

Genetic improvement in coho salmon (*Oncorhynchus kisutch*). II: Selection response for early spawning date

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Abstract

Phenotypic records of within-year spawning date in two cultivated populations of coho salmon, named as even ($n=2272$) and odd ($n=1347$) year classes are analyzed. Both populations were selected for harvest weight and early spawning for four generations, using independent culling levels. Harvest weight was selected using breeding values obtained from an animal model in males and females, while early spawning was selected phenotypically only in females. A post-selection analysis to estimate breeding values in both characters allowed comparison of the phenotypic response (R) and genetic selection response (GR) to selection for early spawning, narrow sense heritability (h^2), and genetic correlation with harvest weight (r_g). Mean spawning dates were 13 and 15 days earlier after four generations of selection in the even and odd year class, respectively. This represents a phenotypic response to selection of -2.74 ± 0.7 ($P=0.03$) and -3.23 ± 1.3 ($P=0.09$) days per generation in the even and odd year classes, respectively. The heritability estimates, by regression of the selection differential on phenotypic change, were $h^2=1.78 \pm 0.37$ ($P<0.05$) for the even year class and $h^2=1.90 \pm 0.42$ ($P<0.05$) for the odd year class. In both cases, calculated values were greater than the highest possible value for heritability ($h^2=1$), which indicates that the response is overestimated due to a positive environmental effect which was not quantified. The estimates of narrow sense heritability using an animal model were high in both populations (even year class $h^2=0.40 \pm 0.05$, odd year class $h^2=0.44 \pm 0.06$). Breeding value analysis showed the genetic selection response was -0.62 and -1.13 days per generation in the even and odd year classes, respectively. The genetic correlation between spawning date and harvest weight was low in both year classes (even $r_g=0.25 \pm 0.13$; odd $r_g=-0.02 \pm 0.24$). The genetic selection differentials (GS) were lower in males than in females (even year class $GS_f=-1.12$ y $GS_m=-0.13$; odd year class $GS_f=-1.46$; $GS_m=-0.36$), which reflects selection practiced only on females.

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1. Introduction

Spawning date within a year or spawning season is a quantitative character of great importance in salmon

culture, since it is the primary determinant of the period of ova production, and also of the date of first feeding. This determines the entrance of juvenile fish into production systems, and therefore conditions the harvest date. A number of studies, mainly in rainbow trout, have shown that this character has an important component of genetic control. There is also evidence of important

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Table 1

Numbers of sires, dams, spawned daughters of the random group per generation in two domesticated populations of coho salmon and percent (%) of random daughters over total females spawned

Population	Generation	Year class	Sires	Dams	Daughters (%)
Even	Base	1992	22	46	208 (76.5)
	1	1994	31	93	198 (69.2)
	2	1996	27	103	349 (76.4)
	3	1998	30	100	232 (38.2)
	4	2000	34	99	1285 (100)
	Total		144	441	2272 (78.0)
Odd	Base	1993	36	96	331 (60.7)
	1	1995	32	101	283 (74.5)
	2	1997	33	100	309 (71.9)
	3	1999	30	98	364 (69.6)
	4	2001	43	100	60 (6.6)
	Total		174	495	1347 (48.3)

genetic variation within stocks; narrow sense heritability estimates have been high (0.53–0.65) for rainbow trout (Siitonen and Gall, 1989; Su et al., 1999), which concurs with the observed modification of spawning date by artificial selection. Fishback et al. (2000) described a closed population of rainbow trout in which phenotypic selection has expanded the spawning season of the broodstock from 2 weeks to 8 months. Other authors have also reported a favorable response to selection for

early spawning (Siitonen and Gall, 1989; Sadler et al., 1992). Siitonen and Gall (1989) indicated a selection response of almost 7 days per generation for 6 generations, advancing the spawning date more than a month. Additionally, recent studies report discovery of several QTL for spawning date in rainbow trout (O'Malley et al., 2003); one of them, in linkage group J, explained 16–64% of the variance in the studied population. These results provide strong evidence that spawning date in rainbow trout is a polygenic character with a few genes of major effect. By contrast, little is known of the genetic architecture of spawning date in other salmon species, since most studies have focused on understanding the genetic nature of the maturation (Nilsson, 1992; Hankin et al., 1993; Wild et al., 1994), especially early maturation (Silverstein and Hershberger, 1992; Heath et al., 1994, 2002). An exception is the study of Gall and Neira (2004) in coho salmon, who reported lower heritability estimates for spawning date (0.24) compared to rainbow trout.

