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[Article]

Comparison of Life History Traits between First-Generation Hatchery and Wild Upper Yakima River Spring Chinook Salmon

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Abstract.—Life history traits in hatchery and wild spring Chinook salmon *Oncorhynchus tshawytscha* from the upper Yakima River were compared to determine whether locally adapted traits had diverged after one generation of state-of-the-art artificial propagation. Sex composition in wild- and hatchery-origin fish differed in three of four brood years ($P \leq 0.01$). The proportion of hatchery males, primarily age 3, increased from 38% to 49% over time. Conversely, the sex composition of wild fish did not exhibit a similar linear trend. Most hatchery- and wild-origin fish reached maturity at age 4 (≥76%), followed in magnitude by ages 3 and 5. Wild mean age at maturation demonstrated no significant trend over time, while hatchery mean age at maturation declined ($P = 0.05$). Mean lengths of 3–5-year-old hatchery fish were shorter than those of wild fish of the same age (differences of 2.7 cm for age 3, 1.7 cm for age 4, and 1.9 cm for age 5). Likewise, body weights of hatchery fish were lower than those of wild fish (differences of 0.3 kg for age 3, 0.3 kg for age 4, and 0.6 kg for age 5), representing a change in body size of between 0.5 and 1.0 standard deviation (SD). Median arrival timing of hatchery and wild fish at a broodstock collection site just downstream of ancestral spawning grounds showed no consistent difference. However, the median arrival date of age-3 fish was 19–20 d later than that for fish of ages 4 and 5 ($P < 0.01$). Mean spawn timing of hatchery fish was significantly earlier (5.1 d) than that of wild fish in a "common-garden" experiment ($P < 0.05$). We estimate that fitness could be reduced by as much as 1–5% for traits diverging from their optima by 0.5–1.0 SD. The degree of genetic determination of the divergence is unknown, but future monitoring will help clarify this. Perhaps the most important conclusion of our study is that even a hatchery program designed to minimize differences between hatchery and wild fish did not produce fish that were identical to wild fish.

Artificial propagation of Pacific salmon *Oncorhynchus* spp. and steelhead *O. mykiss* has been practiced in the Pacific Northwest for over a century. Continuing losses of natural production from overharvest, habitat degradation, and disappearance of spawning habitat due to hydroelectric development, irrigation, logging, and transportation (Lichatowich 1999) have increased the importance of hatchery operations in the region. Over the past century, significant advances have been made in fish culture technology, and now spawner–recruit rates in hatcheries often considerably exceed 1.0. However, what effect artificial production might have on native populations is unresolved (e.g., Waples et al., in press; Goodman 2005). This issue has become even more important recently because of the increasing use of "integrated" hatchery programs in which there is deliberate interbreeding of hatchery- and natural-origin fish (Goodman 2004; Mobrand et al. 2005). In the Columbia River basin, for example, approximately one-third of the nearly 200 hatchery programs currently in place are considered supplementation operations (Goodman 2004) and thus involve some level of

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interbreeding between hatchery- and natural-origin fish. Aspects of the genetic risks of integrated programs have been modeled (Lynch and O'Hely 2001; Ford 2002; Goodman 2005) and the demographic risks of integrated programs recognized (Goodman 2004; Mobrand et al. 2005), but empirical assessments of integrated programs are lacking, as illustrated by a recent review (Berejikian and Ford 2004) that compared the fitness of natural- and hatchery-origin fish. Seventeen of the 18 studies reviewed examined the effects of intentional selection, multiple generation effects, use of nonlocal broodstock, or combinations of these factors. Only one study (Blouin 2003) dealt with conditions that could be considered relevant to the concept of integrated hatchery programs.

The program analyzed by Blouin (2003) and more recently described by Araki et al. (in press) exclusively used natural-origin steelhead as broodstock. In this regard it is not unlike several other extant and pending programs that have restricted broodstock to natural-origin fish or established criteria for the proportion of hatchery-origin adults allowed on spawning grounds. To evaluate the risks and benefits posed by integrated programs, appropriate demographic and genetic data need to be collected (Hard 1995). Whenever possible, data collection should start at the beginning of a program to document whether first-generation hatchery fish are diverging from their native population. Evaluation at this time is critical because progeny of naturally spawning hatchery fish may possess characteristics that are intermediate between those possessed by wild- and hatchery-origin individuals. Consequently, when such individuals are compared with hatchery fish, differences between their traits will be less than those that may occur between pure wild and hatchery individuals.

Life history traits reflect local adaptations affecting population productivity and individual fitness (Stearns 1976; Roff 1992; Brannon et al. 2004). Changes in demographic or life history traits (such as a reduction in age-classes or skewed sex ratio) can reduce phenotypic variation and affect total annual egg production and effective population size (Nunney 1991; Waples 2002). Moreover, changes in adult spawn timing may reduce fitness by shifting fry emergence timing outside a locally adapted temporal window (Brannon 1987; Smoker et al. 1998; Einum and Fleming 2000; Brannon et al. 2004). In general, significant changes in locally adapted life history traits will be maladaptive in the wild (Lynch and O'Hely 2001; Ford 2002; Goodman 2004, 2005), leading to reduced individual reproductive success (Taylor 1991; Fleming and Gross 1993; Fleming et al. 2000) and possibly resulting in lower productivity of a naturally spawning population. Monitoring life history traits of hatchery populations to determine if they are diverging from their native population's distributions is a necessary part of a hatchery monitoring plan (Hard 1995; Goodman 2005). Significant differences may indicate that the artificial rearing environment is causing genetic divergence to occur between the two groups. However, phenotypic changes alone are not sufficient to conclude that genotypic divergence has occurred. To do that, fish from both groups should be spawned, incubated, and reared in a common environment. Observed differences under these circumstances would represent genetic change.

In 1997, an integrated hatchery program was begun to supplement the upper Yakima River population of spring Chinook salmon *O. tshawytscha* (Fast and Craig 1997). The program used only natural-origin fish as broodstock, and no attempt was made to control the proportion of hatchery-origin fish on the spawning grounds. Passage and hatchery facilities in the Yakima River provide excellent access to fish, so our approach has been to measure a variety of fitness-related life history traits on adult returns at different locations in the river. This paper describes the integrated hatchery program targeted on the upper Yakima River and reports on differences between wild-origin and first-generation hatchery-origin fish at several adult life history traits: age and sex composition, size at age, and migration and spawn timing. Finally, we discuss the probable origins of the differences we observed: whether they were genetic with serious implications for long-term impacts (Lynch and O'Hely 2001; Goodman 2004) or simply the result of phenotypic differences caused by hatchery rearing practices.

