

Coho Salmon Broodstock Development: A Case Study of the Domsea Coho Salmon (1977 to 2015)

Robert N. IWAMOTO^{*1}, Richard TOWNER^{*2}, James MYERS^{*3}, Greg HUDSON^{*1},
and Patricia MUNSELL^{*1}

Abstract: There are few long-term studies on Pacific salmon that inform on the potential for gains by systematic selective breeding. As a consequence, there is limited data on the potential for inbreeding losses because of constrained population sizes and matings among closely related individuals over a prolonged period of time. In 1977, Domsea Farms Inc., the University of Washington, and the Washington Sea Grant Program initiated a genetic selection program for coho salmon for Domsea's marine net-pen operations. Because little was known at that time regarding the potential for genetic improvement in coho salmon, the program was initially designed with two central goals: 1) collect basic information (heritabilities, genetic and phenotypic correlations) on the potential for genetic improvement in such economically important traits such as smoltification, growth rate to harvest, flesh color, and reproductive fitness; and 2) using that information, develop selection and mating protocols that would maximize selection gains but minimize inbreeding. Despite significant changes in ownership, rearing environment and operations, the program has remained remarkably consistent over the past 38 years or 19 generations of selection. We have demonstrated that selection for improved growth to the smolt stage (7.1-11.3% per generation) and adult phases (43-53 g per generation) can be achieved. Overall, the growth rate of the Domsea coho salmon has improved between 3% and 8% per generation while reproductive traits such as female weight, egg weight, and survival to ponding have remained unaffected by inbreeding. While traditional genetic approaches have been demonstrably successful for this program, it is anticipated that further consideration and application of molecular approaches will help further characterize and advance this broodstock program for coho salmon.

Key words: Coho salmon, *Oncorhynchus kisutch*, Domsea, selection gains, inbreeding

Introduction

Over the past 50 years or so, the application of genetic selection theory to improve strains of fish and shellfish has been an active and, in many cases, successful endeavor (see Quinton *et al.* 2005-Atlantic salmon; Dunham and Smitherman 1984-catfish; Tave 1999-Tilapia). As a result, the genetic bases for trait improvement are now well characterized for many commercially important aquatic species. However,

there is less known about the effects of long-term intensive selection and the resulting inbreeding on closed populations because of the lack of well-documented, multi-generational selection programs.

This paper presents the results of a 19-generation long and still on-going selection program on a closed-population of coho salmon (*Oncorhynchus kisutch*). It outlines the general facets of the broodstock (commonly known as the Domsea coho) and some major results including trait characterization and

2017年2月28日受理 (Received on February 28, 2017)

^{*1} Riverence LLC, Rochester, WA 98579, U. S. A.

^{*2} GenTec Consulting, Payette, ID 83661, U. S. A.

^{*3} NOAA NMFS Northwest Fisheries Science Center, Seattle, WA 98112, U. S. A.

E-mail: riwamoto@riverence.com

improvement as well as inbreeding effects to date.

Materials and methods

The Domsea coho genetics program was initiated in 1977 as a cooperative effort among Domsea Farms (a then subsidiary of Union Carbide, Inc.), the University of Washington, and the Washington Sea Grant Program. The initial population was founded in 1974 with gametes from the Wallace River Hatchery strain, Skykomish River Basin, in western Washington State. The population had been maintained in captive culture via random mating prior the selection program's start three years later. The initial goals were to develop a population on a two-year spawning cycle and to characterize the genetic bases for several commercially important traits as well as to apply that information to develop a selection program.

Domsea Farms, in the mid to late 1970s, was the first commercial net-pen operation in Puget Sound, WA, and its goal was to produce pan-sized (500 g) coho salmon. Fast growth in fresh and seawater and improved smoltification and subsequent seawater survival were the primary traits of selection interest. Since then, other traits of interest have included fecundity, egg size, and size at maturity.

