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Breeding success of four male life history types of spring Chinook Salmon spawning in an artificial stream

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Abstract In 1997 the Cle Elum Supplementation Research Facility was established to enhance spring Chinook salmon returning to the upper Yakima River, Washington State. This effort increased spring Chinook abundance, yet conditions at the hatchery also significantly elevated the occurrence of jacks and yearling precocious males. The potential genetic effect that a large influx of early maturing males might have on the upper Yakima River spring Chinook population was examined in an artificial stream. Seven independent groups of fish were placed into the stream from 2001 through 2005. Males with four different life history

strategies, large anadromous, jacks, yearling precocious, and sub-yearling precocious were used. Their breeding success or ability to produce offspring was estimated by performing DNA-based pedigree assessments. Large anadromous males spawned with the most females and produced the greatest number of offspring per mate. Jacks and yearling precocious males spawned with more females than sub-yearling precocious males. However, jacks, yearling and sub-yearling precocious males obtained similar numbers of fry per mate. In the test groups, large anadromous males produced 89%, jacks 3%, yearling precocious 7%, and sub-yearling precocious 1% of the fry. These percentages remained stable even though the proportion of large anadromous males in the test groups ranged from 48% to 88% and tertiary sex ratios varied from 1.4 to 2.4 males per female. Our data suggest that large anadromous males generate most of the fry in natural settings when half or more of the males present on a spawning ground use this life history strategy.

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Introduction

Life history strategies in fishes are defined by rates of juvenile development, age of sexual maturation, offspring production, levels of parental investment,

and the onset of senescence and death. They represent pathways designed to maximize reproduction under diverse environmental conditions and their occurrence is controlled by interactions between an individual's genotype and its environment (Thorpe 1994). Salmonid fishes exhibit a large array of life history types that are quite malleable (Caswell et al. 1984; O'Connell and Ash 1993). Thus, environmental variation, among other factors, will change the prevalence of different life history types within a salmonid population from one year to the next.

In the upper Yakima River, Washington State, spring Chinook salmon (*Oncorhynchus tshawytscha*) males exhibit four different life history strategies. Each type matures at a different age; two are anadromous while two others become mature without going to sea. Anadromous males that mature at the same modal age as females are referred to as large anadromous males. Most of them reach maturation at age-4 after spending two years at sea, although a few are age-5 at maturity and have resided in marine waters for three years (Knudsen et al. 2006). Anadromous males that mature a year earlier than the modal female age are referred to as jacks (Healey 1991). In this population they are age-3 and have spent one year at sea. Males that mature after rearing 18 to 20 months in freshwater are called yearling precocious males while non-anadromous males maturing after just 7 to 8 months post emergence are referred to as sub-yearling precocious males.

The occurrence of such a diverse array of male life history types in upper Yakima River spring Chinook is not unusual. Precocious spring Chinook males have been recognized for over 100 years (Rutter 1902 as cited by Pearsons et al. 2009) and their presence in spawning populations can be quite variable, ranging from 1 to 12% or more (Rich 1920 as cited by Larsen et al 2004; Gebhards 1960; Mullan et al. 1992). In the Upper Yakima River, yearling precocious males of hatchery- and wild-origin and wild sub-yearling males have been observed (Pearsons et al. 2009) and numerous jacks and large anadromous males may also be present (Knudsen et al. 2006; Dittman et al. 2010).

In 1997 a spring Chinook supplementation program began in the upper Yakima River with the establishment of the Cle Elum Supplementation Research Facility (CESRF). This program has significantly enhanced the number of spring Chinook salmon returning to the upper

Yakima River (Sampson et al. 2009). However, hatchery conditions have inadvertently increased the number of yearling precocious males in the upper Yakima River. Analyses done by Larsen et al. (2004) indicated that 37–49% of the males produced by the CESRF underwent precocious development and became sexually mature in the second year of life. Many of these fish emigrated downstream or perished after release but a portion of them remained or migrated back upstream and became part of the upper Yakima River spring Chinook spawning population (Larsen et al. 2004; Pearsons et al. 2009). The CESRF also significantly augmented the number of jacks returning to the upper Yakima River (Knudsen et al. 2006; 2010). Increases in the abundance of precocious males and jacks due to artificial culture has been observed in other spring Chinook populations (Gebhards 1960; Mullan et al. 1992; Unwin and Glova 1997) and is likely caused by the growth patterns and energy stores salmon experience under artificial culture (Thorpe 1994; Shearer and Swanson 2000; Larsen et al. 2010).

The enhanced occurrence of jacks and yearling precocious males due to supplementation raised several questions. First, even though large numbers of hatchery-origin yearling precocious males and jacks were produced by the CESRF how many of them are present on upper Yakima River spawning grounds? Second, if they are present, how successful are they in producing offspring? Pearsons et al. (2009) partially addressed the first question with their comprehensive assessment of the occurrence of hatchery-origin yearling precocious males in spring Chinook spawning areas in the upper Yakima River. Their annual surveys of upper Yakima River spring Chinook spawning grounds showed that on average just 22 hatchery precocious males (range 0–78) were found over 60 km of spawning habitat.

Our objective in this paper is to estimate the potential genetic contributions that early maturing hatchery-origin males may make to the Yakima River spring Chinook salmon population, and by extension, the effect that such males may have on other natural populations undergoing supplementation. Concerns about how supplementation may change the genetic composition of salmonid populations prompted Mobrand et al. (2005) to propose that the proportion of natural-origin fish on spawning grounds and in hatchery broodstocks should always be greater than the corresponding proportion of hatchery fish. This

protocol dilutes potential domestication because fifty percent or more of the genes transmitted from one generation to the next by hatchery fish are subjected to natural selection pressures (Mobrand et al. 2005).

In some cases, it is possible to monitor and control the occurrence of hatchery fish on spawning grounds. However, this becomes problematic when dealing with precocious males that reside and mature in freshwater and sometimes with jacks that may be able to pass through weirs or other obstructions designed to stop larger fish. Additionally, early maturing males produced from hatcheries potentially represent a greater source of domestication than hatchery fish maturing at older ages. This happens because they are subject to natural selection pressures for shorter periods of time (Pearsons et al. 2009). And if produced by hatchery-origin parents they may be the most domesticated fish in a population since they have been exposed to an additional generation of artificial culture.

In two previous papers we compared the breeding success of first-generation hatchery and wild female (Schroder et al. 2008) and male (Schroder et al. 2010) spring Chinook salmon spawning in an artificial stream. Because of the ubiquitous presence of precocious males and jacks in the upper Yakima River, and the desire to mimic natural social conditions, we included precocious males and jacks along with large anadromous males and females in seven test groups placed into the artificial stream. Their inclusion in our test groups gave us an opportunity to evaluate offspring production by males having different male life history types when they occurred simultaneously in the same spawning community. Our earlier work (Schroder et al. 2010) indicated no detectable differences occurred in the behavior and breeding success of large anadromous males of hatchery and wild origin. Consequently, here we combine data from hatchery and wild males assuming that both types within the same male life history strategy had similar breeding success values. This increased statistical power and provided an overall estimate that each male life history type had on offspring production in our test groups.

