Correlated response of flesh color to selection for harvest weight in coho salmon (*Oncorhynchus kisutch*)

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ABSTRACT

Chilean coho salmon (*Oncorhynchus kisutch*) represents about 90% of the worldwide production. From a commercial perspective rapid growth to market weights and product quality are important aspects of profitability. The objective of this study was to determine genetic parameters, genetic trends and correlated response of flesh color (FC) after eight generations of selection for harvest weight (HW) in two coho salmon populations spawning independently in even and odd years. A total of 41,597 and 37,319 records for HW and 4946 and 6731 for FC were included in the analysis for the even and odd populations, respectively. A linear bivariate animal model was used to estimate genetic parameters and compute breeding values for both traits. Estimated heritabilities for HW and FC were 0.41 ± 0.03 and 0.08 ± 0.02 in the even population and 0.22 ± 0.03 and 0.04 ± 0.01 the in odd population, respectively. Genetic and phenotypic correlations between HW and FC were 0.15 ± 0.11 and 0.07 ± 0.02 in the even population and 0.25 ± 0.14 and 0.12 ± 0.02 in odd population, respectively. Response to selection was measured as the slope of the linear regression fitted on the mean breeding values per generation per trait. We found a positive genetic trend for both traits after eight generations of selection for HW. The increase in HW per generation was 0.31 ± 0.01 and 0.26 ± 0.02 kg for the even and odd populations, respectively. The correlated increase in FC was 0.04 ± 0.01 and 0.04 ± 0.00 fan units per generation in the even and odd population, respectively, showing that selection for HW can increase FC.
Statement of relevance.
Correlated response in color to selection for growth in coho

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1. Introduction

Farmed coho salmon (*Oncorhynchus kisutch*) production reached about 160,000 tons in 2012 in Chile, representing approximately 90% of the total worldwide production for this species (FAO, 2014). Genetic improvement programs for this species have been developed since the early 1990′s to support this industry in Chile (Neira et al., 2004). These programs have been typically included rapid growth as the most desirable trait given its economic importance (Neira et al., 2014). Other traits, such as carcass quality and disease resistance traits should be also included into the breeding goal in salmon breeding programs (Gjedrem, 2000; 2012; Yáñez and Martínez, 2010; Yáñez et al.,

2014b). Among carcass quality traits, flesh color (FC) has great importance in the profitability of the industry. Based on controlled experiments color has been shown to be associated with the acceptability of food products (Clydesdale, 1993). From this perspective the red-orange color in farmed salmonid fish flesh is associated with market acceptance and price of final product (Sigurgisladottir et al., 1997). Moreover, the supplementation of pigment in the feed represents a substantial proportion of total production costs (Norris and Cunningham, 2004). However, genetic improvement of FC has been hindered by the difficulty in trait measurement, requiring slaughter of the fish. Genetic correlations between HW and FC are favorable in coho salmon (Iwamoto et al., 1990; Whithler and Beacham, 1994) and other salmonid species (Quinton et al., 2005; Rye and Gjerde, 1996), suggesting that by selecting for HW a correlated genetic response would be expected for FC. Thus, the main objectives of the present study were to: i) estimate genetic parameters for FC and HW in two independent coho salmon breeding populations, ii) report genetic trends for HW across eight generations, and iii) assess realised correlated responses in FC from the long-term selection program.

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2. Materials and methods

2.1. Populations, traits and records

This study was carried out in a coho salmon breeding nucleus owned by Pesquera Antares - AquaChile (Puerto Montt, Chile). This breeding nucleus, comprising two populations according to the spawning year (even and odd), was established in 1997. Reproductive management, rearing conditions and HW phenotyping have been previously described in detail by Yáñez et al. (2014a; 2016a). Even and odd populations have been selected for HW across eight generations using single trait best linear unbiased prediction (BLUP) methodology. Pedigree structure from both populations used in this study is summarized in Table 1. Each year an average of 103 and 100 families were produced according to a nested design (1 male to 3–5 females) for the even and odd populations, respectively. Eggs obtained from each full-sib familiy were incubated separately. After hatching, fish were individually PIT-tagged (passive integrated transponder) at 5 to 7 g. Each full-sib group, comprising between 60 and 80 fish, were randomly placed into 2–3 fresh water rearing cages until smoltification, at about 8 months post-spawning. Fish were then transferred to sea water cages and HW was recorded at 20–21 months after spawning at approximately 3 kg. Flesh color (FC) was measured on each fresh carcass using a Roche SalmoFan™ (Hoffmann-La Roche Ltd., Basel, Switzerland) after slaughter at processing plant. The color was assessed using a 20–34 scale, in which 20 represent a low flesh pigmentation degree and 34 corresponds to a high level of flesh pigmentation. Each individual record represents the average of a series of three measures performed along the fillet on the area above the midline. Table 2 shows summary statistics for harvest age (HA), HW and FC for both even and odd populations, separated by year.

