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Inbreeding and inbreeding depression of female reproductive traits in two populations of Coho salmon selected using BLUP predictors of breeding values

José A. Gallardo[a], Ximena García[a],
Jean Paul Lhorente[b], Roberto Neira[a],*

[a] Lab. Genética Cuantitativa, Dpto. de Producción Animal, Fac. Ciencias Agronómicas,
Universidad de Chile, Santa Rosa 11.315 La Pintana, Santiago, Chile
[b] Complejo Piscícola Coyhaique, Instituto de Fomento Pesquero, Coyhaique, Chile

Abstract

Levels of inbreeding and inbreeding depression were studied in two populations of Coho salmon (*Oncorhynchus kisutch*) in Chile. The two populations, termed even year, and odd year were artificially selected by weight at harvest over four generations, using the best linear unbiased prediction (BLUP) of breeding values. Also, general linear models (GLM) were used to analyze the effects of inbreeding on reproductive traits of the females and on survival of the progeny. The selection resulted in 56–76% of the parents of the base population not contributing with descendents in the fourth generation. The inbreeding rate was greater in the even population (ΔF=2.45% per generation) than the odd population (ΔF=1.10% per generation) as a direct consequence of the smaller number of founder individuals in the former population (Ne=61 and 106, respectively). The level of inbreeding in the last generation was 9.5% (S.D.=2.7, range 5–19%) for year-class 2000 and 4.3% (S.D.=2.6, range 1–12%) for year-class 2001. Significant inbreeding depression was estimated for the gonadosomatic index (−5.3% per each 10% increase in inbreeding) in population year 2000, and for body length at spawning (−1.56%) in population year 2001. The inbreeding did not significantly reduce other traits such as weight body at spawning, weight of the gonad, number of green eggs, or relative fecundity. No significant inbreeding depression was observed in either population regarding the survival of eggs in the

* Corresponding author. Tel.: +56-2-5413380; fax: +56-2-6785802.
  E-mail address: rneira@uchile.cl (R. Neira).

eyed stage. Given the deleterious effects of inbreeding on reproductive traits, salmon selection programs should employ methods which limit the rate of increase of this factor.

1. Introduction

Genetic improvement of fishes in aquaculture has recently benefited from incorporation of the "best linear unbiased predictor" (BLUP) for breeding values (BV), when using the animal model for genetic evaluation (Gjoen and Gjerde, 1998; Martínez et al., 1999). This procedure maximises the correlation between the true and the predicted BV, using information from all animals recorded in the present generation, and of preceding generations, as well as the individual's own data. This animal estimation produces a more exact estimation for the breeding value, and increases the genetic response compared with other methods such as phenotypic selection (Belonsky and Kennedy, 1988). However, given that the animal model favours selection of related individuals, it also produces an increase in the rate of inbreeding (ΔF) and a reduction in the genetic variance over the long term (Belonsky and Kennedy, 1988; Quinton et al., 1992). There have been few empirical evaluations of the rate of inbreeding in fish populations subject to artificial selection. In rainbow trout populations, Su et al. (1996) estimated a rate of inbreeding (ΔF) between 1.3% and 1.7% per generation, while Pante et al. (2001a) found rates of inbreeding of between 0.53% and 2% per generation.

