

Genetic improvement in Coho salmon (*Oncorhynchus kisutch*). I: Selection response and inbreeding depression on harvest weight

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Abstract

In this study the genetic response to selection and the effects of inbreeding on harvest weight in two populations (which spawned as even and odd years classes) of Coho salmon are described. Artificial selection was performed using the best linear unbiased prediction (BLUP) of breeding values obtained from an animal model. Both populations were also selected for early spawning date using independent culling levels; these results are presented in a companion paper. The estimation of genetic parameters was based on the phenotypic records of 12,208 animals randomly sampled at harvest time (random group). These fish represented a mean of 64% and 48% of all animals with phenotypic records in the even and odd year classes, respectively. The narrow sense heritability estimated for harvest weight was high and very similar in the two populations, 0.39 ± 0.03 in the even year class and 0.40 ± 0.04 in the odd year class. Due to the mating design, the genetic selection differentials were 2.3 times greater in males than in females. The mean genetic selection response obtained was high in both populations, 383.2 g or $+1.26 \sigma$ and 302.4 g or $+1.23 \sigma$ per generation in the even and odd year classes, respectively. This is equivalent, on the average, to an increase in weight of 13.9% per generation compared to the base population, or 10.2% per generation with respect to the difference between successive generations. After the 4th generation of selection the mean inbreeding level was 9.5% in the even year class and 4.4% in the odd year class, which are close to preliminary estimates based on the records of the random group plus a group of animals with high harvest weight (Gallardo, J.A., García, X., Lhorente, J.P., Neira, R., 2004b. Effects of nonrandom mating schemes to delay the inbreeding accumulation in cultured populations of Coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aqua. Sci. 61, 547–553.). The estimated effects of inbreeding depression on harvest weight were negative, but not significantly different from 0 in either the even year class ($b_f = -7.04 \text{ g}/\Delta F$, s.e. = 3.9; Mean = 4118 g; inbreeding depression per 10% of ΔF was -1.7% ; $P = 0.06$) or the odd year class ($b_f = -4.8 \text{ g}/\Delta F$, s.e. = 0.33; Mean = 3243 g; inbreeding depression per 10% of ΔF was -1.5% ; $P = 0.33$). Other programs in salmon have selected for more than one character, however, there are still no estimates of economic weights published in salmon breeding programs, which are necessary to calculate the total genetic merit for these animals.

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1. Introduction

Mixed models are widely used in animal genetic improvement (Lynch and Walsh, 1998) to estimate genetic parameters (REML, restricted maximum likelihood) and to determine breeding values (BLUP, best linear unbiased predictor). The animal model is perhaps the procedure most often utilized to obtain breeding values, since it maximizes the correlation between the true and the predicted breeding values, using information from all animals recorded in the current generation and preceding generations, as well as the individual's own data. This animal model methodology produces a more exact estimation for breeding values, and increases the genetic response compared with other methods such as phenotypic selection (Belovsky and Kennedy, 1988).

In aquaculture, the methodology of animal models has been gradually incorporated in genetic improvement (Gjoen and Gjerde, 1998). Most studies in aquaculture have utilized these methods in the estimation of genetic parameters for productive traits (Rye and Mao, 1998; Henryon et al., 2002; Pante et al., 2002; Perry et al., 2004; Vandeputte et al., 2004), carcass characters (Neira et al., 2004; Norris and Cunningham, 2004), morphological characters (Martínez et al., 1999; Su et al., 2002), and reproductive traits (Su et al., 1997, 1999, 2002; Gall and Neira, 2004). Animal models have also been used in determining breeding values for artificial selection (Gall et al., 1993; Gall and Bakar, 2002; Fevolden et al., 2002; Bolivar and Newkirk, 2002; Ponzoni et al., 2005; Jerry et al., 2005). In particular, Gall and Bakar (2002) showed that the use of the animal model in a selection program in fish may increase the response to selection by 20–30% over the expected value using phenotypic mass selection.

Although the animal model may increase the response to selection, when the heritability of a character is low the model usually favors the selection of related individuals, which increases the rate of inbreeding (ΔF) and in the long run reduces the genetic variance (Belovsky and Kennedy, 1988; Quinton et al., 1992). Control of the inbreeding rate is important in selection programs, since the higher the level of inbreeding (F), the higher the probability of occurrence of the phenomenon known as inbreeding depression (ID). Estimates of ID in fish have consistently shown that inbred progeny have lower viability, slower growth, and also show less resistance to infection by protozoans (Gjerde et al., 1983; Su et al., 1996; Rye and Mao, 1998; Pante et al., 2001a; Arkush et al., 2002; Gallardo et al., 2004a). There are few studies on the effects of inbreeding on productive traits in Coho salmon; Myers et al. (2001) using controlled mating among full sibs (fast inbreeding) determined that

juvenile fish showed an reduction in body weight of about 10% per each 10% increment in inbreeding.

The objective of this study was to describe the effects of artificial selection using an animal model on the harvest weight in two populations of Coho salmon. In particular, we report the magnitude of selection differentials, genetic response and heritability of harvest weight. In addition, we estimated the effect of the selection on inbreeding levels and the magnitude of inbreeding depression on harvest weight. Response to selection for spawning date is presented in a companion paper (Neira et al., 2006-this issue).