2.2. Statistical analysis

To estimate variance and co-variance components for HW and FC we used a bivariate linear animal model defined as follows:

$$\begin{bmatrix} \mathbf{y}_{HW} \\ \mathbf{y}_{FC} \end{bmatrix} = \begin{bmatrix} \mathbf{X}_{HW} & 0 \\ 0 & \mathbf{X}_{FC} \end{bmatrix} \begin{bmatrix} \mathbf{b}_{HW} \\ \mathbf{b}_{FC} \end{bmatrix} + \begin{bmatrix} \mathbf{Z}_{HW} & 0 \\ 0 & \mathbf{Z}_{FC} \end{bmatrix} \begin{bmatrix} \mathbf{u}_{HW} \\ \mathbf{u}_{FC} \end{bmatrix} + \begin{bmatrix} \mathbf{W}_{HW} & 0 \\ 0 & 0 \end{bmatrix} \begin{bmatrix} \mathbf{c}_{HW} \\ 0 \end{bmatrix} + \begin{bmatrix} \mathbf{e}_{HW} \\ \mathbf{e}_{FC.} \end{bmatrix}$$

Where $\mathbf{y}_{HW}$ and $\mathbf{y}_{FC}$ are vectors of phenotypic records for both traits (HW and FC, respectively); $\mathbf{b}_{HW}$ is a vector of fixed effects for HW, $\mathbf{b}_{FC}$

Table 1
Pedigree structure of even and odd populations of the coho salmon (*Oncorhynchus kisutch*) breeding nucleus used in the present study by year.

Population	Year	Number of Sires	Number of Dams	Total number	Mean per family
Even	1998	42	80	8589	109
	2000	36	73	6557	90
	2002	59	114	9120	80
	2004	49	137	10,749	78
	2006	37	102	10,522	103
	2008	34	98	8821	90
	2010	45	110	8798	80
	2012	61	112	15,944	142
	Total	**363**	**826**	**79,100**	**96**
Odd	1997	25	50	5642	113
	1999	49	80	7144	89
	2001	39	120	8397	70
	2003	41	153	12,240	80
	2005	46	95	8648	91
	2007	41	96	8648	90
	2009	43	95	8640	91
	2011	42	109	15,721	144
	Total	**326**	**798**	**75,080**	**94**

Table 2
Summary statistics for harvest age (HA) measured in days (d), harvest weight (HW) measured in kg and flesh color (FC) measured in Fan units (Fu) in even and odd population separated by year.

