Norwegian University of Life Sciences
Faculty of Veterinary Medicine and Biosciences
Department of Animal and Aquacultural Sciences

Master Thesis 2015
30 credits

Genotype by Environment Interaction for Early Sexual Maturity in Atalntic Salmon (Salmo salar)

Shuwen Xia

Acknowledgments

I would like to express my deepest appreciation to my supervisor, Dr. Bjarne Gjerde for his very useful guidance during the whole period of this thesis work. He was always available for my questions and he was positive and gave generous of his time and vast knowledge. He taught how to use the ASReml for the data analyzing and guaide me how to think a question.Without his guidance and persistent help, this thesis would not been been possible.

I would like to express my deepest gratefulness to my co-supervisor, Panya Sae-Lim for his unwavering support. He takes care of me from beginning to end. He showed me how to deal with problems in data analyzing and taught me how to write a scientific thesis. In addition, he is also happy to help me to improve my poor oral English.

I thank to Nofima that provided me a office, that I can get the advises and helps for supervisor at any time. And all the staffs in Nofima are always very nice to me.

I thank to my family for their moral and financial support in order to finish this study.

In addition, I thank to all my friends for helping me survival all stress this year and not letting me give up.

Shuwen Xia
May, 2015

Summary

Genetic parameters and genotype by environment interactions were estimated for early sexual maturity in Atlantic salmon. About 23984 (24999) individuals from 115 (118) full-sib families were tested in six sea-cages at five different locations in Norway. After 15 to 16 months in the sea, all individuals were classified for indications of maturation. Large variation in percentage of maturing were observed at different farms for two year-classes .

The heritabilities estimated for early sexual maturity ranged from 0.02 to 0.11 on observed scales, and varied from 0.04 to 0.21 on liability scale. Besides, the heritability estimates on observed scale were roughly two times higher than those on the linear scale. The effects common to full-sibs other than additive genetic effects accounted for less than 5% of the total phenotypic variance on observed scale and less than 7% on liability scale .

Gentic correlation were estimated between pairs of test environments, for 0.67 to 0.99 in year-class 1983, and 0.36 to 0.99 in year-class 1987. Most estimates of genetic correlation were significantly different from unity which indicated the presence of genotype by environment interaction. The low and significant correlations of effects common to full-sibs were estimated which indicates the effects common to full-sibs became smaller after separating into production environments.

The genetic gain was calculated based on estimated breeding values of full-sib families, and unfavorable genetic gains were observed in present study both for expect gain and and realized gain.

Table of Contents

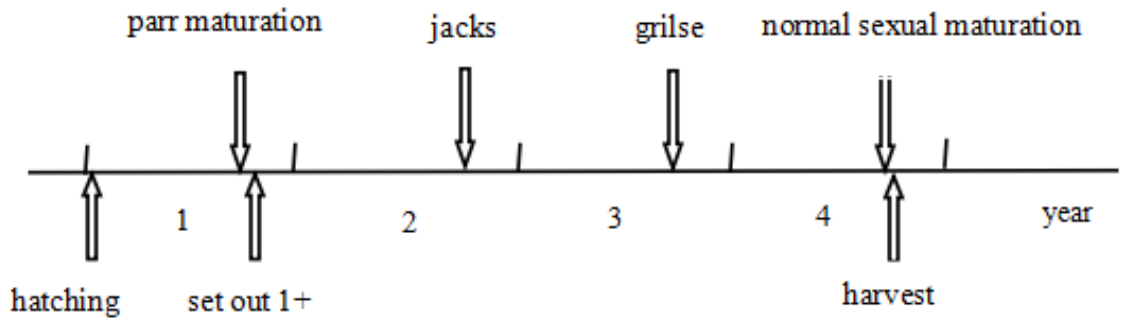
1. Introduction

Norway is the largest producer for Atlantic salmon (*Salmo salar*) and started to rear Atlantic salmon in the late 1960s. Over the past several decades, commercial culturing of anadromous Atlantic salmon expanded rapidly and globally. Correspondingly, in order to obtain higher productivity and production to meet the requirement of the market, AKVAFORSK started a selective breeding program for in Atlantic salmon in the early seventies. Increased growth rate was the selection criterion during the first two generations of selection, while reduced proportion of sexual mature fish was included as an additional breeding objective trait from the third generation.

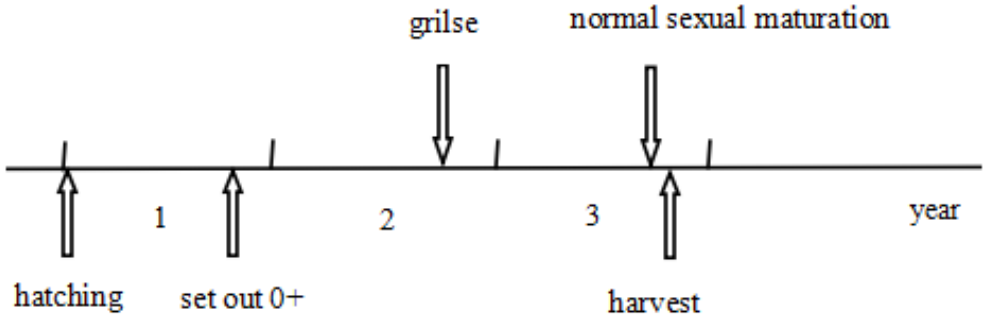
Wild Atlantic salmon, after migrating to sea as smolts, mature sexually either after one sea winter (grilse) or after two or more sea winters. Early sexual maturation; i.e. fish that become sexual mature before desired harvest size, is a major problem in Atlantic salmon farming as maturation leads to reduced flesh quality (Aksnes et al., 1986) and loss of growth during the 4-6 months prior to spawning (Aksnes et al., 1986; Randall et al., 1986).

Atlantic salmon has been named according to their stage of life and time of sexual maturity. More specific, precocious males are fish that become mature before smotifaction at an early stage in freshwater (Rowe and Thorpe 1990); jacks are postsmolts that mature during the first autumn in sea (Duncan et al.,2002); grilse are fish that mature during the second autumn in sea (Duston and Saunders 1999; Duncan et al. 2002), and normal sexual maturing salmon are fish that become sexual mature after two and three winters in the sea. While, in farmed Atlantic salmon the main problem is grilse. The maturation timetable and names in Atlantic salmon are shown in Figure 1.

Male parr often become sexually mature and participate in spawning without first migrating to the sea. Precocious sexual maturation of wild Atlantic salmon parr occurs frequently in males (Buck and Youngson, 1982; Dalley et al., 1983), but has not often been observed in females. Precocious maturation represents a production loss in commercial hatchery production due to reduced growth during the maturation process (Whalen and Parrish, 1999) and negative interference with smoltification (Thorpe and Morgan, 1980, Duston and Saunders, 1992).



a. Reproduction/ maturation in Atlantic salmon (1+)



b. Reproduction/ maturation in Atlantic salmon (0+)

Figure 1. Reproduction /Maturation in Atlantic salmon

Some farmed salmon mature as “jacks” after only a few months in seawater and at a body size of around 0.5 kg (Taranger et al., 2010). Jacks are uncommon in smolts reared under natural

conditions, but has been observed by Herbinger and Newkirk (1990), Duston et al. (1998).
The main problem with early sexual maturity in farmed salmon is at the "grilse" stage, i.e. after 1.5 years in seawater or after one winter in the sea. A high proportion of grilse being reported every year, during 1997–2000, the proportion of grilse in the farmed fish caught during the fishing season was 39.8% (L'Abe'e-Lund et al., 2004).

Normal practices in Norwegian smolt production have been to transfer smolts to seawater in spring about 16 months after hatching (1+). However, 0+ smolts are also produced (Duncan et al. 2002) and transferred to seawater in the autumn about 8 months post hatching (0+ smolt). In commercial farming, 0+ salmon will normally spend one or two winters in the net-cages in the sea depending on size demand from the market or strategy of the farmer.

Early sexual mature 0+ salmon in autumn after one-sea winter were observed in farmed Atlantic salmon (Arge et al., 2012). No term was found for this stage of maturing fish in the previous studies, Therefore, the same term as used for 1+ smolt "grilse" was used in this study. In recent years, in Norway, the ratio of smolt transferred to sea in spring or autumn has been about 60/40 (Kittelsen et al., 2006). The high proportion of 0+ smolt production during these years makes the investigation of early sexual maturity in 0+ smolt vital important.

