

Evolution of Coho Salmon (*Oncorhynchus kisutch*) Breeding Programs

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ABSTRACT: The evolution of Coho salmon breeding programs, breeding objectives, genetic architecture, genetic response and trends, genetics of disease resistance and future implementation of genomic selection in Coho breeding are analyzed. The genetic gain for growth, after 7-8 generations, with a generation interval of 2 years, has been 10-13%. Current breeding objectives are based on estimated breeding values weighted by their marginal economic values including harvest weight, flesh color and disease resistance (SRS). Other traits included are fillet yield fat content and early spawning. The development of genomic resources in Coho salmon is limited; a second generation linkage map is only recently available. It is expected that in the near future whole-genome sequencing studies are applied to Coho salmon and a high-density SNP chip available for this species and the application of genomic information to assist breeding schemes in will be possible.

Keywords: Coho salmon; breeding; breeding objectives; genomic resources

Introduction.

Oncorhynchus kisutch (Walbaum, 1792), known in Canada and Alaska as Coho salmon, also blueback (Canada), silver (USA), ginmaru (Japan) and kizhuch (Russia) is one of the six Pacific salmon species that occurs in North American and Asian continental watersheds, along with *Oncorhynchus gorbuscha* (pink salmon); *Oncorhynchus keta* (chum salmon); *Oncorhynchus nerka* (sockeye salmon); *Oncorhynchus tshawytscha* (chinook salmon) and *Oncorhynchus masou* (masu salmon). Coho salmon is found in coastal streams from California to Norton Sound in Alaska, and from northern Hokkaido in Japan to the Anadyr River in Russia (Sandercock, 1991) and stay in freshwater for 1–2 years and most commonly spend 2 years at sea. Spawning takes place in the autumn or early winter. Females produce between 1,000 and 2,000 eggs/kg of body weight.

Historically, Coho salmon has been a very important fish resource for indigenous people in coastal areas, for recreational and commercial fisheries (Solar, 2009). To support these stakeholders, through state funding, large hatchery programs operate in Japan, Canada and USA making massive alevin releasing (Beamish et al. 1997). Coho salmon represented approximately 4.6% of the total commercial catch of Pacific salmon by 1985 (INPFC 1985), but lately the average abundance of this specie relative to other Pacific salmon species, has been approximately 2.3% (NPAFC 2010). Notably, Coho salmon have disappeared from almost half of the major

ecological provinces they once occupied in northwestern North America (Gustafson et al. 2007). Coho salmon production, after Atlantic salmon and rainbow trout, has been the third species in importance of world farmed salmonid production, increasing its weight since 1980, accounting for 6-7% of farmed salmonids during the last decades (FAO, 2014a). Chilean Coho aquaculture, around 160 thousand tons in 2012 with a value of US\$0,916 billion (Silva, 2012) is about 90% of world production of this specie, with Japan and Canada as other Coho salmon producers (FAO, 2014b). Good fresh water quality and temperature (lakes and springs) have permitted to reduce reproductive cycle of Coho salmon to 2 years (Estay et al., 1997), a very important feature influencing Chilean leading position in this industry.

Economic importance and breeding objectives.

The value of salmon and trout production in Chile in 2013 was USD 3.52 billion, which represent a 13.3% increase compared with 2012, but Coho salmon decreased its importance from 19% to 13% of total value (Salmonchile, pers. comm.). The industry and especially Coho salmon have had to face a series of adverse events. Regarding the market, activity has not only had to face a reduction in international prices, but also a rise in production costs, mainly by i) Weakening of sanitary conditions that have resulted in an increase in costs, mainly by the increase in mortality per cycle and control measures to combat the outbreak of diseases such as piscirickettsia syndrome (SRS) ii) Significant increase in food prices (representing over 50% of the cost ex-cage salmon) and iii) Increase in the value of inputs and services associated with the salmon industry, due to the significant increase in domestic production. We have estimated that a Coho culture with a capacity of 3,000 tonnes per year and a decrease of survival by 5% due to SRS generates losses over US\$ 4.5 million and a 2% increase in costs production (unpublished data). In addition, a 5% increase in food costs generates a decline in profitability over the approximately US\$2 million, the unit cost of production increased by 3%. In industry, while these problems have been addressed through different innovation proposals, the implementation of structured breeding programs has been the most effective.