Population	Variable	Year	n[a]	Mean	SD[b]	Min	Max
Even	HA (d)	1998	898	648.08	6.08	630	658
		2000	1619	626.5	14.82	597	656
		2002	4500	626.6	4.06	621	638
		2004	4455	615.78	7.61	600	639
		2006	6466	621.66	15.29	605	655
		2008	7718	614.36	2.4	609	618
		2010	6327	582.35	2.93	577	587
		2012	8304	570.69	1.92	567	574
	HW (kg)	1998	3214	3.63	0.75	1.39	5.78
		2000	1561	4.21	1.62	0.24	7.2
		2002	4436	3.72	1.74	0.1	7.18
		2004	4391	4.23	1.16	0.1	7.08
		2006	6387	4.9	0.99	1.11	7.5
		2008	7602	2.47	0.9	0.05	4.6
		2010	6106	4.39	0.63	2.49	6.2
		2012	7900	4.44	0.84	0.2	6.9
	FC (Fu)	1998	–	–	–	–	–
		2000	542	29.7	0.83	27	32
		2002	776	27.08	0.78	26	30
		2004	1223	29.68	0.56	27	31
		2006	–	–	–	–	–
		2008	1234	30.49	2.02	25	34
		2010	1171	28.77	1.29	20	33
		2012	–	–	–	–	–
Odd	HA (d)	1997	864	621.83	5.52	615	630
		1999	2915	609.13	14.24	584	644
		2001	3327	616.81	5.55	599	630
		2003	4642	619.36	2.99	613	626
		2005	4992	616.36	16.29	596	641
		2007	6387	618.15	1.45	615	620
		2009	6584	625.8	1.67	622	629
		2011	7608	619.23	2.04	615	623
	HW (kg)	1997	864	2.5	1.22	0.1	5
		1999	2915	3.57	0.9	0.2	6.04
		2001	3327	3.58	1.37	0.16	7
		2003	4642	2.87	1.29	0.68	6.82
		2005	4992	4.2	1.2	0.25	7.48
		2007	6387	3.56	0.8	0.29	5.38
		2009	6584	4.97	0.9	0.44	7.58
		2011	7608	2.87	1.22	0.08	6.5
	FC (Fu)	1997	–	–	–	–	–
		1999	763	30.17	0.67	28	32
		2001	1260	27.06	1.19	24	31
		2003	1299	27.31	1.67	22	30.5
		2005	1135	29.86	0.79	20	32
		2007	–	–	–	–	–
		2009	1071	31.88	1.24	28	34
		2011	1203	28	0.86	20	30

[a] Number of recorded fish.
[b] Standard deviation.

is a vector of fixed effects for FC, both including the contemporary group of sex:cage:year as factor and HA as a covariate; $\mathbf{u}_{HW}$ and $\mathbf{u}_{FC}$ are vectors or random animal genetic effects for HW and FC, respectively; $\mathbf{e}_{HW}$ and $\mathbf{e}_{FC}$ the vectors of residual random effects, for HW and FC, respectively; $\mathbf{c}_{HW}$, is the vector of random common environment effect related to full-sib families for HW; $\mathbf{X}_{HW}$, $\mathbf{Z}_{HW}$ and $\mathbf{W}_{HW}$ are design matrices for HW and $\mathbf{X}_{FC}$ and $\mathbf{Z}_{FC}$ are the design matrices for FC.

For both HW and FC the animal and residual random effects, and for HW the random effect associated to common environment, were assumed to be:

$\mathbf{u} = [\mathbf{u}_{HW}' \mathbf{u}_{FC}']' \sim N(\mathbf{0}, \mathbf{G}_0 \otimes \mathbf{A})$,

$\mathbf{c} = [\mathbf{u}_{HW}']' \sim N(\mathbf{0}, \mathbf{C}_0 \otimes \mathbf{I}_C)$,

$\mathbf{e} = [\mathbf{e}_{HW}' \mathbf{e}_{FC}']' \sim N(\mathbf{0}, \mathbf{R}_0 \otimes \mathbf{I}_N)$,

Where $\mathbf{A}$ is the additive genetic relationship matrix including all fish in the pedigree, $\mathbf{I}_C$ and $\mathbf{I}_N$ is identity matrices with dimension C and N, respectively, $\otimes$ indicates the direct product operator. $\mathbf{G}_0$ and $\mathbf{R}_0$ are the co-variance matrices (2×2) of animal additive genetic and residual effects, respectively. The random effect associated with common

environment of full-sib families was preliminarily assessed using a single-trait likelihood ratio test (Lynch and Walsh, 1998), being statistically significant ($P < 0.05$) only for HW. Therefore, we only included a random common environment effect for HW in the final two-trait animal model and $\mathbf{C_0}$ denotes a scalar (1×1) of this effect. The ASREML software (Gilmour et al., 2009) was used to estimate the variance and co-variance components and breeding values (EBVs) for HW and FC.