A breeding design involving 40 full- and half-sib families initially and later just 40 full-sib families was initially used to evaluate growth performance and estimate heritabilities and genetic correlations for and among traits. The selection strategy included between and within-family selection using a selection index and a mating scheme to minimize inbreeding as much as possible. The program utilized multiple selection events at major life history/rearing transition points (Fig. 1). Each year individuals from the top 10 families were crossed in a circular mating pattern to create six full-sib families within each of the top 10 family crosses^{*1}. The 60 families were then reduced to 40 families after incubation based on assessments of egg size, fecundity, and survival to ponding. Each family was reared separately until

SELECTION SCHEME FOR COHO SALMON STOCK DEVELOPMENT

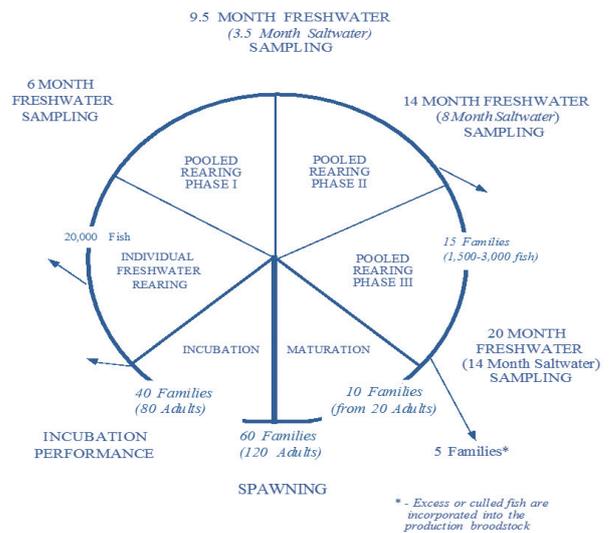


Fig. 1. Selection program for Domsea coho salmon broodstock development. The program has been virtually unchanged for 19 generations with the exception of the change from partial seawater to total freshwater freshwater rearing.

large enough to externally identify with a freeze brand, then families were combined and transferred to marine net-pens. Fish were sampled during the freshwater growth period, at time of transfer to saltwater and at two other periods during saltwater rearing, at 3.5 and 8.0 months post-transfer to assess saltwater survival and growth. The resulting data were then used in the selection index to reduce the number of families to 10^{*2}. After transfer to freshwater for final maturation, the 6-10 largest males and females from each of the selected families were mated using a circular mating design to avoid mating closely-related individuals.

In 1986-1987, because of high pre-spawning mortality for adults maturing in marine net-pens; the survival, maturation, and reproductive success of adults held in freshwater throughout their entire lives were evaluated. As a result of those trials, the broodstock program was then shifted, and has

^{*1} Family crosses were adjusted to avoid first-cousin crosses.

^{*2} In some years the 10 families were selected from the top 15 performing families, due to inbreeding concerns or poor survival post-index selection.

remained ever since, to an all freshwater program. The selection strategy and mating design has remained the same except that the saltwater holding period was then eliminated.

Because of the two-year generational cycle, even- and odd-year lines were established. In 1992, the even-year line was lost due to a hatchery accident, so about half of the odd-year line were subsequently photoperiod-manipulated to spawn two years later, thus re-creating an even-year spawning group. The *de novo* even-year line has been maintained as a separate line ever since.

Pedigrees for both even- and odd-year lines have been maintained from the start, and in combination with population numbers and microsatellite, allozyme, and serum protein (transferrin) data, have been used to estimate inbreeding levels for each generation.

At the initiation of the program, control lines were maintained to assess selection efficacy. However, within two generations, logistics of the program and the space constraints forced the termination of the control lines. Since then, the performance of fish from the founding hatchery population has been

compared with the select line to assess changes to the selected lines.

Results and discussion

Genetic estimates

The first quantitative genetic parameters for coho salmon traits were reported by Iwamoto *et al.* (1982), Saxton *et al.* (1984), and Iwamoto *et al.* (1990) from the Domsea coho program (see Table 1 for a summary). Overall these genetic estimates for freshwater growth, smoltification and initial seawater survival, seawater growth, carcass-related, and reproductive traits for the Domsea coho salmon indicated that a systematic selection program would be successful (Hershberger *et al.*, 1990).

Selection gains for weight and length at 7, 11, and 14 months post-fertilization were predicted using the heritability estimates and a range of selection intensities (Table 2). The range of predicted selection gains was quite high. For example, the predicted improvement for 7-month weight after the first generation of selection varied from 1.4% to 46%.