2. Materials and methods

2.1. Study populations

This study reports on the results of the first four generations of selection for harvest weight performed on 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 two populations, termed 'even' and 'odd' year classes, were started in 1992 and 1993, respectively, from a common base population and managed in a two-year reproductive cycle. Since the initiation of the program, the two populations have been managed as closed populations, maintained by mating approximately 30–35 males with 100 females each season. The fish spawned from late April through June, the eggs of each full-sib family were incubated separately, and at the eyed egg stage 120 families were selected (i.e. higher survival) and moved to separate tanks for hatching and kept until fish were individually marked. Progeny of 100 families were individually PIT tagged in December when the fish averaged about 5–10 g, and transferred to estuary water conditions (Ensenada Baja) where each full-sib family was randomly stocked in equal numbers (60–80) into three rearing cages. Smoltification occurred naturally at eight months post-spawning and weight at harvest was recorded in January, at about 19 months of age. For more information about the characteristics and origins of the populations see Martínez et al. (1999), Winkler et al. (1999) and Gall and Neira (2004).

2.2. Artificial selection

Artificial selection for harvest weight and spawning was applied for four generations, using independent culling levels. In each generation, a random sample of the progeny present at harvest, called the "random"

group, was taken to estimate mean harvest weight and spawning date of the progeny population. Available breeding stock consisted of the random group plus the top 25% for harvest weight of the remaining fish; all these fish remained in sea-cages until they approached sexual maturity. The random group (Table 1) varied from 559 to 3794 and 781 to 1056 individuals for the even and odd year class, respectively, which represented approximately 12% to 39% of the total progeny present at harvest, except in the year 2000, when it was 77%. The random group represented 48–64% of all animals recorded at harvest. Fish were ranked within sex according to their breeding values for weight at harvest. Breeding values were estimated each generation using BLUP predictors with the program MTDFREML (Boldman et al., 1995) based on a single trait animal model. The animal model in each generation included the phenotypic values of all fish recorded at harvest. The general model used in matrix notation was:

$$y = Xb + Za + Ze \quad (1)$$

where y is a vector of harvest weight observations, b is a vector of fixed effects, a is a vector of random additive genetic values, e is a vector of random residual effects. X is a known design matrix relating y with fixed effects and Z is a known matrix relating y with additive genetic values and residual effects respectively. Significant fixed effects detected in a pre-BLUP analyses of variance were included in the model; they usually were sex, cage, year and dam's spawning date. Only the individual was included as a random effect and harvest weight was not available on the founding parents.

From the 300 females with greatest additive genetic value for harvest weight, the 120 with the earliest spawning dates were selected. Once incubation was completed (after shocking) the families with highest egg survival were kept, maintaining a mating design as close as possible to one male to 3–4 females. Full sib mating was avoided.

2.3. Post-selection analysis and estimation of genetic parameters

The post-selection analysis was carried out following the suggestions of Gall and Bakar (2002). Statistical analysis was performed separately for each year class, using data for 12,208 phenotypic records of the random group. Phenotypic data were not available for the parents of the initial generation (1992 and 1993) but all initial parents were taken from a common base population. An analysis of covariance (SAS, Statistical Analysis Systems Institute Inc. 1996) was used to evaluate the influence of the fixed effects. The model included the fixed effects of year, cage, sex, their interactions, with age at harvest as the covariate. The interactions cage–sex and year–cage–sex were not significant ($P > 0.44$) in both year classes, while year–sex was not significant in the odd year class ($P > 0.09$). In consequence, the following reduced model was used to estimate the least square means per generation for both year classes:

$$y_{ijkm} = \mu + Y_i + C_j + S_k + YS_{ik} + b_A A_m + e_{ijkm} \quad (2)$$

where y_{ijkm} is the value of the trait in individual m , μ is the overall mean, Y_i is the effect of year, C_j is the

Table 1

Numbers of sires, dams, estimated number of progeny at harvest (EP), number progeny recorded in the random group (R) and pre-selected selected group (S), and their ratios, in two populations of Coho salmon

Year class	Year	Sires	Dams	EP	Recorded progeny at harvest			R / R+S	R / EP
					R+S		R		
					Both sexes	Males	Females		
Even	1992	22	50	1571	851	372	246	0.73	0.39
	1994	31	93	4566	951	287	272	0.59	0.12
	1996	27	103	4837	1796	636	560	0.67	0.25
	1998	30	100	5400	4458	746	619	0.31	0.25
	2000	34	99	4924	3796	1841	1953	0.99	0.77
	Total	144	445		11,852	3882	3650		
Odd	1993	36	99	4529	1632	396	437	0.51	0.18
	1995	32	101	5390	1746	411	370	0.45	0.15
	1997	33	100	4718	4070	572	484	0.26	0.22
	1999	30	98	4747	2220	526	446	0.44	0.21
	2001	43	100	4909	2159	535	499	0.48	0.21
	Total	174	498		9668	2440	2236		

EP was defined as the number of live animals in the smolt stage minus 10%.

fixed effect cage, S_k is the fixed effect sex, YS_{ik} is the interaction of year by sex, A_m is the age of individual m at harvest, b_A represents the regression coefficient of y on A , and e_{ijkm} is the residual effect of individual m .