The reasons to investigate early sexual maturity in Atlantic salmon, are not only because early sexual maturation lead to reduced flesh quality and loss of growth. But also, during maturation, the immunodepression in Atlantic salmon leads to increased disease susceptibility and mortality rate (Bruno, 1989; Salte et al., 1995; Tranxler et al., 1997; St-Hiaire et al., 1998; Currie and Woo, 2007). Early sexual maturity in Atlantic salmon brings serious economic loss for the farmers, and also has negative effects on animal welfare due to lack of osmoregulation when these fish are not removed from the net-cages (Taranger, 1993). Therefore, it is important to investigate the

causes of early sexual maturity in Atlantic salmon and efforts have to do to reduce the occurrence in the future.

2. Review of literature

Many factors related to the early sexual maturation have been studied in wild and farmed Atlantic salmon during past decades. Maturation strategies have been related to nutritional , environmental, sex and genetic factors or the combined effects of these factors.

2.1 Nutritional factors

For nutritional factors, feed intake was studied by McClure et al. (2007) who found that the use of moist feed were associated with higher risk of grilse. McClure explained that, the moist feed has a higher water content than dry feed and thus more attractive to fish. It has been shown that the incidence of early sexual maturation is associated with energy supply (Rowe and Thorpe, 1990; Thorpe et al., 1994) or lipid reserves (Rowe et al., 1991; Silverstein et al., 1998). Reducing the energy supply and the level of fat reserves resulted in lower risk of early maturation. Besides, the ingredients in the feeds are related to sexual maturation. For example, phosphorus is a macro-mineral that is an essential nutrient for fish, and extra dietary phosphorus is found to reduce early sexual maturity (Fjelldal et al., 2009; Fjelldal et al., 2012). Supplementation of tetradecylthioacetic acid (TTA) in the diets is found to reduce fat reserves in muscle leading to a reduced incidence of early sexual maturation without influencing growth in Atlantic salmon (Alne et al., 2009; Arge et al.,2012).

2.2 Environmental factors

Photoperiod

Photoperiod has been proved related to the risk of early sexual maturity and continuous light is widely used to reduce the proportion of early sexual maturity. For example, Taranger et al. (1999)

found that initiating continuous light in January of the first sea winter reduced grilsing from 91% to 9% in female salmon, and from 74% to 16% in males. Other studies have documented similar effects for Atlantic salmon (Hansen et al., 1992, Oppedal et al., 1997; Taranger et al., 1998; Porter et al., 1999), and for reducing the incidence of precocious parr (Adams and Thorpe, 1989; Thorpe, 1994).

Temperature

Sexual maturation in salmonids is greatly influenced by temperature has been found during past decades. McClure et al. (2007) reported the proportion of grilse was associated with the seawater temperature difference between first winter and second summer, the higher difference the higher risk of grising. Besides, higher water temperature have been found resulted in higher proportion of early sexual maturity because of the higher growth rate (Saunders et al., 1982; Adams and Thorpe,1989; Thorpe,1994; Rowe and Thorpe, 1990; Fleming, 1996; Duston and Sauders, 1999). Similarly, heating was used in the laboratory to accelerate growth and resulted in more mature parr or earlier maturation (Crandell and Gall, 1993).

Cage size

The size of rearing cage in the sea also has been reported related to the proportion of early sexual maturity. McClure et al., (2007) found that the smaller cages had a higher risk of grisling compared to the larger circular cages which also have been reported in other studies. In small cages the lack of proper schooling and swimming activity may affect the energy allocation and the size of energy stores and thus altere the proportion of maturing fish (Kråkenes et al., 1991; Endal et al., 2000).

2.3 Effects of sex

Males were found mature earlier than females in salmonids by Ritter (1975), Naevdal et al. (1978) and Gjerde (1984). In addition, precocious parr were occured frequently in males, but had not often been observed in females (Buck and Youngson, 1982; Dalley et al., 1983). While, the reasons for earlier maturation in male also has been studied. For example, sexes can exhibit genetically different size-at-age thresholds for maturation (Thorpe and Morgan 1980; Saunders et al., 1982; Baum et al. 2004). Similarly, a higher threshold size was reported for female than male maturation in salmonids by Jonsson and Jonsson(2011).

2.4 Genetic factors

Sexual maturity in Atlantic salmon is also associated with genetic factors which has been strongly proved by earlier studies. For example, grilse parents produced higher proportions of grilse than normal maturity parents (Elson, 1973; Piggins, 1974; Ritter and Newbould, 1977; Gjerde, 1984). Between strains of Atlantic salmon reared under the same rearing conditions significant difference have been found in the proportions of maturing fish after one (Navdal et al., 1978) and two winters (Gunnes, 1978; Navdal et al., 1978) in the sea. Also, different levels of sexual maturation between five different North American Atlantic salmon trains were reported by Wolters (2010).

In addition, genetic parameters estimates for early and normal sexual maturity in Atlantic salmon have been studied in recent decades; e.g. heritabilities, magnitude of GxE interaction and genetic correlation with other traits.

Heritabilities

Some previous estimates of hertitabilities for early and normal sexual maturity in Atlantic salmon both on observed and liability scale are given in Table 1. The previous estimates of heratability for this traits vary considerably, from 0.04 to 0.14 for early sexual maturity (Gjerde, 1986; Wild et al., 1994; Gjerde, 1994), and from 0.02 to 0.39 for normal sexual maturity (Gjerde, 1986; Standal and Gjerde, 1987; Gjerde, 1994; Gjerde et al., 1984; Gjerde and Gjedrem, 1984; Lillehammer et al., 2013). These observations strongly indicate that sexual maturity in Atlantic salmon is a heritable trait. Be more specific, the selection programs for sexual maturation can be conducted in both freshwater and seawater production environments to prevent an unfavorable increasing in the frequency of early sexual maturing fish. Besides, Gjerde et al. (1994) concluded that the breeding objective for sexual maturity should be to reduce the frequency of fish that become sexual mature before market size, rather than to select for an increased age at sexual maturity. Selective breeding for reduced frequency of early sexual maturation has proved effective in Atlantic salmon (Gjedrem, 2000) and in rainbow trout (Kause, 2004).

In breeding programs for the aquaculture species, selection takes place in a nucleus, which is usually kept in a well-controlled environment, whereas a wide range of environmental factors (e.g., temperature, salinity, feeding regime, stocking density, light intensity and period) are generally uncontrollable in commercial grow-out rearing environments. Hence, the genotype by environment (G×E) interaction may be resulted by the different rearing environments.

GxE interaction

G×E interaction is the phenomenon that different genotypes respond differently to environmental variation (Falconer and Macky, 1996; Lynch and Walsh, 1998). The presence of G×E interaction might drive the genotype re-ranking which means that the best genotype in one environment is not the best in another environment (Falconer and Mackay, 1996). In addition,

the genotype re-ranking has may reduce the efficiency of the genetic improvement in the selection program (Falconer, 1952; Mulder and Bijma, 2005; Sae-Lim et al.,2013). Mulder and Bijma (2005) demonstrated that the presence of G×E interaction results in losses in genetic gain because the G×E interaction affects both the accuracy of selection, selection intensity, and the genetic variance of the breeding goal. So it is important to quantify the magnitude of G×E interaction for important traits.

The presence of G×E interactions has been documented for many traits in livestock species. While livestock species as pigs or poultryare reared under controlled and thus standardized environmental conditions, for fish reared under natural conditions in cages or ponds the different environmental factors are much more difficult to standardize. Therefore, the potential G×E interaction is likely to be present in the aquaculture species. When starting a breeding program for an aquaculture species it is therefore important to give more attention to potential G×E interaction.

To quantify the magnitude of the G×E interactions, different approaches and statistic models are available. For example, Falconer (1952) presented the magnitude of G×E interaction could be measured in terms of calculating genetic correlation by regarding a trait recorded in the different environments as two separate traits. A genetic correlation between performance in different environments equal to unity implies that the G×E interaction is negligible. In contrast, a genetic correlation statistically different from unity indicates the presence of G×E interaction.

For aquaculture species, the most studies on G×E interactions were measured from the genetic correlations between different test environments. Numerous studies on on G×E interactions were reported for wide species including Altlantic salmon , rainbow trout ,Nile tialpia , Sea bass ect., and also for many economic traits, i.e. growth rate, survival, sexual maturity deformity and so

on. Both significant and non-significant G×E interactions have been revealed. Sae-Lim et al., (2015, in press) reviewed previous studies on G×E interactions and concluded the magnitude of G×E interaction for important traits across 38 aquaculture species : "Re-ranking is moderate for growth and survival , and the average estimates of genetic correlation for these two traits,are 0.72 and 0.54, respectively. Meanwhile, re-ranking is weak for age-at-sexual-maturity and fish appearance (average genetic correlation =0.86), implying that genetic improvement in one environment is expected to be effective in the other environments." This study demonstrate that genotype re-rankings were common exist in the aquaculture species when rearing in different environments. So the magnitude of G×E interactions have to be taken into consideration when conduct the aquaculture species breeding programs in aquaculture species.