In making this evaluation we examined the importance of four factors, relative body size, spawning ground longevity, sex ratios, and the prevalence of each male life history type on the percentage of offspring they produced within a spawning popula-

tion. These factors were chosen because they are linked to male breeding success. Male body weight, for example, is known to be positively correlated with breeding success in large anadromous males (Schroder et al. 2010). Similarly, males that reside on spawning grounds for relatively long periods of time should have more breeding opportunities than those with shorter life times. Additionally, the operational sex ratio or number of males competing for each female, influences intra-sexual competition and the expression of behavioral tactics within and across male life history types (Emlen and Oring 1977; Quinn et al. 1996). Finally, the prevalence of males representing different life history types may also determine how many offspring each type produces and the behavioral tactics that are employed on spawning grounds (Berejikian et al. 2010).

We used DNA-based pedigree assessments to explore the potential importance of each of these factors on the breeding success of males placed into our artificial stream. Results were used to evaluate the effects that increased numbers of early maturing males may have on spawning populations. The insights gained also provided new information about the relative reproductive success of alternative male life history strategies in spring Chinook salmon.

Methods

Origin and collection of spring Chinook salmon

Adult female, large anadromous males, jacks, and yearling precocious males were collected from the upper Yakima River from April through August at the Roza Adult Monitoring Facility. This facility is located at rkm 206 (as measured from the confluence with the Columbia River) and upper Yakima River spring Chinook must pass through it before reaching their spawning grounds. Methods described by Knudsen et al. (2006) were used to collect a representative sample of fish. Collected fish were transported 81 km to the CESRF and females, large anadromous males, and jacks were held in a 30.5 m long by 4.6 m wide by 3 m deep pond while yearling precocious males were placed into a 30.5 m long by 3.5 m wide by 1.1 m deep hatchery raceway. Sub-yearling precocious males were collected off natural redds in the upper Yakima River by using hook and line or electrofishing gear.

After capture they were transported to the CESRF and held in small circular tanks.

Fish selection and introduction into the artificial stream followed the protocols previously described in Schroder et al. (2008, 2010). Briefly, beginning in early September, fish were examined weekly to determine their maturation status. Only ripe fish were selected for use in the artificial stream. Prior to being placed into the stream they were anesthetized in a 1:19,000 part solution of tricaine methanesulfonate (Bell 1964). Once docile, large anadromous males, females, and jacks were weighed to the nearest gram while yearling and sub-yearling precocious males were weighed to the nearest tenth of a gram on electronic balances. Fork lengths to the nearest mm were taken on all fish. The large anadromous fish and jacks were tagged with Petersen disks but no external tags were applied to precocious males due to their small size. A tissue sample from the posterior edge of the dorsal fin was removed from each fish and placed into 100% ethanol for later DNA extraction and genetic analysis. The fish were then transported 200 m and released into the artificial stream. The origin, number, fork lengths, tertiary sex ratios, and the percentage of the males in each test group that represented different life history types are shown in Table 1.

Artificial stream

The artificial stream is located on the grounds of the CESRF. It is 127 m long by 7.9 m wide and has six straight sections that are 15.2 m long by 7.9 m wide plus one curved section that is 21 m long by 7.9 m wide. The sections are separated from one another by concrete cross weirs. Each section has a level gradient and possesses gravel consisting of material ranging from 0.7 to 10.0 cm in diameter with a Fredle Index (Lotspeich and Everest 1981) of seven. A series of 30-cm falls separate one section from another. Water velocity (0.1–2.0 m/s), discharge (0.37 m³/s) and depth (mean 0.4 m) mimicked conditions that spawning Chinook salmon typically prefer (Bjornn and Reiser 1991; Healey 1991). A 2.1-m high wall of camouflage netting was installed on both banks with observation openings at eye level every m along its length (Schroder et al. 2008).

Seven test groups of Chinook salmon were placed into the artificial stream from 2001 through 2005. In

2001 and 2002, the artificial stream was subdivided into an up and downstream part, each having three straight sections (total length equaled 45.6 m). In these two years, test groups were placed into each part of the stream. Single test groups were placed into the entire stream in 2003, 2004, and 2005. In all years, picket barriers were used to confine the fish to parts of the stream set aside for their test group. Fish were introduced into a test group on the same day over a 2 to 3 h period. They were always released into the uppermost section of the artificial stream allotted to their test group and could move freely within the part of the stream that had been sequestered for their population. In those years where two test groups were placed into the stream, seven days elapsed between when fish were placed into the upper and lower parts of the artificial stream (Schroder et al. 2010).

Estimating male breeding success

In 2001 and 2002 modified fyke nets with floating live boxes were placed just below each part of the stream that contained a test group. In 2003, 2004, and 2005 the traps were installed immediately below the last section of the artificial stream. The traps captured newly emerged fry and parr (Allan and Ritter 1977) hereafter referred to collectively as fry, as they emigrated from the stream. Traps were installed prior to emergence and were in continuous operation until fry migration ceased, then electrofishing gear and seines were used to capture any remaining juveniles. Ten percent of each day's catch was preserved in 100% ethanol and used in microsatellite DNA pedigree assessments. The pedigree analyses indicated the number of fry each male had contributed to the ten percent sample collected from his test group. The breeding success of each male was estimated by dividing the number of fry he produced in the pedigree sample by the total number of fry in the sample.

Pedigree analyses

Methods used to perform the pedigree analyses have been previously described in Schroder et al. (2008, 2010). For test groups 2001A and 2001B, genomic DNA was extracted from the fry and adult samples by digesting their tissues in a 5% chelex solution containing 0.4 mg proteinase K. Following digestion

Table 1 The number, fork length, tertiary sex ratio, and percentage of males using different life history strategies in the test groups placed into the artificial stream from 2001–2005