The main traits studied in breeding programs have been growth, carcass traits (fillet weight, carcass, and visceral fat content), quality aspects (fillet color and fat content) and disease resistance (Gjedrem, 2005; Neira et al., 2004). However, there is a shortage of studies to determine the economic values of each of these traits. The derivation of economic values is a fundamental step

to fulfill breeding objectives (Wolfová and Wolf, 2013). According to Byrne et al. (2010) and Pravia et al. (2014), the definition of these objectives not only simplifies selection decisions (optimal strategy), but also the identification of traits that have high impact on the economic performance of the activity. In fish, breeding objectives have been designed for Atlantic salmon (*Salmo salar*), Tilapia (*Oreochromis niloticus*) and carp (*Cyprinus carpio*). In these investigations economic values were estimated for production traits, especially growth rate, sexual maturity, survival and cumulative food intake (Gjedrem et al., 2012; Ponzoni et al., 2008)

Traits to incorporate into the breeding objective require a marginal economic value, defined as the change in a profit function expressed per animal unit. This change is due to variation in one unit in the genetic merit of the considered trait (Kömlösi et al., 2009). There are two approaches to derive economic values: 1) The subjective approach, providing economic values through the allocation of values for characters that may be intangible, such as consumer preferences; and 2) normative methods using profit equations or bioeconomic models (Krupová et al., 2008).

A profit equation is a single equation designed to represent the relationship between animal performance in traits of economic interest and the economic profit of the company (Steine et al., 2008). Economic values are obtained through the partial derivative of the profit function for each trait considered in the breeding objective. The main advantage of this approach is the simplicity and ease of interpretation of the results. However, the description of the production system through a single equation makes it inaccurate to describe the complex relationships between biological characteristics, factors of production and economic elements. Bioeconomic models consist of a set of equations characterizing the biological relationships simulating technical, biological and economic situations that determine the profitability of the production system (Ivkovic and Kumar, 2009). An advantage over other methods is its precision; it incorporates uncertainty sources that require a risk analysis (Anderson and Seijo, 2010). In this case, for each trait economic values are obtained through simulation of the effect of increasing the genetic merit on the profit function (Aby et al., 2012).

Currently, Coho salmon production in Chile uses breeding objectives based on estimated breeding values weighted by their marginal economic values. The traits studied have been harvest weight, disease resistance (SRS) and flesh color. However, there is no reported research on economic values. We estimated (unpublished data) economic values through the normative approach applying a bioeconomic model including the effects of temperature, photoperiod and individual weight. The model has been calibrated through historical observations of Coho salmon production, scientific literature, market and technical parameters. The economic profit function was described as follows:

$$NPV = Y(t) e^{-it} - \int_{t=0}^{t=T} C(t) e^{-it} dt$$

where NPV is the net present value in continuous time (Bjørndal 1990), t is time (in days), $Y(t)$ and $C(t)$ correspond to the function of revenues and costs respectively which are described in continuous time. Revenues are affected mainly by the improved harvest weight and SRS (survival). The total costs are mainly affected by the flesh color (pigment cost and astaxanthin retention). The economic function (NPV) was solved by numerical integration and discounted according a discount rate from time $t=0$ to the final harvest time $t = T$. This procedure was done by incorporating a discount factor e^{-it} for the discounted value of the economic benefits achieved in the culture. The assumptions of the model considered the current production system in Chile, i.e., 18 sea cages with a maximum capacity of 3,000 tons per production cycle. Simulations were carried out over a time horizon of one production cycle. A base scenario that included a change in the productive output of each trait was evaluated. This was carried out through a *ceteris paribus* condition, where each trait is changed by one unit, while all others remain constant. An economic efficiency ratio (EER; returns divided by costs) was calculated for each alternative scenario (Sadeghi-Sefidmazgi et al., 2009). For each trait, the economic weight was estimated as the difference between the EER ratio obtained in the base case scenario and the new ratio achieved after the modification in the output for the trait. After evaluating all economic weights, results indicated that harvest weight was the most important trait, representing 60.2% (USD 0.024) of total profit (USD 0.041), followed by SRS and flesh color, with values of 35.1% (USD 0.014) and 4.7% (USD 0.002), respectively. We confirmed these results by means of stochastic analysis. Uncertainty in the price of different sale products and input costs (e.g., smolt, food, pigment and processing) revealed that there is a probability of 60% of achieving an economic weight between USD 0.022 and USD 0.027 for harvest weight. These results will be useful for the development of multi-trait selection indexes for the genetic improvement of Coho salmon under Chilean production conditions.