Methods

Yakima River spring Chinook salmon and the Yakima spring Chinook salmon enhancement project.—The Yakima River is a large tributary to the Columbia River located in south-central Washington State (Figure 1). It contains three genetically distinct wild spring Chinook salmon populations (Busack and Marshall 1991) that are reproductively isolated in both space and time: the American River (a tributary of the Naches River), the Naches River basin (excluding the American River), and the upper Yakima River (Figure 1). These three populations exhibit significant differences in spawn timing, age composition, and size at age (Major and Mighell 1969), as well as sex composition (Knudsen et al. 2005). All three populations are "stream-type" Chinook salmon (Healey 1991); adults migrate into the basin in the spring and spawn in the early fall, and juveniles spend a full year in freshwater before migrating to the ocean. Some

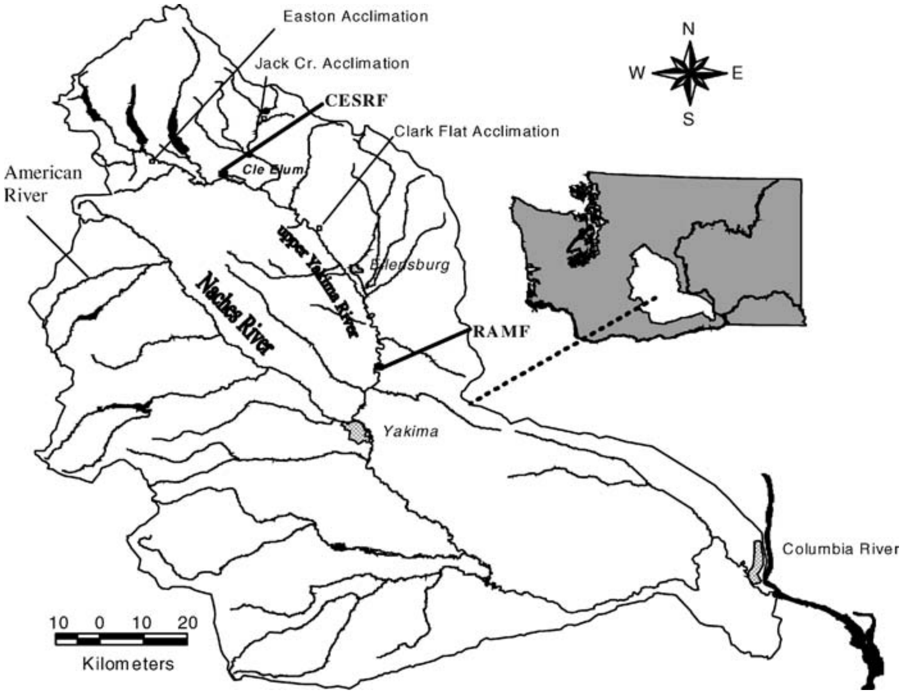

FIGURE 1.—Map of the Yakima River basin, Washington, showing the upper Yakima River, Roza Adult Monitoring Facility (RAMF), Cle Elum Supplementation Research Facility (CESRF), spring Chinook salmon acclimation sites, Naches River, and the American River.

males mature precociously in freshwater in their first or second year (see Larsen et al. [2004] and Pearsons et al. [2004] for a full description of hatchery and wild precocious male production in the upper Yakima River).

The Yakima–Klickitat Fishery Project (YKFP) began a spring Chinook salmon hatchery program at the Cle Elum Supplementation Research Facility (CESRF) near Cle Elum on the upper Yakima River (river kilometer [rkm] 297, measuring from the confluence with the Columbia River; Figure 1) in 1997. This program is a supplementation effort targeting the upper Yakima River population and is designed to test whether artificial propagation can be used to increase natural production and harvest opportunities while limiting ecological and genetic impacts. It is an integrated hatchery program (Mobrand et al. 2005) because only natural-origin broodstock are used and returning hatchery-origin adults are allowed to spawn in the wild. The program includes a domestication monitoring effort that compares several traits of the supplemented population with those of a hatchery-only control line founded from first-generation hatchery returns, and with those of a wild control line (the unsupplemented Naches River population; Busack et al. 2004).

A note on nomenclature is in order at this point. As integrated programs proceed, it is inappropriate to call fish resulting from natural spawning "wild" because they may be the progeny of naturally spawning hatchery fish. These fish are more appropriately called "natural-origin" fish. We call the naturally produced fish in this study wild because they occurred before significant numbers of naturally produced fish of hatchery ancestry were possible (Table 1). Hatchery-origin, age-3 males from the 1997 brood year (BY) may have made some contribution to the 2000 brood, but this influence was probably slight as these fish accounted for only 5% of the natural spawning population (Yakama Nation [YN], unpublished data). The natural-origin upper Yakima River spring Chinook salmon in this study can be considered wild also because this population had been subjected to only negligible levels of hatchery activity in the past.

Broodstock collection and fish culture.—Broodstock were collected exclusively from wild adults between 1997 and 2000 at the Roza Adult Monitoring Facility (RAMF) located adjacent to Roza Dam (rkm 206; Figure 1). Roza Dam is an irrigation diversion structure

TABLE 1.—Degree of hatchery ancestry among natural-origin spring Chinook salmon from the upper Yakima River through the first three generations of integrated hatchery operation. Data are shown for return years 2000–2008, which correspond to brood years 1997–2005. Entries are fish ages at return. Those in ordinary type indicate fish with wild ancestry only, whereas those in bold italics indicate fish with substantial hatchery ancestry. The one entry with an asterisk indicates fish with a small hatchery influence from age-3 males (see text for further details).

Brood year	Generation 1 (Initiation of hatchery operations and broodstock collection)				Generation 2 (Hatchery fish begin returning to spawn naturally)				Generation 3 (First returns of natural-origin fish produced by naturally spawning hatchery fish)			
	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	2007	2008
1997				3	4	5						
1998					3	4	5					
1999						3	4	5				
2000							3	4	5			
2001								3*	***4***	***5***		
2002									***3***	***4***	***5***	
2003										***3***	***4***	***5***
2004											***3***	***4***
2005												***3***

that all upper Yakima River salmon must pass through before reaching their spawning grounds. The RAMF was operated daily between April and September. No more than 50% of the wild fish collected on any given day at RAMF were used as broodstock. All returning fish were enumerated, and a subsample was selected and taken by truck to CESRF, where they were held until they reached maturity. Most fish collected were used as broodstock for the supplemented line or for the hatchery control line, but additional wild- and hatchery-origin fish were collected at RAMF for other research purposes. All fish transferred to CESRF were tagged with passive integrated transponder (PIT) tags (Prentice et al. 1990) in the pelvic girdle at RAMF so that individual data collected at the two sites could be linked. Considerable attention was paid to collecting fish randomly over the entire run. In 1997 and 1998, broodstock was collected randomly based on a list of random numbers developed from the broodstock need and the predicted run size. This method, however, created the potential for significant over- or under-collecting if run predictions were inaccurate. For this reason, from 1999 onward broodstock collection has been based on average migration timing patterns past RAMF (Bosch 2005). We used the same method for hatchery-origin adults, which began returning in 2001.