The estimation of variance components and the calculation of breeding values were made with the program ASREML (Gilmour et al., 2002) using a simple animal model. The animal model included a compound fixed effect year–cage–sex with 30 levels, the covariate age and a random animal effect.

2.4. Estimation of response to selection

The estimates of the least squares mean per generation were used to determine phenotypic trend over generations, while the genetic selection differentials (GS) were calculated as the difference between the mean breeding value of the individuals selected as parents and mean of all animals of the same sex by generation. Genetic selection response (GR) per generation was calculated as the difference between mean breeding values in successive generations. Mean genetic selection response was expressed as a proportion of the least square means of each generation (%R), as a proportion of the least square mean of the base population and in units of genetic standard deviations (R_{SD}) and as the difference between the initial and final mean breeding values as a proportion of the least square mean of the base population. We also calculated the ratio (GR / GS) between the genetic selection response and the genetic selection differentials (Gall and Bakar, 2002).

2.5. Rate of inbreeding and inbreeding depression

A previous study reported the level and rate of inbreeding for all animals recorded for harvest weight (Gallardo et al., 2004a). In the present study, the mean level of inbreeding was determined using only the random group, to obtain a less biased estimate of inbreeding. Individual inbreeding coefficients were calculated using the PEDIGREE program (Kinghorn and Kinghorn, 1999). Inbreeding was assumed to be zero in the base population. The rate of inbreeding in each generation (ΔF) was calculated following Falconer and Mackay (1996) as:

$$\Delta F = (F_t - F_{t-1}) / (1 - F_{t-1})$$

where F_t and F_{t-1} are mean coefficients of inbreeding in generations t and $t-1$, respectively. The average rate of

inbreeding for each year class was calculated as the simple mean of the inbreeding rates per generation.

The effect of inbreeding was evaluated for harvest weight of random group. The analysis included only data from 1996 to 2000 in the even year class and data from 1997 to 2001 in the odd year class, in which the coefficients of inbreeding were generally greater than zero. The following linear model was used to estimate the magnitude of inbreeding depression on harvest weight:

$$y_{ij} = \mu + YCS_i + b_a A_{ij} + b_f F_{ij} + e_{ij} \quad (3)$$

where y_{ij} is the value of the trait in individual j , μ is the overall mean, YCS_i is the composite fixed effect year–cage–sex, A_{ij} is the age of individual j at harvest, b_a represents the linear regression coefficient of y on A , F_{ij} is the inbreeding coefficient of individual j , b_f represents the linear regression of y on F , and e_{ij} is the residual unique to the j th individual.

Table 2
Descriptive statistics for harvest weight of the random progeny per year of two domesticated populations of Coho salmon

Year class	Year	Sex	Min	Max	Mean	CV	Least square mean
Even	1992	Males	790	3990	2602	22	2483
		Females	470	3610	2414	22	
		Average			2508		
	1994	Males	824	4080	2770	20	2840
		Females	391	6184	2752	19	
		Average			2761		
	1996	Males	610	6930	4560	19	4412
		Females	590	6150	4177	20	
		Average			4369		
	1998	Males	500	5900	3968	20	3902
		Females	501	5260	3764	17	
		Average			3866		
2000	Males	750	7000	4282	25	4083	
	Females	730	6250	3972	25		
	Average			4127			
Odd	1993	Males	981	3430	2502	16	2481
		Females	762	3742	2352	17	
		Average			2427		
	1995	Males	783	4541	3141	17	3113
		Females	430	4186	2979	16	
		Average			3060		
	1997	Males	762	4750	3009	21	2911
		Females	1025	4460	2874	17	
		Average			2942		
	1999	Males	1050	6500	3898	26	3827
		Females	610	5241	3705	22	
		Average			3802		
2001	Males	1028	4520	3155	20	2950	
	Females	840	4290	2862	20		
	Average			3009			

3. Results

3.1. Phenotypic and genetic performance

The least squares means of harvest weight showed a tendency to increase in both populations, primarily in the even year class (Table 2). In all generations of both year classes, males had a greater phenotypic mean than females, however, the phenotypic variation (CV) was similar in males and females. The heritability estimated for harvest weight was high and similar in both populations, 0.39 ± 0.03 in the even year class and 0.40 ± 0.03 in the odd year class.

The mean breeding values increased over generations in both populations (Table 3). The post selection analysis showed that the genetic selection differentials were 2.2 and 2.4 (odd and even year classes, respectively) times greater in males than in females, reflecting the higher selection intensity on males than on females. The genetic selection differentials were markedly higher in the last two generations for the even year class but remained relatively consistent for the odd year class. The intensity of genetic selection, measured as the ratio of selection differential to genetic (EBV) standard deviation was greater than one standard deviation in all generations except 1994.