The objective of this study is to contribute to the understanding of the genetic architecture of the character spawning date in coho salmon. In particular, narrow sense heritability and genetic correlation with harvest weight were estimated. The effects of artificial selection for early spawning in two populations of

Table 2

Phenotypic performance for spawning date and harvest weight in two domesticated populations of coho salmon

Population	Trait	Year class	N ^a	Mean	SD	CV	Min	Max
Even	Spawning date	1992	238	141.0	8.3	5.9	124	160
		1994	248	137.3	9.0	6.5	125	160
		1996	398	137.2	8.8	6.4	117	157
		1998	295	136.0	7.2	5.3	121	151
		2000	1285	127.9	6.1	4.7	115	154
		Total	2464					
	Harvest weight	1992	238	2498	505	20.2	1023	3564
		1994	248	2875	510	17.8	1121	3987
		1996	398	4342	801	18.4	1013	6109
		1998	295	4123	537	13.0	2141	5292
2000		1285	4070	827	20.3	1131	6061	
Odd	Spawning date	1993	381	142.5	10.0	7.0	123	172
		1995	310	130.7	7.9	6.0	120	156
		1997	358	134.7	8.0	6.0	121	165
		1999	419	127.3	7.2	5.6	102	142
		2001	60	128.1	4.9	3.9	112	139
		Total	1528					
	Harvest weight	1993	381	2502	365	14.6	1368	3816
		1995	310	3102	450	14.5	1275	4213
		1997	358	2921	474	16.2	1428	4389
		1999	419	3878	747	19.3	1129	5505
2001		60	3203	516	16.1	1423	4140	

^a Number of spawned females of the random group plus non-random females selected as mothers of the next generation and used in the genetic analysis.

coho salmon are also described. The selection scheme used was that of multiple characters using independent culling levels; first for harvest weight and then for spawning date. We compare the selection differentials, response to selection and realized heritability for early spawning based on a phenotypic analysis and the breeding values obtained from a post-selection analysis using an animal model. The direct response for harvest weight is presented in a companion paper (Neira et al., 2006).

2. Materials and methods

2.1. Study populations

The study was based on data from two coho salmon populations from the genetic improvement center (CMG) maintained by the Institute for Fisheries

Development (IFOP) and the University of Chile in Coyhaique (XI Region, Chile). The coho populations were produced using a two-year breeding cycle and consisted of two subpopulations formed from a common base population in 1992 and 1993, and referred to as even and odd year classes. The spawning season lasted between late April and June, each full-sib family was individually incubated, and alevin progeny individually PIT tagged in December at an average 5–10 g. Each full-sib family was randomly stocked in equal numbers (60–80) into three rearing cages under estuary water conditions (Ensenada Baja) where smoltification occurred naturally at eight months post-spawning; weight at harvest time was recorded at an age of 19 months in January. More detailed information about the general management of the fish in this breeding program is given in the companion paper (Neira et al., 2006) and also for the origin of the

