



Inbreeding and effective population size in a coho salmon (*Oncorhynchus kisutch*) breeding nucleus in Chile[☆]

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ABSTRACT

A commercial breeding nucleus of coho salmon (*Oncorhynchus kisutch*) was established in Chile in 1997. This nucleus consists of two independent populations corresponding to different year-classes (even and odd, depending on the spawning year), which have been successfully selected for harvest weight (approximate genetic gain per generation of 10%). In order to constrain the buildup of inbreeding a strategy based on avoiding full-sib mating in each generation was used. In this study we assess the inbreeding levels and effective population size of the two year-classes to evaluate the outcome of the mating strategy within the nucleus. The average rate of inbreeding in the two year classes was around 1% per generation. However, rapid increase of inbreeding coefficients in the latest generations suggests that the simple mating strategy used should be improved in order to constrain maximum inbreeding values in further generations. The effective population size calculated based on the regression of the average rate of co-ancestry across generations was 34 and 39 for the odd and even populations, respectively. The effective population number is 50 for both, odd and even populations, based on the regression of the average rate of inbreeding over generations. The results indicate that the mate allocation strategy has contained the rate of inbreeding within acceptable values to date, but that current effective population size must be increased in order to be adequate for the viability of the breeding program in the medium to long term. However, the effective population size of these populations is far below 500, the minimum number suggested for retaining the evolutionary potential to adapt to new environmental conditions. Further strategies to constrain maximum inbreeding levels across all the individuals belonging to the nucleus and to maintain a satisfactory effective population size for ensuring the sustainability of this breeding scheme are proposed.

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1. Introduction

Genetic improvement programs have been successfully carried out in different salmonid species for increasing the productivity of economically important traits (Gjedrem, 2000, 2012). It has been early recognized that one of the negative consequences of selective breeding may be the accumulation of inbreeding (Robertson, 1961). Inbreeding may put at risk a breeding scheme because it could reduce the additive genetic variance (Falconer and Mackay, 1996, chapter 15) and increase the variance of genetic gain due to an increase in the relationship between individuals (Meuwissen, 1991). Furthermore, due to the limited resources and the need to breed only from fish of high genetic merit, selected lines may have a small population size (Ponzoni et al., 2010). Populations with a small effective number are more susceptible to the following: inbreeding

depression, increase in recessively inherited disorders, reduction in additive genetic variance, and random genetic drift (Kause et al., 2005). Thus, monitoring and managing of inbreeding and effective population size are key issues during the implementation of genetic improvement programs.

Genetic improvement programs in aquaculture frequently use “best linear unbiased predictor” (BLUP) procedures for calculating breeding values (BV), using an animal model for genetic evaluation (Gjoen and Gjerde, 1998). This procedure maximizes the correlation between the true and the predicted BV and is expected to increase the response to selection. However, when the heritability of a character is low the model favors the selection of related individuals, which may increase the rate of inbreeding (ΔF) and reduce the genetic variance in the long run (Belonsky and Kennedy, 1988; Quinton et al., 1992). Several methods have been devised to reduce the rate of inbreeding while maintaining a high genetic gain (Meuwissen, 1997; Villanueva et al., 1996; Wu and Schaeffer, 2000). However, their implementation is in many cases difficult to manage with aquaculture species. Breeding schemes with exclusion of full-sib mating have been recommended (Hansen and Jensen, 2005; Sekino et al., 2004).

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Only a few empirical evaluations of the rate of inbreeding in fish populations subject to artificial selection exist. In rainbow trout populations, Su et al. (1996) estimated a rate of inbreeding (ΔF) between 1.3% and 1.7% per generation, and Pante et al. (2001a) found a ΔF between 0.53% and 2% per generation. In Coho salmon (*Oncorhynchus kisutch*) Gallardo et al. (2004) reported a ΔF from 1.1 to 2.45% per generation after 4 generations of selection using BLUP for harvest body weight as a selection criteria, avoiding FS mating as inbreeding control strategy, with an average genetic gain of 10.2% per generation (Neira et al., 2006).