It was not possible to collect broodstock by sex at RAMF because adults pass RAMF 1–5 months prior to reaching full maturity and consequently have not fully developed their distinguishing secondary sexual characteristics. For this reason, we collected two age–size categories of broodstock: age-4 and older returns (where sex identification was ambiguous) and age-3 returns, which could be accurately identified based on their significantly smaller body size and which were known to be nearly all males (Washington Department of Fish and Wildlife [WDFW] and YN, unpublished data).

Hatchery and wild adults transferred to CESRF were held together in a single concrete raceway until reaching maturity and then artificially spawned. Fertilized eggs from each female were sequestered from one another until they reached the eyed stage of development. By that time, pathogen screenings were completed. Eggs from females deemed to be pathogen free were combined and placed into Heath trays supplied with rugose substrate and incubated until yolk absorption. After completion of the incubation period, fry were transferred and reared in concrete raceways (30 m long × 3.3 m wide × 3.1 m deep) with a water flow of 2,200 L/min for approximately 16 months and then were moved to three acclimation sites (Figure 1) for an additional 8–10 weeks of rearing. Mean rearing densities ranged annually from approximately 36,000 to 46,000 fish per raceway. In mid-March, raceway screens were pulled and fish were allowed to volitionally emigrate over the following 2 months. Total smolt releases ranged from 370,000–834,000 fish for BYs 1997–2000, and fork lengths and

TABLE 2.—Mean hatchery smolt body weights and fork lengths by brood year for upper Yakima River spring Chinook salmon. Fish were sampled just prior to the initiation of volitional releases from the acclimation sites.

Brood year	Sample date	Body weight (g)	Fork length (mm)	*N*
1997	Mar 11 1999	17.9	116.7	654
1998	Mar 13 2000	15.6	111.6	1,007
1999	Mar 12 2001	18.5	118.6	1,078
2000	Mar 18 2002	20.1	121.7	1,079

body weights averaged between 115 and 122 mm and 17.2 and 20.1 g, respectively, in mid-March as volitional releases began (Table 2). In mid-May, any juveniles still remaining at the acclimation sites were forced out of their raceways. The first release of hatchery yearling smolts occurred in 1999. All hatchery releases were adipose fin clipped for post-release monitoring and to allow unambiguous identification of hatchery fish upon return as adults.

Data collection.—Both wild and hatchery adults were sampled at two sites each year. At RAMF, passage date, body length, weight, and age data were collected as fish migrated upstream. At CESRF, maturation date and gender were noted as fish were artificially spawned, and these data were linked back to the fish's RAMF passage date, size data, and age data by means of an adult PIT tag applied at RAMF.

Upstream migrants were processed daily at RAMF over the course of the run each year. All hatchery fish were identified by their missing adipose fins and were diverted to a holding tank containing an anesthetic solution of MS-222 (tricaine methanesulfonate; Bell 1964) at a concentration of approximately 130–260 mg of MS-222/L of water. Each fish was examined for marks and tags and was visually classified as either age 3 or older based on body size; some were sampled for additional biological information. The proportion (0.10–0.25) of hatchery fish selected for biological sampling depended on the magnitude of the forecasted run size. Selected hatchery fish were measured for postorbital hypural plate (POHP) length, body weight, age (scale sample), and arrival date at RAMF. After being sampled, fish were briefly held to recover from the anesthetic and released back to the river to complete their spawning migration or transferred to CESRF if they had been selected as potential broodstock or for other purposes. Similarly, all the wild fish selected for broodstock were anesthetized, measured, and weighed at RAMF before being transferred to CESRF.

Sex and age composition.—Estimates of the percentages of adult females and males passing RAMF were made on the basis of fish collected at RAMF and taken to CESRF, where sex was identified by post mortem inspections of wild fish selected for broodstock and wild and hatchery adults that met other experimental needs. As mentioned above, fish transferred to CESRF were intramuscularly PIT-tagged in the pelvic girdle, allowing them to be linked back to their collection date at RAMF. This ability to link individual fish back to when they were sampled at RAMF allowed us to identify the sex of the fish and therefore to estimate age-specific sex ratios for each return year. These ratios were then multiplied by age-specific RAMF return numbers to calculate age- and sex-specific total return numbers. Fish produced in any particular BY returned at age 3, 4, or 5. Data were organized on a BY basis for both sex and age composition analyses. Comparisons of hatchery and wild sex composition were made for each BY using a χ^2 test with Yates correction (Zar 1999).

As noted above, age-3 returns (jacks) were identified by their significantly smaller body size. The age composition of wild age-4 and age-5 adults was estimated from fish taken to CESRF. Acetate impressions were made from scales that had been placed on labeled gummed cards, and ages were determined by examining the impressions using a microfiche reader. Two scale analysts independently aged all scales and resolved disagreements. Ages were designated as the number of years from conception (BY) to return year. Thus, a fish produced from parents spawning in the fall of 1998 and returning in 2003 is identified as age 5. We evaluated temporal trends in age structure by regressing age-class proportions over the four BYs.

All means were calculated as unweighted averages, and all statistical tests were considered significant if the P-value was 0.05 or less.

Size at age.—Lengths and body weights of wild-origin fish were taken when the fish arrived at RAMF, and size data for hatchery-origin fish were also collected at RAMF. This was done to ensure that both types of fish would be in similar stages of maturity when size measurements were made. Within each BY, hatchery and wild size-at-age distributions were compared by age-class by means of a two-way analysis of variance (ANOVA; origin × year). If the interaction effect was significant ($P < 0.05$), we performed a t-test for each BY to examine origin effects. Sexual dimorphism in size is common in Pacific salmon and does occur in the Naches and American River populations of spring Chinook salmon; however, upper Yakima hatchery- and natural-origin adults do not exhibit significant sexual dimorphism in either body weight or length (WDFW and YN, unpublished data). Therefore, males and females were combined within age-classes in all body size analyses.

Adult passage timing.—We analyzed passage timing by return year rather than BY, because although populations of adult Pacific salmon demonstrate consistent patterns in upstream migration timing, there can be significant year-to-year variation resulting from interannual differences in river discharge (Keefer et al. 2004) and ocean water temperature regimes (Hodgson and Quinn 2002). Passage data were obtained by recording when fish were passed upstream through RAMF. We compared hatchery and wild passage timing distributions but grouped returns into two types

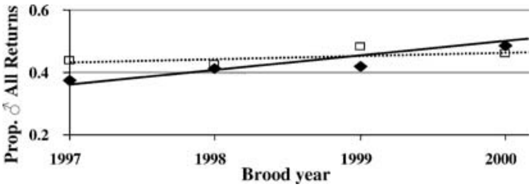

FIGURE 2.—Proportion of hatchery (diamonds; solid line) and wild (squares; dashed line) spring Chinook salmon returns to the upper Yakima River, Washington, composed of males, by brood year.

for analysis: age 3 and ages 4 and 5 combined. The data were analyzed with a three-way ANOVA testing for origin (hatchery, wild), type (age 3, ages 4–5), and year (2001–2004) effects, as well as interactions. All RAMF passage dates were converted to ordinal dates (day of year). The passage dates were $\log_e$ transformed to normalize distributions during analyses.