The control of inbreeding rate is important in selection programs as the higher the level of inbreeding (F), the higher is the probability of occurrence of the phenomenon known as inbreeding depression (ID). Estimations of ID in fishes has consistently shown that consanguineous progeny has lower viability, less growth, and also shows lower resistance to infection by protozoans (Gjerde et al., 1983; Su et al., 1996; Rye and Mao, 1998; Pante et al., 2001b; Arkush et al., 2002). Gjerde et al. (1983) found a strong decrease in survival in various early stages of development in rainbow trout, as well as a low growth rate in adults with high levels of inbreeding (F=0.25, 0.375, and 0.5). Estimates obtained from artificially selected populations (Su et al., 1996) showed that the magnitude of the inbreeding depression (ID) for body weight increased with age (ID=+1.73%, −0.85%, and −2.26% for each 10% increment in inbreeding at 168, 280, and 364 days, respectively). Similarly, Pante et al. (2001b) estimated an average decrease of between −1.0 and −2.6 for each 10% increase in inbreeding. Rye and Mao (1998) estimated ID of between −0.6% and −2.6% for each 10% increase in inbreeding for the same trait in Atlantic salmon. Arkush et al. (2002) recently demonstrated that inbreeding could also increase the severity of a protozoan infection in Chinook salmon (*Oncorhynchus tshawytscha*). In spite of the harmful effects of the preceding data, little is known concerning the effects of inbreeding on reproductive traits. These traits are determining factors in the long-term success of selection programs. In rainbow trout, Su et al. (1996) estimated that for each 10% increase in inbreeding the numbers of eggs decreased

significantly by 6.1%. It was also shown that inbreeding of the dam, but not the sire, affected the survival of the progeny (ID=−11.6% and 2.0%, respectively). Data on the effects of inbreeding in reproductive traits in Coho salmon (*Oncorhynchus kisutch*) have not been published.

The objectives of the present study were: (1) to determine the effect of artificial selection, following the animal model, on the levels of inbreeding in two populations of Coho salmon; (2) to investigate the effects of inbreeding on reproductive traits in females; and (3) to evaluate the effects of inbreeding on egg survival.

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 two populations, termed 'even' and 'odd', were produced in 1992 and 1993, respectively, and are managed in a 2-year reproductive cycle. Individuals were ranked using their breeding values for body weight at harvest time and the 25% best individuals (1000 approximately) were kept as breeding stock. Spawning season occurred between April and June each year. The first 300 spawning females and 60 males were randomly mated, but each male was used to fertilize eggs of females spawning at the beginning, at the middle and at the end of the spawning period. Additionally, full siblings (FS) mating were avoided. The eggs of each full-sib family were incubated separately, and at eyed eggs stage 120 families were selected and moved to individual tanks considering the following criterion: (1) keeping a mating design as close as possible to one male to three to four females; and (2) keep families with highest eggs survival (>50%). Then, the progeny of only 100 families were individually PIT tagged in December when the fish averaged about 5–7 g. At this age fish are 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 8 months post-spawning and weight at harvest time was recorded in February, at 20–21 months of age. For more information about the characters and origins of the populations see Martinez et al. (1999), Winkler et al. (1999), and Gall and Neira (2004).

Artificial selection was practised for four generations in both the even and the odd populations. Characters selected included the weight at harvest, using BLUP predictions of breeding values obtained from the MTDFREML program (Boldman et al., 1995) by means of the animal model, and early spawning by means of phenotypic selection.

2.2. Data

The level and rate of inbreeding in the even and odd populations were determined on the basis of the genealogical records of the animals (Table 1). All together, each generation was composed of between 850 and 4400 individuals in the even population, and between

Table 1
Numbers of sires, dams, and sexed progeny per generation in two domesticated populations of Coho salmon

Year class	Year	Sire	Dam	n
Even	1992	22	50	851
	1994	33	93	951
	1996	27	103	1796
	1998	30	100	4458
	2000	34	99	3796
	Total	146	445	11 852
Odd	1993	36	99	1632
	1995	32	102	1746
	1997	33	100	4070
	1999	31	98	2220
	2001	43	100	2159
	Total	132	399	9668

1600 and 2200 in the odd population (Table 1). The effective size (Ne) of the base population was 61 for the even population and 106 for the odd population.