G×E interaction studies for sexual maturity are few in aquaculture species compared with other traits. In Atlantic salmon, only Wild et al. (1994) reported a significant G×E interaction for early sexual maturity by estimating of the variance of cage×sire interaction and cage×sire interaction effects. In that study, the estimation of G×E interaction was conducted on more than 23000 individuals which were reared in six cage at five different location at year-classes 1983 and 1987. The sire by cage interaction and dam by cage interaction both accounted less than 4% of the total variance on the underlying scale. However, the sire by cage interaction accounted for 23 to 54% of the sire variance and the dam by cage interaction accounted for 61% and 105% of the dam variance. In rainbow trout, a high genetic correlation (0.96±0.03) between proportion of sexual mature fish in freshwater and seawater rearing environment was reported by Kause et al. (2003). And the negligible G×E interaction for sexual maturity in rainbow trout could be concluded from this high genetic correlation estimation. A rather low genetic correlation (0.71) between two locations for sexual maturity in Atlantic cod was given by Kolstad et al.(2006), but the timing for recording of sexual maturity was reported as the factor attributed to the rather low genetic correlation not rather than G×E interaction. Consequently, as there are few studies of

G×E interaction for sexual maturity in salmonids as well as other farmed aquaculture species it is vital important to conduct more G×E interaction studies in order to decide whether it is necessary to establish a separate breeding program or not.

Genetic correlation with other traits

As sexual maturity have been found have negative effects on some growth, mortality and some other traits by previous studies (Aksnes et al., 1986; Randall et al., 1986; Bruno, 1989; Salte et al., 1995; Tranxler et al., 1997; St-Hiaire et al., 1998; Currie and Woo, 2007). Some studies have been conducted for the genetic correlation between sexual maturity and other economic traits. For example, significant positive genetic correlations between growth rate and normal sexual maturation (Gjerde, 1986; Gjerde et al., 1994; Lillehammer et al.,2013) and early sexual maturity (Gjerde and Gjedrem, 1984) .While, Lillehammer et al (2013) reported a tendency towards weak to moderately unfavorable genetic correlations between sexual maturation and health status. In that study, outbreaks of infectious pancreatic necrosis (IPN) in Atlantic salmon were observed, and genetic correlations were conducted between traits. Therefore, the low genetic correlation between sexual maturation and survival (0.19-0.22) was observed.

To conclude, the causes of early sexual maturity in Atlantic salmon are numerous. Strategies for reducing early sexual maturation also have widely conducted based on these studies. However, further studies have to conducted for sexual maturity, especially from the genetic perspective because of the lacking of studies and high potential.

Table 1

Estimates of heritability with standard errors for early and normal sexual maturity in Atlantic salmon

	No. fish	Maturing fish(%)	Ns	Nd	h_P^2±S.E.	h_x^2±S.E.	Reference
Early maturity	1704	6.5	26	115	0.09±0.04	0.34±0.13	Gjerde et al. (1994)
	24481	9.8	30	119	0.05	0.16±0.13	Wild et al. (1994)
	25212	25.9	24	119	0.07	0.12	Wild et al. (1994)
	-	27.9	17	-	0.14	0.25	Gjerde (1986)
	-	10.3	14	-	0.04	0.12	Gjerde (1986)
	-	26.0	19	-	0.04	0.07	Gjerde (1986)
Normal maturity	2725	10.6	18	43	0.14±0.08	0.40±0.23	Gjerde and Gjedrem (1984)
	3054	1.0	30	84	0.06±0.05	0.84±0.70	Gjerde and Gjedrem (1984)
	3709	52.9	35	90	0.39±0.12	0.61±0.19	Gjerde and Gjedrem (1984)
	-	72.3	17	-	0.11	0.20	Gjerde (1986)
	-	76.6	14	-	0.02	0.04	Gjerde (1986)
	-	61.3	19	-	0.09	0.15	Gjerde (1986)
	20664	39.2	17	130	0.17±0.07	0.27±0.11	Standal and Gjerde (1987)
	18124	42.7	22	102	0.08±0.04	0.13±0.06	Standal and Gjerde (1987)
	1704	55.5	26	115	0.15±0.08	0.24±0.13	Gjerde et al.(1994)
	14391	29.0	152	294	0.33 ±0.05	0.58±0.09	Lillehammer et al.(2013)

h_P^2=heritabilty on the observed scale; h_x^2=heritabilty on the liability scale; “-” not available

3. Own study

This study is a reanalyze of earlier data on early sexual maturity in Atlantic salmon published by Wild et al. (1994). In that study, the five production environments were combined together from which an overall estimate of heritabilty and G×E interaction was obtained using different univariate ANOVA based statistical models. Whereas, in present study, the heritabilies were obtained both within and across the test environments in two year-classes, and estimates of the genetic correlations between pairs of test environments using a more up-to-date statistical mixed models than was available earlier.

The main objectives of this study were i) to obtain estimates of the heritability for early sexual maturity in Atlantic salmon, ii) to investigate the existence and magnitude of G×E interactions, iii) to evaluate the expected and realized response to one generation of selection.

4. Materials and methods

4.1 Materials

The materials used and the rearing methods for this study are described in Wild et al. (1994) and can be summarized as follows.

The data used comprise two year-classes (year when startfed) of Atlantic salmon, 1983 and 1987 produced AKVAFORSK (Institute of Aquaculture Research Ltd.), Norway. In early seventies AKVAFORSK started a selective breeding program for Atlantic salmon by using the fertilized eggs from wild strains and then selected for high growth rate and against early sexual maturity with 2/3 positive relative weight on growth and 1/3 negative relative weight on early sexual maturity. Four nucleus populations were produced in year 1972, 1973, 1974 and 1975 (Gjerde and Korsvoll,1999) during this breeding program. The two year-classes originate from the same population founded in 1975, except 7 dams of 1987 year-class were selected from year-class 1982 (2^{nd} generation of base population 1974). A hierarchical mating system was used to produce the full- and half-sib families. Each male was mated with one to nine females and each female to one male only. A total of 115 and 118 full-sibs families were produced for the two year classes, 1983 and 1987, respectively. The families of each year-class were starfed at three different dates; the 1983 year-class families on February 23, March 10 and March 21, and the 1987 year-class families on February 17, March 7 and March 19. The structure of the two year-classes data was provided in the Table 2.

In the freshwater phase, the full-sibs were reared together in one tank and until all members grew to a body size suitable for marking. The individuals from the same full-sibs family were marked with the same mark by fin clipping and freeze-branding (Gunnes and Refstie, 1980).

After that, all marked fish were reared in the same concrete pond until smotification in May. After smotification, a random sample of the fish from all families were stocked into a net cage (about 500 m^3) at six different test farms (Figure 2) distributed in different parts of Norway with different environment condition like lights, temperature etc. In 1983, farm 02, 05, 06, 15 and 19 were used, while for year-class1987, farm 06 was omitted and replaced with farm 21. At farm 02 (AKVAFORSK marine experimental unit) the breeding candidates were reared in two replicated cages, while there was one cage in each of the four other farms. Of the total number of recorded fish, 53% (year-class 1983) and 59% (year-class 1987) were reared at farm 02.