Recently, Ponzoni et al. (2010) calculated the accumulation of inbreeding and the effective population size, using four different approaches, in the Malaysian breeding nucleus of the GIFT strain of Nile tilapia (*Oreochromis niloticus*). These authors highlight the importance of these parameters in the sustainability of a genetic improvement program and point to the paucity of similar studies in aquatic species.

A commercial breeding nucleus of Coho salmon (*O. kisutch*) was established in 1997. After seven and six generations of selection for body weight, in odd and even populations, respectively, a genetic gain of ~10 to 13% per generation has been achieved (Neira, personal communication). In the present study we estimate both the levels of inbreeding and the effective population size in order to discuss the present and prospective status of these populations and the sustainability of this breeding scheme.

2. Materials and methods

2.1. Breeding populations

This study is based on pedigree data from a coho salmon breeding program run by Pesquera Antares in Chile. This breeding program involves two independent populations corresponding to even and odd spawning years, which have been selected for harvest weight during six and seven generations, respectively. The populations were established in 1997 and 1998, and are managed in a two-year reproductive cycle. Using BLUP breeding values for body weight at harvest, 30% of the best individuals of the population are preselected as candidates and spawned in May of each year to produce the nucleus of the next generation and multipliers. Using hormone induced spawning, all families of each generation are generated within one or two weeks, thus minimizing the effect of date of spawning on weight at harvest. An average of 100 families per year was produced using a nested design (one male to three to five females). Inbreeding was controlled by avoiding only full-sib mating in first generations and half- and full sib matings in later generations. No restriction to the family contribution to the following generation was applied.

Eggs of each full-sib family were incubated separately, and at eyed stage 2000 eggs of each selected families were moved to individual tanks (400 l each) for hatching considering the following criteria: (1) keeping a mating design as close as possible to one male to four females; and (2) keeping the families with highest egg survival (>80%). Then, the progeny of an average of 100 families were individually identified using PIT (passive integrated transponder) tags between November and December of each year when the fish were about 5 to 7 g. At this stage fish were transferred to smoltification sites in fresh water conditions where each full-sib family was randomly stocked in equal numbers (60–80) into two or three rearing cages. Smoltification occurred naturally at eight months post-spawning and weight at harvest time (~3 kg) was recorded at 20–21 months of age.

2.2. Data and analysis

The basic information of the structure for the even and odd year-classes included in the breeding nucleus is shown in Table 1. Data from a total of 290 sires and 689 dams with 59,471 offspring in seven generations from the odd year-class and of 256 sires and 603

Table 1

Number of sires, dams and tagged progeny in each generation in the two populations (odd and even) of the coho salmon (*Oncorhynchus kisutch*) breeding nucleus. **Sires_{os}** and **Dams_{os}** represent the number of sires and dams whose offspring became selected to be parents in following generations, respectively.

Population	Year	Sires	Sires _{os}	Dams	Dams _{os}	Progeny
Odd	1997	30	9	48	14	5750
	1999	49	26	80	40	7147
	2001	39	27	120	55	8398
	2003	41	27	153	52	12,240
	2005	46	17	96	23	8648
	2007	41	25	96	38	8648
	2009	44	20	96	28	8640
	Total	290	151	689	250	59,471
Even	1998	41	24	79	36	7037
	2000	37	25	73	44	6558
	2002	59	23	114	31	9120
	2004	49	32	137	66	10,763
	2006	37	24	102	48	10,524
	2008	34	23	98	47	8821
	Total	257	151	603	272	52,823

dams with 52,823 offspring in six generations from the even year class (including base populations in both cases) were analyzed.

Co-ancestry between individuals, inbreeding levels and effective population size were calculated using the pedigree data available for both populations, even and odd. This was carried out using the approaches implemented in POPREP software (Groeneveld et al., 2009). For calculation of all parameters only fish whose offspring were selected to be parents in the following generations were taken into account (Ponzoni et al., 2010).

The inbreeding coefficient (F) of an individual i , is equal to the co-ancestry coefficient (f_{sd}) between its parents s and d (Falconer and Mackay, 1996, p. 85), thus, $F_i = f_{sd}$. In a large population under random mating the rate of inbreeding (ΔF) and the rate of co-ancestry (Δf) would be expected to be the same due to the fact that all individuals would have the same chance to leave offspring. Therefore, the effective population size can be estimated either as $1/(2\Delta F)$ or as $1/(2\Delta f)$. Differences between both estimates are an indication of deviation from random mating.