Inbreeding depression (ID) of reproductive traits in females was evaluated in the last generation of each population, in 2000 and 2001. The reproductive traits evaluated included weight (SW), and body length at spawning (SL), gonad weight (GW), gonadosomatic index (GSI=GW/SW ratio), number of green eggs (GE=GW×(egg per 10 g)/10) where 'egg per 10 g' is the number of eggs in 10 g of gonad, and finally, the relative fecundity (RF) calculated as the number of green eggs per female divided by the SW. The effect of inbreeding on the survival of eggs was determined on eggs in the eyed stage. Survival was determined as the fraction of eggs remaining alive after shocking, in relation to the total number of eggs successfully fertilized. The survival post-fertilization was evaluated 2–4 h after fertilized eggs were hydrated, as the number of green eggs minus the total number of dead eggs counted manually, in relation to the total number of green eggs.

2.3. Data analysis

The effect of selection on the long-term contribution of the parents of the base population was studied based on pedigree records in order to determine which had failed to leave descendants in the last generation. The level of inbreeding was calculated for each generation as a mean of the coefficients of inbreeding of all the animals at harvesting time. Individual coefficients of inbreeding were calculated using the PEDIGREE program (Kinghorn and Kinghorn, 1999). Inbreeding was assumed to be zero in both base populations. 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 rate of inbreeding for each population was calculated as the simple mean of the inbreeding rates per generation.

The effects of inbreeding were evaluated from reproductive data and survival of progeny, separately, in 2000 and 2001. The following linear models were used to estimate the magnitude of inbreeding depression on reproductive traits (Eq. (1)) and on survival of eggs (Eq. (2))

$$y_i = u + b_{sd}SD_i + b_f F_i + e_i \tag{1}$$

$$y_i = u + b_{sd}SD + b_D F_D + b_S F_S + b_o F_o + e_i \tag{2}$$

where y_i is the record of each trait in the female or the progeny i; SD is the spawning date, defined as the correlative number of days $(1, 2, 3,\ldots,n)$ between the first day of spawning and the day of the respective observation. F_i is the coefficient of inbreeding of the female; b_{sd} represents the partial regression coefficient of y on SD; b_f is the partial regression coefficient of y on F. The date of spawning was included as an attempt to increase the precision of the estimations of ID. F_D, F_S, and F_o represent the coefficients of inbreeding of the dam, sire, and progeny (eggs), respectively.

3. Results

3.1. Reproductive performance and survival of eyed eggs

The females from 2001 showed the highest values for all the reproductive traits analyzed, except for relative fecundity, when compared with data from the year 2000 group (Table 2). Similarly, survival of eyed eggs was greater in 2001 (mean=69%,

Table 2

Average values for different morphological and reproductive traits in females of two domesticated populations of Coho salmon

Year	Trait	Mean	Min	Max	S.D.	n
2000	SW (g)	4958	3000	6700	641	317
	SL (cm)	69.0	61.0	78.0	3	318
	GW (g)	914	531	1339	149	317
	GE (number)	5695	2982	8834	955	317
	GSI (%)	18.5	12	24	2	316
	RF (no. of eggs×kg^{-1})	1164.9	620	1989	220	316
2001	SW (g)	5550	3085	6927	540	221
	SL (cm)	70.5	64.0	75.5	2	221
	GW (g)	1065	500	1474	153	221
	GE (number)	5977	3390	8672	916	221
	GSI (%)	19.2	12.4	24.1	2	220
	RF (no. of eggs×kg^{-1})	1082	715	1923	176	220

SW, spawn weight; SL, spawn length; GW, gonad weight; GE, green eggs; GSI, gonadosomatic index; RF, relative fecundity; n, number of individuals measured.

Table 3
Number of family selected (sire's and dam's families) by the animal model, and number parents selected from each family full-sib (dam's families) per generation

Year class	Year	Families selected				Parents selected per full-sib family		
		Sires	Dams	% Sires	% Dams	Mean (DS)	Min	Max
Even	1992[a]	20	39	90.9	78.0	3.2 (4.0)	1	24
	1994	23	41	69.7	44.1	3.1 (2.5)	1	10
	1996	17	38	63.0	36.9	3.4 (3.7)	1	19
	1998	21	40	70.0	40.0	3.2 (2.4)	1	12
	Mean			73.4	49.7			
Odd	1993	31	57	86.1	57.6	2.3 (1.8)	1	9
	1995	25	51	78.1	50.0	2.6 (1.9)	1	9
	1997	27	46	81.8	46.6	2.8 (1.9)	1	8
	1999	20	49	64.5	50.0	3.0 (1.9)	1	8
	Mean			77.6	50.9			

[a] No BLUP selection this year, within family selection was practiced instead.