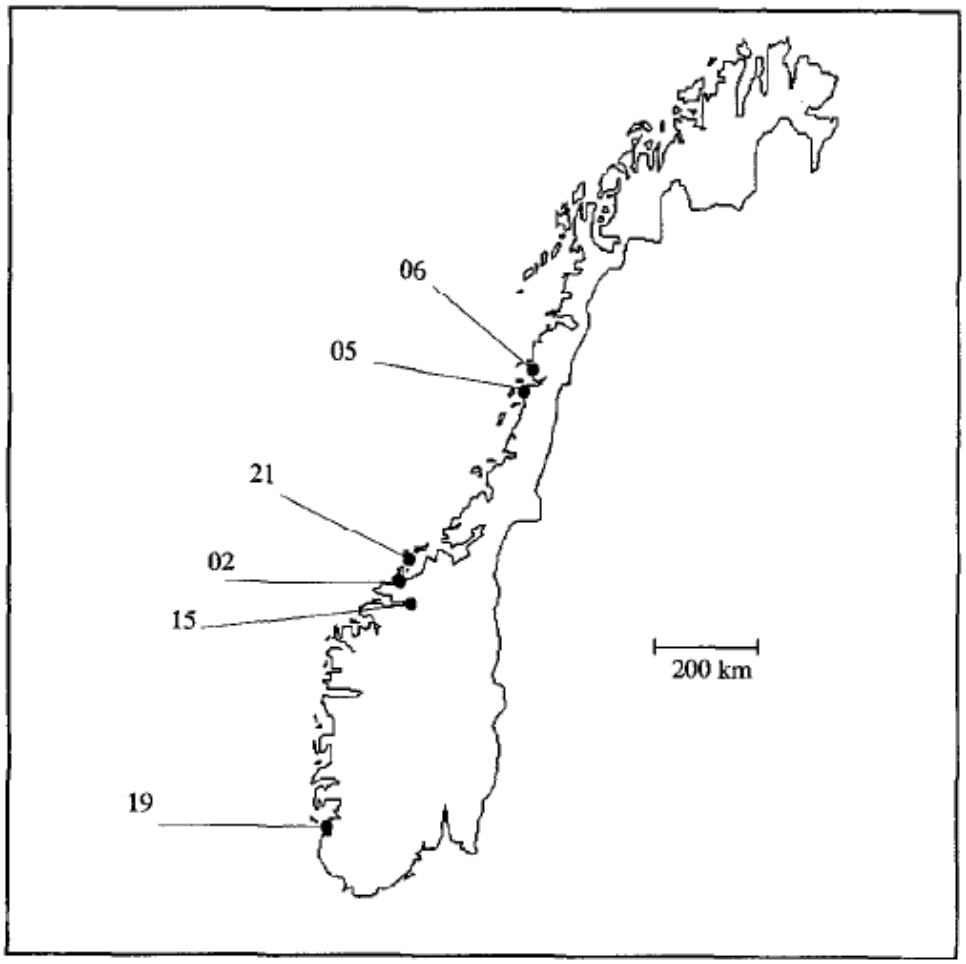


Figure 2. Location of the test farms in Norway

Table 2

Structure of the data sets in the two year-classes

	1983	1987
No. of test environments (net cage)	6	6
No. of sires	26	24
No. of dams	115	118
No. of recorded offspring	23984	24999
No. of offspring/sire	329-1704	186-2193
No. of offspring/dam	93-347	108-331
No. of offspring/dam within cages	4-111	4-132
No. of families for the three start feeding dates	73/26/16	72/34/12

Table 3

Number of fish and percentage of early sexual mature fish at the different farms and cages in the two year-classes, the location have been cited out in Figure 2.

Farm-cage	1983		1987	
	No. of fish	Percentage(%)	No. of fish	percentage(%)
205	5816	5.9	7500	26.7
207	7001	6.4	7334	27.8
0501	3820	17.3	2474	31.1
0601	2381	6.5	-	-
1501	2414	11.5	1925	13.1
1901	2552	26.4	3780	20.9
2101	-	-	1986	42.9
Average		12.3		28.1

"-": not application

The classification of early sexual maturity (sexual maturing or immature) took place in August to October after 15 to 16 months in the sea, and was based on the secondary sex characters. The proportion of the sexual mature fish of the two-year-classes at the different locations are shown in Table 3.

4.2 Data analysis

Data were analyzed with a linear mixed sire and dam model using ASReml software (Gilmour et al., 2009) in which the observed early sexual maturity trait were treated as binary trait (immature fish were coded as zero and sexual maturing fish were coded as one). The genetic variance components were estimated by restricted maximum likelihood (REML), while prediction of genetic effects (estimated breeding values) was processed with the best linear unbiased prediction (BLUP) method. In the matrix nation, the sire and dam model may be written as:

$$\mathbf{y}=\mathbf{Xb}+(\mathbf{Z_s}+\mathbf{Z_d})\mathbf{u}+\mathbf{Z_c c}+\mathbf{e}$$

Where **y** = the vector of observed early sexual maturity

b = the vector of fixed effects

u = the vector of half the sire- dam additive genetic effects

c= the vector of random effects common to full-sibs other than additive genetics

e = the vectors of residual errors

The year-class, farm-cage and start feeding dates were all considered as fixed effects and sire, dam and the effect common to fullsibs as random effects. The effects common to full-sibs were included tank effects, dominance effect, and maternal effect and so on. $\mathbf{Z_s}$, $\mathbf{Z_d}$ and $\mathbf{Z_c}$ are known design matrices assigning observations to the level of **u** and **c**, respectively.

In addition, a binary model including the same fixed and random effects as in the linear model was used to obtain parameter estimates for the binary trait early sexual maturity also on the underlying liability scale. Hence, the early sexual maturity was taken as a continuous but non-observable liability scale.

The estimates on the underlying liability scale assume that the susceptibility for the early sexual maturity is determined by an underlying liability that is distributed normally and inherited in a polygenic manner. Early sexual maturing fish exceed the threshold of liability, while normal fish lie below the threshold.

For the estimation of heritabilities and correlations between traits, both observed and liability scale were considered. For both models, estimates of heritabilies for sexual maturity were obtained using a single trait analysis for each farm and across all farms within each of the two year-classes, as well as across all farms of both year-classes.

For the above model, estimated heritability for early sexual maturity was calculated as:

$$h^2 = \frac{4\sigma_s^2}{2\sigma_s^2 + \sigma_c^2 + \sigma_e^2}$$

and the relative proportion of the effects common to full-sibs was calculated as:

$$c^2 = \frac{\sigma_c^2}{2\sigma_s^2 + \sigma_c^2 + \sigma_e^2}$$

Where, ∂_s^2 was the variance component for sire, ∂_e^2 was the variance component for residual error and ∂_c^2 was the veiance of effects common to full-sibs. In this sire-dam model, it was assumed that $\partial_s^2 = \partial_d^2 = \sigma_u^2 = 1/4\sigma_a^2$. On the observed scale variance components for sire (∂_s^2), effects common to full-sibs (∂_c^2) and residual error (∂_e^2) need to be estimated. On the liability scale, the residual variance (∂_e^2) is set equal to 1 and hence only sire (∂_s^2) and full-sibs common (∂_c^2) need to be estimated.

Genotype by environment effects for early sexual maturity were expressed by genetic correlations when the same traits in the two different locations (Falconer,1952). The residual covariance between the traits in two locations was set to zero because individual fish can not produce simultaneous records in more than one environment.

Estimates of genetic and common environment correlations between sexual maturity at different farms were obtained within year-classes. Convergence of log likelihood and parameters could not be obtained for more than two traits at a time. Consequently, the estimated correlations between trait pair of traits (locations) within year-class had to be used.

To test if the estimated effects common to full-sibs correlation between two different test environment was significantly different from the model which omitted the common environment effects, the significance of the effects common to full-sibs correlation was tested by omitting the common environment effects. A test for full model and reduced model was obtained by the following log likelihood-ratio test (Lynch and Walsh, 1998):

$$LR=-2(LogL_R-LogL_F)$$

Where L_R is the log of the restricted likelihood of the reduced model and L_F is the log of the restricted likelihood of full model. The asymptotic distribution of likelihood ratio follows Chi-square (χ^2) distribution with a mixture (50:50) of degrees of freedom between 0 and 1 (Stram and Lee, 1994). When $\alpha=0.05$, the critical value was 2.71.

The two year-classes originate from the same population founded in 1975, and the parents of 1987 year-class were selected from the year-class 1983. Consequently, both the predicted and

realized genetic gain could be calculated through the difference of these two generations. Here, both expected and realized genetic gains were estimated on observed scale and liability scale.

After getting the estimates breeding values for all sires and dams, the breeding values for each full-sib families could be figured out. The estimated breeding values of full-sib families were calculated as the sum of estimated breeding value of sire and and the estimated breeding value of dam. For example, the breeding values for full-sib family 1 is equal to the sum of estimates breeding values of sire 1 and estimates breeding values of dam 1. After getting the estimates breeding value for full-sibs family, both expected genetic gain and realized genetic gain could be calculated.