Test Group	Sex	Type	No.	Fork Length-Range (mm)	Mean Fork Length	Tertiary Sex Ratio ^e	% Males ^f
2001 A	Female	Large Anadromous ^a	16	589–774	729	1.5	
	Male	Large Anadromous	21	591–908	743		87.5%
		Jack ^b	3	526–531	528		12.5%
		Yr-Precocious ^c	0	–	–		0.0%
		Sub-Yr Precocious ^d	0	–	–		0.0%
2001 B	Female	Large Anadromous	17	668–770	715	1.8	
	Male	Large Anadromous	18	560–821	716		60.0%
		Jack	2	498–519	509		6.7%
		Yr-Precocious	5	177–227	203		16.7%
		Sub-Yr Precocious	5	77–87	81		16.7%
2002 A	Female	Large Anadromous	22	662–832	756	1.4	
	Male	Large Anadromous	22	660–841	733		73.3%
		Jack	2	442–458	450		6.7%
		Yr-Precocious	6	142–190	166		20.0%
		Sub-Yr Precocious	0	–	–		0.0%
2002 B	Female	Large Anadromous	17	660–760	718	1.4	
	Male	Large Anadromous	16	650–880	749		66.7%
		Jack	2	492–520	506		8.3%
		Yr-Precocious	6	145–206	184		25.0%
		Sub-Yr Precocious	0	–	–		0.0%
2003	Female	Large Anadromous	24	655–900	757	2.1	
	Male	Large Anadromous	24	560–890	758		48.0%
		Jack	6	470–580	545		12.0%
		Yr-Precocious	7	122–203	163		26.0%
		Sub-Yr Precocious	13	85–117	102		14.0%
2004	Female	Large Anadromous	20	644–800	721	2.4	
	Male	Large Anadromous	29	560–900	728		61.7%
		Jack	4	402–521	469		8.5%
		Yr-Precocious	12	122–221	177		25.5%
		Sub-Yr Precocious	2	114–115	115		4.3%
2005	Female	Large Anadromous	23	610–767	703	2.0	
	Male	Large Anadromous	25	680–920	772		55.6%
		Jack	4	494–530	514		8.9%
		Yr-Precocious	8	170–215	191		17.8%
		Sub-Yr Precocious	8	61–110	93		17.8%

^a Anadromous fish maturing at ages 4 or 5

^b Anadromous males maturing at age 3

^c Non-anadromous males maturing after 18 to 20 months of freshwater residency

^d Non-anadromous males maturing after 7 to 8 months of freshwater residency

^e Number of males per female

^f Percentage of males in a test group representing a life history type

the samples were heated to denature proteins and DNA extracts were stored at 5°C until all analyses were completed. Spin-column extraction kits from Machery-Nagel were used to purify genomic DNA from fish in test groups 2002A–2005. Adults and fry were genotyped at 10 to 13 loci. The number of alleles per locus ranged from 5 in Ots-1 to 40 at Ots-100. Microsatellite DNA loci were amplified via the polymerase chain reaction (PCR) using fluorescent-labeled primers obtained from Applied Biosystems or Integrated DNA Technologies. Data were collected using an ABI-3100 Genetic Analyzer. Applied Biosystems Genemapper 3.0 software was used to collect, analyze and determine genotypes at each locus. Allele identification on sampled fry was attempted on all loci and fry had to be genotyped at six or more loci before they were assigned to a parent fish. A maximum likelihood procedure in Cervus 2.0 (Marshall et al. 1998) was used to infer parent-offspring relationships. The procedure uses allele frequency data to assign likelihoods to parent-offspring combinations and allows mismatching genotypic data to be evaluated concurrently with matching genotype data.

Data analysis

Statistical analyses were performed using SYSTAT 12 software (SYSTAT 2007). All tests were two-sided and an alpha level of 0.05 was used.

Body lengths and longevity Body length comparisons were performed using a two-step process. First, Model I, 2-way ANOVAs were performed on the fork length data collected on males within a life history type. One fixed factor was test group origin while the other fixed factor was male origin, i.e. were the fish of wild or hatchery-origin. These analyses were performed to determine if all the length data obtained from males having the same life history could be pooled. A one-way ANOVA was then performed to assess whether males with different life histories had different mean fork lengths at maturity. A *post hoc* Tukey's Honestly-Significant-Difference Test was used to determine which male life history types had different mean fork lengths.

Longevity or the number of hours a male resided in the artificial stream was calculated by subtracting the median time and date his test group entered the

artificial stream from the time and date he was first observed dead. Mean longevity values for males representing each life history type within a test group were calculated by summing all the longevity data for a given male type and then dividing this value by the number of males of that type that were present. The resulting mean longevity values were used in a non-parametric (Friedman's Test) randomized block analysis of variance and subsequent Student-Newman Multiple range test to determine if longevity differences existed among males having different life histories. The longevity of sub-yearling precocious males was not compared to the other male life history types because too few were recovered.

The effect of body length on breeding success in all four types of males was examined by using regression analyses. Data from each test group were analyzed separately. Seven regressions, one for each test group, were performed on large anadromous males. In these regressions fork length (log 10) was the independent variable and breeding success, after it had been normalized by the arcsine transformation, was the dependent variable. Six similar regressions were conducted on data obtained from yearling precocious males, and three each were run on jacks and sub-yearling precocious males. The *p* values obtained from the regressions performed on each male type were used in meta-analyses referred to as combined probability tests (Sokal and Rohlf 1995). The combined probability tests allowed us to discover if fork length affected breeding success within a male life history type across multiple test groups.

The effect of longevity on breeding success within each male type was evaluated by using non-parametric Kendall tau rank correlations. In this instance, individual breeding success values were correlated with longevity values. Seven such correlations were performed on data collected from large anadromous males. Four were performed on yearling precocious males while three were conducted on jacks. Not enough longevity data were collected on sub-yearling precocious males to assess the importance of this trait on their breeding success.

Tertiary sex ratios Each test group had a different tertiary sex ratio or absolute number of males per female (Table 1). Because all the fish placed into the test groups were ripe at the time of entry and no new recruits were allowed to enter any of the test groups,

the tertiary sex ratio was used to estimate male intra-sexual competition for females in each of the test groups. Regression analyses were performed to determine how much variation in male breeding success (the dependent variable) could be explained by the tertiary sex ratios in the test groups (independent variable). Three regressions were performed; one for large anadromous males, another for jacks, and one for yearling precocious males.

The effect of male intra-sexual competition for females on the proportion of fry produced by each male life history type in the test groups was also examined by regression. Four separate regressions were performed, one for each male life history type. The independent variable in these analyses was the tertiary sex ratio that was present in each test group. The dependent variable was the percentage of the fry population in a test group that a male life history type had produced. The arcsine transformation was used to normalize the percentage of the fry population in a test group that had been fathered by a male type. No data transformation was used on the tertiary sex ratios.

Prevalence of male life history types Four regression analyses, one for each male life history type, were performed to assess how much variation in fry paternity could be explained by how prevalent a male type was in a spawning population. In these analyses the percentage of the male spawning population representing a life history type was the independent variable. The dependent variable was the percentage of the fry population that had been fathered by that life history. Prior to performing the regressions both percentages were normalized by using the arcsine transformation.