Genetic Architecture

Estimation and use of genetic parameters are fundamental in the design and implementation of genetic improvement programs. Genetic parameters allow the breeder to understand the relative importance of heritable and environmental variation. This is especially true since only phenotypes are measured. However, the breeding value of the selection candidates will influence rates of genetic gain in proceeding generations. Furthermore, most selection is based on multi-trait genetic evaluations, allowing increases in accuracy as information from correlated traits is used; and reduces bias by taking into account the notion that for traits measured after sequential rounds of selection, only the better individuals are evaluated.

Multi-trait evaluations also provide greater opportunity for implementation of selection indexes composed of Economically Relevant Traits (ERTs) weighted by marginal economic values. As profitability is deter-

mined by costs of production and income derived from the breeding program, the choice of ERTs should directly influence either a cost of production or a source of income. These traits should be the focus of genetic improvement.

This paper is not an exhaustive catalog of genetic parameters associated with salmon. See Carlson and Seamons (2008) for an excellent review. We will highlight some studies to provide a general view of variation and genetic relationships important for breeding program design.

In general, reproductive traits will express lower genetic variation than traits associated with morphology (Carlson and Seamons, 2008). Some traits, like early spawning date, are highly heritable in Coho (Gall & Neira, 2004; Neira et al., 2006a), with low genetic correlation with harvest weight. Thus, selection can be effective with little effect on growth potential.

Harvest weight is the single most studied trait in salmonid species, and likely has the greatest economic value (Neira et al., 2006b; Neira et al., 2004). It is easy to measure, moderately heritable, and possesses certain beneficial genetic relationships with other ERTs, as shown below.

Carcass composition and product quality traits have great influence on product yield and ultimately consumer preference (Neira et al., 2004). Traits such as flesh color, fat, and filet yield, while expensive to measure, are important components of profitability. Heritability estimates tend to be low to intermediate for most traits (Neira et al., 2004; Carlson and Seamons, 2008). There are certain beneficial genetic correlations for carcass quality and composition that would be of importance in a breeding program. Neira et al (2004) found a high positive correlation between filet yield and harvest weight (0.98) and fat content of flesh and harvest weight (0.73). The heritability of fat content of flesh was low (0.15) but still points to the utility of including fat content in a breeding objective to control level of leanness. In their study, there was little genetic control of texture (heritabilities about 0.06 to 0.09), but a high genetic correlation with harvest weight (0.70). There is likely some intermediate optimum for texture, which would require a non-linear component in a breeding objective.

At a minimum, the breeding objective for Coho salmon should include traits associated with harvest weight (main source of income) and survival (number of fish available for market). Enhanced objectives should take into account quality traits as well as some measure of disease resistance.

Any breeding objective should include the cost of feed, which by some estimates account for approximately 45% of the cost of production (e.g., Marine Harvest, 2013). Selection for reduced feed intake or allied traits (e.g., residual feed intake) has been successful in a number of livestock species (ref.). However, to achieve similar results in fish would require (1) the ability to

account for day-to-day variation in feed intake; (2) the ability to measure feed intake over a continuum of age classes; and (3) overcome the technical difficulties of recording individual feed intake on a large number of fish in a single tank (Kause et al., 2006). There is sufficient genetic variation for feed intake in salmonids, with heritability ranging between 0.10 and 0.17 in fish. The genetic correlation between feed intake and harvest weight in Atlantic salmon is between 0.65 and 0.70, so is a good indicator for the ERT.