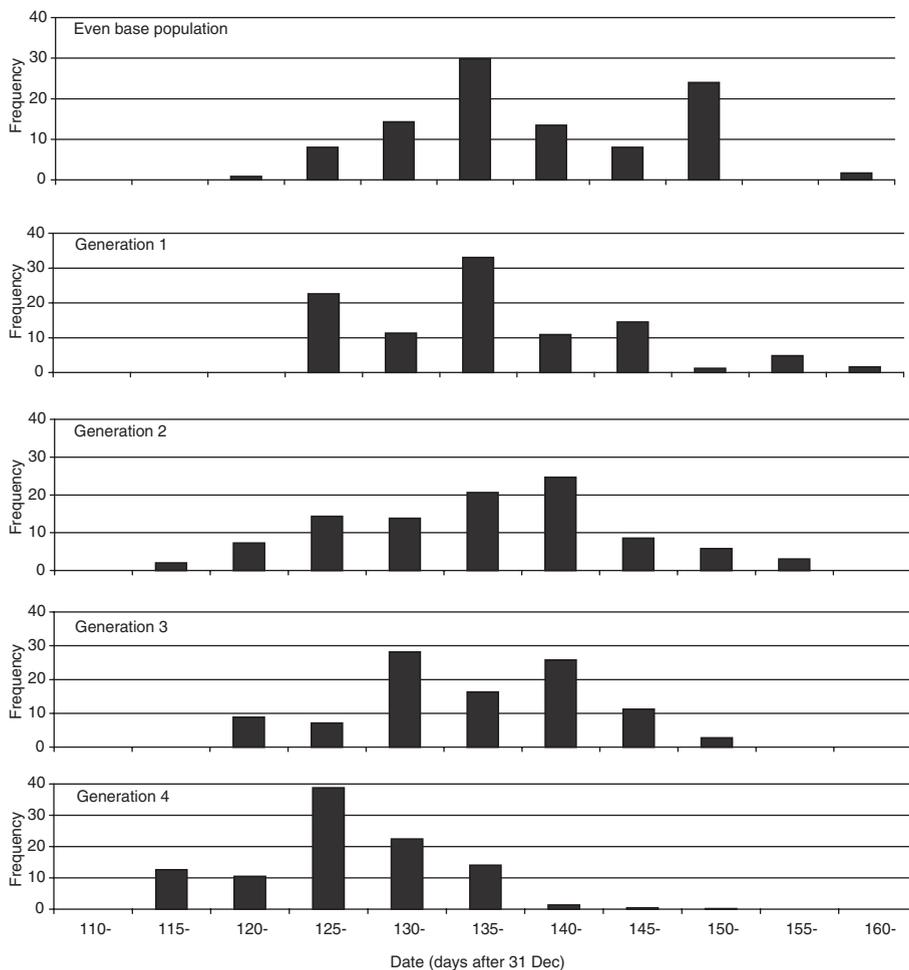


Fig. 1. Frequency distribution of spawning females of the base population and four generations of selection in the even population of coho salmon.

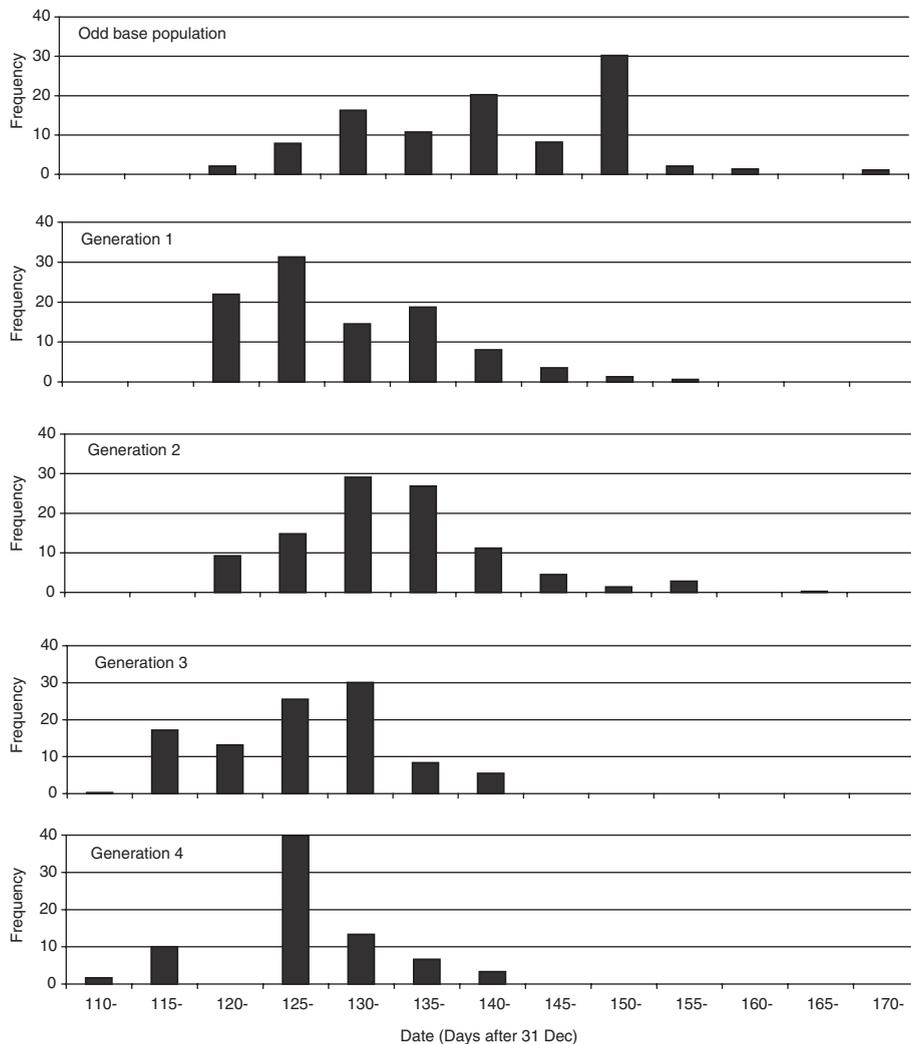


Fig. 2. Frequency distribution of spawning females of the base population and four generations of selection in the odd population of coho salmon.

populations see [Winkler et al. \(1999\)](#), and [Gall and Neira \(2004\)](#).