S.D.=19.1, range 15–98%, n=198) than in 2000 (mean=55%, S.D.=23.7, range 5–92%, n=197).

3.2. Effect of BLUP selection on the genetic contribution and on the level of inbreeding

The BLUP selection and the mating design resulted in an average of 75% of sire's families and 50% of dam's families contributing with progeny per generation in both year classes (Table 3). However, in the even year class, the average number of parents selected
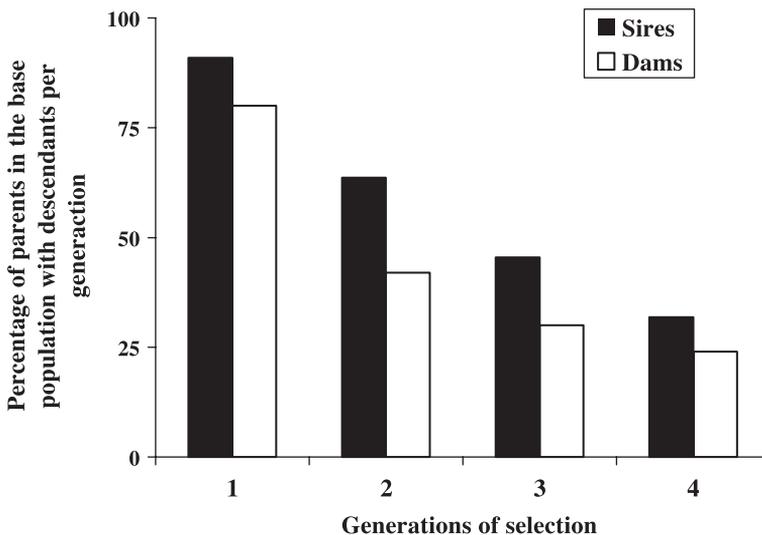

Fig. 1. Genetic contribution of the parents of the base population for the even class year for each generation of selection (n sires=22; n dams=50).
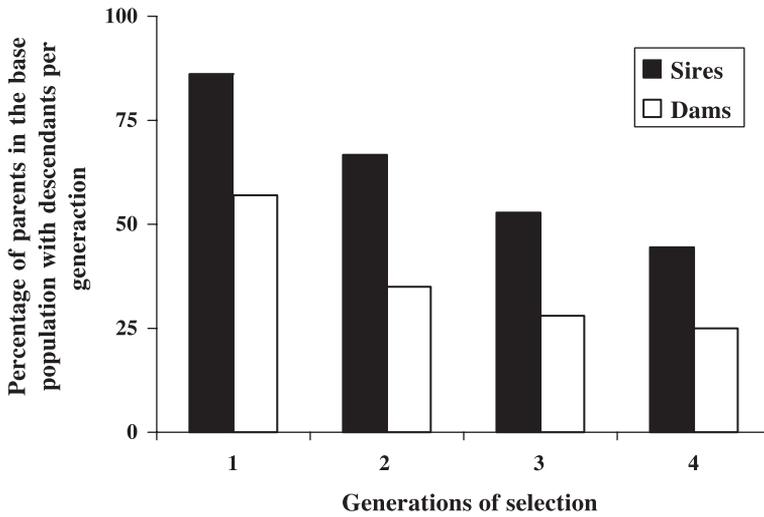
Fig. 2. Genetic contribution of the parents of the base population for the odd class year for each generation of selection (*n* sires=33; *n* dams=99).

by full-sib family was greater and more variable than in the odd year class. Consequently, the long-term genetic contribution of the parents of the base population was different between populations and between sexes (Figs. 1 and 2). In the even population, only 31% of the sires and 24% of the dams contributed their genes after four generations of selection. However, in the odd population, although the contribution of the sires was greater than in the even population (44%), the genetic contribution of the dams was similar (25%). Therefore, in both populations, the genetic contribution of the founder females dropped faster than founder males.

