balstad, T., and Lamberg, A. 2000. Lifetime success and interactions of farm salmon invading a native population. Proc. R. Soc. B Biol. Sci. **267**(1452): 1517–1523. doi:10.1098/rspb.2000.1173.

Ford, M.J. 2002. Selection in captivity during supportive breeding may reduce fitness in the wild. Conserv. Biol. **16**(3): 815–825. doi:10.1046/j.1523-1739.2002.00257.x.

Ford, M.J., and Williamson, K.S. 2009. The aunt and uncle effect revisited — the effect of biased parentage assignment on fitness estimation in a supplemented salmon population. J. Hered. **101**(1): 33–41. doi:10.1093/jhered/esp068.

Ford, M., Fuss, H., Boelts, B., LaHood, E., Hard, J., and Miller, J. 2006. Changes in run timing and natural smolt production in a naturally spawning coho salmon (*Oncorhynchus kisutch*) population after 60 years of intensive hatchery supplementation. Can. J. Fish. Aquat. Sci. **63**(10): 2343–2355. doi:10.1139/F06-119.

Fritts, A.L., Scott, J.L., and Pearsons, T.N. 2007. The effects of domestication on the relative vulnerability of hatchery and wild origin spring Chinook salmon (*Oncorhynchus tshawytscha*) to predation. Can. J. Fish. Aquat. Sci. **64**(5): 813–818. doi:10.1139/F07-057.

Gerber, S., Mariette, S., Streiff, R., Bodénès, C., and Kremer, A. 2000. Comparison of microsatellites and amplified fragment length polymorphism markers for parentage analysis. Mol. Ecol. **9**(8): 1037–1048. doi:10.1046/j.1365-294x.2000.00961.x. PMID:10964223.

Gerber, S., Chabrier, P., and Kremer, A. 2003. FaMoz: a software for parentage analysis using dominant, codominant and uniparentally inherited markers. Mol. Ecol. Notes, **3**(3): 479–481. doi:10.1046/j.1471-8286.2003.00439.x.

Greig, C., and Banks, M.A. 1999. Five multiplexed microsatellite loci for rapid response run identification of California's endangered winter Chinook salmon. Anim. Genet. **30**(4): 318–324. doi:10.1046/j.1365-2052.1999.00445-3.x.

Greig, C., Jacobson, D.P., and Banks, M.A. 2003. New tetranucleotide microsatellites for fine-scale discrimination among endangered chinook salmon (*Oncorhynchus tshawytscha*). Mol. Ecol. Notes, **3**(3): 376–379. doi:10.1046/j.1471-8286.2003.00455.x.

Healey, M.C. 1983. Coastwide distribution and ocean migration patterns of stream- and ocean-type chinook salmon, *Oncorhynchus tshawytscha.* Can. Field Nat. **97**: 427–433.

Healey, M.C. 1991. The life history of chinook salmon (*Oncorhynchus tshawytscha*). *In* Life history of Pacific salmon. *Edited by* C. Groot and L. Margolis. University of British Columbia Press, Vancouver, B.C. pp. 311–394.

Hill, M.S., Zydlewski, G.B., and Gale, W.L. 2006. Comparisons between hatchery and wild steelhead trout (*Oncorhynchus mykiss*) smolts: physiology and habitat use. Can. J. Fish. Aquat. Sci. **63**(7): 1627–1638. doi:10.1139/F06-061.

Hoffnagle, T.L., Carmichael, R.W., Frenyea, K.A., and Keniry, P.J. 2008. Run timing, spawn timing, and spawning distribution of hatchery- and natural-origin spring Chinook salmon in the Imnaha River, Oregon. N. Am. J. Fish. Manage. **28**(1): 148–164. doi:10.1577/M05-145.1.

Independent Scientific Advisory Board. 2003. Review of salmon and steelhead supplementation, Portland. Available from http://www.nwcouncil.org/library/isab/isab2003-3.htm.

Independent Scientific Advisory Board. 2005. Monitoring and evaluation of supplementation projects. Available from http://www.nwcouncil.org/library/isrp/isrp2005-15.htm.

Jamieson, A., and Taylor, S.C. 1997. Comparisons of three probability formulae for parentage exclusion. Anim. Genet. **28**(6): 397–400. doi:10.1111/j.1365-2052.1997.00186.x. PMID:9616104.