In this study we calculated the effective population size in four different ways as described by Ponzoni et al. (2010). First, we used the number of parents:

$$N_p = (4N_s N_d) / (N_s + N_d)$$

where N_s and N_d are the number of sires and dams, respectively.

Second, we used the equation (Falconer and Mackay, 1996, p. 68) which incorporates variance of family size:

$$N_v = 8N / (V_s + V_d + 4)$$

where V_s and V_d are the variances of family sizes of each sire and dam, respectively (Hill, 1979). In this case, we used the variances calculated from the data (N_{v1}), and also the values assuming a Poisson distribution of family size (N_{v2}), where the variance is equal to the mean of family size.

Third, we used the rate of inbreeding (ΔF):

$$N_f = 1 / (2\Delta F), \text{ where} \\ \Delta F = (F_t - F_{t-1}) / (1 - F_{t-1}).$$

And fourth, we used the rate of co-ancestry (Δf) among all sires with all dams:

$$N_f = 1 / (2\Delta f), \text{ where} \\ \Delta f = (f_t - f_{t-1}) / (1 - f_{t-1}).$$

We also calculated the average rate of inbreeding and co-ancestry per year based on the slope of the linear regression fitted on the estimated f values per generation. This value was used for calculating the average effective population size for each of the populations.

3. Results

3.1. Pedigree quality and number parents by generation

The reliability of the estimated inbreeding coefficient for a particular individual depends on the amount of pedigree information. The pedigree completeness index (MacCluer et al., 1983) implemented in POPREP package (Groeneveld et al., 2009) was used to determine the amount of information contained in the pedigree analyzed. Excluding the base population (i.e. fish with unknown parents at the foundation of the pedigree), pedigree completeness was 100% on each generation for even and odd populations. This means that both parents were known for all individuals included in the studied populations.

The total number of sires, dams and progeny on each generation is shown in Table 1, as well as, the number of sires and dams whose offspring were selected and became parents in subsequent generations (Sires_{os} and Dams_{os}, respectively). Only these individuals were included for inbreeding, co-ancestry and effective population size calculations.

3.2. Family size

The family size is defined as the number of offspring of an individual that become parents in the following generation (Falconer and Mackay, 1996, p. 67). Thus, fish that did not produce offspring (with a minimum family size equals to 0) were not taken into account in the analysis in order not to have distorted results (Ponzoni et al., 2010). Minimum, maximum and mean family sizes by year-class for sires and dams on each generation, as well as the variance in family size are shown in Table 2.

The simple mating strategy used for containing the buildup of inbreeding in these populations (i.e. avoiding full-sib mating), has led

to an uneven and variable family contribution over generations. The overall average sire family size and dam family size across the two populations were 5.9 and 3.6, respectively, and were very similar for both even and odd year classes. Only 41% of selected dams and 55% of selected sires had offspring which became selected to be parents in following generations. The variation for family size was high (CV over 80%). The variation of sire and dam family size was similar in the odd year class (82% and 80%, respectively). However, in the even year class the variation of sire family size (CV = 89%) was higher than that of dam family size (CV = 78%).

3.3. Inbreeding

The minimum, maximum, mean and standard deviation of the inbreeding coefficients for the two year-class populations are shown in Table 3. The levels of inbreeding were low in the first generations for the two year-classes but in the later generations this level increased, as expected, due to the inevitable mating of distantly related fish. The number of inbred animals increased with the number of generations. Whereas the minimum inbreeding in the later generations in both populations was around 3%, the maximum was 13% and 8% for the odd and even populations, respectively. The rate of inbreeding by generation, based on the slope of the regression of the average of inbreeding coefficients over five and six generations of selection in the even and odd populations, was in both cases 0.01.