The realized genetic gain was calculated as:

$\Delta G_R = \bar{X}_{87} - \bar{X}_{83}$

$\bar{X}_{83}$ and $\bar{X}_{87}$ is the average estimated breeding value for all full-sib families in 1983 and 1987, respectively. Those two values calculated from the estimated breeding value from ASReml. The estimated breeding value for full-sib families were calculated as the sum of estimated breeding values of sire and dam. In addition, $\bar{X}_{83}$ and $\bar{X}_{87}$ were getting from the predicted breeding values analyzed base on the data combined two year classes.

and the expected genetic gain was calculated as:

$\Delta G_E = \bar{X}_s - \bar{X}_{av}$

$\bar{X}_s$ was the average estimated breeding value of the selected full-sib families which were selected from 1983 year class for next generation (year-class 1987). $\bar{X}_{av}$ was the average

estimated breeding value of all full-sib families in 1983. Where, $\overline{X}_s$ and $\overline{X}_{av}$ was calculated based on the estimated breeding value only from 1983 year class (the data of year-class1987 was not included into this part of calculation).

5. Results

5.1 Means

Table 3 shows the percentage of early sexual maturing fish in year-class 1983 and 1987 at the different farms. The total average of cumulative mature fish for 1983 and 1987 year-class were 12.3% and 28.1%, respectively. The proportion of mature fish showed large fluctuations between farms, varying from 5.9% to 26.4% for year-class 1983 and from 13.1% to 42.9% for 1987. The proportions of early sexual maturing fish were quite similar between the two replicated cages at farm 2 in both year-classes. The maturing fish were males, except in the farm 21, which had the similar numbers of maturing fish between two sexes (Table 4).

Table 4
Numbers of early sexual mature males and females, and the proportion of the maturing females of the total number of maturing fish at the different farms and cages in the two year-classes

Farm-cage	1983			1987		
	EMF	EMM	Ratio(%)	EMF	EMM	Ratio(%)
205	35	271	11.44	395	1552	20.29
207	64	342	15.68	312	1677	15.69
0501	54	566	8.71	57	674	7.80
0601	6	125	4.58			
1501	8	235	3.29	9	212	4.07
1901	73	565	11.44	139	611	18.53
2101				409	412	49.82

EMM: early sexual maturity male; EMF: early sexual maturity female; Ratio=EMF/(EMM+EMF)

Table 5

Least square means for percentage of early sexual maturing fish for the three different startfeeding dates for the different farms-cages of each of the two year-classes obtained from a single trait observed and liability scale model

Farm-cage		83 year class				87 year class			
		Start feeding date				Start feeding date			
		23/02	10/03	21/03	F-value	17/02	07/03	19/03	F-value
0205	Observed	7.0±1.5	6.7±1.8	9.0±1.9	1.28^{NS}	21.2±4.0	23.2±4.3	24.1±5.3	0.53^{NS}
	Liability	5.8±1.6	5.4±1.7	8.3±2.4	1.73^{NS}	18.0±3.7	19.5±4.1	21.4±5.3	0.46^{NS}
0207	Observed	7.4±2.0	8.0±2.2	8.4±2.3	0.31^{NS}	22.8±4.7	25.9±4.9	30.9±6.1	1.73^{NS}
	Liability	5.8±1.8	6.7±2.2	7.0±2.4	0.55^{NS}	19.6±4.5	22.2±5.1	29.0±7.1	2.10^{NS}
0501	Observed	16.7±4.0	16.3±4.4	17.5±4.5	0.07^{NS}	24.9±5.3	34.01±5.6	30.1±6.8	4.06^{*}
	Liability	14.1±3.6	15.1±4.3	13.9±3.9	0.09^{NS}	22.0±4.8	30.2±6.0	27.8±7.0	3.76^{*}
0601	Observed	6.1±1.6	6.0±2.1	5.9±2.4	0.01^{NS}				
	Liability	4.8±1.3	4.5±1.7	4.5±1.9	0.03^{NS}				
1501	Observed	9.3±1.7	12.8±2.3	15.9±2.7	4.10^{*}	11.4±2.9	14.0±3.2	8.7±4.0	1.09^{NS}
	Liability	8.0±1.3	11.4±2.3	14.1±3.0	4.31^{*}	9.5±2.6	11.7±3.2	7.7±2.9	1.08^{NS}
1901	Observed	26.4±4.9	21.6±5.5	27.7±5.8	1.26^{NS}	19.4±3.3	18.2±3.6	13.4±4.7	1.13^{NS}
	Liability	23.8±4.7	19.5±4.8	25.4±5.8	1.25^{NS}	16.8±3.0	16.1±3.1	12.0±3.4	1.06^{NS}
2101	Observed					43.1±4.0	38.8±4.5	39.9±6.1	0.77^{NS}
	Liability					40.9±4.2	36.2±4.6	37.7±6.2	0.88^{NS}

NS: Not significant; *: significant ($p < 0.05$)

5.2 Effect of start feeding date

Least squares means of proportion of early sexual maturing fish for the three different start feeding dates and the statistical significance for this effect are showed in Table 5. For both year-class 1983 and 1987, the means from the linear model were higher than those from the liability model. For farm 15 in year-class 1983 and farm 05 in year-class 1987, the effect of start feeding date was significantly different from zero, and with a lower proportion of sexual maturing fish among the oldest fish in both year-classes and both models.

Table 6
Estimates of heritabilities and the effect common to full-sibs with standard errors

Farm-cage	Observed scale		Liability scale	
	h^2±se	c^2±se	h^2±se	c^2±se
83 year-class	0.05 ± 0.02	0.01±0.01^{NS}	0.14±0.06	0.02±0.01
0205	0.04 ± 0.02	0.01±0.01^{NS}	0.14±0.08	0.01±0.02
0207	0.05 ± 0.03	0.01±0.01^{NS}	0.18±0.09	0.03±0.03
0501	0.10 ± 0.04	0.01±0.01^{NS}	0.21±0.05	0.00±0.00^{NS}
0601	0.03 ± 0.03	0.03±0.01	0.11±0.10	0.06±0.04
1501	0.02 ± 0.02	0.02±0.01	0.04±0.05	0.05±0.03
1901	0.11 ± 0.06	0.02±0.01^{NS}	0.18±0.10	0.03±0.03
87 year-class	0.05±0.02	0.02±0.01	0.11±0.05	0.04±0.01
0235	0.06±0.03	0.03±0.01	0.14±0.06	0.06±0.02
0237	0.08±0.05	0.05±0.02	0.18±0.09	0.07±0.03
0501	0.10±0.05	0.02±0.02^{NS}	0.19±0.09	0.02±0.03
1501	0.04±0.04	0.03±0.02^{NS}	0.13±0.10	0.02±0.04
1901	0.04±0.03	0.04±0.01	0.08±0.06	0.06±0.02
2101	0.03±0.04	0.04±0.02	0.06±0.06	0.06±0.03^{NS}
Across year-class	0.05±0.02	0.02±0.01	0.13±0.04	0.03±0.01

NS: the effect common to full-sibs not significantly different from zero (P>0.05, likelihood-ratio test)

5.3 Heritabilities

The estimated heritabilities with standard errors for early sexual maturity both on observed and liability scale are given in Table 6. The estimates of hertabilities within test environment on liability scale (varying from 0.04 to 0.19) were roughly two times higher than those on the linear scale (varying from 0.02 to 0.11). The estimated heritabilities of across environments were very similar, estimate for 0.05 on the linear scale in both yea-classes, and 0.14 and 0.11 on the liability scale.

5.4 The effect common to full-sibs

The estimates of the effects common to fullsibs as a proportion of the total phenotypic variances are showed in Table 6. In 1983, the common environment effects of each farm cage explained 0 to 3% (on linear scale) and 0 to 6% (on liability scale) of the total variation in the tested traits, whereas the proportions were 2 to 5% and 2 to 7% for linear and liability scale in 1987, respectively. In year-class 1983, this effect common to full-sibs were 20% (observed scale) and 14% (liability scale) of the additive genetic variance, and 40% (observed scale) and 37% (liability scale) for year-class 1987.

The likelihood-ratio test for the effect common to full-sibs were tested both within and across the test environment for each year-class, and the estimates not significantly different from zero were marked with a ‘NS’ in Table 5. In the farm 05, the effects common to full-sibs are not significantly different from zero both on linear and liability scale for two year-classes.

5.5 Genetic correlations

Estimates of genetic correlation between early sexual maturity at every two different locations for each year-class both on linear and liability model are given in Table 7. The genetic correlation estimates were moderate to high, ranging from 0.67 to 0.99 (linear scale) and from 0.72 to 0.99 (liability scale) in 1983 year-class. In year-class 1987, the genetic correlation estimates were low to high, varying from 0.53 to 0.99 on the linear model, and from 0.36 to 0.99 on liability model. Besides, genetic correlations (on the linear scale) between the cages in farm 02 were quite high which almost reach to the boundary (0.99) for both two year-classes.