Genetic bases of Coho salmon breeding programs. Coho salmon is, after *O. mykiss*, the most widely and successfully translocated species of the genus *Oncorhynchus* (Solar, 2009). First attempts to introduce Coho salmon to Chile in the early 20th century, and several others afterwards until late the 60's aimed to initiate sea ranching with Coho were unsuccessful. Later, between 1968 and 1976 when eggs were imported from releasing hatcheries from Oregon and Washington this species was considered introduced (Vila et al., 1978; Campos, 1981). Since 1980 the panorama for Coho salmon started to change significantly when the complete production cycle was successfully accomplished and Coho farming in sea cages began. During that decade, importations of eggs were realized from Oregon and Kitimat River related to salmon culture activity (Lhorente, pers. comm.) and became the genetic basis of broodstocks present in the Chile. In the USA Coho salmon broodstock used to develop a breeding program at Washington State University came from eggs taken from Skykomish River and that were kept in captivity from 1971 to 1977 where from the program begun (Hershberger et al., 1990). Canadian program was initiated in 1985 and both selective year classes were composed by eggs coming from five different Rivers of British Columbia: Kitimat, Bella Coola, Big Qualicum, Robertson Creek and Pallant Creek (Swift, 1991).

Response and genetic trends.

Family-based breeding programs for genetic improvement of aquaculture species, were first introduced for salmonids in the 1970s (Gjedrem, 2012). Now they are established as an industry standard and according to Rye et al., (2010) 13 breeding programs have been implemented in Atlantic salmon, 13 in rainbow trout and 4 in Coho salmon. Coho salmon have been selectively bred for improved performance for culture in United State (Hershberger et al., 1990), Canada (Swift, 1991) and Chile (Neira et al. 2006 a,b). These breeding programs began as research project funded by state and led by competent Universities, whose focus was to support and improve the productivity of Coho salmon industry. In addition, direct or indirectly related to these initiatives, commercial breeding programs are underway mainly in Chile (Solar, 2009) (Table 1). Reported genetic responses in Coho salmon are related to the Chile and U.S. programs, as no information was found related to Canadian case, which makes us suspect that this program may have been discontinued, as has the IFOP breeding program in Chile.

Table 1. Family-based selective breeding programs of Coho salmon

Company- Country*	Start	Selected traits in addition to growth
(A) IFOP-U.- Chile	1992	Early spawning
(B) AquaChile - Chile	1997	Flesh color, fat content
(C) Marine Harvest - Chile	1998	Flesh color, fat content, fillet yield
(D) Invertec - Chile	2000	-
(E) Aquaseed/Domsea -USA [†]	1978	Shape

*IFOP: Institute of Fisheries Department; UCh: University of Chile; [†]: Equivalent to Domsea Farm Inc.

Table 2. Response to selection in growth rate

Country-Institute*	Trait selected	ΔG per gen	N° of generation	Author
(A)	HW, 3.0 k	9.9-10.5	4	Neira et al. (2006a)
(B)	HW, 3.0 k	10-13	7-8	Neira, pers. com.
(C)	GF3	5.0-6.0	7	Deerenberg, pers. com.
(D)	HW 0.3 k	10.1	4	Hershberger et al. (1990)

*As in Table 1; HW: harvest weight; ΔG : Genetic gain; GF3: Growth Factor 3

Main published genetic gain results from large-scale breeding programs in Coho salmon are related with growth in on-growing phase. After 4 generations Hershberger et al. (1990) have shown a genetic response of 10,1 % per generation in fish of 300 g. Almost equal results have been reported in Coho salmon of 3,0 kg after 4 generation of selection (Neira et al. 2006a). Actually, the most important commercial breeding program in Chile shows similar magnitude of genetic gain for growth at harvest as a result of 7-8 generations of selection (Table 2). Similar ranges in genetic response for growth has been reported and summarized in Atlantic salmon and rainbow trout (Gjedrem, 2000), indicating that selection process for growth has been very efficient in salmonids.

Associated with the IFOP Coho salmon breeding program initiated in 1992 in Chile, an independent culling selection scheme for early spawning (days) measured in females was included as a second selection stage in both year classes of selection (Neira et al. 2006,b). After four generations of selection, a phenotypic reduction of 13-14 days was obtained in both selected year classes, which represents an average phenotypic response to selection for onset of spawning of -3 days per generation for the two populations of Coho.