Knudsen, C.M., Schroder, S.L., Busack, C.A., Johnston, M.V., Pearsons, T.N., Bosch, W.J., and Fast, D.E. 2006. Comparison of life history traits between first-generation hatchery and wild upper Yakima River spring Chinook salmon. Trans. Am. Fish. Soc. **135**(4): 1130–1144. doi:10.1577/T05-121.1.

Kostow, K., Marshall, A., and Phelps, S. 2003. Naturally spawning hatchery steelhead contribute to smolt production but experience low reproductive success. Trans. Am. Fish. Soc. **132**(4): 780–790. doi:10.1577/T02-051.

LaHood, E.S., Miller, J.J., Apland, C., and Ford, M.J. 2008. A rapid, ethanol-free fish tissue collection method for molecular genetic analyses. Trans. Am. Fish. Soc. **137**(4): 1104–1107. doi:10.1577/T07-181.1.

Lande, R., and Arnold, S.J. 1983. The measurement of selection on correlated characters. Evolution, **37**(6): 1210–1226. doi:10.2307/2408842.

Leider, S.A., Hulett, P.L., Loch, J.J., and Chilcote, M.W. 1990. Electrophoretic comparison of the reproductive success of naturally spawning transplanted and wild steelhead trout through the returning adult stage. Aquaculture, **88**(3-4): 239–252. doi:10.1016/0044-8486(90)90151-C.

Lynch, M., and O'Hely, H. 2001. Captive breeding and the genetic fitness of natural populations. Conserv. Genet. **2**(4): 363–378. doi:10.1023/A:1012550620717.

Mallinson, J.J.C. 1995. Conservation breeding programmes: an important ingredient for species survival. Biodivers. Conserv. **4**(6): 617–635. doi:10.1007/BF00222518.

McClure, M.M., Holmes, E.E., Sanderson, B.L., and Jordan, C.E. 2003. A large-scale, multispecies status assessment: anadromous salmonids in the Columbia River Basin. Ecol. Appl. **13**(4): 964–989. doi:10.1890/1051-0761(2003)13[964:ALMSAA]2.0.CO;2.

Meagher, T.R., and Thompson, E. 1986. The relationship between single parent and parent pair genetic likelihoods in genealogy reconstruction. Theor. Popul. Biol. **29**(1): 87–106. doi:10.1016/0040-5809(86)90006-7.

Mobrand, L.E., Barr, J., Blankenship, L., Campton, D.E., Evelyn, T.T.P., Flagg, T.A., Mahnken, C.V.W., Seeb, L.W., Seidel, P.R., and Smoker, W.W. 2005. Hatchery reform in Washington State: principles amd emerging issues. Fisheries, **30**(6): 11–33. doi:10.1577/1548-8446(2005)30[11:HRIWS]2.0.CO;2.

Morgan, M.T., and Conner, J.K. 2001. Using genetic markers to directly estimate male selection gradients. Evolution, **55**(2): 272–281. PMID:11308085.

Mullan, J.W., Williams, K.R., Rhodus, G., Hillman, T.W., and McIntryre, J.D. 1992. Production and habitat of salmonids in mid-Columbia River tributary streams. US Fish. Wildl. Serv. Monograph I.

Murdoch, A., Pearsons, T., Maitland, T., Ford, M., and Williamson, K. 2008. Monitoring the reproductive success of naturally spawning hatchery and natural spring Chinook salmon in the Wenatchee River. BPA Project No. 2003-039-00. Bonneville Power Administration, Portland, Ore. Available from http://pisces.bpa.gov/release/documents/documentviewer.aspx?doc=P106770.

Myers, J.M., Kope, R.G., Bryant, G.J., Teel, D., Lierheimer, L.J., Wainwright, T.C., Grant, W.S., Waknitz, F.W., Neely, K., Lindley, S.T., and Waples, R.S. 1998. Status review of chinook salmon from Washington, Idaho, Oregon and California. NOAA Tech. Memo. NMFS-NWFSC-35.

Naish, K.A., and Park, L.K. 2002. Linkage relationships for 35 new microsatellite loci in chinook salmon *Oncorhynchus tshawytscha*. Anim. Genet. **33**(4): 316–318. doi:10.1046/j.1365-2052.2002.t01-4-00886.x. PMID:12139517.

Naish, K.A., Taylor, J.E., III, Levin, P.S., Quinn, T.P., Winton, J.R., Huppert, D., and Hilborn, R. 2007. An evaluation of the effects of conservation and fishery enhancement hatcheries on wild populations of salmon. Adv. Mar. Biol. **53**: 61–194. doi:10.1016/S0065-2881(07)53002-6.