2.3. Heritabilities, genetic correlations and genetic trends

For HW and FC, the heritabilities were calculated as follows:

$$h_i^2 = \frac{\sigma_{Gi}^2}{\sigma_{Gi}^2 + \sigma_{Ci}^2 + \sigma_{Ei}^2},$$

where, i is HW or FC, σ_{Gi}^2 denote the additive genetic variances from $\mathbf{G_0}$ matrix, σ_{Ci}^2 denotes the variance of common environment effect related to full-sib groups for HW from $\mathbf{C_0}$ and σ_{Ei}^2 denote the residual variances from $\mathbf{R_0}$ matrix. The genetic correlation (r_{xy}) between HW and FC was computed as follows (Falconer and Mackay, 1996):

$$r_{HW,FC} = \frac{\sigma_{aHW,aFC}}{\sqrt{\sigma_{aHW}^2 \ \sigma_{aFC}^2}},$$

where $\sigma_{aHW,aFC}$ is the additive genetic covariance between HW and FC, σ_{aHW}^2 is the additive genetic variance of HW, and σ_{aFC}^2 is the additive genetic variance of FC. Genetic trends for HW and FC were determined by regressing mean EBV on generation number for each population (Estany et al., 1989; Sorensen and Kennedy, 1984)

3. Results

3.1. Variance components and heritabilities

Variance components and heritabilities for both traits in each population are shown in Table 3. Significant additive genetic variation was detected for HW and FC in both populations. Heritabilities of low to moderate magnitude were estimated for HW (0.41 ± 0.03 and 0.22 ± 0.03, for even and odd populations, respectively). Low values of heritability were also observed for FC (0.08 ± 0.02 and 0.04 ± 0.01, for even and odd populations, respectively). The variance components associated with common environment represented 1.6% and 4.9% of the phenotypic variance for HW for even and odd populations, respectively.

3.2. Phenotypic and genetic correlations

Phenotypic and genetic correlations between HW and FC for both populations are presented in Table 4. Low positive phenotypic correlations between HW and FC were estimated for both populations: 0.07 ± 0.02 and 0.12 ± 0.02. Low to moderate, but positive genetic correlations between HW and FC were estimated for both populations: 0.15 ± 0.11 and 0.25 ± 0.14, for even and odd population, respectively.

3.3. Genetic trends for HW and FC

Genetic trends determined by fitting a linear regression of the mean EBV on generation for each population is presented in Fig. 1. A positive

Table 3

Phenotypic, additive, common environment and residual variance components (σ_p^2, σ_a^2, σ_c^2, σ_e^2, respectively) and heritabilities (h^2) for harvest weight (HW) and flesh color (FC) in even and odd coho salmon breeding populations ($\pm$ standard errors).

Value	Even population		Odd population	
	HW	FC	HW	FC
σ_p^2	0.64 ± 0.01	1.86 ± 0.04	0.81 ± 0.01	1.36 ± 0.02
σ_a^2	0.27 ± 0.02	0.16 ± 0.03	0.18 ± 0.03	0.06 ± 0.02
σ_c^2	0.01 ± 0.00	–	0.04 ± 0.01	–
σ_e^2	0.37 ± 0.01	1.69 ± 0.04	0.60 ± 0.01	1.26 ± 0.03
h^2	0.41 ± 0.03	0.08 ± 0.02	0.22 ± 0.03	0.04 ± 0.01

Table 4

Genetic (r_g) and phenotypic (r_p) correlations between harvest weight (HW) and flesh color (FC) for even and odd populations of coho salmon ($\pm$ standard error).

Correlation	Even population	Odd population
$r_{g \ (HW, FC)}$	0.15 ± 0.11	0.25 ± 0.14
$r_{p \ (HW, FC)}$	0.07 ± 0.02	0.12 ± 0.02

genetic response for both HW and FC was found in both populations. There were no significant differences ($p > 0.05$) in the EBVs between the two populations for the two analyzed traits. The regression of the mean EBVs on generation number showed that the estimated increases in HW were 0.31 ± 0.01 (9.3%) and 0.26 ± 0.02 (9.8%) kg per generation in even and odd population, respectively, while the correlated responses in FC were 0.04 ± 0.01 (0.4%) and 0.04 ± 0.00 (0.6%) fan units per generation in even and odd population, respectively. Over eight generations, the mean EBVs increased by an estimated 2.06 and 1.71 kg for even and odd population, respectively, while the correlated increase in the mean EBVs for FC were 0.28 and 0.24 fan units for even and odd populations, respectively. The genetic responses to selection were very similar for both traits in the two populations.