Adult spawn timing.—We were able to use a "common-garden" experiment to test for differences in maturation timing at CESRF because hatchery- and wild-origin adults were held together in a single concrete raceway. Beginning in early September and continuing into early October, adults were checked for ripeness and were spawned weekly. Ripe fish were identified when either eggs or milt were extruded with gentle manual pressure; fish were then transferred to a separate raceway for holding until spawning the next day. Hatchery- and wild-origin spawn timing distributions were compared with a three-way ANOVA (origin × return year × sex). For these analyses, we divided sex into three categories: age-3 males, age-4 males, and age-4 females. As with passage date and for the same reasons, analysis was done on a return year rather than BY basis, and all dates were converted to ordinal dates. Spawn timing appeared to be normally distributed, so dates were not $\log_e$ transformed. Age-5 returns were not included because they were not represented by one or both sexes in some years and represented 1–6% of total returns.

Exploration of fitness impacts.—The fitness cost of differences between wild- and hatchery-origin fish for traits in which standard deviations could be estimated was explored using Lande's (1976) stabilizing selection model for quantitative variation, in which fitness declines in a Gaussian pattern as trait value deviates from an optimum. The severity of the fitness loss depends on the strength of selection. Mean fitness in the notation of Ford (2002) is given by

$$\overline{W} \propto \exp\left[\frac{-(\bar{z}-\theta)^2}{2(\omega^2+\sigma^2)}\right],$$

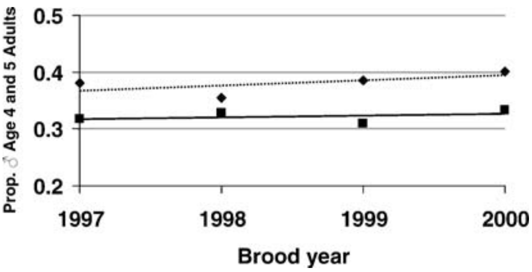

FIGURE 3.—The proportion of male spring Chinook salmon returns (ages 4 and 5 only) to the upper Yakima River, Washington, by origin (wild [squares; solid line] or hatchery [diamonds; dashed line]) and brood year.

where $\bar{z}$ is the mean trait value, θ is the optimum trait value, ω is the selection intensity, and σ^2 is the trait variance. We assumed that the wild component of the population was at the optimum.

Results

Sex Composition

The proportions of female and male wild- and hatchery-origin adults differed significantly in three of four BYs (χ^2 tests; BY 1997 and 1999–2000: $P < 0.01$; BY 1998: $P = 0.192$). Females were predominant in wild returns in all years, while the proportion of hatchery males steadily increased from 0.38 to 0.49 (Figure 2; hatchery linear regression: $P = 0.049$, $r^2 = 0.855$). Conversely, wild returns showed no significant trend in the proportion of males over time (linear regression: $P = 0.388$). When just age-4 and age-5 returns were examined, the proportion of males for both hatchery and wild returns showed no trend over time (wild linear regression: $P = 0.386$; hatchery regression: $P = 0.638$; Figure 3), indicating that the trend in increasing proportion of males over time was a consequence of the increase in age-3 returns. However, the proportion of age-4 and age-5 males was always lower in the hatchery returns than in the wild returns by an average of 0.06.

Age Composition

The majority of hatchery- and wild-origin fish within a brood returned at age 4 ($\geq$76%; Table 3), followed, in descending order, by ages 3 and 5. In three of four BYs, hatchery- and wild-origin age compositions were significantly different ($P < 0.01$; Table 4). There were significant temporal trends in hatchery age composition that were not observed in wild age composition. In general, for wild-origin adults, the proportion of fish returning at ages 3 and 4 showed no temporal trend over BYs (all wild-origin linear regressions: $P \geq 0.61$). In contrast, the proportion of age-3 hatchery returns

TABLE 3.—Age and sex composition of upper Yakima River wild- and hatchery-origin spring Chinook salmon by brood year based on scales and mark recoveries at the Roza Adult Monitoring Facility (RAMF) or the Cle Elum Supplementation Research Facility (CESRF). Sample sizes for sexing are in parentheses and represent fish examined post mortem at CESRF.

Origin	Brood year	Age	Age-class (%)[a]	Male (%)	Female (%)
Wild	1997	3	9.4	9.4 (41)	0.0 (0)
		4	88.3	33.5 (181)	54.8 (297)
		5	2.3	1.0 (12)	1.3 (17)
	1998	3	12.8	11.6 (28)	1.2 (2)
		4	82.8	29.2 (177)	53.6 (325)
		5	4.3	1.7 (25)	2.6 (38)
	1999	3	17.4	16.5 (37)	0.9 (2)
		4	77.8	30.3 (121)	47.5 (190)
		5	4.8	1.6 (1)	3.2 (2)
	2000	3	9.9	9.9 (55)	0.0 (0)
		4	88.7	35.6 (202)	53.1 (302)
		5	1.4	0.5 (3)	0.9 (5)
Hatchery	1997	3	8.5	8.5[b]	0.0
		4	89.4	28.4 (35)	61.0 (75)
		5	2.1	0.7 (1)	1.4 (2)
	1998	3	12.7	12.7 (5)	0.0 (0)
		4	81.3	25.9 (57)	55.4 (113)
		5	6.0	2.7 (21)	3.3 (26)
	1999	3	15.9	15.9 (10)	0.0 (0)
		4	82.2	26.1 (25)	56.1 (41)
		5	1.9	0.0 (0)	1.9 (2)
	2000	3	22.9	22.9 (26)	0.0 (0)
		4	75.6	25.3 (37)	50.3 (60)
		5	1.5	0.4 (2)	1.1 (5)

[a] For ages 4 and 5, age-class was determined from scales and tags or marks. Age-3 percentages are based on visual counts as fish passed RAMF. Age-4 and age-5 percentages were then adjusted to account for the age-3 component.

[b] No brood year 1997 hatchery age-3 returns were taken to CESRF for post mortem sexing. All were assumed to be males.