Genetic improvement programs in Coho salmon frequently use "Best Linear Unbiased Prediction" (BLUP) procedures for calculating breeding values (BV)

and genetic trends (Yañez et al., 2013) and commonly only consider direct additive effects as random (Neira et al., 2004; Neira et al., 2006b). Results published by Gallardo et al. (2010) conclude that common environment and non-additive variances are also an important component for harvest weight in Coho salmon, thus not including it in BLUP analyses may produce an overestimation of predicted response.

Animal model procedures produce a more exact prediction of BV and increase genetic response compared with other more traditional selection schemes (e.g., Belonsky and Kennedy, 1988). However, given that this procedure favors selection of related individuals, it also produces an increase in the rate of inbreeding (ΔF), and a reduction in genetic variance over the long term (Belonsky & Kennedy, 1998; Quinton et al. 1992). Applying a mating scheme where crosses between half and full-sibs were avoided (Gallardo et al. 2004a), an accumulated inbreeding of 4.4-9.5% and a rate of inbreeding of 1.1-2.4% has been calculated in Coho salmon breeding program of IFOP-UCh after 4 generation of selection in even and odd populations (Neira et al. 2006a). Using the same mating scheme, a similar magnitude (5.3 to 7.0%) and rate of inbreeding (1 % per generation) has been reported in commercial breeding programs (Yañez et al. 2013b). Although the rate of inbreeding remained at the upper limit accepted for a viable breeding program (Bijma, 2000), Coho salmon studies show that the mating scheme is efficient only in the first 1-2 generations and subsequently is not effective producing a reduction in effective population size (N_e) and generating a future risk in sustainability of breeding programs (Yañez et al., 2013a). Non-random mating schemes have been evaluated in Coho salmon, showing that it is possible to control increase in inbreeding and maintain genetic response by applying optimization algorithm in salmonids (Gallardo et al., 2004a). For example, using mate selection analysis approach an algorithm was developed to derive alternative investment mating schemes that are widely used in beef cattle, dairy cattle and swine to optimize mate selection decisions (Kinghorn, 2011). One of the big challenges today is implementing and evaluating mate selection tools to automate selection and mate allocation decisions in Coho salmon.

High inbreeding increases the probability of occurrence of inbreeding depression (ID), thereby reducing mean phenotypic value in characters related with reproductive capacity or physiological efficiency (Falconer & Mackay, 1996). Estimation of ID in salmonids has consistently shown that consanguineous progeny have lower viability and less growth (Gjerde et al. 1983; Pante et al. 2001). Few studies have been published in Pacific salmon. In Chinook salmon, it has been reported that ΔF could increase the severity of a protozoan infection (Arkush et al. 2002) and reduce relative fecundity in spawning females. The effect of inbreeding on different traits has been studied in Coho salmon. Significant ID was observed in gonadosomatic index and body length in spawning females (-5,3%, and -1,56% per each 10%

increase of inbreeding, respectively) (Gallardo et al. 2004b). There is no evidence of significant impact of inbreeding on other traits as body weight and fecundity (Gallardo et al. 2004; Neira et al. 2006a).

Coho salmon production has clear growth potential, but its harvest is seasonally limiting. Once sexual maturation begins, the organoleptic quality of the meat destined for consumption is severely affected. In Chile, the Coho harvest begins in December and ends in February, concentrating the use of processing plants into a few months. Thus, opportunities for creating new markets and increasing existing ones are lost. One alternative for expanding the harvest season is to produce sterile specimens, partially or completely suppressing sexual development by using triploid individuals (Taranger et al., 2010). Triploid Coho salmon are currently used in a commercial farming operation in Chile. The increase in total weight and survival for triploid and diploid fish under the same treatment showed no significant differences and the gonad somatic index is significantly lower for the triploid (unpublished data).