4. Discussion

Various studies have shown the presence of significant genetic variation for growth traits in coho salmon. For instance, an early study demonstrated the presence of heritability for body weight with an intermediate value (0.3 ± 0.1) in a commercial coho salmon population (Hershberger et al., 1990). Moreover, Neira et al. (2004) obtained low to medium heritability (0.13 ± 0.04–0.24 ± 0.05) for body weight at 20–21 months of age. In a similar study, Neira et al. (2006) reported heritability values for HW of 0.39 ± 0.03 and 0.40 ± 0.04 in two populations. None of these previous estimates accounted for a common environment effect which should be included in the genetic evaluation model for HW according to the results presented by Gallardo et al. (2010). We also found a significant common environment effect due to rearing of full sib-groups in common tanks prior to tagging. The range of heritabilities for HW ($h^2 = 0.22$–0.41) and the magnitudes of common environment effects in the present study ($c^2 = 0.016$–0.049) were somewhat similar to those reported by Gallardo et al. (2010) ($h^2 = 0.21$–0.38 and $c^2 = 0.02$–0.06). In addition, similar levels of heritability values (0.21–0.43) have been previously found for body weight in other salmonid species such as rainbow trout and Atlantic salmon (Elvingson and Johansson, 1993; Gjerde and Schaeffer, 1989; Rye and Refstie, 1995).

Flesh color should be accurately and inexpensively phenotyped at processing plant (Norris and Cunningham, 2004). In most markets, salmon products are categorized and given different prices depending on perceived color. In the present study the trait was defined based on perceived color rather than quantifying pigment retention in the flesh. Here we used visual determination of color by means of the Roche SalmoFan™ (Hoffmann-La Roche Ltd., Basel, Switzerland). Different studies have demonstrated the presence of additive genetic variation for FC in coho salmon and other related salmonid species. For example, Araneda et al. (2005) reported moderate values of heritability (0.20–0.23) for FC in coho salmon phenotyped using visual evaluation. In addition, Norris and Cunningham (2004) and Vera et al. (2007) have estimated a range of heritability values (0.05 ± 0.03 to 0.20 ± 0.02) for FC in Atlantic salmon when using the Roche SalmoFan™ and other alternative methods for phenotyping. Our results shown heritability values in the lower range of the previous studies reported in the literature. Nevertheless, our estimates are still significant. Low values of heritability reported here may be related with high levels of pigment present in the commercial feed in order to obtain good and uniform flesh color in typical production conditions. Even though feeding composition changed depending on the year and stage of the production cycle, pigments levels (astaxanthin) were kept constant at 60 ppm along the whole
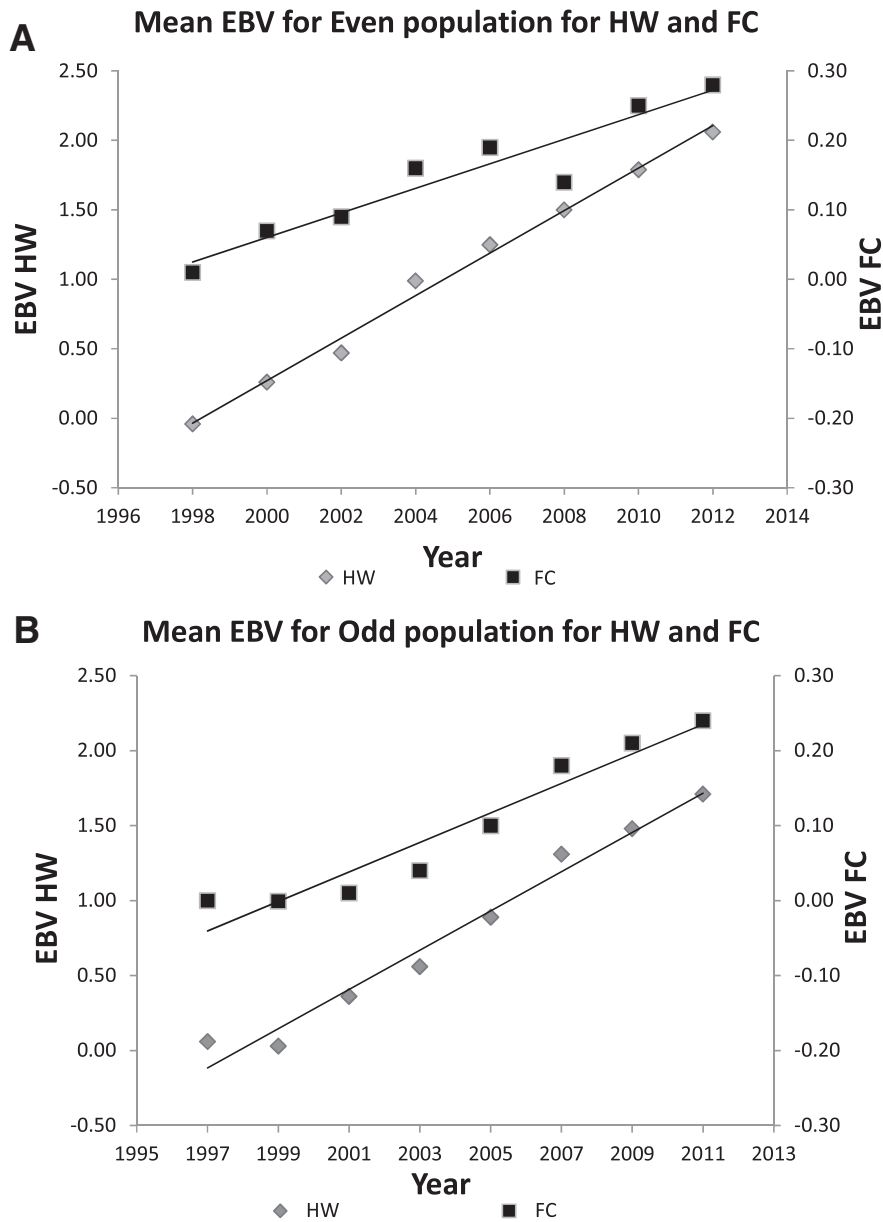
Fig. 1. Genetic trends for harvest weight (HW) and flesh color (FC) for even (A) and odd (B) populations of coho salmon after eight generations.