As Table 4 shows, the average genetic selection response in harvest weight was 383.2 g per generation in the even year class and 302.4 g per generation in the odd year class. The average genetic response per generation expressed as a proportion of the least square mean of the previous generation averaged 10.5% and 9.9% per generation for the two year classes. Genetic selection response expressed in genetic standard deviation units was similar in the two populations, +1.26 SD and +1.23 SD

Table 4

Genetic selection response (GR) in grams and the ratio GR / GS (GS = genetic selection differential) for harvest weight in two year classes of Coho salmon

Year class	Year	GR (g)	%R	R _{SD}	GR / GS
Even	1992	–	–	–	–
	1994	351.4	14.3	1.12	1.05
	1996	264.4	9.3	1.05	1.12
	1998	473.8	10.7	1.44	1.05
	2000	443.0	11.4	1.42	1.08
	Mean	383.2	10.5	1.26	1.08
Odd	1993	–	–	–	–
	1995	271.3	10.9	1.27	1.04
	1997	263.9	8.5	1.22	1.09
	1999	300.8	10.3	1.27	1.10
	2001	372.8	9.8	1.14	1.01
	Mean	302.4	9.9	1.23	1.06

%R, and R_{SD} are genetic selection responses expressed as a proportion of the least square mean of the previous generation and in standard deviation units, respectively.

per generation in the even and odd year classes, respectively. Genetic selection response calculated as total genetic selection response relative to the base population phenotypic least squares mean harvest weight was 61.7% and 48.7%, equaling 1.22 and 1.42 genetic standard deviations per generation, for the even and odd year classes, respectively. The ratios G / GS were close to one in both populations, which agrees with a post selection analysis based on breeding values (Gall et al., 1993).

3.2. Inbreeding and inbreeding depression on harvest weight

The estimation of the mean level of inbreeding per generation and the rate of inbreeding calculated using the

Table 3

Average harvest weight estimated breeding values (EBV) and standard deviation (SD) of random progeny and selected parents, genetic selection differentials (GS) and genetic intensity (GI) of selection

Year class	Year	EBV of random progeny				EBV of selected parents			GS			GI
		Males	Females	Mean	SD	Sires	Dams	Mean	Sires	Dams	Mean	(GS / SD)
Even	1992	33.3	48.4	40.9	313.0	521.4	234.0	377.7	485.1	185.5	335.3	1.07
	1994	378.6	405.9	392.3	250.7	721.3	549.2	635.3	327.8	143.4	235.6	0.94
	1996	643.1	670.3	656.7	329.4	1252.0	962.5	1107.0	610.0	292.3	451.1	1.37
	1998	1127.0	1134.0	1130.0	312.4	1734.0	1346.0	1540.0	606.9	212.4	409.6	1.31
	2000	1577.0	1569.0	1573.0	384.8	–	–	–	–	–	–	–
	Mean	–	–	–	–	–	–	–	507.4	208.4	357.9	–
Odd	1993	22.4	24.0	23.2	213.3	377.5	189.9	283.7	353.6	167.5	260.6	1.22
	1995	292.7	296.2	294.5	215.8	643.3	431.9	537.7	347.2	139.2	243.2	1.13
	1997	556.2	560.6	558.4	236.9	956.8	706.2	831.5	396.3	150.0	273.1	1.15
	1999	858.5	860.0	859.2	327.3	1345.0	1110.0	1228.0	485.9	251.7	368.8	1.13
	2001	1229.0	1236.0	1232	228.8	–	–	–	–	–	–	–
	Mean	–	–	–	–	–	–	–	353.6	167.5	260.6	–

Table 5

Average level of inbreeding (F) and rate of inbreeding (ΔF) for random group (R) and for random plus selected group (R+S) in two populations of domesticated Coho salmon

Year class	Year	Random group (R)					R+S	
		F_R	SD	Min	Max	ΔF_R	F_{R+S}	ΔF_{R+S}
Even	1992	0	0	0	0	–	0	
	1994	0.9	3.9	0	25.0	0.9	1.1	1.1
	1996	5.5	3.9	0	18.8	4.6	5.4	4.3
	1998	6.9	2.8	2.3	15.6	1.5	6.9	1.6
	2000	9.5	2.8	5.1	18.8	2.8	9.5	2.8
	Mean					2.5		2.5
Odd	1993	0	0	0	0	–	0	
	1995	0.1	1.3	0	12.5	0.1	0.2	0.2
	1997	1.6	2.4	0	9.4	1.5	1.8	1.6
	1999	3.2	2.6	0	10.9	1.6	3.2	1.4
	2001	4.4	2.6	0.6	11.7	1.2	4.3	1.2
	Mean					1.1		1.1

R+S data were obtained from Gallardo et al. (2004a,b) over the same populations.

random group was almost identical to that obtained using all animals with phenotypic records (Table 5). After 4 generations of selection, the mean level of inbreeding was 9.5% in the even year class and 4.4% in the odd year class. This difference is explained by the difference in the number of founding adults taken from the base population (Table 1). The analysis of covariance showed no significant effect of inbreeding on harvest weight, neither in the even year class ($b_f = -7.04$ g/ ΔF , s.e. = 3.9; Mean = 4118 g; inbreeding depression per 10% of ΔF was -1.7% ; $P = 0.06$) nor in the odd year class ($b_f = -4.8$ g/ ΔF , s.e. = 0.33; Mean = 3243; inbreeding depression per 10% of ΔF was -1.5% ; $P = 0.33$).