The even population showed twofold the rate of inbreeding (ΔF=2.45) of the odd population (ΔF=1.10), result that may be a direct consequence of having a smaller number

Table 4
Average level of inbreeding and rate of inbreeding (ΔF) for each generation in two populations of domesticated Coho salmon

Year class	Year	Mean	S.D.	Min	Max	ΔF
Even	1992	0	0	0	0	
	1994	1.1	4.2	0	25	1.1
	1996	5.4	3.9	0	18.8	4.3
	1998	6.9	2.8	2.3	15.6	1.6
	2000	9.5	2.8	5.1	18.8	2.8
					Mean	2.5
Odd	1993	0	0	0	0	
	1995	0.2	1.6	0	12.5	0.2
	1997	1.8	2.5	0	9.4	1.6
	1999	3.2	2.7	0	10.9	1.4
	2001	4.3	2.6	0.6	11.7	1.2
					Mean	1.1

Table 5
Inbreeding depression (ID) for different reproductive traits in two populations of domesticated Coho salmon

Year	Trait	b	S.E.	Mean	ID (%)	P
2000	SW (g)	−8.28	13.54	4959	−1.67	0.541
	SL (cm)	−0.03	0.05	69.2	−0.39	0.615
	GW (g)	−6.11	3.13	914	−6.68	0.052
	GSI (%)	−0.10	005	18.5	−5.32	0.039
	GE (number)	−7.87	20.42	5695	−1.38	0.700
	RF (no. of eggs×kg^{-1})	0.74	4.70	1165	0.63	0.876
2001	SW (g)	2.02	13.57	5550	0.36	0.880
	SL (cm)	−0.11	0.05	70.5	−1.61	0.019
	GW (g)	7.21	3.69	1065	6.77	0.058
	GSI (%)	0.13	0.05	19.2	6.77	0.013
	GE (number)	41.81	22.54	5977	6.99	0.067
	RF (no. of eggs×kg^{-1})	−9.16	4.39	1082	−8.47	0.330

ID, inbreeding depression measured in percentage of mean per 10% of inbreeding; SW, spawn weight; SL, spawn length; GW, gonad weight; GE, green eggs; GSI, gonadosomatic index; RF, relative fecundity.
P=level of significance.

of founder individuals (Ne=61 and 106, respectively). Consequently the average level of inbreeding was greater in the even population than in the odd population in equivalent generations (Table 4). For example, in the last generation the average inbreeding for the even population was 9.5% (S.D.=2.7, range 5–19%) while in the odd population it was only 4.3% (S.D.=2.6, range 1–12%).

3.3. Inbreeding depression

Significant inbreeding depression (ID) was only observed in a few reproductive traits in the two populations studied (Table 5). In 2000, almost all evaluated traits showed reduction in their values; however, only GSI was significantly associated with inbreeding (−5.3% per each 10% increase of inbreeding). In 2001 the length at spawning was significantly reduced by inbreeding, although by a low value (−1.61% per each 10% increase in inbreeding), while the reverse was observed with GSI, which increased significantly with inbreeding (+6.77%). As shown in Table 6, in neither year class a

Table 6
Effect of inbreeding of the sire (F_S), dam (F_D), and progeny (F_O) on survival of the progeny at the eyed egg stage

F	Year 2000			Year 2001		
	Mean (S.D.)	ID (%)	P	Mean (S.D.)	ID (%)	P
F_D	6.0 (2.6)	−6.3	0.60	3.1 (2.7)	−4.7	0.52
F_S	6.9 (2.5)	−12.3	0.32	3.5 (2.9)	4.6	0.51
F_O	9.7 (2.7)	−3.3	0.78	4.2 (2.6)	10.9	0.16

ID, inbreeding depression measured in percentage of mean per 10% of inbreeding.
P=level of significance.

significant ID in egg survival associated with any of the components of inbreeding (of dam, sire, or progeny) was demonstrated.