3.4. Co-ancestry

The mean and the rate of the co-ancestry across generations for both populations are shown in Table 4. For comparative purposes, the corresponding values of inbreeding are also shown. Note the discrepancies between Δf and ΔF , which is indicating a deviation from random mating in both populations. Note also the presence of a negative value for Δf and zeros for ΔF , which makes it impossible to estimate the effective population size in such cases. The rate of change of co-ancestry by generation, based on the slope of the regression of the average co-ancestry coefficients from 1997 to 2011 for the odd population, and between 1998 and 2010 for the even populations was 0.0148 and 0.0128, respectively.

3.5. Effective population size

Effective population size calculated from: the number of parents (N_p), the variance in family size obtained from the data and assuming Poisson distribution (N_{v1} and N_{v2}), the rate of inbreeding (N_f), and

Table 2
Sire and dam family sizes in each generation of the two populations (odd and even) in the coho salmon (*Oncorhynchus kisutch*) breeding nucleus.

Population	Year	Parent	N	Mean	Min	Max	Variance
Odd	1997	Sire	9	2.11	1	4	1.61
		Dam	14	1.36	1	2	0.25
	1999	Sire	26	6.12	1	22	23.39
		Dam	40	3.98	1	11	8.54
	2001	Sire	27	7.19	1	24	51.70
		Dam	55	3.53	1	11	7.14
	2003	Sire	27	5.26	1	15	14.43
		Dam	52	2.73	1	12	5.30
	2005	Sire	17	8.06	1	26	69.81
		Dam	23	5.96	1	23	41.41
	2007	Sire	25	5.60	1	17	23.50
		Dam	38	3.68	1	17	12.33
2009	Sire	20	7.60	1	17	29.20	
	Dam	28	5.43	1	16	22.70	
Even	1998	Sire	24	3.54	1	13	10.78
		Dam	36	2.36	1	8	4.87
	2000	Sire	25	6.92	1	29	52.33
		Dam	44	3.93	1	12	8.02
	2002	Sire	23	8.09	1	38	66.72
		Dam	31	6.00	1	20	20.67
	2004	Sire	32	4.34	1	13	12.75
		Dam	66	2.11	1	6	1.97
	2006	Sire	24	5.50	1	17	20.09
		Dam	48	2.75	1	11	6.57
	2008	Sire	23	6.74	1	17	22.02
		Dam	47	3.30	1	10	4.87

Data for generation 2010 was not yet available.

Table 3
Inbreeding coefficients (F) within each generation of the two populations (odd and even) in the coho salmon (*Oncorhynchus kisutch*) breeding nucleus.

Population	Year	Number of parents	Inbred parents	F				
				Min	Max	Mean	SD	
Odd	1997	23	0	0.0000	0.0000	0.0000	0.0000	
	1999	66	0	0.0000	0.0000	0.0000	0.0000	
	2001	82	0	0.0000	0.0000	0.0000	0.0000	
	2003	79	0	0.0000	0.0000	0.0000	0.0000	
	2005	40	13	0.0000	0.1328	0.0182	0.0310	
	2007	63	56	0.0000	0.0781	0.0247	0.0234	
	2009	48	48	0.0073	0.1489	0.0526	0.0289	
	2011	151	151	0.0315	0.1255	0.0703	0.0272	
	Even	1998	60	0	0.0000	0.0000	0.0000	0.0000
		2000	69	0	0.0000	0.0000	0.0000	0.0000
2002		54	0	0.0000	0.0000	0.0000	0.0000	
2004		98	18	0.0000	0.0625	0.0102	0.0223	
2006		72	60	0.0000	0.1719	0.0368	0.0349	
2008		70	70	0.0078	0.1445	0.0428	0.0297	
2010		155	155	0.0254	0.0811	0.0533	0.0143	

Table 4

Average levels and rate of co-ancestry (f) and inbreeding (F) within each generation of the two populations (odd and even) in the coho salmon (*Oncorhynchus kisutch*) breeding nucleus.