Breeding success Average breeding success values for each male life history type were determined in the 2001B, 2003, 2004, and 2005 test groups. These test groups were chosen because males with all four male life history types were present. Mean values were calculated by summing individual breeding success values of all the males within the same life history type and then dividing that sum by the number of males having that strategy. These average values estimated the mean percentage of fry produced from a test group that had been fathered by males in each life history type. They were normalized by using the arcsine transformation. A randomized block analysis of variance and a *post hoc* Student-Newman Kuels

multiple range test were used to determine if life history type affected male breeding success. Differences in breeding success were observed. To help explain why there were differences we also evaluated whether male history type affected mate number and progeny produced per mate.

Number of mates The pedigree analyses revealed the number of different females each male in a test group had spawned with. These data were sorted by male type, summed, and divided by the number of males in each life history type. The resulting quotients were used to estimate the mean number of mates males with different life history types had spawned with. Average mate numbers were determined for each male life history type in the 2001B, 2003, 2004, and 2005 test groups. A randomized block analysis of variance and *post hoc* Student-Newman Kuels multiple range test were used to see if male life history affected mean mate numbers.

Number of fry per mate The pedigree analyses also indicated the number of fry produced by each female a male spawned with. These values were sorted by male life history type, summed and divided by the number of male x female pairs that occurred within a male type. The quotients equaled the average number of progeny produced per mate in the fry used for the pedigree analysis. Estimates of the number of fry produced per mate were determined by dividing the above average values by the percentage of the fry from a test group that had been used in a pedigree assessment. For example, in the 2004 test group, 86 different large anadromous male x female pairs produced 2699 fry. The average number of fry produced by each pair was 31 (2,699/86). This test group produced 47 140 fry and 2892 or 6.1% of them were assigned to parental fish. Consequently, large anadromous males produced an average of 511 fry per mate. Similar calculations were done for each male life history type in the 2001B, 2003, 2004, and 2005 test groups. The resulting values were used in a randomized block analysis of variance and a *post hoc* Student-Newman Kuels multiple range test to compare the mean number of fry produced per mate among the four male life history types.

Relative breeding success To estimate the relative breeding success of jacks and both types of precocious males compared to large anadromous males, we

determined the mean number of fry each type of male produced in every test group. This was done by dividing the total number of fry a male type had contributed to the fry used in our pedigree assessments by the number of males having that life history type. Relative breeding success was then calculated by dividing the mean fry values of jacks, and the two types of precocious males by the mean value obtained from the large anadromous males that had been in their test group.

Results

Production of juveniles from the test groups varied from 18 960 (test group 2001 A) to 64 494 (test group 2003). Altogether 30 683 fry were sampled from the test groups for DNA analysis. A total of 13 779 were analyzed and 96% of those were assigned to parental fish. The percentage of the fry population produced from a test group that were successfully assigned to parental fish ranged from 1.8% (test group 2001B) to 6.1% (test group 2004) and averaged 4.3% (Schroder et al. 2010).

Fork length

The fixed factor two-way ANOVAs that examined whether male origin (first-generation hatchery or wild) or test group affected fork lengths in large anadromous males and jacks were non-significant ($p=$

0.169 for origin and $p=0.116$ for test group in large anadromous males; $p=0.915$ for origin and $p=0.133$ for test group in jacks) and therefore length data within these two male types were pooled. Test group origin also had no effect on the fork lengths of yearling or sub-yearling precocious males ($p=0.394$ for yearling precocious; $p=0.093$ for sub-yearling precocious males). However, hatchery-origin yearling precocious males were significantly longer than wild yearling precocious males ($p<0.001$). The one-way ANOVA and *post hoc* Tukey's Honestly Significant Difference tests that compared the fork lengths among males with different life histories indicated that there were dissimilarities in the mean fork lengths among all the life history types, with large anadromous males being the largest followed by jacks, hatchery yearling precocious, wild yearling precocious, and wild sub-yearling precocious males (Table 2).

Longevity

Male life history type affected longevity or the number of hours males with different life histories resided in the artificial stream ($p=0.027$). On average, yearling precocious males lived for longer periods of time than both large anadromous males ($p=0.017$) and jacks ($p=0.035$). No difference, however, was observed between the longevity of large anadromous males and jacks ($p=0.416$). Large anadromous males had a mean longevity of 152 h; jacks had an overall

Table 2 Results of the randomized block and *post hoc* tests used to compare the fork lengths and spawning ground longevity of spring Chinook males having different life history strategies that were placed into the artificial stream

Trait	Male life history types compared	Mean values	Difference	<i>p</i> value	Conclusion
Fork Length (mm)	Large Anadromous vs. Jack	744 vs. 510	234	<0.001	Reject H_0
	Large Anadromous vs. Hatchery Yearling Precocious	744 vs. 194	550	<0.001	Reject H_0
	Large Anadromous vs. Wild Yearling Precocious	744 vs. 141	603	<0.001	Reject H_0
	Large Anadromous vs. Sub-Yearling Precocious	744 vs. 93	651	<0.001	Reject H_0
	Jack vs. Hatchery Yearling Precocious	510 vs. 194	316	<0.001	Reject H_0
	Jack vs. Wild Yearling Precocious	510 vs. 141	369	<0.001	Reject H_0
	Jack vs. Sub-Yearling Precocious	510 vs. 93	417	<0.001	Reject H_0
	Hatchery Yr Precocious vs. Wild Yearling Precocious	194 vs. 141	53	<0.001	Reject H_0
	Hatchery Yr Precocious vs. Sub-Yearling Precocious	194 vs. 93	101	<0.001	Reject H_0
	Wild Yr Precocious vs. Sub-Yearling Precocious	141 vs. 93	48	<0.001	Reject H_0
Spawning Ground Longevity (hrs)	Yearling Precocious vs. Large Anadromous	216 vs. 152	64	0.017	Reject H_0
	Yearling Precocious vs. Jack	216 vs. 173	43	0.035	Reject H_0
	Jack vs. Large Anadromous	173 vs. 152	21	0.416	Fail to reject H_0

longevity value of 173 h while yearling precocious males lived for an average of 216 h (Table 2).