5.6 Correlations between the effects common to full-sibs

Within the test environments, the estimated correlations of effects common to full-sibs were moderate to high in 1983 year-class, while the estimates were quite low in year-class 1987 both on observed and liability scale (Table 7). In year-class 1987, the correlation was negative between farm 19 and farm 21 (-0.01±0.26), but with large standard error, meaning that the correlation could not be accurately estimated. Besides, when omitting the effect common to full-sibs, the genetic correlation had a minor change. In year-class 1987, the correlation of effects common to full-sibs were significantly different from zero for all pairs of two test environments ($P<0.05$, likelihood-ratio test). However, on the liability scale, the correlations of effect common to full-sibs for all the pair of combination for every two test environments were significantly different from zero ($P<0.05$, likelihood-ratio test) in 1983 and 1987 year-classes, except the correlation of effect common to full-sibs between farm 05 and 21 in 1987 year-class.

Table 7

Estimated genetic (above diagonal) and effects common to full-sibs (below diagonal) correlation between two locations for both two year-classes

	Observed model					Liability model				
83 year class										
Farm	02	05	06	15	19	02	05	06	15	19
02	-	0.90±0.08*	0.99[B]	0.77±0.36	0.77±0.20	-	0.87±0.11	0.99[B]	0.83±0.28	0.82±0.18
05	0.99[B]	-	0.99[B]*	0.99[B]*	0.83±0.12*	0.99[B]	-	0.99[B]	0.99[B]	0.84±0.12
06	0.73±0.24	0.99[B]	-	0.99[B]	0.96±0.26	0.72±0.24	0.99[B]	-	0.99[B]	0.89±0.24
15	0.88±0.39	0.99[B]	0.91±0.28	-	0.67±0.50	0.99[B]	0.99[B]	0.96±0.36	-	0.72±0.45
19	0.61±0.38	0.99[B]	0.68±0.36	0.62±0.40	-	0.57±0.45	0.99[B]	0.72±0.48	0.71±0.46	-
87 year-class										
Farm	02	05	15	19	21	02	05	15	19	21
02	-	0.94±0.16	0.91±0.47	0.99[B]	0.51±0.47	-	0.98±0.12	0.83±0.34	0.99B	0.36±0.43
05	0.44±0.25	-	0.99[B]	0.96±0.30	0.86±0.48	0.36±0.29	-	0.99[B]	0.96±0.30	0.77±0.46
15	0.33±0.24	0.03±0.58	-	0.95±0.36	0.67±0.69	0.30±0.33	-0.22±0.85	-	0.99[B]	0.53±0.59
19	0.48±0.17	0.05±0.42	0.57±0.25	-	0.99[B]	0.49±0.19	0.03±0.43	0.66±0.37	-	0.99[B]
21	0.56±0.22	0.10±0.45	0.28±0.35	-0.01±0.26	-	0.66±0.25	0.14±0.47*	0.28±0.35	-0.01±0.26	-

B: fixed at a boundary; * : the effects common to full-sibs were not significantly different from zero (P>0.05, likelihood-ratio test)

5.7 Genetic gain

The estimated genetic gains on observed and liability scale are provided in Table 8. The gains were unfavorable (more sexual mature fish) and significantly different from zero ($P<0.05$). The realized gain was higher than the expected gain, and quite similar on the two scales.

Table 8
Expected and realized genetic gain for early sexual maturity on observed and liability scale

	Linear model	Liability model
Expected gain	0.79±0.25	0.47±0.16
Realized gain	1.44±0.60	1.73±0.66

6. Discussion

6.1 Phenotypic observation

Early sexual maturation is a major problem in Atlantic salmon farming as maturation leads to reduced flesh quality and loss of growth, increase disease susceptibility and mortality rate during grow-out period (Aksnes et al., 1986; Randall et al., 1986; Bruno, 1989; Salte et al., 1995; Tranxler et al., 1997; St-Hiaire et al., 1998; Currie and Woo, 2007).

In this study, large variation in percentage of sexual maturing Atlantic was found in a comparison between fish farms rearing fish from the same full-sib families and between year-classes of fish reared at the same farm. For year-class 1983 and 1987 the percentage of maturing fish was 12.3% and 28.1%, respectively. At a time, none of the fish had reached marketing size because of the rather lower growth rate. It is reasonable to conclude that a series of environmental sources of variations (water temperature, salinity, photo-period, latitude, feeding regime, densities, etc.) with macro- environment must be responsible for this large variation between farms within the same year-class of fish, while differences between year-classes within a farm might also reflect a genetic component.

Different start feeding dates arise because of different production and hatching time of families. In 10 out of the 12 cases (farms), this effect had a non-significant effect on the percentage of early sexual maturing Atlantic salmon. In the two farms for each year-class with a significant effect, a lower proportion of sexual maturing fish was seen among the oldest fish. Yet, no further studies on effect of different start feeding dates on sexual maturity in Atlantic salmon were conducted. If this is a real biological effect or a coincidence, we do not know.

6.2 Genetic parameters

Sexual maturity in Atlantic salmon is a heritable trait, which have been strongly proved by earlier studies. In present study, estimates of heritabilities (h^2) for early sexual maturity in Atlantic salmon range widely from 0.02-0.11 (on the linear scale) and 0.04-0.21 (on the liability scale) among the farms of the two year-classes. This was consistent with the estimates reported by Wild et al. (1994) based on the same data but obtained using a different statistical model. In that study, heritabilities were estimated from sire and dam component separately, and also from both of them jointly. The heritabilty derived from the estimated sire component on the liability scale was 0.16 and 0.12 in year-class 1983 and 1987, respectively. While, the heritablities estimated from the dam component within sire, and the sire-dam component (full-sib component) were much higher because the dam component contains the effects common to full-sibs. Several previous estimates of hertitability for early and normal sexual maturity in Atlantic salmon both on linear and liability scale are given in Table 1. Meanwhile, the estimates of heritability in present study for early sexual maturity were comparable magnitude with the study reported by Gjerde (1986) and Gjerde et al.,(1994).

Our study has different traits definition compared with previous study. Similar heritabilty estimates for normal sexual maturity reported by Standal and Gjerde (1987), and higher estimates given by Gjerde (1984), Gjerde and Gjedrem (1984), Gjerde (1994) and Lillehammer (2013) for normal sexual maturity. While, early and normal sexual maturity are two traits for incomparable, however, the heritable of sexual maturity can be concluded.

Besides, earlier reports (Gjerde and Gjedreem, 1984; Gjerde, 1986; Gjerde et al., 1994) showed that a significant additive genetic variation for growth and sexual maturity in Atlantic salmon. Besides, males were found mature earlier than females (Ritter, 1975; Navdal et al., 1978; Gjerde, 1984), and the maturing males were reported significantly heavier than maturing female by

Ritter (1975), Navdal et al. (1978), Gjerde and Gjedrem (1984), Gjerde and Refstie (1984), and Gjerde (1984). In present study, the proportion of maturing females is also much lower than males. Consequently, estimates of heritabilities for sexual maturity may be biased if the sex ratio in the families depart from 1:1.

Few studies have explored the effects common to full-sibs (c^2) for early sexual maturity in Atlantic salmon. Low and significant effects common to full-sibs for this trait were observed in present study, 0.01 to 0.05 on observed scale and 0.01-0.07 on liability scale. Besides, the effects common to full-sibs was higher in year-class 1987 than in 1983 both on observed and liability scale. This estimates was consistent with Kause et al. (2003), in that study, the random tank effect explained 3-5% of the total variation for the maturity trait in rainbow trout. This results suggested that common environmental effects could reduce the accuracy of genetic evaluation if mating designs and statistical analyses are inappropriate (Winkelman and Peterson, 1994). So efforts should be done to minimized the effects common to full-sibs. Nevertheless, environmental effects common to full-sibs should be minimalized in testing schemes applied in breeding programs by standardizing the rearing environment in all tanks prior to tagging, or alternatively communal rearing of the families and parental assignment using genetic markers. The method by synchronizing the breeding to minimize the difference in family production and hatching time before communal testing also can be considered.