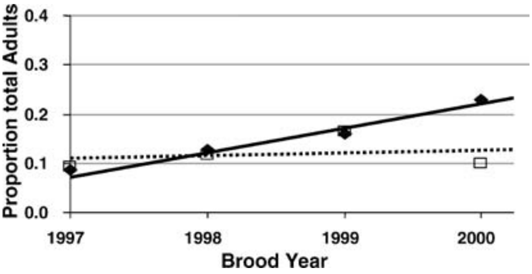

FIGURE 4.—The proportion of spring Chinook salmon adults returning as age-3 spawners to the upper Yakima River, Washington, by origin (wild [squares; dashed line] or hatchery [diamonds; solid line]) and brood year.

significantly increased over time (regression: $P = 0.003$, $r^2 = 0.912$; Figure 4), more than doubling from 0.09 to 0.23. The wild and hatchery proportions of age-3 returns were nearly identical for the first three BYs and then deviated sharply in 2000, driving the trend observed in hatchery returns in Figure 4. The increase in the proportion of hatchery age-3 returns (nearly exclusively male) resulted in a significant decrease in hatchery mean age at maturation over time (regression: $P = 0.05$, $r^2 = 0.85$), while wild mean age at maturation showed no trend (regression: $P = 0.55$).

Size at Age

The mean POHP lengths and body weights of hatchery- and wild-origin returns by BY and age are given in Table 5 along with sample sizes and standard deviations (SDs). For each BY, age-3 hatchery returns were smaller than wild-origin age-3 returns (length and body weight ANOVAs, origin effects: $P < 0.001$; Table 6). On average, hatchery age-3 fish were 2.7 cm and 0.3 kg smaller than wild-origin fish, representing

TABLE 4.—Age composition χ^2 test results for origin (hatchery–wild) effects by brood year for upper Yakima River spring Chinook salmon. The sexes were combined within age-classes.

Brood year	*P*
1997	0.072
1998	0.002
1999	0.002
2000	<0.001

TABLE 5.—Mean postorbital hypural plate (POHP) lengths (cm), body weights (BW, kg), and sample sizes (*N*) of hatchery- and wild-origin spring Chinook salmon returns to the upper Yakima River for brood years 1997–2000.

Brood year	Age	Origin	POHP (SD)	BW (SD)	*N*
1997	3	Hatchery	38.3 (3.8)	1.2 (0.4)	635
		Wild	41.3 (3.5)	1.5 (0.4)	41
	4	Hatchery	59.3 (4.0)	4.3 (0.8)	2,342
		Wild	61.3 (4.2)	4.6 (0.9)	483
	5	Hatchery	67.0 (6.3)	5.8 (1.4)	34
		Wild	71.2 (4.0)	7.1 (2.0)	30
1998	3	Hatchery	39.9 (3.5)	1.4 (0.4)	473
		Wild	42.9 (3.1)	1.7 (0.4)	32
	4	Hatchery	59.2 (3.8)	4.1 (0.8)	1,535
		Wild	60.9 (3.6)	4.5 (0.8)	535
	5	Hatchery	71.4 (4.1)	6.8 (1.2)	215
		Wild	72.3 (4.5)	7.1 (1.3)	62
1999	3	Hatchery	38.7 (4.1)	1.2 (0.4)	26
		Wild	41.6 (4.0)	1.5 (0.4)	46
	4	Hatchery	60.6 (4.4)	4.4 (1.0)	255
		Wild	62.4 (4.3)	4.7 (0.9)	312
	5	Hatchery	71.0 (2.8)	5.9 (0.8)	2
		Wild	69.3 (2.5)	6.2 (0.1)	3
2000	3	Hatchery	41.8 (3.7)	1.5 (0.4)	394
		Wild	43.5 (3.7)	1.6 (0.5)	55
	4	Hatchery	59.5 (3.9)	4.1 (0.8)	451
		Wild	59.8 (4.1)	4.1 (0.8)	515
	5	Hatchery	70.1 (3.8)	6.4 (1.6)	18
		Wild	70.8 (5.2)	6.5 (1.9)	12

TABLE 6.—Comparisons of postorbital hypural plate (POHP) length and body weight distributions of age-3 Yakima River spring Chinook salmon returns using a two-way ANOVA (origin × brood year [BY]) of hatchery and wild origin for BYs 1997–2000.

Source	Sum of squares	df	Mean square	*F*-ratio	*P*
POHP length					
Origin	801.60	1	801.60	58.57	<0.001
BY	761.81	3	253.94	18.55	<0.001
Origin × BY	57.63	3	19.21	1.40	0.240
Error	23,184.60	1,694	13.69		
Body weight					
Origin	6.15	1	6.15	39.09	<0.001
BY	6.09	3	2.03	12.90	<0.001
Origin × BY	1.11	3	0.37	2.36	0.070
Error	266.62	1,694	0.16		

a divergence from wild distributions of between 0.5 and 1.0 SD. Hatchery age-4 fish were also 1.5 cm shorter and 0.3 kg lighter on average than wild-origin returns except in BY 2000. The mean differences represent a shift in body size distributions of up to 0.5 SD. Initial analysis of age-4 size distributions using a two-way ANOVA (origin × BY effects) indicated there were significant origin ($P < 0.001$), BY ($P < 0.001$), and origin × BY interaction ($P < 0.001$) effects; the interaction was obviously caused by BY 2000. We then reanalyzed the age-4 length and body weight distributions by BY using a *t*-test to assess origin effects. Wild returns were significantly larger than hatchery returns in all BYs but 2000 (POHP length and body weight *t*-test: $P < 0.001$). In 2000, wild fish were longer but not significantly so (*t*-test: $P = 0.223$) and were equal in body weight to hatchery returns (*t*-test: $P = 0.967$). The sample size for age-5 fish in BY 1999 was very small, so we limited the age-5 analysis to BYs 1997, 1998, and 2000. Within those BYs, age-5 wild fish were significantly larger than hatchery returns: 1.9 cm larger and 0.6 kg heavier (length and body weight ANOVAs, origin effects: $P < 0.01$; Table 7). These differences represent an average divergence in trait distributions of approximately 0.4 SD.

TABLE 7.—Two-way ANOVA results comparing postorbital hypural plate (POHP) length and body weight distributions of age-5 hatchery- and wild-origin spring Chinook salmon returns to the upper Yakima River for brood years (BYs) 1997, 1998, and 2000.

Source	Sum of squares	df	Mean square	*F*-ratio	*P*
POHP length					
Origin	117.75	1	117.75	6.09	0.014
BY	324.02	2	162.01	8.38	<0.001
Origin × BY	95.32	2	47.66	2.46	0.086
Error	7,059.28	365	19.34		
Body weight					
Origin	13.230	1	13.230	7.429	0.007
BY	15.890	2	7.945	4.461	0.012
Origin × BY	12.731	2	6.365	3.574	0.029
Error	650.029	365	1.781		

TABLE 8.—Three-way ANOVA results of the $\log_e$ transferred passage date of spring Chinook salmon at the Roza Adult Monitoring Facility on the upper Yakima River. The ANOVA tested for effects of origin (hatchery versus wild), type (age 3 versus ages 4–5), return year (RY; 2001–2004), and all interactions.