4. Discussion

This study reports a significant progress in improving harvest weight of Coho salmon. The mean genetic improvement was about 1.25 SD per generation, which is equivalent to an increase in harvest weight of 10.2–13.9% per generation depending on the way the weight increase is expressed, in relation to the phenotypic mean in each generation or to the base population. These results are similar to those reported for this and other fish species. Hershberger et al. (1990) reported an increase in weight of 10.1% per generation using a program of family selection. In Tilapia, *Oreochromis niloticus*, Gall and Bakar (2002) and Ponzoni et al. (2005) indicated an increase in body weight per generation of about 13% and 10% respectively; both studies used BLUP selection. Similar results have been obtained in rainbow trout *Oncorhynchus mykiss* (Gjerde, 1986) and in Atlantic

salmon, *Salmo salar* (Gjerde, 1986; Gjerde and Korsvoll, 1999; O'Flynn et al., 1999).

Both year classes in the present study were also selected for early spawning date, using independent culling levels. Date of spawning was advanced by 0.62 and 1.13 days per generation in the even and odd year classes, respectively, equivalent to 0.19 and 0.24 standard deviation units (Neira et al., 2005). The lower response to selection in spawning date is explained mainly by the selection method applied. Spawning date was selected using phenotypic selection and not by BLUP selection as in harvest weight, and spawning date selection was practiced only with fish meeting a minimum harvest weight. This resulted in lower selection intensities applied to spawning date than to harvest weight. Most genetic improvement programs involve selection for more than one character; however, estimates of economic weights necessary to calculate the total genetic merit per animal are still scarce in the literature. One exception is the estimation of economic values in a commercial production system of the freshwater crayfish (*Cherax tenuimanus*) by Henryon et al. (1999).

It should be noted that the heritability used for the predicted response may be biased upwards because it was obtained from a model with animal as the only random effect. A complete study on the effects of random full-sib family effect to account for a possible tank effect caused by the separate rearing of the full-sib families until tagging and a possible non-additive genetic effect common to full-sibs has been completed and will be reported separately. Preliminary results indicate that the effects of common environment are irrelevant, probably due to the fact that alevins were pit tagged and communally raised since 5–10 g.

As predicted by Gjedrem (1983), the great progress obtained in genetic improvement of fish has been due to a high genetic variability present in the characters under selection. The majority of the species utilized in aquaculture today have been domesticated only recently; thus they should be expected to possess high genetic variability and prolificacy, which results in higher selection intensities compared to terrestrial farm animals. Another reason for the progress is the use of advanced methods of genetic evaluation such as BLUP selection (Gall et al., 1993) which is today standard in genetic improvement in aquaculture (Fevolden et al., 2002; Bolivar and Newkirk, 2002; Ponzoni et al., 2005; Jerry et al., 2005).

Gjedrem (2000) estimated that about 1% of the world production of aquaculture comes from genetically improved animals. In addition, the production of

improved animals is very heterogeneous at the global level, for example, in countries like Norway close to 70% of the production of salmon and trout is genetically improved (Fjalestad et al., 2003). Something similar occurs in Chile, since the large salmon-producing companies have maintained genetic improvement programs for the last 10 years. Fish have certainly received the greatest attention; genetic improvement programs have been developed for tilapia, *Oreochromis niloticus* (Longalongo et al., 1999), in Atlantic salmon, *Salmo salar* (Gjerde, 1986; Gjerde and Korsvoll, 1999), in Coho salmon, *Oncorhynchus kisutch* (Hershberger et al., 1990; present study), in rainbow trout, *Oncorhynchus mykiss* (Kincaid et al., 1977; Gjerde, 1986), in channel catfish, *Ictalurus punctatus* (Rezk et al., 2003) and in common carp, *Cyprinus carpio* (Tran and Nguyen, 1993), among others. In contrast, only a few genetic improvement programs have been described in other aquatic organisms such as shrimp, *Panaeus vannamei* (Fjalestad et al., 1997; Hetzel et al., 2000), freshwater crayfish, *Cherax destructor* (Jerry et al., 2005) and in the Pacific oyster, *Crasostrea gigas* (Ward et al., 2000).

One of the principal drawbacks of BLUP selection is the high level of inbreeding which results from the tendency of the procedure to select relatives as future parents (Quinton et al., 1992; Sonesson et al., 2005), especially when the heritability of the character is low. The levels of inbreeding rate reported here (ΔF odd=1.1%, ΔF even=2.4%) are similar to those predicted by simulation studies of fish breeding schemes (Sonesson et al., 2005) using BLUP selection, and to those obtained in other salmon populations subjected to artificial selection (Su et al., 1996; Rye and Mao, 1998; Myers et al., 2001; Pante et al., 2001b). The estimated level and rate of inbreeding obtained in this study show that our preliminary estimates (Gallardo et al., 2004b) were not biased by including only those individuals selected by weight, and that inbreeding rates were just above or near the limits recommended by various authors to prevent the detrimental effects of inbreeding (Tave, 1999; Meuwissen and Woolliams, 1994). Various methods have been devised to reduce tendencies toward increase in the rate of inbreeding produced by artificial selection (Villanueva et al., 1996; Meuwissen 1997; Wu and Schaeffer 2000). However, to date, few studies have evaluated in practice the methods cited above (Sanchez et al., 1999; Weigel and Lin 2000). Gallardo et al. (2004b) evaluated in practice the use of non-random mating to control the increase of inbreeding in the populations of Coho salmon of this study. These authors demonstrated that a crossing scheme that minimizes the

mean co-ancestry of the selected groups reduces the increment and the variance of inbreeding by 14 to 50 percent, thus reducing the possibility of inbreeding depression.