Besides, the estimation of hertability also had been conducted when omitting the effect common to the full-sibs, higher estimates of heritabilty were revealed. So it could be concluded that the presence of effects common to fullsibs other than additive genetics on the age at sexual maturity in Atlantic salmon may lead to the upward biased hertabilities if not accounted for in the model. However, including common effects to full-sibs in the mixed model may results in difficulty in disentangling additive genetic effects from common effects to full-sibs when the population

structure, i.e., mating design, number of family, family size is suboptimal. Consequently, additive genetic variance may be underestimated. Nevertheless, omitting common effects to full-sibs in the mixed model will inflate magnitude of additive genetic variance (Martinez et al.,1999). It is therefore important that these common effects to full-sibs are accounted for. Hierarchical mating design, i.e., 1 sire to 2 dams, is commonly used in aquaculture breeding programs. This allows separating the additive genetic effects from the common effects to full-sibs when (paternal) half-sib families are kept in different family tanks. However if survival rate of a half-sib family is low, such mating ratio will be 1 to 1 with may result in difficulty in estimating the common effects to full-sibs. Alternatively 2x2 partial factorial design may be more powerful in estimating both additive genetic effects and common effects to full-sibs simultaneously. This has been shown in the previous study by Berg and Henryon (1998).

6.3 Genotype by environment interaction

Genetic correlation between early sexual maturity recorded in different test environments is considered as a measurement of the genotype by environment interactions. The genetic correlation for early sexual maturity between pairs of test environments were varied widely within year-class: 0.67 to 0.99 on observed scale and 0.72 to 0.99 on liability scale in year-class 1983, and 0.51 to 0.99 on observed scale and 0.36 to 0.99 on liability scale in year-class 1987. In present study, the low to moderate estimates of for pairs of test environment genetic correlation were observed which indicated the presentce of G×E interactions, even though some estimates were high (close to unity). Besides, the low genetic correlation explained for the strong re-ranking of genotype between test environments.

In addition, according to the preset study, the rather low genetic correlations were only involved in farm 21. This suggests that a significant GxE interaction occurred for early sexual maturity in

the farm 21 compared with the other test environments. But the low numbers of recording fish reared in this test environment which only accounted for 7.9% of the total population and low average number of fish per full-sib family may had caused a downward bias of genetic correlation (Sae-Lim et al., 2010).

Besides, the rather lower genetic correlation in year-class 1983 and a high genetic correlation in year-class 1987 were observed between test environment 15 and 19, for 0.67 and 0.95, respectively. This explained that the strong re-ranking in year-class 1983 and weak re-ranking in year-class 1987 for the same two test environments in different generations. Especially, the environmental conditions were varying a lot in different periods, i.e. temperature, salinity and photo-period, the uncoordinated estimates between the same test environment during different periods might be attributed to the environmental conditions. However, substantial standard errors were presented which meant that the estimates of genetic correlation could not be calculated very accurately. And the large standard errors probably were attribute to the rather low heritabilty, small numbers of recording and small size of full-sibs family. So the bias of the estimation of genetic correlation might be contributed to the substantial standard errors. In addition, in order to get higher accuracy of estimates, the number of recordings should be large enough to minimize standard errors (Falconer and Mackay, 1996).

While, Wild et al. (1994) used the same data and showed the existence of G×E interaction. In that study G×E interactions were calculated as variance component of sire × net interaction and dam × net interaction which both accounted for less than 4% of the total variation in the early sexual maturity trait, but from for 23 to 54% of the sire variance and from 61 to 105% of the dam variance. In present study, larger magnitude of G×E re-ranking were observed in year-class 1987 than year-class 1983, meant that a stronger genotype re-ranking in year-class 1987 than 1983. However, the variances of interactions for two year-classes were not comparable for

genotype re-ranking in Wild's study. In that study, interaction model was used to calculate the variance of interaction components, whereas, multi-traits model was used to calculated genetic correlations in present study. Be more specific, for the interaction model, it is not possible to separate the two forms of GxE interaction , genotype re-ranking and heterogeneity of genetic variation (Sae-Lim, 2015, in press). While, for multi-traits model, both heterogeneity of variance and genotype re-ranking can be identified (Sae-Lim et al., 2015, in press). So in that study, the variance of interaction only proved the presence of GxE interaction, and the re-rankings of genotype between test environments were not clear. Hence, the multi-traits is more suitable to quantify the genotype re-ranking for numbers test environments.

Few previous studies for early sexual maturity in Atlantic salmon, another study on sexual maturity in rainbow trout was given by Kause et al.(2003). In that study, a negligible G×E interaction for sexual maturity in rainbow trout was observed because of the high genetic correlation estimate (0.96±0.03). Even though, few studies were on G×E interactions for early sexual maturity, the numerous studies were widely conducted on G×E interactions in aquaculture species through multiple environments and generations. Sae-Lim et al. (2015, in press) conclude a quantitative review for genotype by environment interactions across 38 species Atlantic salmon is considered as one of the most important economic species worldwide. Surprisingly, a study of GxE interaction on sexual maturity are lacking in aquaculture species.

When there is re-ranking GxE interaction, genetic gain in the production environment may be lower than expected. Hence, it is important to account for GxE interaction in a breeding program. Two options are commonly considered; incorporating sib information from different production environments and establishing separate breeding programs. The decision making are usually referred to the magnitude of 0.8 as suggested by Robertson (1959). Robertson suggested that when genetic correlation is 0.8, GxE is considered important. However, his suggestion based on

personal opinion rather than economical point of view. As the genetic correlation differs from a unity, the ranking of animals are different across production environemnts. Including sib information into a selection index can increase genetic gain and a breeding program may maintain genetic gain in selection and production environments (Martinez et al., 2006; Sea-Lim et al., 2013). Nevertheless, when the genetic correlation is significant low. It may not be possible to maintain the genetic gain in the production environments. Mulder and Bijma et al. (2005) recommends that when the genetic correlation is lower than a break-even point correlation, i.e., intersection of genetic correlations when the genetic gain of two different breeding strategies are equal, a breeding program should be divided into two environment-specific breeding programs. In fish breeding program, Sae-Lim et al.,(2013) expected that the break-even point correlation is higher than 0.71. In this current study, we found that the genetic correlation between several pairs, i.e., farm 21 and farm 02, 15 in year-class 1987, are lower than 0.71 and thus a breeding program may not be able to maintain the genetic gains in these particular environments. Although based on statistical evidence, the breeding program should be separate, it is important to consider economic point of view. More study is required to compare different breeding strategies to optimize for GxE interaction of early sexual maturity in Atlantic salmon, i.e. a comparison of genetic gain, rate of inbreeding and running cost, using either deterministic or stochastic simulation (Sae-Lim et al., 2015, in press).

In present study, most of the estimates of genetic correlation for pairs of test environment were high, however, strong re-rankings were still observed a few pairs of the investigated test environments. It would be more favorable to take a separate breeding program in that case for the strong re-ranking . While, the data used in this G × E interaction study were collected in early years and the breeding program had been conducted before the present detailed analyses. In recent years, there is no G × E interaction studies for early sexual maturity in Atlantic salmon, hence, more studies on this should be conducted.

The effects common to full-sibs correlations of pairs of two test environment were low and significant in year-class 1987 when compared year-class with 1983 both on observed and liability scale. While, the low r_c indicates that the effects common to full-sibs resulting from the environment the full-sibs shared early in their life became smaller due to the separation into two environments during the grow-out period (Khaw et al.,2012). Besides, previous studies had shown that the effects common to full-sibs diminishes over time in salmonid species (Gunnes and Gjedrem, 1978, Elvingson and Johansson, 1993, Gjerde et al., 1994 and Winkelman and Peterson, 1994). Hence, the effects common to full-sibs would smaller after transferring into production environments, the different shrinking rate might contribute to the varying correlations between the pairs of test environments.

6.4 Genetic gain

Based on the estimated breeding values for full-sibs, unfavorable genetic gains were observed in present study both for expect and realized gains. The expected gentic gain was 0.79% on observed scale and 0.47% on liability scale, which is slightly higher compared to expected genetic gain (-0.34%) calculated for the same population reported by Gjøen and Gjerde (1997). However, four populations were conducted in this breeding program, comparing with the estimated genetic gains for other three population, -8.3%, -5.9% and -9.1% (Gjøen and Gjerde, 1997), the genetic gain of this population was rather low and almost close to zero. To some degree, the response to selection of the population analyzed in present study was not as favorable as other three populations. Whereas, in that study, the response to selection was calculated based on the method of selection differential, which is related to estimates of heritability, accuracy of selection and selection intensity. However, in present study, both the expected and realized genetic gains were calculated from the estimated breeding value of full-sib families. So those two different methods for calculating the genetic gain might

contribute to the slight difference of the estimates.