4. Discussion

BLUP selection (animal model) resulted in a high proportion of the parents of the base population not contributing with descendents in the fourth generation. These results were expected according to simulations of BLUP selection in populations with population structures similar to the ones presently studied (Bijma and Woolliams, 2000). Rearing families that do not contribute to the following generations may appear to represent an important loss of resources for the first generations of selection, as suggested by Bijma and Woolliams (2000). However, a selection program must consider the occurrence of this loss, estimate costs (inbreeding) and benefits (genetic gain), and make decisions according to the initial size of the selection program. Particularly, in this study the genetic contribution of the founder females dropped faster than the founder males. This phenomenon has not been reported before and probably occurred as a direct consequence of how the selection was practiced. Commonly, in each generation, 50% of dam's families were represented in the best 25% of individuals selected by the animal model. However, due to the fact that the mating design was nearly one male by three females, a highest percentage of sires of the previous generation ($\sim 75\%$) could contribute descendents to the next generation.

In the present study, the calculated rate of inbreeding (1.1% and 2.4%) was similar to other salmon populations subject to artificial selection (Su et al., 1996; Rye and Mao, 1998; Myers et al., 2001; Pante et al., 2001a). All of these studies registered the pedigree accurately, which allowed controlling the increment of inbreeding, for example limiting the possibility of mating closely related individuals. Additionally, several other methods may be applied which may restrain increases in levels of inbreeding in selection programs (Grundy et al., 1994; Caballero et al., 1996; Sanchez et al., 1999; Weigel and Lin, 2000; Sonesson and Meuwissen, 2000). Few of these, however, have been evaluated to be used in practical conditions. Recently, Gallardo et al. (in press) evaluated the use of nonrandom mating schemes for the reduction of the rate of inbreeding on the Coho salmon populations analyzed in this study. Gallardo et al. (in press) showed that the mating scheme that minimized the average coascendence of the group selected was more efficient in reducing the increase in inbreeding, thus limiting the expression of inbreeding depression, when compared with the other mating schemes applied to the Coho salmon program (random mating of selected individuals and compensatory mating schemes). This minimum coancestry mating scheme also reduced the variance of inbreeding, producing more homogeneous families in relation to this parameter.

In this study, variations in the magnitude of the inbreeding depression were found between populations and traits. Similarly, previous authors working with fish have described variations in the magnitude of ID among traits within the same population (Su et al., 1996; Heath et al., 2002). Su et al. (1996) showed that the weight at spawning and the number of eggs were significantly reduced by inbreeding (4−6% per 10% increase in inbreeding), while egg size, age at spawning, and juvenile weight were not affected.

Heath et al. (2002) recently found significant ID in relative fecundity in females of *O. tshawytscha* using a measure correlated with inbreeding as related to multi-locus heterozygosity. However, this was not true for the GSI in males or for egg size. Differences between populations can be explained by differences in the level of inbreeding and in the level of genetic load, while differences among traits within the same population may be attributed to variations in the amount of dominance variance present (Lynch and Walsh, 1998; De Rose and Roff, 1999), and to differences in genetic load too. An explanation of the lower (or lack of) inbreeding depression in the odd population, compared to the even population, may be the lowest level of inbreeding in the odd population. However, we cannot explain differences between traits because we do not have estimates of dominance variance present nor of differences in the initial genetic load. On the other hand, an increment in the gonadosomatic index in the odd population may be explained by effects of genetic drift and by the effect of artificial selection based on the weight at harvest applied to this population, given that there exists a moderate genetic correlation ($r=0.46$) between weight at harvest and gonadal weight (Gall and Neira, in press).