2.2. Artificial selection using independent culling levels

Artificial selection for spawning and harvest weight was applied for four generations, using independent culling levels ([Neira et al., 2006](#)). At harvest time, a random sample of the progeny was taken and kept until spawning; the main purpose of this random group was to estimate the average spawning date of the progeny population in every generation and was also used to estimate the average harvest weight. The random group generally represented between 12–39% of the total progeny size: the number per generation and year class is given in [Neira et al. \(2006\)](#). Breeding

females consisted of the females of the random group plus all remaining females in the top 25% for harvest weight. Breeding males consisted of a group of around 100 best ranked males for harvest weight. All these fish remained in sea-cages until they were sent to the hatchery as approaching maturity, generally in March.

Ranking of all fish available for selection was performed within sex according to their breeding value for harvest weight, estimated using BLUP predictors obtained with the program MTDFREML ([Boldman et al., 1995](#)) using a simple animal model. More details of the animal model and the selection response for harvest weight are given in [Neira et al. \(2006\)](#). At sexual maturity, males and females were maintained separately in freshwater tanks at the hatchery, and females were examined manually to determine the state of maturation

Table 3

Phenotypic selection differential per generation (S) in days, and accumulated selection differential (AS) on spawning date in females of two populations of coho salmon

Population	Generation	Year class	S	AS
Even	Base	1992	-0.9	-0.9
	1	1994	-1.8	-2.7
	2	1996	-0.4	-3.1
	3	1998	-2.5	-5.6
		Mean		-1.4
Odd	Base	1993	-4.6	-4.6
	1	1995	-1.5	-6.1
	2	1997	-0.8	-6.9
	3	1999	-1.2	-8.1
		Mean		-2.0

every 5 days in some years and weekly or bi-weekly in other years. Mature females were spawned and eggs fertilized using mature males with the highest ranking for harvest weight. Spawning date can be judged only in females, since all males are capable of releasing sperm throughout the spawning period. The spawned females representing the 300 highest rankings for harvest weight were identified and the fertilized eggs from the 120 females with earliest spawning dates were retained. After shocking, 100 families were finally selected keeping a mating design as close as possible to 1 male to 3–4 females and culling families with low egg survival (<50%). To avoid a confounding effect between spawning date and sire effects, males were used for at least two weeks of spawning. Full-sib mating was avoided. The character spawning date was measured as the number of days between December 31 and date of spawning (Gall and Neira, 2004).

2.3. Phenotypic analysis

Data analysis for spawning date was performed for the even and odd year classes separately. A total of 2272 females were analyzed in the even year class and 1347 in the odd year class (Table 1). The random females comprised 48% and 78% of all spawned females in the odd and even year classes, respectively. Since only females were selected for spawning date, the selection differential per generation (S) was calculated as half the difference between the phenotypic mean of selected females, adjusted for number of daughters and the population phenotype mean, assuming that the selection differential of males was 0. The phenotypic response to selection (R) was estimated from the regression of mean spawning date of the group on generations of selection.

2.4. Genetic analysis using an animal model

Both random females and non-random mothers were included to estimate genetic parameters in each generation (Table 2). The estimation of variance components and breeding values for spawning date was made using the ASREML program (Gilmour et al., 2002) using a bivariate animal model with harvest weight as the second character. The animal model included a compound year-cage effect with 15 levels and the random animal effect. The character harvest weight was first adjusted to a mean harvest age of 620 days using multiplicative correction factors. It should be noted that breeding values for males were derived from the performance of all female relatives. The genetic selection differentials for dams (GS_d) and sires (GS_s) selected as parents in each generation were calculated as the difference between the mean breeding value of selected parents, adjusted for number of daughters, and the mean of each population. The average genetic selection differential per generation (GS_{mean}) was calculated as the arithmetic mean of the selection differentials for dams and sires. The genetic selection response per generation (GR) was calculated as the difference between the mean breeding values in successive generations. We did not express the genetic selection response as a proportion of the phenotypic mean of each generation, since the measurement of the character is relative to an arbitrary date (December 31). The ratio between the mean genetic selection differential (GS_{mean}) and the genetic selection response per generation (GR) was calculated following Gall and Bakar (2002).