Population	Year	Number of parents	Co-ancestry		Inbreeding		
			Average	Δf	Average	ΔF	
Odd	1997	23	0.0000	–	0.0000	–	
	1999	66	0.0004	0.0004	0.0000	0.0000	
	2001	82	0.0105	0.0101	0.0000	0.0000	
	2003	79	0.0301	0.0199	0.0000	0.0000	
	2005	40	0.0461	0.0165	0.0182	0.0182	
	2007	63	0.0752	0.0305	0.0247	0.0066	
	2009	48	0.0802	0.0054	0.0526	0.0286	
	2011	151	0.0909	0.0117	0.0703	0.0187	
	Even	1998	60	0.0000	–	0.0000	–
		2000	69	0.0055	0.0055	0.0000	0.0000
2002		54	0.0307	0.0254	0.0000	0.0000	
2004		98	0.0585	0.0286	0.0102	0.0102	
2006		72	0.0578	–0.0007	0.0368	0.0269	
2008		70	0.0624	0.0049	0.0428	0.0062	
2010		155	0.0728	0.0110	0.0533	0.0110	

the rate of co-ancestry (N_f) is shown in Table 5. The effective population size could not be calculated when the rate of co-ancestry was negative and when the rate of inbreeding was zero. In general, there was low to moderate agreement between the four methods. This may have resulted from the selection strategy and the relatively unbalanced contribution of families to the next generations. The best agreement was found between N_p and N_{v2} .

4. Discussion

The results revealed the inbreeding levels and effective population size of a particular breeding program of coho salmon in Chile. This breeding program has been successful in terms of the genetic gain achieved for body weight at harvest (around 10 to 13% per generation, Neira, personal communication). These results are similar to those reported by Neira et al. (2006), under comparable management. A recent study has given emphasis on the balance among the short and long term genetic gains, for ensuring the viability of the genetic improvement program. Ponzoni et al. (2010) have analyzed the inbreeding levels and determined the effective population size to make inferences about the long term sustainability of the genetic improvement program of the GIFT strain of tilapia in Malaysia. In the present study we used the same approach that was used by Ponzoni et al. (2010) in order to: (i) have an insight about the present and future status of the breeding nucleus, and (ii) evaluate and make decisions about the mating strategy used up to date within the population.

Table 5

Effective population size of the two populations (odd and even) in the coho salmon (*Oncorhynchus kisutch*) breeding nucleus estimated in each generation based on the number of parents (N_p), based on the variance of family size (N_{v1} and N_{v2}), based on the co-ancestry coefficient (N_f), and based on the inbreeding coefficient (N_F).

Population	Year	N_p	N_{v1}	N_{v2}	N_f	N_F	
Odd	1997	22	31	25	–	–	
	1999	63	15	37	50	–	
	2001	72	10	45	25	–	
	2003	71	27	53	30	27	
	2005	39	3	18	16	76	
	2007	60	13	38	92	17	
	2009	47	7	23	43	27	
	Even	1998	58	24	48	92	–
		2000	64	9	37	20	–
2002		53	5	24	17	49	
2004		86	42	75	–	19	
2006		64	19	47	102	80	
2008		62	18	40	45	46	

A negative consequence of inbreeding, known as inbreeding depression (ID), is the decline in the mean phenotype for a particular trait with increasing homozygosity in a population (Lynch and Walsh, 1998). The effect of inbreeding on different traits has been studied in coho salmon. For example, significant inbreeding depression has been detected for the gonadosomatic index and body length at spawning in two independent populations (Gallardo et al., 2004). There is no evidence of significant impact of F on other traits, such as, body and gonad weight, number and survival of eggs and fecundity (Gallardo et al., 2004; Neira et al., 2006). In other salmon species, significant inbreeding depression has been reported for growth in Atlantic salmon (ID: –0.6 to –2.6%; Rye and Mao, 1998) and rainbow trout (ID: –1.6 to –5.0%; Pante et al., 2001) for each 10% increment of inbreeding. In this regard, it has been proposed that a rapid increase of inbreeding has a greater negative effect than slower accumulation of inbreeding (Bentsen and Olesen, 2002). This may be due to the fact that selection may act against fixation of deleterious genes if the rate of inbreeding is low, therefore, avoiding inbreeding depression (Pirchner, 1983, p. 314).