Fork length and longevity effects on breeding success

The effect of fork length on male breeding success was examined by using regression analyses. For large anadromous males, regression coefficients ranged from 15 to 47% and averaged 25%. The combined probability test that examined the importance of this trait on breeding success in large anadromous males showed this trait was positively associated with breeding success ($p < 0.001$). The combined probability tests that examined the importance of length on male breeding success in the other male life history types were all non-significant ($p = 0.429$ for jacks, $p = 0.942$ for yearling precocious, and $p = 0.254$ for sub-yearling precocious males). Figure 1 illustrates how

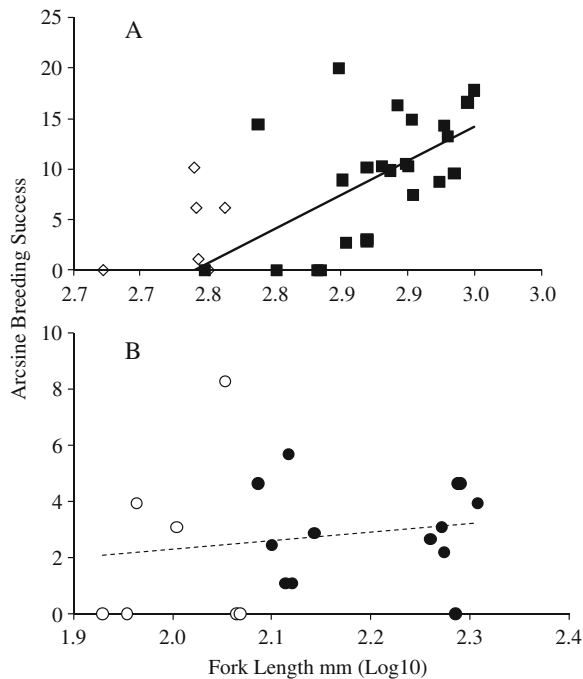


Fig. 1 The effect of fork length on the breeding success of large anadromous males (black squares), jacks (white diamonds), yearling (black circles) and sub-yearling precocious males (white circles) spawning in the 2003 test group. Part A illustrates the significant relationship ($r^2 = 0.314$; $p = 0.004$) between these two variables (solid line) in large anadromous males and the non-significant association between them in jacks ($r^2 = 0.163$; $p = 0.428$). Part B shows the non significant relationship ($r^2 = 0.035$; $p = 0.431$) between fork length and breeding success (dashed line) in yearling and sub-yearling precocious males

fork length and breeding success were associated with one another in all four types of males placed in the 2003 test group.

In two of the test groups, significant negative Kendall tau rank correlations between spawning ground longevity and breeding success in large anadromous males were found. The combined probability test that examined the overall effect of longevity on breeding success showed that longevity in large anadromous males was negatively correlated to breeding success ($p = 0.046$). Conversely, both positive and negative relationships between these two variables were seen in jacks and yearling precocious males and thus no consistent trends occurred in these two life history types.

Tertiary sex ratio

As the absolute number of males per female or tertiary sex ratios in the test groups increased, mean breeding success in large anadromous males decreased (Fig. 2). Similar, but non-significant decreases in mean breeding values occurred in jacks ($r^2 = 0.411$, $p = 0.121$) and yearling precocious males ($r^2 = 0.432$, $p = 0.156$). The effect that tertiary sex ratios had on the proportion of fry each male life history type produced was also examined by regression. These analyses showed that tertiary sex ratios in our test group did not influence the percentage of fry each male life history type produced (Fig. 3). Regression coefficients equaled 0.002 ($p =$

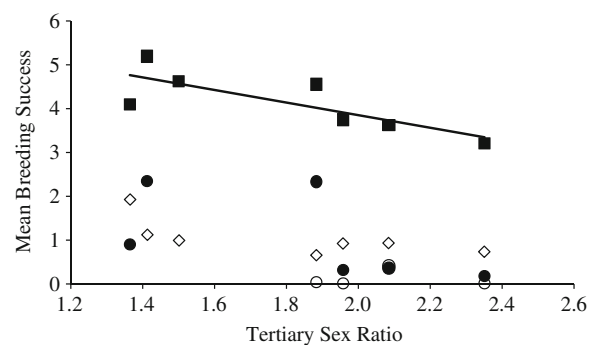


Fig. 2 The influence of tertiary sex ratios on mean breeding success in large anadromous males (black squares), jacks (white diamonds), yearling (black circles) and sub-yearling precocious males (white circles). A significant negative relationship between these two variables occurred in large anadromous males ($r^2 = 0.643$; $p = 0.030$). Negative, but non-significant relationships occurred in jacks ($r^2 = 0.411$; $p = 0.121$) and yearling precocious males ($r^2 = 0.432$; $p = 0.156$)

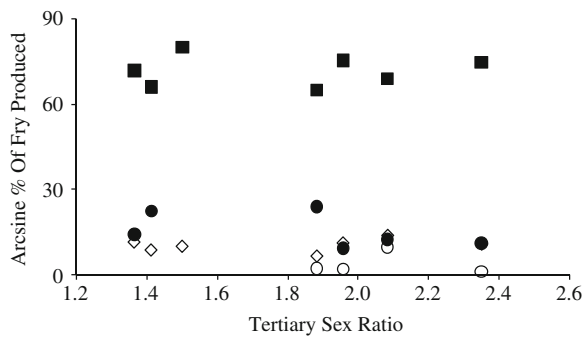


Fig. 3 The proportion of fry fathered by large anadromous males (*black squares*), jacks (*white diamonds*), yearling (*black circles*) and sub-yearling precocious males (*white circles*) under different tertiary sex ratios in the test groups

0.919) for large anadromous males, 0.063 ($p=0.587$) for jacks, 0.228 ($p=0.338$) for yearling precocious, and 0.003 ($p=0.946$) for sub-yearling precocious males. Thus, under the array of tertiary sex ratios present in our test groups, large anadromous males consistently produced around 89% of the offspring and on average jacks produced 3%, yearling precocious 7% and sub-yearling males 1%.

Prevalence of male life history types

If each male life history type were equally successful at producing offspring, then there would be a one-to-one relationship between the percentage of a male type present on a spawning ground and the percentage of the fry population originating from that type of male. The relationship between the prevalence of male life history types spawning in our test groups and the paternal origin of fry produced from those groups is shown in Fig. 4. In every test group, large anadromous males produced about 89% of the fry regardless of their relative occurrence. No relationship was found between the percentage of large males in the test groups and the percentage of fry that life history type produced ($r^2=0.334$, $p=0.174$). Similarly, the percentage of jacks ($r^2=0.142$; $p=0.405$), yearling ($r^2=0.048$; $p=0.676$) and sub-yearling precocious males ($r^2=0.068$; $p=0.740$) in our test groups did not influence the percentage of fry they were able to produce.

Mean breeding success comparisons

Mean breeding success values among the four male life history types were different ($p<0.001$, Table 3). Large

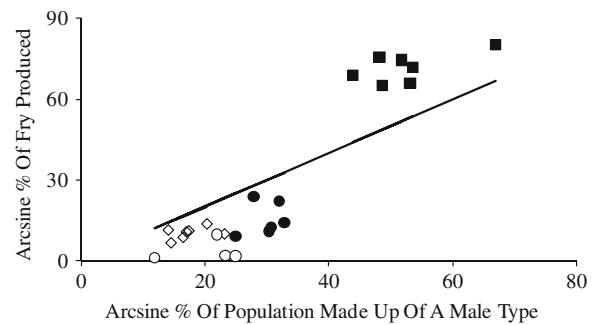


Fig. 4 The occurrence of male life history types in the test groups versus the proportion of juveniles they fathered. The *black diagonal line* represents the percentage of fry each male life history type would be expected to produce if individuals within each type had an equal ability to produce offspring. Large anadromous males are represented by *black squares*, jacks by *white diamonds*, yearling precocious males by *black circles* and sub-yearling precocious males by *white circles*

anadromous males had greater mean breeding values than jacks ($p=0.001$), yearling precocious ($p<0.001$) and sub-yearling precocious males ($p<0.001$). No difference was found in the breeding success values of jacks and yearling precocious males ($p=0.555$). However, both had higher mean breeding success values than sub-yearling precocious males ($p=0.016$ for jacks and $p=0.020$ for yearling precocious males).