3. Results

3.1. Phenotypic performance

After 4 generations of selection, spawning date was advanced in both populations (Figs. 1 and 2; Table 2: parameter estimates for harvest weight given for

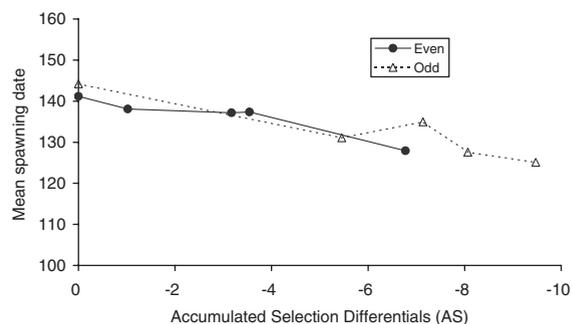


Fig. 3. Mean spawning date of females of two populations of coho salmon over accumulated selection differential (AS).

reference only); there was a decrease of 13 and 15 days in the even and odd year classes, respectively. This was accompanied by a reduction in the minimum and maximum spawning dates in both populations and in the coefficient of variation, principally in the odd year class (Table 2).

The mean selection differential was highly variable in both populations (Table 3); it was lower in the even year class (mean = -1.4) than in the odd year class (mean = -2.0). The change per generation, or phenotypic response (R) for spawning date was -2.74 ± 0.7 ($P=0.03$) and -3.23 ± 1.3 ($P=0.09$) days per generation, in the even and odd year classes, respectively. Fig. 3 shows, for both populations, the relation between accumulated selection differentials (AS) and response to selection (R). Based upon this relation, the realized heritability was $h^2=1.78 \pm 0.37$ for the even year class ($P<0.05$) and $h^2=1.90 \pm 0.42$ for the odd year class ($P<0.05$). In both cases, the result is greater than the maximum possible value for heritability ($h^2=1$), which indicates that this parameter was overestimated due to a positive environmental correlation which was not quantified.

3.2. Genetic performance

The estimation of genetic parameters by the animal model gave a high heritability for spawning date for females, low heritability for harvest weight in females and low phenotypic and genetic correlations between these characters. The heritability estimated for spawning date was identical in the two populations ($h^2=0.44 \pm 0.05$ for the even year class and $h^2=0.44 \pm 0.06$ for the odd year class). By contrast, the heritability estimate for

harvest weight for females in the even year class ($h^2=0.20 \pm 0.04$) was greater than that of the odd year class ($h^2=0.07 \pm 0.03$). The genetic and phenotypic correlations between spawning date and female harvest weight were positive and significantly greater than zero for even year class ($r_p=0.12 \pm 0.02$; $r_g=0.25 \pm 0.13$), but were negative and not significant for the odd year class ($r_p=-0.11 \pm 0.03$; $r_g=-0.02 \pm 0.24$).

The post-selection analysis of the data (Table 4) showed that both the realized genetic selection differential and the genetic selection response were different between sexes and between populations. In both populations, the average genetic selection differential was much lower in males than in females (even year class: $GS_f=-1.12$ y $GS_m=-0.13$; odd year class $GS_f=-1.46$; $GS_m=-0.36$). Average genetic selection intensity was variable from generation to generation and averaged -0.16 and -0.17 standard deviations for the even and odd year classes, respectively. Total, or accumulated, genetic selection response was -2.48 d, giving an average of -0.62 d per generation for the even year class and -4.53 , giving an average of -1.13 d for the odd year class. Table 4 also shows that the ratio (GR/GS) was 1.0 in both populations, which concurs with the post-selection analysis (Gall et al., 1993).

4. Discussion

The results demonstrate that the genetic progress per generation estimated by the analysis of breeding value was less than that calculated on the basis of phenotypic analysis. The results of the phenotypic selection response were similar to those reported by Siitonen and Gall (1989) in rainbow trout. However, up to the

Table 4

Breeding values (BV), genetic selection differential (GS), genetic selection intensity (GI), genetic selection response (GR) and the ratio (GR/GS) for spawning date in two populations of coho salmon