Source	Sum of squares	df	Mean square	*F*-ratio	*P*
RY	0.453	3	0.151	4.254	0.005
Type	0.187	1	0.187	5.258	0.022
Origin	0.082	1	0.082	2.312	0.129
RY × type	0.170	3	0.057	1.600	0.187
RY × origin	0.042	3	0.014	0.391	0.759
Type × origin	0.009	1	0.009	0.258	0.612
RY × type × origin	0.063	3	0.021	0.593	0.620
Error	49.322	1,390	0.035		

Passage Timing

Hatchery and wild passage timing at RAMF did not differ significantly in the three-way ANOVA (origin effects: $P = 0.129$; Table 8), and hatchery and wild median passage timing followed no consistent pattern across years (Table 9). We did find that age-4 and age-5 adults passed RAMF on average 19 d earlier than did age-3 adults (average difference over return years and origins; type effect: $P = 0.022$). There were also significant return year effects ($P = 0.005$), driven to a large degree by later passage in 2002.

Spawn Timing

Beginning with the first hatchery-origin age-4 adults artificially spawned at CESRF in 2001, hatchery returns have matured significantly earlier than wild fish (origin: $P < 0.001$; Table 10), spawning 5.1 d earlier on average than wild fish (Table 11). Contrary to fish origin, age of maturation within hatchery or wild fish did not affect when the fish matured, as spawn timing of age-3 and age-4 males and females were similar (sex effect: $P = 0.113$). The observed difference in spawn timing was equal to approximately 0.7 SD.

Exploration of Fitness Impacts

On the basis of recent reviews, Hard (2004) concludes that selection intensity (ω) for life history traits is unlikely to be outside the range of 1–4 SD. Application of Lande's (1976) model with these values suggests that the differences in body size and spawn

TABLE 9.—Median passage timing (day of year) of hatchery- and wild-origin spring Chinook salmon at the Roza Adult Monitoring Facility (RAMF), Yakima River, for age-3 and age-4–5 returns (types used in three-way ANOVA in Table 8). Sample sizes (*N*) are total age-5 returns passing RAMF; na = not applicable.

Type	Return year	Origin	Median	*N*
Age 3	2000	Wild	166.5	474
		Hatchery	164.0	618
	2001	Wild	160.0	336
		Hatchery	167.0	990
	2002	Wild	175.0	131
		Hatchery	177.5	86
	2003	Wild	167.0	774
		Hatchery	166.0	1,133
	2004	Wild	159.0	711
		Hatchery	163.0	216
Ages 4–5	2000	Wild	142.0	10,619
		Hatchery[a]	na	
	2001	Wild	142.0	5,010
		Hatchery[b]	145.0	6,1808
	2002	Wild	160.0	2,361
		Hatchery	163.0	6,133
	2003	Wild	146.0	784
		Hatchery	144.0	1,151
	2004	Wild	141.0	7,144
		Hatchery	143.0	2,985

[a] No age-4 or age-5 returns occurred in this year.

[b] No age-4 returns occurred in this year.

timing ($\bar{z} - \theta$) observed in this study (0.5–1.0 SD) would equate to a relative fitness of approximately 77–99% for a single trait. For the more-likely ω range of 3–4 SD (Hard 2004), the relative fitness range would be 95–99%.

Discussion

Sex Composition

While females were predominant in wild returns in all years and showed no trend over time, the proportion of hatchery males steadily increased over time. It appears some facet of hatchery rearing incrementally increased the portion of fish maturing as age-3 males. When we examined the mean fork lengths of migrating hatchery and wild smolts captured in a juvenile trap at Roza Dam during March 15 to May 21 between 1999 (BY 1997) and 2002 (BY 2000), we noticed two trends: (1) there was an increasing difference in length between hatchery and wild smolts and (2) hatchery smolts were stable in size over time, while natural-origin smolts decreased in size over time (Figure 5). Larger juvenile size at release can result in increased production of age-3 males (jacks) in Chinook salmon (Vøllestad et al. 2004), but mean release sizes of CESRF juveniles did not increase steadily over time (Table 2) and in-river hatchery smolt samples demonstrated a flat temporal trend in length (Figure 5) that does not parallel the increase in hatchery age-3 production. In addition, while mean wild smolt lengths decreased over time likely as a result of density-dependent interactions (Pearsons et al. 2004), the proportion of wild age-3 adults produced from these BYs remained relatively stable over time. All of this indicates that smolt length does not appear to be a good predictor of age-3 male production in upper Yakima

TABLE 10.—Three-way ANOVA of spawn timing for spring Chinook salmon in the upper Yakima River. The ANOVA tested for the effects of year, origin (hatchery, wild), and sex (age-4 males, age-4 females, and age-3 jacks) and all possible interactions.

Source	Sum of squares	df	Mean square	*F*-ratio	*P*
Origin	3,604.0	1	3,604.0	67.0	<0.001
Year	1,028.9	4	257.2	4.8	0.001
Sex	235.4	2	117.7	2.2	0.113
Year × sex	639.5	8	79.9	1.5	0.157
Year × origin	224.0	4	56.0	1.0	0.385
Sex × origin	12.2	2	6.1	0.1	0.893
Year × sex × origin	276.8	8	34.6	0.6	0.742
Error	114,653.5	2,130	53.8		

TABLE 11.—Mean spawning date (day of year) for hatchery- and wild-origin spring Chinook salmon in the upper Yakima River. Ages and sexes are combined because there were no significant differences between age-3 returns (primarily males), age-4 males, and age-4 females (Table 10), which represent between 94% and 99% of all returns.

Return year	Origin	Mean	SD	*N*
2001	Hatchery	256.9	7.3	79
	Wild	261.3	8.0	413
2002	Hatchery	260.5	7.2	92
	Wild	267.9	7.2	385
2003	Hatchery	259.8	6.8	127
	Wild	266.0	7.8	369
2004	Hatchery	262.8	8.4	60
	Wild	265.2	6.7	347

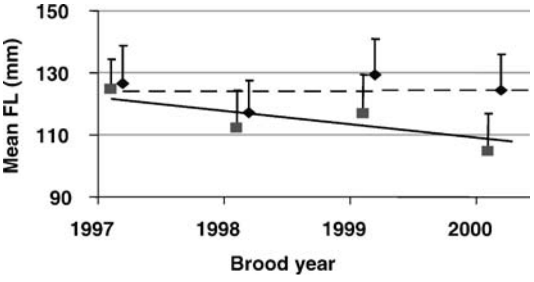

FIGURE 5.—Mean + SD fork lengths (FLs) of hatchery (diamonds; dashed line) and wild (squares; solid line) spring Chinook salmon smolts sampled at the Roza Dam smolt trap on the Yakima River, Washington.