study. Differences of astaxanthin content of 70 ppm versus 35 ppm in the food resulted in heritability values of 0.13 and 0.23 of flesh color respectively at harvest in coho salmon (Neira, unpublished data). The absence of a significant common environment effect for FC was expected because this is usually found to be present for traits during early growth and also to be greater for growth-related traits than for carcass quality traits (Nguyen et al., 2010).

Differences in heritability between even and odd populations for HW ($h^2 = 0.22$ to 0.41) and FC ($h^2 = 0.04$ to 0.08) are considerable in magnitude. Similar differences have been reported for HW ($h^2 = 0.21$ to 0.38) in two independent coho salmon breeding populations by Gallardo et al., (2010). These differences are based on the relative importance of the estimated variance components of each independent population. In the present study, it is evident that higher genetic variation and lower residual variation for both HW and FC were measured in the even population when compared to the odd population. For instance, the residual variance represented 57.8% and 74.1% and the additive genetic variance represented 42.2% and 22.2% of the total phenotypic variance for HW in the even and odd populations,

respectively. Alternatively, the residual variance represented 90.9% and 92.6% and the additive genetic variance represented 8.6% and 4.4% of the total phenotypic variance for FC in the even and odd populations, respectively. The magnitude of residual and additive genetic variance components explaining total phenotypic variation for both HW and FC in a specific population may change with environmental conditions (e.g. given by different year, management practices and others) and heritability can vary accordingly (Falconer and Mackay, 1996; Visscher et al., 2008).

It has been demonstrated in earlier studies that genetic relationships between HW and FC are positive in coho salmon (Iwamoto et al., 1990; Whithler and Beacham, 1994), which is favorable as large size and high levels of pigmentation are desirable features for production. Moreover, there are a number of studies in Atlantic salmon and rainbow trout that have shown positive genetic correlations between HW and FC, indicating that the selection for HW would increase FC (Gjerde and Schaeffer, 1989; Johnston et al., 2006; Norris and Cunningham, 2004; Quinton et al., 2005; Rye and Gjerde, 1996). In accordance with previous studies, we found low but positive genetic correlations between HW

and FC in both populations analyzed. Although there is consensus that body weight and color traits are positively correlated in salmonids, to date there are no published studies reporting correlated responses between these traits after long-term selective breeding.