Table 1. Heritability estimates (standard error in parentheses) for various traits at different generations. Estimates are based on sire (S), pooled sire and dam (S + D), full-sib (FS), or pooled full-sibs/double first cousin (FS + DFC) components. Other abbreviations: SW = saltwater; FW = freshwater.

Component	Trait	Generations under selection				
		1	2	3	5	14
h^2_S	8 m SW Weight	0.19 (0.11)				
		0.62 (0.21)				
h^2_{S+D}	8 m SW Weight	0.20 (0.06)				
		0.33 (0.10)				
h^2_{FS}	8 m SW Weight		0.40 (0.15)	0.30 (0.07)	0.21 (0.09)	
				0.29 (0.08)	0.22 (0.09)	
h^2_{FS+DFC}	8 m SW Weight			0.26 (0.07)	0.20 (0.07)	
				0.30 (0.07)	0.24 (0.07)	
h^2_{FS}	24 m FW Weight					0.422 (0.146)
h^2_{FS}	24m FW Fecundity					0.237 (0.108)
h^2_{FS}	24 m FW Egg Size					0.432 (0.135)
h^2_{FS}	Carotenoid		0.50 (0.16)	0.30 (0.14)		
h^2_{FS}	Lipid		0.18 (0.13)	0.19 (0.23)		

Table 2. Prediction of selection gains based on different selection intensities

Trait		Mean	Max Estimate	%	Min Estimated	%
7 Month	Weight	14.46 g	6.61 g ^a	46	0.2 g	1.4
	Length	101.45 mm	11.63 mm ^a	11	0.6 mm	0.6
11 Month	Weight	136.71 g	27.79 g ^b	20	3.3 g	2.4
	Length	210.42 mm	28.97 mm ^b	14	0.7 mm	0.3
14 Month	Weight	374.17 g	72.00 g ^c	19	7.9 g	2.1
	Length	305.37 mm	21.76 mm ^c	7	3.2 mm	1.0

^a Based on selecting 60 individuals out of 10,000

^b Based on selecting 60 individuals out of 7,000

^c Based on selecting 60 individuals out of 3,000

^d Based on index results and selecting 10 families out of 40

Improvements

The 7-month weight of the odd-year line changed from 11.2 g in 1977 to 24.7 g in 2011, while the even-year line increased from 11.2 g in 1977 to 34.1 g in 2012 (Fig. 2). The increase for the odd-year line represented a 7.1% per generation increase, while the increase for the even-year line was equivalent to an 11.3% per generation increase. While the total increase could not be attributed to directed selection alone, it does indicate that there has been substantial improvement for that trait. This is despite changes in level of care and husbandry over the past 38 years due to changes in ownership of the company. The fluctuations in care and husbandry are partially reflected by the yearly variability in performance reflected in Fig. 2.

Although adult weight was not a selected trait until fairly late in the program, the fairly high genetic correlation between spawn weight and 7-month weight, led to increases in spawn weight. The average spawn weight of the odd-year females in 2011 was 2568 g compared with 1669 g for the first generation (Fig. 3). This was an increase of 53 g per generation or an overall increase of 54% over 17 generations.

Because of the changes in ownership, and the differences in husbandry and rearing environment over the many generations, it is difficult to precisely estimate the improvement in growth due to genetics or other causes. The best estimate for this line of coho salmon is that growth rate is improving between 3% and 8% per generation.