Predicting the magnitude of inbreeding depression in a population is a complex issue, since it depends not only on the level of inbreeding, but also on the genetic load present in the population (Bijlsma et al., 1999), the character under analysis (Su et al., 1996; DeRose and Roff, 1999; Gallardo et al., 2004a) and the environment in which it is evaluated (Dahlgard and Hoffmann, 2000; Gallardo and Neira, 2005). The magnitude of the estimates of inbreeding depression for harvest weight in both year classes of this study were low and within the range of previously reported values (−0.6% to −2.6% for each 10% increase in F) and in other salmon populations (Su et al., 1996; Pante et al., 2001b; Rye and Mao, 1998). Various reasons may explain the low inbreeding depression for body weight in these populations: (1) the mean inbreeding levels after a few generations are still low (i.e. $F < 10\%$); (2) the effect of selection on body weight may mask the real magnitude of inbreeding depression; (3) the slow accumulation of inbreeding may provide a greater opportunity to purge deleterious genes. Wang et al. (2001) analyzed estimates of inbreeding and inbreeding depression reported for salmon and suggested the last of these reasons. They observed that when the increase in inbreeding is rapid (i.e., full sib crosses), the deleterious effects of inbreeding tend to be greater than when the increase in inbreeding is slow as in programs of artificial selection.

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References

- Arkush, K.D., Giese, A.R., Mendonca, H.L., McBride, A.M., Marty, G.D., Hedrick, P.W., 2002. Resistance to three pathogens in the endangered winter-run Chinook salmon (*Oncorhynchus tshawytscha*): effects of inbreeding and major histocompatibility complex genotypes. *Can. J. Fish. Aquat. Sci.* 59, 966–975.
- Belonsky, G.M., Kennedy, B.W., 1988. Selection on individual phenotype and best linear unbiased predictor of breeding value in a closed swine herd. *J. Anim. Sci.* 66, 1124–1131.