About a 1% of inbreeding accumulation per generation may be tolerated without great preoccupation in animal breeding (Franklin, 1980). Although, a more conservative threshold (0.5% per generation) has been suggested by Nicholas (1989) in order to maintain the variance in response to selection at low levels (coefficient of variation < 10% over a ten-year period), by contrast, Bijma (2000) suggested a level of 0.5 to 1.0% per generation as an upper limit for rate of inbreeding in a viable breeding program. Our findings show that the rate of change of the mean inbreeding levels calculated from the regression across generations for the odd and even populations was 1%. Thus, our results were in agreement with the threshold suggested by Franklin (1980) and Bijma (2000), but above that one proposed by Nicholas (1989). Therefore, although the mate allocation strategy has been successful in containing average levels of inbreeding at a certain level, it will be necessary to explore and implement other approaches in order to have a better control of both the rate of increase and the maximum levels of inbreeding obtained by generation (Table 3). Moreover, further studies are necessary in order to examine if there is evidence of the negative impact of inbreeding levels in productive and reproductive traits in these populations.

The results in terms of the estimated effective population size using different approaches are shown in Table 5. As it has been previously shown by Ponzoni et al. (2010) the estimate from the rate of inbreeding (N_F) was not as informative as the other estimates given that it was not possible to calculate it when the ΔF was zero. Effective population size calculated from number of parents (N_p) and variance in family size (N_{v1} and N_{v2}) was the more informative measure. In general the values obtained by these three methods were very variable depending on the year and the agreement between them was not as good as demonstrated by Ponzoni et al. (2010). This may be mainly due to the fact that selection intensity was relatively high and genetic gain was prioritized instead of maintaining the family contribution on each generation. This situation can also be depicted from the relatively low number of parents whose offspring become selected to be parents on each generation (**Sires_{OS}** and **Dams_{OS}**) compared with the total number of sires and dams (Table 1) and the variable and higher values for maximum family sizes and family variances (Table 2).

The most reliable method to estimate effective population size is N_f , and it has been proposed to be the method of choice for monitoring this parameter (Meuwissen, 2007; Ponzoni et al., 2010). The effective population size calculated based on the regression of the average rate of co-ancestry across generations is 34 and 39 for the odd and even populations, respectively. The effective population size is 50, for both odd and even populations, considered separately, if estimated based on the regression of the average rate of inbreeding over generations. However, ΔF is more affected than Δf when the mating allocation strategy tends to avoid the accumulation of inbreeding.

Ponzoni et al. (2010) give a detailed discussion about the minimum effective population size in order to ensure the sustainability of a breeding program. In this regard, the results showed in the present study indicate that the effective population size of the populations of the breeding nucleus is below or at least just at the minimum number suggested by FAO (1998, p. 69) and Hall (2004) if this is calculated based on Δf or ΔF , respectively. As well, the populations kept in the nucleus are far below the minimum number of effective population size (500) suggested in order to have the chance of retaining their evolutionary potential (Franklin, 1980; Franklin and Frankham, 1998).

Immediate measures for increasing the effective population size to a number which allows ensuring the viability of the breeding program could be done through the connection of the two populations by means of cryopreserved sperm from selected males. If this measure is coupled with the implementation of more effective mate allocation strategies for containing inbreeding levels in aquaculture species, such as the one described by Ponzoni et al. (2010) or the computational algorithm approach based on optimal contributions developed by Hinrichs et al. (2006), the rate of increase of inbreeding will be better controlled.

However, these two interventions will hardly permit reaching the minimum effective population size necessary to allow the adaptation of these populations to abrupt modifications in the environment. This issue is getting more relevant during the last years because of the increasing evidence of the possible impact of climate change on fish production (Brander, 2007). The link between genetic material coming from different genetically improved coho salmon populations within Chile and abroad could increase the effective population size to a number which may give more resilience of these populations to unexpected changes in the environmental conditions.

5. Conclusion

The effective population size of the breeding nucleus of coho salmon studied here is just below the number which would guarantee the sustainability of the genetic improvement program in the medium term. This situation may have an impact in the rate of increase of inbreeding levels in future generations. Measures such as linking both populations using frozen semen from highly ranked sires and modifying the mate allocation strategy may both increase the effective population number and contain levels of inbreeding. Finally, we would have to take major measures, such as the involvement of other companies and institutions, in order to connect different coho salmon breeding nuclei, for increasing the effective population size to a number which allows retaining the evolutionary potential of these populations to cope with environmental changes or to enable the development of new breeding objectives.

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