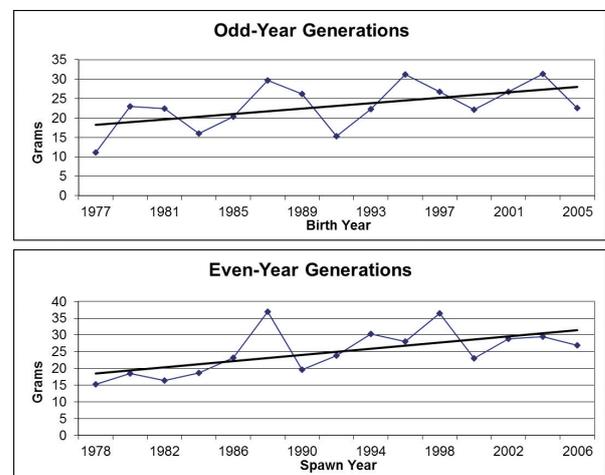


Fig. 2. Change in 7-month weight after 14 generations of selection

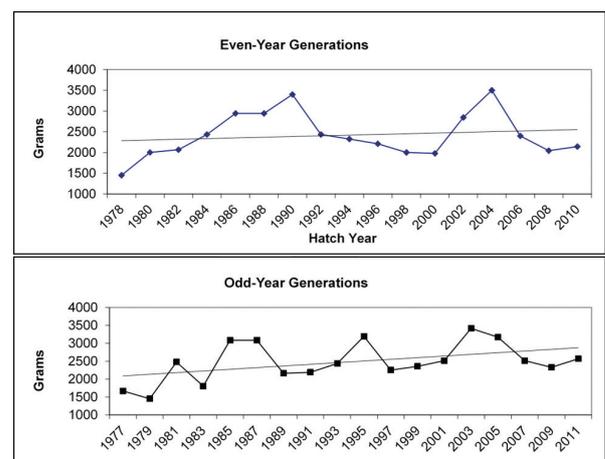


Fig. 3. Change in female weight at spawn over the course of 16 and 17 generations for the odd- and even-year broodstocks.

Inbreeding

Despite the circular mating scheme, inbreeding could not be avoided but merely delayed because of the intense selection the closed populations were subjected to every generation. Over the life of the program, inbreeding has been estimated in various ways. For example, Myers *et al.* (2001) estimated that after 9 and 10 generations of selection for the even- and odd-year lines respectively, inbreeding had increased by 13 - 48% depending on the method of estimation. Overall, via allozyme analysis, the authors determined that the two lines had undergone little change in average heterozygosity but significant changes in loss of variability at several loci. Pedigree-based inbreeding estimates show a progressive increase in inbreeding of about 1.5% per generation (Fig. 4). The inbreeding estimates for the even-year line shows a striking decrease in inbreeding within the last two generations as a result of deliberate outcrossing with the founder strain.

There have been no obvious indications of inbreeding depression despite the relatively high levels of inbreeding. If the current level of inbreeding is 25% or higher, it would be equivalent to that of full-sib matings – levels at which other studies have indicated can negatively affect reproductive success and early growth and survival of fish (Bondari and Dunham, 1987; Wang *et al.*, 2002). Because of the absence of a control group, the effects of inbreeding on overall growth and survival could not be assessed. It is possible that had inbreeding levels been lower over the course of the program, larger improvements per generation might have been observed.

Conclusion

The Domsea coho broodstock program has and continues to provide important data on the efficacy of a long-term genetic selection program to improve commercially important traits. More importantly, it provides an opportunity to address the question of the effects inbreeding may have on a sustained basis. As the program matures, it will be informative to incorporate genomics theory into the current quantitative genetics-based program to further characterize the genetic basis for commercially important traits and concomitant effects of

inbreeding.

References

- Bondari K. and Dunham R. A., 1987: Effects of inbreeding on economic traits of channel catfish. *Theor. Appl. Genet.* **74**(1), 1-9.
- Dunham R. A. and Smitherman R. O., 1984: Ancestry and breeding of catfish in the United States. Alabama Agricultural Experiment Station Circular 273. Auburn University, Auburn, AL
- Hershberger W. K., Myers J. M., Iwamoto R. N., McAuley W. C., and Saxton A. M., 1990: Genetic changes in the growth of coho salmon (*Oncorhynchus kisutch*) in marine net-pens, produced by ten years of selection. *Aquaculture* **85**, 187-197.
- Iwamoto R. N., Myers J. M., and Hershberger, W. K., 1990: Heritability and genetic correlations for flesh coloration in pen-reared coho salmon. *Aquaculture* **86**, 181-190.
- Iwamoto R. N., Saxton A. M., and Hershberger W. K., 1982: Genetic estimates for length and weight of coho salmon (*Oncorhynchus kisutch*) during freshwater rearing. *J. Hered.* **73**, 187-191.
- Myers J. M., Heggelund P. O., Hudson G., and Iwamoto R. N., 2001: Genetics and broodstock management of coho salmon. In: Lee, Cheng-Sheng and Donaldson, E. M. Reproductive biotechnology in finfish aquaculture. *Aquaculture* **197**, 43-62.
- Myers J. M., Iwamoto R. N., Teel D., Van Doornink D., and Hershberger W. K., 1999: Coho salmon broodstock development---1977-1998. Ten generations of systematic selective breeding. *Bull. Natl. Res. Inst. Aquac. Suppl.* **1**, 63-70.
- Quinton C. D., McMillan I., and Glebe B. D., 2005: Development of an Atlantic salmon (*Salmo salar*) genetic improvement program: Genetic parameters of harvest body weight and carcass quality traits estimated with animal models. *Aquaculture* **247**, 211-217.
- Saxton A. M., Hershberger W. K., and Iwamoto R. N., 1984: Smoltification in the net-pen culture of coho salmon: quantitative genetic analysis. *Trans. Am. Fish. Soc.* **113**, 339-347.
- Tave D., 1999: Inbreeding and brood stock