Genomic resources to assist selective breeding

The development and application of novel genomic approaches, such as next generation sequencing methods and high-throughput genotyping technologies, have allowed the dissection of the genetic architecture of phenotypic variation for several complex traits in species of economic importance (Goddard and Hayes (2009)). Although, the development of genomic resources in Coho salmon is somewhat limited, there is an increasing availability and application of genomic tools in related species, such as Atlantic salmon and rainbow trout (Yáñez and Martínez (2010)). For instance, the International Collaboration to Sequence the Atlantic salmon Genome (ICSASG), aimed at both providing a reference genome sequence and identifying and locating all genes for this species, will help in the generation of genomic resources and the sequences of other species, including Pacific salmon (Davidson et al. (2010)).

The generation of a genetic map is the first stage towards the implementation of genomic strategies aimed at unraveling the genetic basis of economically important traits. The construction of a genetic map depends on the availability of molecular markers, such as microsatellites and SNPs (Single Nucleotide Polymorphisms). A considerable number of molecular markers have been characterized for Coho salmon, most of them initially discovered for related species and proven to have cross-reaction (Olsen et al. (1996); Williamson et al. (2002); McClelland and Naish (2008)) and some others primarily discovered for this species (Smith et al. (1998); Kodama et al. (2014); Campbell and Narum (2011)). The first linkage map available for Coho salmon, was built using 148 AFLP markers and 133 microsatellites, covered 26 chromosomes and identified two homeologous chromosomes using information from duplicated loci (McClelland and Naish (2008)). A second generation linkage map constructed using 8,681 restriction site

associated DNA (RAD) loci, comprising 30 linkage groups and identifying 8 homeologous chromosomes has been recently reported (Kodama et al. (2014)).

There are some studies aimed at detecting loci or genes associated to relevant traits in Coho salmon. For example, Sequence Characterized Amplified Regions (SCAR) markers associated with flesh color (Araneda et al. (2005)) and spawning date (Araneda et al. (2009)) have been identified in farmed populations. Furthermore, Quantitative Trait Loci (QTLs) of minor effect for growth rate, length and weight were detected in seven linkage groups and colocalization between them suggested pleiotropic effects, which may have been accounted for phenotypic correlations between these traits (McClelland and Naish (2010)). Clock genes *Cryptochrome2b* and *OtsClock1b* mapped to some of these previously identified QTLs for growth and length in a stage-specific basis, suggesting temporal expression of these genes influencing growth related traits in different life stages (O'Malley et al. (2010)). A recent study fine-mapped QTLs associated to weight, length, growth and age at sexual maturation in several linkage groups using RAD markers (Kodama et al. (2014)). However, to our knowledge, up to date none of these loci associated to economically important traits have been implemented to assist breeding schemes in this species. In this regard, more studies are needed in order to identify variants in high linkage disequilibrium with the causative mutations for these and other traits, such as disease resistance and carcass quality, in order to ensure that the marker-trait associations is maintained across both populations and for a considerable number of generations.

It is expected that in the near future whole-genome sequencing studies are applied to Coho salmon and a high-density SNP chip is available for this species. This has been the case for the some related species, including Atlantic salmon (Houston et al. (2014); Yáñez et al. (2014)) and rainbow trout (Palti, personal communication), for which high-density SNP arrays are currently available. These tools can assist the identification of loci involved in complex traits of economic importance through the implementation of genome-wide association studies. This information will be useful for accelerating the genetic progress through the use of genome-wide information to assist selective breeding (i.e. genomic selection), especially for traits that are difficult to measure in the selection candidates in a typical aquaculture selective breeding scheme, including disease resistance and carcass quality traits (Sonesson and Meuwissen (2009); Villanueva et al. (2011); Taylor (2013)). Finally, it is important to mention that further studies are needed in order to determine a cost-effective way of applying genomic information to assist breeding schemes in aquaculture in practice, including Coho salmon breeding programs, as it has been recently addressed using in simulation studies to test the output of using low-density SNP panels (Lillehammer et al. (2013)).

Conclusion

A genetic gain of 5-6% per year in Coho salmon breeding programs is the highest achieved in salmonid species, because the generalized use of 2 years generation interval in Chile. The development of genomic resources in Coho salmon is still limited. It is expected that in the near future whole-genome sequencing studies are applied to Coho salmon and a high-density SNP chip available for this species and the application of genomic information to assist breeding schemes in will be possible.

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