To understand why differences in breeding success had occurred we evaluated whether male life history type affected the average number of mates individuals in each life history type spawned with. Male life history type did influence mate number ($p=0.002$). On average large anadromous males mated with more females than sub-yearling precocious males ($p<0.001$), yearling precocious males ($p=0.034$), and jacks ($p=0.029$). Jacks and yearling precocious males had similar mean mate numbers ($p=0.686$) and both had higher mean mate numbers than sub-yearling precocious males ($p=0.020$ for jacks and $p=0.017$ for yearling precocious males) (Table 3). Male life history type also influenced the average number of progeny produced per mate ($p<0.001$). Large anadromous males produced an average of 580 fry per mate which was greater than the 131 fry per mate for sub-yearling precocious males ($p=0.002$), 175 fry per mate in yearling precocious ($p=0.004$) and 212 fry per mate for jacks ($p=0.006$). No differences, however, were seen in fry production per mate among jacks and the two types of precocious males ($p=0.506$ for jacks and yearling precocious males; $p=0.332$ for jacks and

Table 3 Results of the randomized block and *post hoc* tests used to compare the breeding success, number of mates, and number of fry produced per mate of spring Chinook salmon males possessing different life history strategies that were used in the test groups

Trait	Male life history types compared	Mean values	Difference	<i>p</i> value	Conclusion
Breeding Success ^a	Large Anadromous vs. Sub-Yearling Precocious	9.3 vs. 0.8	8.5	<0.001	Reject H ₀
	Large Anadromous vs. Yearling Precocious	9.3 vs. 3.8	5.5	0.001	Reject H ₀
	Large Anadromous vs. Jack	9.3 vs. 4.5	4.8	0.001	Reject H ₀
	Jack vs. Sub-Yearling Precocious	4.5 vs. 0.8	3.7	0.016	Reject H ₀
	Jack vs. Yearling Precocious	4.5 vs. 3.8	0.7	0.555	Fail to reject H ₀
	Yearling Precocious vs. Sub Yearling Precocious	3.8 vs. 0.8	3.0	0.020	Reject H ₀
Mate Number ^b	Large Anadromous vs. Sub-Yearling Precocious	3.4 vs. 0.5	2.9	0.001	Reject H ₀
	Large Anadromous vs. Yearling Precocious	3.4 vs. 1.9	1.5	0.034	Reject H ₀
	Large Anadromous vs. Jack	3.4 vs. 2.1	1.3	0.029	Reject H ₀
	Jack vs. Sub-Yearling Precocious	2.1 vs. 0.5	1.6	0.020	Reject H ₀
	Jack vs. Yearling Precocious	2.1 vs. 1.9	0.2	0.686	Fail to reject H ₀
	Yearling Precocious vs. Sub Yearling Precocious	1.9 vs. 0.5	1.4	0.017	Reject H ₀
Progeny Per Mate ^c	Large Anadromous vs. Sub-Yearling Precocious	580 vs. 131	449	0.002	Reject H ₀
	Large Anadromous vs. Yearling Precocious	580 vs. 175	405	0.004	Reject H ₀
	Large Anadromous vs. Jack	580 vs. 212	368	0.006	Reject H ₀
	Jack vs. Sub-Yearling Precocious	212 vs. 131	81	0.332	Fail to reject H ₀
	Jack vs. Yearling Precocious	212 vs. 175	37	0.506	Fail to reject H ₀
	Yearling Precocious vs. Sub-Yearling Precocious	175 vs. 131	44	0.369	Fail to reject H ₀

^a Breeding success is the arcsine transformed average percentage of fry in a pedigree analysis produced by males in each life history strategy

^b Mate number equals the mean number of different females males in each life history strategy spawned with as indicated by the pedigree analyses

^c Progeny per mate is the mean number of fry males in each life history strategy produced per female they spawned with

sub-yearling precocious males; and *p*=0.369 for yearling and sub-yearling precocious males, Table 3).

The biological consequences of differences in average mate number, fry per mate, and overall breeding success in the four male life history types can be examined by comparing their relative breeding success values (Table 4). On average, jacks and yearling precocious males had breeding success values that were 25.0% and 22.0% respectively of those obtained by large anadromous males. Overall sub-yearling precocious males had breeding success values that were 3.2% of that realized by large anadromous males. These values were variable however. For example, within our test groups, breeding success of jacks relative to large anadromous males ranged from 16.6% to 46.8%. Comparable variation was found in yearling precocious males whose breeding success relative to large anadromous males varied from 8.5% to 51.0%. Similarly, breeding success in sub-yearling precocious males relative to

large anadromous males fluctuated from 0.3% to 11.2%.

Discussion

Spring or stream-type Chinook salmon (Healey 1991) populations probably possess the most diverse array of male life history strategies in semelparous Oncorhynchids. Some males reach maturation after just 7 to 8 or 18 to 20 months of freshwater growth (sub-yearling and yearling precocious males), while others utilize an anadromous life history strategy and reach maturation after spending one or more years in the ocean (jacks and large anadromous males) before returning to freshwater to spawn. In our experimental setting, large anadromous males achieved significantly higher mean individual breeding success values than the other three male life history phenotypes examined even when they were outnumbered by

Table 4 The breeding success of jacks, yearling precocious and sub-yearling precocious males in each test group relative to that achieved by large anadromous males

Test group	Breeding success relative to large anadromous males ^a		
	Jacks	Yearling precocious	Sub-yearling precocious
2001 A	16.6%	–	–
2001 B	14.1%	51.0%	0.6%
2002 A	46.8%	14.3%	–
2002 B	21.3%	39.2%	–
2003	25.3%	9.7%	11.2%
2004	26.4%	9.4%	0.5%
2005	24.2%	8.5%	0.3%
Over All Average	25.0%	22.0%	3.2%

^a Relative breeding success was estimated by dividing the mean number of offspring produced in a test group by either jacks, yearling, or sub yearling precocious males by the mean number of offspring produced by large anadromous males

males using different life history strategies. Jacks and yearling precocious males had comparable mean breeding success values, while sub-yearling precocious males had the lowest breeding success values.