- Bijlsma, R., Bundgaard, J., Van Putten, W.F., 1999. Environmental dependence of inbreeding depression and purging in *Drosophila melanogaster*. *J. Evol. Biol.* 12, 1125–1137.
- Boldman, K.G., Kriese, L.A., Van Vleck, L.D., Van Tassell, C.P., Kachman, S.D., 1995. A Manual for Use of MTDFRML: A Set of Programs to Obtain Estimates of Variances and Covariances (draft). U.S. Department of Agriculture, Agricultural Research Service.
- Bolivar, R.B., Newkirk, G.F., 2002. Response to within family selection for body weight in Nile tilapia (*Oreochromis niloticus*) using a single-trait animal model. *Aquaculture* 204, 371–381.
- Dahlgard, J., Hoffmann, A.A., 2000. Stress resistance and environmental dependency of inbreeding depression in *Drosophila melanogaster*. *Conserv. Biol.* 14, 1187–1192.
- DeRose, M.A., Roff, D.A., 1999. A comparison of inbreeding depression in life-history and morphological traits in animals. *Evolution* 53, 1288–1293.
- Falconer, D.S., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics, 4th Edition. Pearson Education Ltd., Essex, England.
- Fevolden, S.-E., Roed, K.H., Fjalestad, K.T., 2002. Selection response of cortisol and lysozyme in rainbow trout and correlation to growth. *Aquaculture* 205, 61–75.
- Fjalestad, K.T., Gjedrem, T., Carr, W.H., Sweeney, J.N., 1997. Final report: the shrimp breeding program. Selective breeding of *Penaeus vannamei*. AKVAFORSK Rep. No. 17/97. 85 pp.
- Fjalestad, K., Moen, T., Gomez-Raya, L., 2003. Prospects for genetic technology in salmon breeding programmes. *Aquacult. Res.* 34 (5), 397–406.
- Gall, G.A.E., Bakar, Y., 2002. Application of mixed-model techniques to fish breed improvement: analysis of breeding-value selection to increase 98-day body weight in tilapia. *Aquaculture* 212, 93–113.
- Gall, G.A.E., Neira, R., 2004. Genetic analysis of female reproductive traits of farmed Coho salmon (*Oncorhynchus kisutch*). *Aquaculture* 234, 143–154.
- Gall, G.A.E., Bakar, Y., Famula, T., 1993. Estimating genetic change from selection. *Aquaculture* 111, 75–88.
- Gallardo, J.A., Neira, R., 2005. Environmental dependence of inbreeding depression in cultured coho salmon (*Oncorhynchus kisutch*): aggressiveness, dominance and intraspecific competition. *Heredity* 95, 449–456.
- Gallardo, J.A., Garcia, X., Lhorente, J.P., Neira, R., 2004a. Inbreeding and inbreeding depression of female reproductive traits in two populations of Coho salmon selected using BLUP predictors of breeding values. *Aquaculture* 234, 111–122.
- Gallardo, J.A., Garcia, X., Lhorente, J.P., Neira, R., 2004b. Effects of nonrandom mating schemes to delay the inbreeding accumulation in cultured populations of Coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 61, 547–553.
- Gilmour, A.R., Cullis, B.R., Welham, S.J., Thompson, R., 2002. ASReml reference manual, 2nd edition. Release 1.0 NSW Agriculture Biometrical Bulletin, vol. 3. NSW Agriculture, Locked Bag, Orange, NSW 2800, Australia.
- Gjedrem, T., 1983. Genetic variation in quantitative traits and selective breeding in fish and shellfish. *Aquaculture* 33, 51–72.
- Gjedrem, T., 2000. Genetic improvement of cold-water fish species. *Aquacult. Res.* 31, 25–33.
- Gjerde, B., 1986. Growth and reproduction in fish and shellfish. *Aquaculture* 57, 37–56.
- Gjerde, B., Korsvoll, A., 1999. Realised selection differentials for growth rate and early sexual maturity in Atlantic salmon. *Aquac. Eur.* 99, 73–74 Trondheim, Norway. (abstract).
- Gjerde, B., Gunnes, K., Gjedrem, T., 1983. Effects of inbreeding on survival and growth in rainbow trout. *Aquaculture* 34, 327–332.
- Gjoen, H.M., Gjerde, B., 1998. Comparing breeding schemes using individual phenotypic values and BLUP breeding values as selection criteria. Proceedings of the 6th World Congress on Genetics Applied to Livestock Production, vol. 27. University of New England, Armidale, New South Wales, Australia, pp. 111–114.
- Henryon, M., Purvis, I.W., Berg, P., 1999. Definition of a breeding objective for commercial production of the freshwater crayfish, marron (*Cherax tenuimanus*). *Aquaculture* 173, 179–195.
- Henryon, M., Jokumsen, A., Berg, P., Lund, I., Pedersen, P.B., Olesen, N.J., Slierendrecht, W.J., 2002. Genetic variation for growth rate, feed conversion efficiency, and disease resistance exists within a farmed population of rainbow trout. *Aquaculture* 209, 59–76.
- Hershberger, W.K., Myers, J.M., Iwamoto, M., Mcauley, W.C., Saxton, A.M., 1990. Genetic changes in the growth of coho salmon (*Oncorhynchus kisutch*) in marine net-pens, produced by 10 years of selection. *Aquaculture* 85, 187–197.
- Hetzel, D.J.S., Crocos, P.J., Davis, G.P., Moore, S.S., Preston, N.C., 2000. Response to selection and heritability for growth in the Kuruma prawn, *Penaeus japonicus*. *Aquaculture* 181, 215–223.
- Jerry, D.R., Purvis, I.W., Piper, L.R., Dennis, C.A., 2005. Selection for faster growth in the freshwater crayfish *Cherax destructor*. *Aquaculture* 247, 169–176.
- Kincaid, H.L., Bridges, W.R., Von Limbach, B., 1977. Three generations of selection for growth rate in fall spawning rainbow trout. *Trans. Am. Fish. Soc.* 106, 621–629.
- Kinghorn, B., Kinghorn, S., 1999. PEDIGREE VIEWER Program. Version 4.9. University of New England, Australia.
- Lynch, M., Walsh, B., 1998. Genetics and Analysis of Quantitative Traits. Sinauer Associates, Sunderland, MA.
- Longalong, F.M., Eknath, A.E., Bentsen, H.B., 1999. Response to bi-directional selection for frequency of early maturing females in Nile tilapia (*Oreochromis niloticus*). *Aquaculture* 178, 13–25.
- Martínez, V., Neira, R., Gall, G.A.E., 1999. Estimation of genetic parameters from pedigreed populations: lessons from analysis of alevin weight in Coho salmon (*Oncorhynchus kisutch*). *Aquaculture* 180, 223–236.
- Meuwissen, T.H.E., 1997. Maximising the response of selection with a predefined rate of inbreeding. *J. Anim. Sci.* 75, 934–940.
- Meuwissen, T.H.E., Woolliams, J., 1994. Effective sizes of livestock populations to prevent a decline in fitness. *Theor. Appl. Genet.* 89, 1019–1026.
- Myers, J.M., Heggelund, P.O., Hudson, G., Iwamoto, R.N., 2001. Genetics and broodstock management of Coho salmon. *Aquaculture* 197, 43–62.
- Neira, R., Lhorente, J.P., Aranceda, C., Diaz, N.F., Bustos, E., Alert, A., 2004. Studies on carcass traits in two populations of Coho salmon (*Oncorhynchus kisutch*): phenotypic and genetic parameters. *Aquaculture* 241, 117–131.
- Neira, R., Diaz, N.F., Gall, G.A.E., Gallardo, J.A., Lhorente, J.P., Alert, A., 2006-this issue. Genetic improvement in Coho salmon (*Oncorhynchus kisutch*). II: Selection response to early spawning date. *Aquaculture*. doi:10.1016/j.aquaculture.2006.03.001.
- Norris, A.T., Cunningham, E.P., 2004. Estimates of phenotypic and genetic parameters for flesh colour traits in farmed Atlantic salmon based on multiple trait animal model. *Livest. Prod. Sci.* 89, 209–222.
- O'Flynn, F.M., Bailey, J.K., Friars, G.W., 1999. Responses to two generations of index selection in Atlantic salmon (*Salmo salar*). *Aquaculture* 173, 143–147.