During the first eight generations this commercial coho salmon breeding program has only been focused on the improvement of HW. Here we demonstrated significant genetic progress with realised selection responses close to 10%. These values are similar to those reported by Neira et al. (2006) for the same species and other important fish species with lower generation interval (e.g. tilapia) (Bolivar and Newkirk, 2002; Nguyen et al., 2010).

Despite that the first generations of the present breeding program has only been focused on improvement of HW, there is interest in including other economically important traits into the breeding objective, such as disease resistance (Correa et al., 2015a; Yáñez et al., 2016a) and flesh color.

To our knowledge, this is the first report of a correlated response between two economically important traits, such as HW and FC, in a salmonid species after a long-term selection. Furthermore, although no selection for FC was performed across the eight generations, a small correlated response for this trait was observed after direct selection for HW. A similar correlated response between HW and FC was observed in two independent populations from the same breeding nucleus. Previous work has also reported a correlated response in a carcass quality trait (i.e. fillet weight) to selection for HW in tilapia (Nguyen et al., 2010). However, the magnitude of the correlated response in this previous study are much higher (15.8%–22.5%) than those reported in the present work (0.4%–0.6%), which is mainly due to the higher magnitude of the genetic correlations between fillet weight and HW (0.96 ± 0.02).

In practical terms, the present study demonstrated that a highly relevant carcass quality trait (FC) could be somewhat improved by means of direct selection for HW. Based on the present results, improvement of FC through indirect selection for HW is possible, but not very effective. Breeding programs focused at selecting exclusively for HW will achieve relatively slow genetic progress for FC. Therefore, in order to accomplish a more rapid genetic gain for FC, direct selection for this trait should be considered, by means of selection index, weighting the different traits included into the breeding goal based on their economic relative importance (Hazel, 1943). It is also important to mention that carcass quality traits, including FC, are difficult to measure on selection candidates and selection can only be applied using between-family information. This situation will affect the level of genetic gain achievable on each generation due to lower accuracies of EBVs when using only information from siblings compared to the accuracies achieved when using information from potential breeders themselves (Falconer and Mackay, 1996). Genomic information might be included in genetic evaluations to predict genomic EBVs (Meuwissen et al., 2001). This approach will be particularly useful for improving traits difficult to measure on selection candidates (Sonesson and Meuwissen, 2009; Villanueva et al., 2011; Taylor, 2014), as is the case of FC. Genomic tools required to implement genomic selection schemes (i.e. dense single nucleotide polymorphisms panels) are now available for salmonid species, including Atlantic salmon (Houston et al., 2014; Yáñez et al., 2016b) and rainbow trout (Palti et al., 2015). Moreover, these panels have been already used to identify genomic regions controlling economically important traits (Correa et al., 2015b; 2017; Tsai et al., 2015; 2016) and even utilized to assess the efficiency of genomic selection on these salmonid species (Ødegård et al., 2014; Vallejo et al., 2016; Tsai et al., 2015; 2016). It is expected that in the near future, these genomic tools will be routinely available for several aquaculture species (Yáñez et al., 2015), including coho salmon, allowing the technical feasibility for implementation of genomic selection for FC and other traits. Nevertheless, an economic evaluation of the costs and benefits of the implementation of genomic selection to accurately estimate EBVs and thus accelerate the genetic progress for FC is required.

5. Conclusion

A positive genetic trend demonstrated the success of selection for weight at harvest in two independent coho salmon populations after eight generations. We also showed that selection for weight at harvest resulted in a significant but small correlated response in flesh color in this species. In order to accelerate the genetic progress for flesh color, direct selection for this trait should be considered in genetic improvement programs. Further studies aimed at quantifying the impact of direct selection for weight at harvest on changes in other economically important traits in coho salmon (e.g. fillet weight, fillet yield, resistance to specific pathogens) are still needed.

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