Some authors have shown that traits in the progeny may be affected by the inbreeding of their parents (Su et al., 1996; Margulis, 1998; Keller, 1998). Su et al. (1996) showed that survival of eggs from fertilization to hatching in rainbow trout (*Oncorhynchus mykiss*) was significantly reduced by inbreeding of the dam, and slightly reduced by inbreeding of the progeny, but not affected by the inbreeding of the sire. We did not find such effects, probably due to the low level of inbreeding of parents (3–6%) in this study. Similarly, Heath et al. (2002) did not find any association between egg survival from eyed egg to hatching, and the genetic variation measured as heterozygosity in microsatellites.

5. Conclusions

In agreement with theoretical predictions, BLUP selection (animal model) resulted in a high proportion of the parents of the base population (56–76%) not contributing descendents in the fourth generation. However, the levels of inbreeding in these populations were similar to those previously described in other fish populations, using other methods of genetic evaluation (individual or family selection). The prejudicial effects of the inbreeding, although significant with regard to some reproductive traits such as the GSI or body length at spawning, may not limit the viability of a genetic improvement program in the medium term. However, methods that limit inbreeding should be employed as a precautionary measure.

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.

Bijma, P., Woolliams, J.A., 2000. Prediction of rates of inbreeding in populations selected on best linear unbiased prediction of breeding value. Genetics 156, 361–373.

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). US Department of Agriculture, Agricultural Research Service.

Caballero, A., Santiago, E., Toro, M.A., 1996. System of mating to reduce inbreeding in selected populations. Anim. Sci. 62, 431–442.

DeRose, M.A., Roff, D.A., 1999. A comparison of inbreeding depression in life-history and morphological traits in animals. Evolution 53, 1288–1292.

Falconer, D.S., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics, 4th edition. Logman Group. 464 pp.

Gall, G.A.E., Neira, R., 2004. Genetic analysis of female reproductive traits of farmed Coho salmon (*Oncoorhyncus kisutch*). Aquaculture 234, 143–154.

Gallardo, J.A., García, X., Lhorente, J.P., Neira, R., 2004. Effects of nonrandom mating schemes to delay the inbreeding accumulation in cultured populations of Coho salmon (*Oncorhynchus kisutch*). Can. J. Fish. Aquat. Sci. 234, 143–154.

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.

Grundy, B., Caballero, A., Santiago, E., Hill, W.G., 1994. A note on using biased parameter values and nonrandom mating to reduce rates of inbreeding in selection programmes. Anim. Prod. 59, 465–468.

Heath, D.D., Bryden, C.A., Shrimpton, J.M., Iwama, G.K., Kelly, J., Heath, J.W., 2002. Relationship between heterozigosity, allelic distance (d2), and reproductive traits in chinook salmon *Oncorhynchus tshawytsha*. Can. J. Fish Aquat. Sci. 59, 77–84.

Keller, L.F., 1998. Inbreeding and its fitness effects in an insular population of song sparrows (*Melospiza melodia*). Evolution 52, 240–250.

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.

Margulis, S.W., 1998. Relationships among parental inbreeding, parental behaviour and offspring viability in old field mice. Anim. Behav. 55, 427–438.

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.

Myers, J.M., Heggelund, P.O., Hudson, G., Iwamoto, R.N., 2001. Genetics and broodstock management of Coho salmon. Aquaculture 197, 43–62.

Pante, M.J., Gjerde, B., McMillan, I., 2001. Inbreeding levels in selected populations of rainvow trout, *Oncorhynchus mykiss*. Aquaculture 192, 213–224.

Pante, M.J., Gjerde, B., McMillan, I., 2001. Effects of inbreeding on body weight at harvest in rainbow trout, *Oncorhynchus mykiss*. Aquaculture 192, 201–211.

Quinton, M., Smith, C., Goddard, M.E., 1992. Comparison of selection methods at the same level of inbreeding. J. Anim. Sci. 72, 1060–1067.

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., Meuwissen, T.H.E., 2000. Mating schemes for optimum contribution selection with constrained rates of inbreeding. Genet. Sel. Evol. 32, 231–248.

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.

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. Diary 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.