Pop.	Year class	BV				GS			GI ($GS_{\text{mean}}/S.D.$)	GR	Ratio (GR/GS)
		Population		Selected parents		Dams	Sires	Mean			
		Average	S.D.	Dams	Sires						
Even	1992	-0.44	3.71	-0.88	-0.84	-0.44	-0.41	-0.42	-0.11		
	1994	-0.86	4.18	-2.7	-1.75	-1.84	-0.89	-1.37	-0.33	-0.42	1
	1996	-2.22	4.17	-2.01	-2.25	0.22	-0.02	0.1	0.02	-1.36	1
	1998	-2.12	3.45	-4.53	-1.32	-2.4	0.8	-0.8	-0.23	0.1	1.02
	2000	-2.93	2.74	-0.88	-0.84	-	-	-	-	-0.81	1
	Mean			-2.53	-1.54	-1.12	-0.13	-0.62	-0.16	-0.62	1
Odd	1993	-0.04	4.53	-4.39	-1.14	-4.35	-1.1	-2.72	-0.16	-	
	1995	-2.77	3.58	-3.83	-4.01	-1.06	-1.24	-1.15	-0.32	-2.72	1
	1997	-3.92	3.63	-4.48	-4.43	-0.56	-0.51	-0.54	-0.15	-1.15	1
	1999	-4.46	3.55	-5.58	-3.55	-1.13	0.9	-0.11	-0.03	-0.54	1
	2001	-4.57	2.42	-	-	-	-	-	-	-0.12	1.03
	Mean			-4.57	-3.28	-1.78	-0.9	-1.13	-0.17	-1.13	1.01

present there are no other published studies with which to compare the genetic selection response on the basis of breeding values. In the present study, parameters such as realized heritability and phenotypic selection response reflect an important environmental effect, which was not possible to estimate. Davies and Bromage (2002) recognized the photoperiod as a primary environmental factor which regulates the maturation process, while water temperature modulates the time of maturation and spawning. All of the reproducers in this study (males and females) were maintained under a natural photoperiod, without artificial light, which should not have varied during the study. However, the water in which the fish were maintained came from the Simpson River, for which there are no registers of temperature.

The estimate of heritability for spawning date for the populations, obtained using the animal model, was 0.44, which is slightly less than the values reported for rainbow trout (Siitonen and Gall, 1989; Su et al., 1999). However, this estimate was greater than the 0.24 obtained by Gall and Neira (2004) in a previous study of these same populations. The difference is probably due to the fact that the estimations in the present study were based principally on phenotypic registers of randomly sampled individuals, and not just those whose descendants were within the selection program; the previous study therefore may have excluded some source(s) of variation. In both populations of the present study, the selection differential of males was much less than that of females, which reduced the realized selection differential by almost one half. Additionally, in the odd year class there was a tendency for the selection differential to decrease over generations, which was probably produced by chance and not by a systematic change in the selection, since this effect was not observed in the even year class.

In this study selection was applied to two traits, harvest weight and early spawning date, using independent culling levels. Quantitative genetic theory (Lush, 1945) predicts that when two characters are selected phenotypically using independent culling levels, the relative response in each will be 30% less than that expected for selection on just one character, assuming the characters are uncorrelated (Relative response = $\frac{1}{\sqrt{n}}$, where n is the number of characters under selection). In this case the reduction in relative response may not be as large as 30%, based on the estimated genetic correlation for the even year class.

A comparison of selection intensities for harvest weight (Neira et al., 2006) and spawning date may be of interest. In both populations the selection intensity was greater for harvest weight than for

spawning. In the even year class, the mean genetic selection intensity for harvest weight (GI_{mean}) was 6.7 times greater than that for spawning date (GI_{mean} harvest weight=1.17, GI_{mean} spawning date=0.17). In the odd year class, the mean genetic selection intensity for harvest weight (GI_{mean}) was 6.1 times greater than that for spawning date (GI_{mean} harvest weight=1.16, GI_{mean} spawning date=0.19). The difference was a direct reflection of the partitioning of selection intensity for the two characters, established arbitrarily in designing the study. Alternative selection intensities could be achieved by selecting a large proportion (number of fish) at harvest time which would provide greater opportunity for selection on spawning date.

Other methods besides artificial selection have been used to advance spawning date, such as changes in the photoperiod (Billard, 1985; Davies and Bromage, 2002) and the use of hormonal implants (Mylonas and Zohar, 2000). However, independent of the methodology utilized, some hatchery practices such as removing the smallest individuals which were born late in the season may have had an effect on advancing spawning date. Quinn et al. (2002) suggest that this hatchery practice, together with the low rate of smolting of the offspring of late spawners, are the principal causes of involuntary advancement of spawning date in domesticated populations of coho and chinook salmon in the USA.

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