- Pante, M.J., Gjerde, B., McMillan, I., 2001a. Effects of inbreeding on body weight at harvest in rainbow trout, *Oncorhynchus mykiss*. Aquaculture 192, 201–211.
- Pante, M.J., Gjerde, B., McMillan, I., 2001b. Inbreeding levels in selected populations of rainbow trout, *Oncorhynchus mykiss*. Aquaculture 192, 213–224.
- Pante, M.J., Gjerde, B., McMillan, I., Misztal, I., 2002. Estimation of additive and dominance genetic variances for body weight at harvest in rainbow trout, *Oncorhynchus mykiss*. Aquaculture 204, 383–392.
- Perry, G., Tarte, P., Croisetière, S., Belhumeur, P., Bernatchez, L., 2004. Genetic variance and covariance for 0+ brook char (*Salvelinus fontinalis*) weight and survival time of furunculosis (*Aeromonas salmonicida*) exposure. Aquaculture 235, 263–271.
- Ponzoni, R.W., Hamzah, A., Tan, S., Kamaruzzaman, N., 2005. Genetic parameters and response to selection for live weight in the GIFT strain of Nile Tilapia (*Oreochromis niloticus*). Aquaculture 247, 203–210.
- Quinton, M., Smith, C., Goddard, M.E., 1992. Comparison of selection methods at the same level of inbreeding. J. Anim. Sci. 72, 1060–1067.
- Rezk, M.A., Smitherman, R.O., Williams, J.C., Nichols, A., Kucuktas, H., Dunham, R.A., 2003. Response to three generations of selection for increased body weight in channel catfish, *Ictalurus punctatus*, grown in earthen ponds. Aquaculture 228, 69–79.
- Rye, M., Mao, I.L., 1998. Nonadditive genetic effects of inbreeding depression for body weight in Atlantic salmon (*Salmo salar* L.). Livest. Prod. Sci. 57, 15–22.
- Sanchez, L., Toro, M.A., García, C., 1999. Improving the efficiency of artificial selection: more selection pressure with less inbreeding. Genetics 151, 1103–1114.
- Sonesson, A.K., Gjerde, B., Meuwissen, T.H.E., 2005. Truncation selection for BLUP-EBV and phenotypic values in fish breeding schemes. Aquaculture 243, 61–68.
- SAS Institute Inc., 1996. SAS user's guide: Statistics, Windows Version 6.03. edition.
- Su, G.-S., Liljedahl, L.-E., Gall, G.A.E., 1996. Effects of inbreeding on growth and reproductive traits in rainbow trout (*Oncorhynchus mykiss*). Aquaculture 142, 139–148.
- Su, G.-S., Liljedahl, L.-E., Gall, G.A.E., 1997. Genetic and environmental variation of female reproductive traits in rainbow trout (*Oncorhynchus mykiss*). Aquaculture 154, 115–124.
- Su, G.-S., Liljedahl, L.-E., Gall, G.A.E., 1999. Estimates of phenotypic and genetic parameters for within-season date and age at spawning of female rainbow trout. Aquaculture 171, 209–220.
- Su, G.-S., Liljedahl, L.-E., Gall, G.A.E., 2002. Genetic correlations between body weight at different ages and with reproductive traits in rainbow trout. Aquaculture 213, 85–94.
- Tave, D., 1999. Inbreeding and brood stock management. FAO Fisheries Technical Paper, vol. 392. FAO, Rome. 122 pp.
- Tran, M.T., Nguyen, C.T., 1993. Selection of common carp (*Cyprinus carpio* L.) in Vietnam. Aquaculture 111, 301–302.
- Vandeputte, M., Kocour, M., Magera, S., Dupont-Niveta, M., De Guerrya, D., Rodinab, M., Gelab, D., Vallodc, D., Chevassusa, B., Linhart, O., 2004. Heritability estimates for growth-related traits using microsatellite parentage assignment in juvenile common carp (*Cyprinus carpio* L.). Aquaculture 235, 223–236.
- Villanueva, B., Woolliams, J.A., Gjerde, B., 1996. Optimum designs for breeding programmes under mass selection with an application in fish breeding. Anim. Sci. 63, 563–576.
- Wang, S.Z., Hard, J., Utter, F., 2001. Salmonid inbreeding: a review. Rev. Fish Biol. Fish. 11, 301–319.
- Ward, R.D., English, L.J., McGoldrick, D.J., Maguire, G.B., Nell, J.A., Thompson, P.A., 2000. Genetic improvement of the Pacific oyster *Crassostrea gigas* (Thunberg) in Australia. Aquac. Res. 31, 35–44.
- Weigel, K.A., Lin, S.W., 2000. Use of computerised mate selection programs to control inbreeding of Holstein and Jersey Cattle in the next generation. J. Dairy Sci. 83, 822–828.
- Winkler, F.M., Bartley, D., Diaz, N.F., 1999. Genetic differences among year classes in a hatchery population of Coho salmon (*Oncorhynchus kisutch* (Walbaum, 1792)) in Chile. Aquaculture 173, 425–433.
- Wu, L., Schaeffer, L.R., 2000. Reducing the effect of parent averages from animal solutions in mixed model equations. J. Anim. Breed. Genet. 117, 361–374.