National Research Council. 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Nelson, R.J., and Beacham, T.D. 1999. Isolation and cross species amplification of microsatellite loci useful for study of Pacific salmon. Anim. Genet. **30**(3): 228–244. doi:10.1046/j.1365-2052.1999.00404-4.x. PMID:10442988.

Nielsen, R., Mattila, D.K., Clapham, P.J., and Palsbøll, P.J. 2001. Statistical approaches to paternity analysis in natural populations and applications to the North Atlantic humpback whale. Genetics, **157**(4): 1673–1682. PMID:11290722.

Olsen, J.B., Bentzen, P., and Seeb, J.E. 1998. Characterization of seven microsatellite loci derived from pink salmon. Mol. Ecol. **7**(8): 1087–1089. PMID:9711869.

Pearsons, T.N., Fritts, A.L., and Scott, J.L. 2007. The effects of hatchery domestication on competitive dominance of juvenile spring Chinook salmon (*Oncorhynchus tshawytscha*). Can. J. Fish. Aquat. Sci. **64**(5): 803–812. doi:10.1139/F07-058.

Quinn, T.P. 1993. A review of homing and straying of wild and hatchery-produced salmon. Fish. Res. **18**(1-2): 29–44. doi:10.1016/0165-7836(93)90038-9.

Quinn, T.P. 2005. The behavior and ecology of Pacific salmon and trout. American Fisheries Society, Bethesda, Md.

Quinn, T.P., and Fresh, K. 1984. Homing and straying in chinook Salmon (*Oncorhynchus tshawytscha*) from Cowlitz River hatchery, Washington. Can. J. Fish. Aquat. Sci. **41**(7): 1078–1082. doi:10.1139/f84-126.

Reisenbichler, R.R., and McIntyre, J.D. 1977. Genetic differences in growth and survival of juvenile hatchery and wild steelhead trout, *Salmo gairdneri*. J. Fish. Res. Board Can. **34**: 123–128.

Rich, W.H. 1920. Early history and seaward migration of Chinook salmon in the Columbia and Sacramento Rivers. Bull. Bureau Fish. Vol. 37.

Riddell, B.E., and Swain, D.P. 1991. Competition between hatchery and wild coho salmon (*Oncorhynchus kisutch*): genetic variation for agonistic behaviour in newly-emerged wild fry. Aquaculture, **98**(1-3): 161–172. doi:10.1016/0044-8486(91)90381-G.

Sancristobal, M., and Chevalet, C. 1997. Error tolerant parent identification from a finite set of individuals. Genet. Res. **70**(1): 53–62. doi:10.1017/S0016672397002851.

Schroder, S.L., Knudsen, C.M., Pearsons, T.N., Kassler, T.W., Young, S.F., Busack, C.A., and Fast, D.E. 2008. Breeding success of wild and first-generation hatchery female spring Chinook salmon spawning in an artificial stream. Trans. Am. Fish. Soc. **137**(5): 1475–1489. doi:10.1577/T07-123.1.

Schwenke, P.L., Rhydderch, J.G., Ford, M.J., Marshall, A.R., and Park, L.K. 2006. Forensic identification of endangered Chinook Salmon (*Oncorhynchus tshawytscha*) using a multilocus SNP assay. Conserv. Genet. **7**(6): 983–989. doi:10.1007/s10592-006-9133-x.

Seamons, T.R., Bentzen, P., and Quinn, T.P. 2004. The effects of adult length and arrival date on individual reproductive success in wild steelhead trout (*Oncorhynchus mykiss*). Can. J. Fish. Aquat. Sci. **61**(2): 193–204. doi:10.1139/f03-158.

Upper Columbia Salmon Recovery Board. 2007. Upper Columbia spring Chinook salmon and steelhead recovery plan. Available from http://www.ucsrb.com/theplan.asp.

Utter, F.M., Chapman, D.W., and Marshal, A.R. 1995. Genetic population structure and history of chinook salmon of the Upper Columbia River. Am. Fish. Soc. Symp. **17**: 149–168.

Winans, G.A., Paquin, M.M., Van Doornik, D.M., Baker, B.M., Thornton, P., Rawding, D., Marshall, A., Moran, P., and Kalinowski, S. 2004. Genetic stock identification of steelhead in the Columbia River Basin: an evaluation of different molecular markers. N. Am. J. Fish. Manage. **24**(2): 672–685. doi:10.1577/M03-052.1.