Significant differences existed among the male life history types in their body sizes, spawning ground longevity, and their ability to fertilize eggs from multiple females. Of these factors, body size was probably the proximate factor responsible for the detected differences in breeding success. Large anadromous males were on average over 200 mm longer than jacks, the next largest male life history type, and obviously had even greater size advantages over the precocious males (Table 2). Their superior size allowed them to be socially dominant over the other three male life history types and provided them with a greater number of opportunities to spawn with females. For example, on average, large anadromous males in our test groups mated with 3.4 females, jacks with 2.1, yearling precocious with 1.9 and sub-yearling precocious with 0.5 females (Table 3).

Even though there was a large disparity in their body sizes, jacks and yearling precocious males spawned with a similar number of females. Both located themselves in close proximity to spawning pairs but used slightly different tactics to participate in spawnings. Jacks typically positioned themselves just downstream of a dominant pair and persistently remained in this location even though they were often subject to repeated attacks by both members of the dominant pair. When able to detect a spawning event,

they rushed upstream and participated by lying adjacent to a spawning pair or in a few cases by inserting themselves between the dominant male and the spawning female. Yearling precocious males, on the other hand, were often seen in the nest depression or lying closely adjacent to a dominant male or female. Initially these small fish were subject to repeated chases and attacks by both members of a courting pair. Their ability to use shallow water refugia, great maneuverability, tenacious fidelity to a developing nest, and the eventual habituation of their presence by the dominant pair, allowed them to be in close proximity to the larger fish during egg deposition. This same tactic was employed by sub-yearling precocious males (Schroder and Knudsen unpubl. data). The capacity of sub-yearling precocious males to mate with different females, however, may have been limited by the amount of milt they were able to produce.

Although important, the ability to spawn with numerous females only partially explained why differences existed among the male life history types in their mean individual breeding success values. The number of fry produced per mate was another critical factor. In our test groups large anadromous males produced three to four times as many fry per mate as jacks, yearling precocious and sub-yearling precocious males (Table 3). A variety of factors may have contributed to this difference. The aggressive behavior of large anadromous males, for instance, often delayed sperm release by competitors. This gave their sperm precedence over

any released by rivals and therefore increased the likelihood they would fertilize most of the eggs in a multiple-male spawning (Berejikian et al. 2010). Large salmonid males also release significantly greater volumes of milt (Taborsky 1998) at higher pressures (Mjølnerod et al. 1998) than smaller competitors. Together these two factors may enhance their ability to fertilize eggs as sperm released by rivals could be flushed out or numerically overwhelmed (Mjølnerod et al. 1998). A proclivity for salmonid females to prefer relatively large mates (Taborsky 1998; Blanchfield and Ridgway 1999) might have further contributed to their higher breeding success values. The number of offspring produced per mate in jacks and the two types of precocious males was similar. Thus, even though precocious males and jacks used alternative tactics to obtain fertilizations, they produced comparable numbers of progeny per mate.

The effects that body size, longevity, and different tertiary sex ratios had on individual breeding success values helped expose the selection pressures males in each life history type experienced while spawning. Large anadromous males mainly competed among themselves for access to females and in this life history type; body size was positively associated with social dominance and breeding success (Fig. 1). In the present study, body size did not influence the breeding success of jacks and the two precocious male life history types. As male densities around a courting pair increased it becomes more difficult for any male to exclude all his potential rivals. In brook trout, for example, per capita aggressive interactions among males surrounding an active female decreased as male numbers increased (Blanchfield and Ridgway 1999). The inability to exclude multiple rivals leads to scramble competition among peripheral males and under this circumstance body size is not as important as being in close proximity when spawning events occur (Jones and Hutchings 2001).

The negative relationship between longevity and male breeding success in large anadromous males was probably due to energy expenditures. Large anadromous males expend a considerable amount of effort on agonistic interactions and courtship. In our test groups, large anadromous males with high breeding success values engaged in more attacks and courting activities than those that had lower breeding success values (Schroder et al. 2010). Conversely, spring Chinook jacks and precocious males engage in less

courtship and agonistic behavior (Schroder unpubl. data); instead they spend time and energy avoiding attacks and on finding and remaining in close proximity to spawning pairs. Because their breeding success is often determined by the outcomes of scramble competition (but see Grimardias et al. 2010a, 2010b), we speculate that energy expenditures directed toward excluding rivals does not affect their breeding success as strongly as it does in large anadromous males. Support for this speculation can be found in the relationship between tertiary sex ratios in the test groups and how this factor influenced individual breeding success values in the various male life history types. A negative relationship occurred between these two variables within each male life history type (Fig. 2). However, it was only significant in large anadromous males, suggesting that intra-sexual competition among males possessing the same life history type is probably more important for large anadromous males than it is for the other male life history types.

Individuals typically mating at a disadvantage, such as jacks and precocious males, are theoretically expected to employ behavioral, physiological or morphological tactics designed to offset this disadvantage (Andersson 1994; Gage et al. 1995; Taborsky 1998). Precocious males and jacks did have longer spawning ground longevity than large anadromous males. Relatively long spawning ground residency may be a reproductive adaptation by these life history types to increase their likelihood of participating in spawning events. Additionally, Mjølnerod et al. (1998) found that the recent spawning history of large anadromous Atlantic salmon (*Salmo salar*) had an effect on their ability to fertilize eggs. Individuals that had spawned extensively prior to a spawning event released fewer sperm. This meant that secondary males associated with such a spawning were able to achieve high breeding success values even though they had been socially dominated. Relatively long spawning ground residency may increase the probability of jacks and precocious males participating in a spawning of this type. The possible reproductive advantage associated with increased longevity was not fully evaluated in our experiment because additional males and females were not introduced into our test groups over time. Consequently, females were available to all the males over a shorter time period than they would have been under natural conditions.

Other reproductive adaptations observed in precocious males include higher gonadosomatic indices (GSI) than anadromous males (Gage et al 1995; Vladic and Jarvi 2001; Koseki and Maekawa 2002). And when adjusted for body size, precocious males also produce greater quantities of sperm that are more motile and live longer (but *see* Mjølnerod et al. 1998) than those produced by anadromous males (Gage et al. 1995; Vladic and Jarvi 2001). Alternatively, when Hoysak et al. (2004) examined sperm competition between sockeye jacks (3-yr-old fish) and large anadromous males (5 yr-old fish) they found no differences in sperm quality. Instead they hypothesized that the relatively small size of jack sockeye allowed them to gain closer access to females during spawning and thus enhanced their fertilization success. Precocious spring Chinook salmon have significantly higher GSI values than those found in large anadromous males (Knudsen and Schroder unpubl. data). No evaluations, however, have been made on gamete quality in jack and precocious male spring Chinook to determine whether their sperm and milt have traits similar to those found in other salmonid species with early maturing males.