management. FAO Fisheries Technical Paper #392, 123p.

Wang S., Hard J. J., and Utter F., 2002: Salmonid inbreeding: a review. *Rev. Fish Biol. Fish.* **11**, 201-319.

Annotated bibliography

(1) a. Iwamoto R. N., Saxton A. M., and Hershberger W. K., 1982: Genetic estimates for length and weight of coho salmon (*Oncorhynchus kisutch*) during freshwater rearing. *J. Hered.* **73**, 187-191.

b. Saxton A. M., Hershberger W. K., and Iwamoto R. N., 1984: Smoltification in the net-pen culture of coho salmon: quantitative genetic analysis. *Trans. Am. Fish. Soc.* **113**, 339-347.

c. Hershberger W. K., Myers J. M., Iwamoto R. N., McAuley W. C., and Saxton A. M., 1990: Genetic changes in the growth of coho salmon (*Oncorhynchus kisutch*) in marine net-pens, produced by ten years of selection. *Aquaculture* **85**, 187-197.

d. Iwamoto R. N., Myers J. M., and Hershberger W. K., 1990: Heritability and genetic correlations for flesh coloration in pen-reared coho salmon. *Aquaculture* **86**, 181-190.

The papers cited above provide much of the early quantitative genetic parameters for coho salmon traits. Genetic estimates for freshwater growth, smoltification and initial saltwater survival, seawater growth, and flesh coloration for the Domsea coho salmon were derived from full- and half-sib analyses. In almost every case, the magnitude of the derived heritabilities and genetic correlations indicated that a systematic selection program would be successful.

(2) Myers J. M., Park L. K., Neely K., Swanson P., Elz A., and Hard J. J., 2011: Feeding ration, genetics, and reproductive traits in female coho salmon: Is bigger better? *J. World Aquac. Soc.* **42**, 812-823.

The authors examine reproductive traits and the relationship between environment (feeding ration) and genetics (family) in the Domsea coho salmon stock after 15 generations of selection. Results suggested that phenotypic improvements could be achieved through changes in ration and/or direct selection.

(3) Myers J. M., Iwamoto R. N., Teel D., Van Doornink D., and Hershberger W. K., 1999: Coho salmon broodstock development - 1977-1998. Ten generations of systematic selective breeding. *Bull. Natl. Res. Inst. Aquac. Suppl.* **1**, 63-70.

The authors summarize the concept of the Domsea coho salmon broodstock program from the selection scheme to the circular mating design. They also present allozyme comparisons of the founder strain and the broodstock after 10 generations of selection and indicate that significant genetic changes had occurred in the broodstock as a result of genetic selection and drift.

(4) Myers J. M., Heggelund P. O., Hudson G., and Iwamoto R. N., 2001: Genetics and broodstock management of coho salmon. In: Lee, Cheng-Sheng and Donaldson, E. M. (Eds.) Reproductive biotechnology in finfish aquaculture, *Aquaculture* **197**, 43-62.

This paper summarizes the information collected on the Domsea coho salmon broodstock program after 13 generations of implementation. It discusses the results of sib trials in marine net pens and two freshwater environments and consequently the importance of considering genotype-environment interactions in broodstock programs for specific applications. It tracked theoretical (pedigree data) and genetic changes (allozyme data and individual traits) in the broodstock population.