River hatchery or wild returns. The female-skewed sex ratios of both hatchery and wild age-4 and age-5 returns are in large part attributable to age-1 (wild) and age-2 (wild and hatchery) nonanadromous precocious males and to age-3 returns maturing and thus not contributing to the older male age-classes in the cohort. Larsen et al. (2004) estimated that the CESRF hatchery produced significantly more age-2 precocious males than the naturally spawning wild population, which produced both age-1 and age-2 precocious males (Pearsons et al. 2004). Larsen et al. (2004) hypothesized that in hatchery-origin adults, the increased production of precocious males should result in a sex ratio that is even more highly skewed toward females, since naturally spawning precocious males are unlikely to survive postspawning and therefore "drop out" of a cohort. Our results do not support this hypothesis and indicate that just the opposite appears to be occurring: the proportion of males is increasing in adult hatchery BY returns over time primarily because of increasing proportions of age-3 hatchery males.

Age Composition

We observed a consistent flat temporal trend in wild age composition by BY, indicating that the upper Yakima River wild population has maintained a stable age distribution, perhaps due to stabilizing selection. Reduced mean age at maturity of hatchery fish due to increases in the proportion of hatchery age-3 returns has been observed in other spring Chinook salmon hatchery programs (Hankin 1990) such as those in the Tucannon (Gallinat 2004), Grand Ronde (Carmichael and Messmer 1995), and Wenatchee (Murdoch et al. 2005) rivers. The cause of the increase in age-3 males in the YKFP is unclear as discussed above, and smolt length does not appear to explain the trend.

One factor that differs in wild and hatchery juvenile populations is the capacity of wild fish to migrate from their rearing areas at any time during the year. Wild juvenile passage at a downstream juvenile trap occurs over a much broader temporal period and begins earlier than the hatchery juvenile out-migration (unpublished data). Hatchery juvenile releases do not begin until mid-March, 3–4 months after wild juvenile Chinook salmon have begun moving downstream in the Yakima River (Bosch 2005). Perhaps the restriction of hatchery smolt movements and the constraint to a later migration period have enhanced the occurrence of age-3 fish. We are unsure why such an increase has occurred and will continue to monitor this trend in the future.

Size at Age

The magnitude of the one-generation shift in length and body weight distributions represents a response of approximately 0.4–1.0 SD/generation. These exceed rates of declining body size in Chinook salmon populations observed by Ricker (1995) and Bigler et al. (1996). In fish that mature at multiple ages, such as Chinook salmon, decreases in average body size can be due to either reduced mean age at maturation, such as when older age-classes are fished out in newly exploited populations, or decreases in growth reflected in lower size at age. Since the changes we observed were changes in size at age, they represent decreases in growth rate. Adult size at age is subject to environmentally driven phenotypic plasticity (Riddell 1986; Hard 1995), such as the growth response to the ocean environment (Wells et al. 2006), and can also be significantly affected by size and time of smolt releases in hatchery programs (Bilton 1980). Size at age and growth rate are also influenced by both natural and sexual selection pressures (Quinn and Foote 1994; Hendry 2001) and have been shown to respond to selection (Gjerde and Gjedrem 1984; Su et al. 2002). Irrespective of causes, smaller body size can reduce maternal fitness by (1) adversely affecting a female's ability to compete in the wild for nest sites and to construct and guard redds (van den Berghe and Gross 1989; Foote 1990); (2) decreasing redd depth, thereby increasing redd vulnerability to scour during flood events (van den Berghe and Gross 1989; Steen and Quinn 1999); and (3) reducing mean fecundity (Healey and Heard 1985; Beacham and Murray 1993). Smaller body size can also influence spawning distribution by reducing the ability of fish to colonize more-distant or higher-elevation spawning areas (Beacham and Murray 1993; Kinnison et al. 2001) and larger portions of river systems (Rogers 1987; Blair et al. 1993; Hendry and Quinn 1997). In addition, lower mean body weight also reduces the average carcass biomass returning to the natal basin, potentially reducing exogenous nutrients available to rearing juveniles (Bilby et al. 1996); however, this would only be a significant problem if nutrients are limiting production and demographic benefits of supplementation are not realized.

The observed difference in POHP length between first-generation hatchery- and natural-origin fish is similar to the results reported in three other hatchery projects using natural-origin broodstock: Tucannon River spring Chinook salmon, Sacramento winter Chinook salmon, and Cedar River sockeye salmon *O. nerka*. Tucannon River hatchery-origin returns were smaller at age during the initial years of operation (Gallinat 2004). The Sacramento River winter Chinook salmon program has been in operation at some level since 1989. In 2003, hatchery-origin females were on average 1.3 cm shorter in fork length (~0.33 SD) than natural-origin females, and hatchery-origin males were on average 4.9 cm shorter (~0.75 SD) than natural-origin males (USFWS 2004). Fresh et al. (2003) found that the mean POHP length of first-generation age-4 Cedar River hatchery sockeye salmon females was 1.5 cm shorter than that of wild conspecifics. In addition, Unwin and Glova (1997) found that New Zealand hatchery-reared male Chinook salmon returned 0.6 cm smaller than natural-origin males.

In both the Tucannon River and New Zealand studies, hatchery fish were much larger at juvenile release than their natural-origin counterparts, and this larger size was probably the primary cause of the observed difference in size at age. As noted above (see also Figure 5), CESRF spring Chinook salmon smolts are larger than upper Yakima River wild smolts migrating contemporaneously and, due to wild smolt size decreasing over time, the difference between hatchery and wild smolt sizes increases over time. Thus, if smolt size is affecting adult size, we would expect (1) the difference in hatchery and wild adult body sizes to increase over time and (2) the wild body size at age to decrease (reflecting the trend in Figure 6). However, these trends were not observed. Thus, it does not appear that differences in smolt size would cause the observed differences in adult body size.

It is clear, however, that because size differences were consistently observed in age-3 fish, the causal mechanism(s) responsible for the shift in size distribution must act during the 18 months between juvenile release and return at maturation. One possibility is that the hatchery juveniles undergo a period of depressed growth while they transition to natural food sources, and subsequent growth never entirely compensates for this energy deficit. Another is that hatchery-origin juveniles out-migrate more slowly than natural-origin juveniles, arriving in marine waters later. Bilton (1980) noted that earlier releases of coho salmon *O. kisutch* returned at a larger size because they had the opportunity to rear for a longer period in the more-productive marine environment.