Even though precocious males and jacks may have made greater investments in relative gonad size and possessed more motile and longer lived sperm; large anadromous males consistently produced about 89% of the fry generated from each of our test groups. Similar results in other salmonid species have been found. In an 8 km long Scottish river containing 34 to 66 anadromous Atlantic salmon females, 38 to 43 large anadromous males competed with an estimated two to three thousand precocious males for fertilization opportunities. In this population, large anadromous males represented just 1 to 2% of the male population yet they still fertilized about 50% of the eggs that were deposited (Taggart et al. 2001). Additionally, Hutchings and Myers (1988) established populations in simulated streams where large anadromous male Atlantic salmon represented 5% of the spawning males, yet these individuals fertilized approximately 75% of the deposited eggs. In another study using Atlantic salmon spawning in an artificial stream, 16% of the males were large anadromous individuals while the remaining 84% were precocious parr; in this setting anadromous males fertilized between 63 and 77% of the deposited eggs (Jones and Hutchings 2002). In a natural spawning popula-

tion of brook trout, Blanchfield and Ridgway (1999) and Blanchfield et al. (2003) found that male size and a female preference for large males meant that over 90% of the fry produced originated from large males, even though there were numerous smaller “peripheral” males on the spawning grounds. In aggregate, our study and those cited above indicate that the largest males in a breeding population often produce a disproportionate number of fry when salmonids are allowed to spawn naturally.

The reproductive tactics used by each male life history type are conditional and may change with the relative abundance of the other types. For example, jacks will court females and fight among themselves for primary male status if large anadromous males become scarce (Allen et al. 2007). Even precocious males may assume this role if other male life history types are absent (Hutchings and Myers 1985; Beall et al. 1997; Martinez et al. 2001). Thus, the potential genetic contribution rates of different male life history types is dynamic; it may increase or decrease depending upon its prevalence in a spawning population. Similarly, the amount of intra-sexual competition occurring among males will alter how genes are exchanged. When there are just a few males competing among themselves for numerous sexually active females, each male, regardless of life history type, is expected to be successful. As intra-sexual competition among males escalates, average breeding success values for individuals within each life history type will decline. This decline is probably asymmetric as breeding success values in males using life history strategies that reach maturation at relatively small sizes should decline more sharply than those belonging to the male life history type that has the largest size at maturation. This occurs because when intra-sexual competition is high, large males that would normally assume primary courting roles will be forced by competitors to employ a peripheral or satellite tactic. Their utilization of this tactic further diminishes fertilization opportunities for males that matured at earlier ages and smaller body sizes because they must now compete with larger fish for satellite positions. Habitat complexity is another factor that could affect the relative breeding success of males adopting different life history strategies (Beall and de Gaudemar 1999). Grimardias et al. (2010a) for example, found a positive relationship between substrate complexity and the number of precocious

males that fertilized eggs in Atlantic salmon redds. They speculated that substrate diversity provided precocious males with shelters that protected them from male aggression and allowed them close access to spawning females.

The primary purpose of our investigation was to estimate the potential genetic impact that a large influx of early maturing hatchery males might have on the upper Yakima River spring Chinook salmon population. Under the conditions in the artificial stream, jacks and precocious males fathered about 10% of the fry produced from each test group. The applicability of this result depends upon how closely conditions in the test groups resembled those occurring in the upper Yakima River. Currently, multiple thousands of anadromous spring Chinook spawn in the upper Yakima River (Dittman et al. 2010). Data from Pearsons et al. (2009) and Knudsen et al. (2010) were used to estimate the percentage of males representing each life history type present on upper Yakima River spawning grounds. From 1999 through 2007, 50 to 89% ($\bar{x} = 76\%$) of the males were large anadromous fish, 2 to 47% ($\bar{x} = 19\%$) were jacks, and 1 to 8% ($\bar{x} = 4\%$) were precocious males (sub-yearling and yearlings combined). In our test groups 48 to 87% ($\bar{x} = 65\%$) were large anadromous males, 7 to 13% ($\bar{x} = 9\%$) were jacks and 20 to 40% ($\bar{x} = 26\%$) were precocious males (Table 1). The proportion of large anadromous males in the test groups was similar to that found in the upper Yakima River, although the test groups did have fewer jacks and a greater percentage of both types of precocious males. Data from the artificial stream, however, suggest that when 50% or more of the males on a spawning ground are large anadromous individuals they typically produce 90% of the offspring. Since the majority of males spawning in the upper Yakima used the large anadromous strategy it is likely that they accounted for most of the progeny production. Thus, in the upper Yakima River, intra-sexual competition among male life history types has likely limited gene flow from early maturing hatchery fish to the naturally reproducing population.

Under different circumstances (e.g., low abundance of large anadromous males) early maturing hatchery males could make significant genetic contributions to natural populations, becoming potential agents of genetic change and domestication (Garant et al. 2003). Nevertheless, their occurrence on natural

spawning grounds in the upper Yakima River appears to be quite low (Pearsons et al. 2009). Beckman and Larsen (2005) suggest two reasons for this; first, mortality during the downstream migration period may be high. And second, many of these fish appear to migrate downstream to the nearest large reservoir they encounter where they stay until they mature and attempt to ascend back upstream. Their upstream migration is several months later than that used by the large anadromous fish and consequently they may encounter thermal blocks which prevent them from completing a migration to a spawning area (Beckman and Larsen 2005). Thus, the principal impacts of hatchery precocious males in the upper Yakima River appear to be linked to the potential loss of adult salmon for harvest or broodstock (Zimmerman et al. 2003; Beckman and Larsen 2005) and to interactions they may have with native fishes in the natural environment (Beckman and Larsen 2005).

Conversely, the production of early maturing males from a local or native population may be beneficial when hatcheries are used as agents of conservation. The infusion of genes from these males would increase the effective size of a recipient population and therefore help retain its genetic diversity and variation (Saura et al. 2008). They could also be used as hatchery broodstock. Flain (1971) and more recently Unwin et al. (1999) report that precocious male Chinook salmon can survive from one spawning season to the next if held under artificial culture. Consequently, when fish abundance is extremely low precocious males could be used as broodstock over several spawning seasons.

Our investigation examined a small part of a larger question, what is the genetic legacy of supplementation? Recent reviews by Araki (2008) and Araki and Schmid (2010) suggest that rapid domestication occurs when salmonids are under culture and that domestication will often lead to reduced performance under natural conditions (also see Blanchet et al. 2008; Roberge et al. 2008). Alternatively, significant benefits from salmonid supplementation programs have been reported (e.g. Sharma et al. 2006; Berejikian et al. 2008; Small et al. 2009). Because supplementation is a human enterprise, social and economic values along with biological considerations will determine whether it is instituted, maintained or stopped. Importantly, every supplementation project has the potential to provide managers with information if its effects are

monitored and evaluated. Consequently careful assessments and planned evaluation programs should be incorporated into every supplementation program since data derived from such efforts will help refine how supplementation is used in the future.

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