One strong selection factor that could impact the trait distributions of CESRF returns are the hatchery-selective fisheries in the lower Columbia River that target adipose fin–clipped hatchery fish. If these fisheries selectively remove larger hatchery fish, they could shift the size distribution of survivors lower. However, the commercial and sport hatchery-selective fisheries did not occur until 2002 (WDFW and ODFW 2002) and thus did not interact with hatchery-origin age-3 returns from BYs 1997 and 1998 and age-4 returns from BY 1997. Since we observed that each of these hatchery groups was significantly smaller than wild returns, it does not appear that lower Columbia River hatchery-selective fisheries could be responsible for the divergence in body size.

Passage and Spawn Timing

Run and spawn timing have been shown to be heritable traits in salmonids (Siitonen and Gall 1989; Smoker et al. 1998; Quinn et al. 2002). After one generation of hatchery influence, we observed significant differences between hatchery and wild fish passing RAMF, and median passage dates of hatchery fish lagged by 3 d on average. Passage at RAMF occurs over approximately 5 months, so a lag in median passage timing of 3 d is unlikely to have a significant impact on the reproductive success of naturally spawning hatchery fish because we found no correlation between RAMF passage date and date of maturation. More noteworthy was the consistent, significantly earlier maturation of hatchery fish relative to wild fish after being held in a common vessel under the same environmental conditions. Earlier maturation was also noted by Quinn et al. (2002) in three Chinook salmon hatcheries and was attributed to inadvertent selection. A shift toward earlier hatchery maturation timing advances embryo development through additional development days, resulting in early hatchery fry emergence. Based on September 2000–2004 upper Yakima River mean daily water temperatures, eggs that were spawned 5.2 d earlier than the mean natural spawning date would acquire 77°C in additional temperature units. This should result in earlier emergence timing, which could cause higher mortality for the early emerging fish due to suboptimal rearing conditions. Conversely, early emergence could allow hatchery fry to establish prior residence when early rearing condition are better than average, allowing them to displace wild fry downstream from preferred rearing areas (Berejikian et al. 1996; Rhodes and Quinn 1998).

Fitness Implications

The development of differences in traits between hatchery- and natural-origin fish derived from the same native stock may have a significant genetic component as a result of domestication, either through unintentional directional selection or relaxation of natural selection pressures in the hatchery (Hard 1995; Lynch and O'Hely 2001; Ford 2002). They may also be caused by phenotypic plasticity due to environmental variation (Stearns 1989) or result from a complex interaction of both factors (Riddell 1986; Taylor 1991; Hard 1995). Irrespective of the underlying causes, whether genetic or environmental, a significant shift in body size and maturation timing from the locally adapted optimum will result, on average, in some loss in overall productivity of naturally spawning hatchery fish through selection against the smallest and earliest spawners and a reduction in the proportion of largest and latest spawners.

A complete analysis for the traits considered here would need to evaluate all the traits simultaneously as well as other correlated traits (e.g., fecundity, egg size, fry size, and fry emergence timing) in a multivariate treatment such as in Lande (1980); this would include accounting for phenotypic and genetic covariation between traits (see Hard 2004 for an example). However, if hatchery-origin fish differ phenotypically from the optimum at several traits, each of which depresses fitness by approximately 5%, the overall effect could be considerable. For example, differences at four traits could depress fitness by nearly 20%, which could seriously affect the demography of a supplementation program (Goodman 2004).

It is likely that counterselection operating in the wild would act on hatchery fish representing the extremes of the divergent traits; in the absence of an infusion of hatchery-origin spawners each year, natural selection would eventually drive trait distributions back toward their locally adapted optima over generations (Lande and Arnold 1983; Law 1991; Hendry 2001). However, the intent is to have the Yakima River supplementation program be an integrated program with a constant infusion of hatchery-origin spawners each year and to use natural-origin fish only as hatchery broodstock. Such programs should incur less domestication than traditional hatchery programs with heavy gene flow from the hatchery to the natural-origin component and little gene flow in the other direction (Goodman 2004).

Results in Perspective

We would like to conclude by putting these results in the context of the continuous debate over the risks and benefits of artificial propagation, especially integrated hatchery programs, in recovery efforts. In numerous ways, the YKFP spring Chinook salmon program is designed to minimize genetic impacts. Only natural-origin broodstock, collected randomly over the course of the run, is used. The relative size of the program (adult returns) is limited so as not to overwhelm the naturally spawning population (Lynch and O'Hely 2001; Ford 2002). No more than 50% of the natural-origin returns can be used as broodstock. Factorial matings (Fiumera et al. 2004; DuPont-Nivet et al. 2006) are used in the hatchery to increase effective population size and maintain genetic diversity. The proportion of age-3 males that are taken as broodstock is limited to historical BY levels. Additionally, "best culture practices," such as low rearing densities and volitional release of juveniles, are used. The intent is to increase natural production of spring Chinook salmon while at the same time producing hatchery returns that are equivalent to naturally produced returns in terms of life history and reproductive success, at rates comparable to their natural-origin conspecifics. Our purpose as researchers is to intensively monitor this program from its inception to assess how well it meets these objectives.

This hatchery program is in the beginning of its third generation (Table 1). The first hatchery fish have returned to spawn in the wild, and their naturally produced progeny have begun to return (Pearsons 2002). At this point, the program appears to be successful in producing returning hatchery adults, yielding as many as 33 recruits per spawner (authors' unpublished data), but it is too early to determine its success at increasing natural production. In this study, we reported that the first-generation hatchery returns in this program differ from their wild counterparts at size at age, age and sex composition, and spawn timing. These differences are large enough to potentially have some effect on fitness, but at this point the magnitude of that effect and the impact on overall population productivity are unclear. Araki et al. (in press) determined through a pedigree study that first-generation hatchery steelhead in the Hood River, Oregon, were just as fit as their wild counterparts. It is plausible that in our program, the total effect of all differences between wild and hatchery fish (as well as effects we did not observe) amount to a similar quantity of fitness change. Also unclear in our study is the degree of genetic determination of these differences. A common assumption in criticizing hatcheries is that any changes observed as a result of hatchery culture are genetic; in fact, such changes may be the result of a mix of genetic and environmental causes. We would not be surprised to learn that the changes we have observed are largely environmental in origin. Comparing future generations of returns with our hatchery control line should allow us to partition the effects into genetic and nongenetic causes.

In the meantime, perhaps the most important observation to be derived from this study is that hatcheries do not produce fish that are identical to wild fish, even in a program designed to minimize the differences between the two production types. The early hatchery and natural rearing environments experienced by upper Yakima River spring Chinook salmon differ sufficiently to cause differences of 0.5–1.0 SD after 2.5 years of growth in a common environment. The significance of these differences is unclear, but as some of them have been observed in several programs, their implications for population productivity clearly need to be better understood as we proceed with the use of conservation hatcheries to sustain salmon and steelhead production.

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