Besides, Gjerde and Korsvoll (1999) and Gjøen and Gjerde (1997) reported the aim for this selection program were to increase the growth rate and to reduce the proportion of early sexual maturity. However, the significant positive genetic correlation between body weight and age at first maturation in Atlantic salmon were found by earlier papers (Gjerde and Gjedrem, 1984; Gjerde, 1986; Gjerde, 1994). Genetic selection differential for slaughter weight and early sexual maturity from previous report and estimated breeding value of full-sibs families for early sexual maturity from present study are showed in the Appendix I. A large proportion of sires and dams were selective from the individuals which have unfavorable early sexual maturity genetic index, but high selection differential for slaughter weight. This might have been showed the case in this present analysis, resulting in a possible unfavorable change of sexual maturity.

7. Reference

Adams, C.E., Thorpe, J.E., 1989. Photoperiod and temperature effects on early development and reproductive investment in Atlantic salmon (Salmo salar L.). Aquaculture 79, 403–409.

Alne, H., Thomassen, M., Sigholt, T., Berge, R.K., Rørvik, K.-A.., 2009. Reduced sexual maturation in male post-smolt 1 + Atlantic salmon (Salmo salar L.) by dietary tetradecylthioacetic acid. Aquaculture Research 40, 533-541.

Arge R., Thomassen M., Berge R.K., Zambonino-Infante J. L., Terjesen B. F., Oehme, T., Rørvik K.-A., 2012. Reduction of early sexual maturation in male S0 Atlantic salmon (Salmo salar L.) by dietary supplementation of tetradecylthioacetic acid (TTA). Aquaculture Research, 1-12.

Aksnes, A., Gjerde, B., Roald, S.O., 1986. Biological,chemical and organoleptic changes during maturation of farmed Atlantic salmon, Salmo salar. Aquaculture 53,7–20.

Baum, D., Laughton, R., Armstrong, J. D. & Metcalfe, N. B. (2004). Altitudinal variation in the relationship between growth and maturation rate in salmon parr. Journal of Animal Ecology 73, 253–260.

Berg, P., Henryon, M., 1998.A comparison of mating designs for inference on genetic parameters in fish. Proc. 6th WCGALP, 27, 115-118.

Bruno, D.W., 1989. Fungal infections of farmed salmon and trout. Aquaculture Information S. 5, 1–5.

Buck, R.G.J. and Youngson, A.F., 1982. The downstream migration of precociously mature Atlantic salmon, *Salmo salar,* parr in autumn; its relation to the spawning migration of mature adult fish. J. Fish Biol., 20, 279-288.

Crandell, P. A. & Gall, G. A. E. (1993). The genetics of body weight and its effect on early maturity based on individually tagged rainbow trout. Aquaculture 117, 77–93.

Currie, J., Woo, P., 2007. Susceptibility of sexually mature rainbow trout, Oncorhynchus mykiss to experimental cryptobiosis caused by Cryptobia salmositica. Parasitol. Res. 101, 1057–1067.

Dalley, E.L., Andrews, C.W. and Green, J.M., 1983. Precocious male Atlantic salmon in insular Newfoundland. Can. J. Fish. Aquat. Sci., 40, 647-652.

Duston, J., Saunders, R.L., 1999. Effect of winter food deprivation on growth and sexual maturity of Atlantic salmon (Salmo salar) in sea water. Canadian Journal of Fisheries and Aquatic Science 56, 201–207.

Duston, J., Saunders, R.L., 1992. Effects of 6-, 12- and 18-month photoperiod cycles on smolting and sexual maturation in juvenile Atlantic salmon (Salmo salar) Can. J.Fish. Aquat. Sci., 49, pp. 2273–2280.

Duncan, N.J., Thrush ,M.A., Elliott, J.A.K. , Bromage, N.R., 2002. Seawater growth and maturation of Atlantic salmon (Salmo salar) transferred to sea at different times during the year. Aquaculture 213, 293–309.

Endal, H. P., Taranger, G. L., Steffansson, S. O. and Hansen, T., 2000. Effects of continuous additional light on growth and sexual maturity in Atlantic salmon, Salmo salar, reared in sea cages. Aquaculture 191, 337- 349.

Elson, P.F., 1973. Genetic polymorphism in Northwest Miramichi salmon, in relation to season of river ascent and age at maturation and its implications for management of the stocks. ICNAF Res. Dot. 73/76, 6 pp.

Elvingson, P., Johansson, K., 1993. Genetic and environmental components of variation in body traits of rainbow trout (Onchorhynchus mykiss) in relation to age. Aquaculture 118, 191 – 204.

Falconer, D.S., 1952. The problem of environment and selection. The American Naturalist 86, 293-298.

Falconer, D.S., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics. Longman, Essex, UK.

Fjelldal, P.G., Hansen, T., Breck, O., Sandvik, R., Waagbø, R., Berg, A., Ørnsrud, R., 2009. Supplementation of dietary minerals during the early seawater phase increase vertebral strength and reduce the prevalence of vertebral deformities in fast-growing under-yearling Atlantic salmon (Salmo salar L.) smolt. Aquaculture Nutrition 15, 366–378.

Fjelldal, P.G., Hansen, T., Vaccination and elevated dietary phosphorus reduces the incidence of early sexual maturation in Atlantic salmon (Salmo salar L.) Aquaculture 364–365, 333–337.

Gilmour, A.R., Gogel, B.J., Cullis, B.R., and Thompson, R., 2009. ASReml User Guide Release 3.0 VSN International Ltd, Hemel Hempstead, HP1 1ES, UK www.vsni.co.uk

Glebe, B.D., Saunders, R.L., 1986. Genetic factors in sexual maturity of cultured Atlantic salmon (Salmo salar) parr and adults reared in sea cages. In: Meerburg, D.J. (Ed.), Salmonid Age at Maturity. Can. Spec. Publ. Fish. Aquat. Sci., 89,24–29.

Gjedrem, T., 2000. Genetic improvement of cold-water fish species. Aquaculture Research 31, 25–33.

Gjerde, B., 1984. Response to individual selection for age at sexual maturity in Atlantic salmon. Aquaculture, 38:229-240.

Gjerde, B., 1986. Growth and reproduction in fish and shellfish. Aquaculture 57, 37-55.

Gjerde, B. and Gjedrem, T., 1984. Estimates of phenotypic and genetic parameters for carcass traits in Atlantic salmon and rainbow trout. Aquaculture 36, 97-l 10.

Gjerde, B. and Refstie, T., 1984. Complete diallel cross between five strains of Atlantic salmon. Livest. Prod. Sci., 11,207-226.

Gjerde, B., Simianer, H., Refstie, T., 1994. Estimates of genetic and phenotypic parameters for body weight, growth rate and sexual maturity in Atlantic salmon. Livestock Production Sciences 38, 133–143.

Gjerde, B., Korsvoll, A., 1999. Realised selection differentials for growth rate and early sexual maturity in Atlantic salmon. Aquac. Eur. 99, 73–74 Trondheim, Norway.

Gjerde, B., Pante, J.R.P., Baeverfjord, G., 2005. Genetic variation for a vertebral deformity in Atlantic salmon (Salmo salar). Aquaculture 244, 77–87.

Gjoen H.M., Gjerde B., 1997. Selection differential for Atlantic salmon. Year Classes 1980-92 (Seleksjiondifferenser for laks. Arsklasse 1980-92). Report No. 31/97. AKVAFORSK

Gunnes, K. and Gjedrem, T., 1978. Selection experiments with salmon. IV. Growth of Atlantic salmon during two years in the sea. Aquaculture 15,19-33.

Herbinger, C. M. and Newkirk, G. F. 1990. Sources of family variability for maturation incidence in cultivated Atlantic salmon. Aquaculture 85, 153–162.

Hansen, T., Steffansson, S. and Taranger, G. L., 1992. Growth and sexual maturation in Atlantic salmon, Salmo salar L., reared in sea cages at two different light regimes. Aquacult. Fish. Man. 23, 275-280.

Johnnson, B., Jonsson, N., 2011. Ecology of Atlantic salmon and brown trout: habitat as a template for life histories. Fish and Fisheries Series 33.

Kause, A., Ritola, O., Paananen, T., Mantysaari, E., Eskelinen, U., 2003 Selection against early maturity in large rainbow trout *Oncorhynchus mykiss*: the quantitative genetics of sexual dimorphism and genotype-by-environment interactions. Aquaculture 228, 53-68.

Khaw, H.L., Ponzoni, R.W., Hamzah, A., Abu-Bakar, K.R., Bijma, P., 2012. Genotype by production environment interaction in the GIFT strain of Nile tilapia (*Oreochromis niloticus*). Aquaculture 326–329, 53-60.

Kittelsen, A., Rosten, T., Ulgenes, Y., Selvik, J., Alne, H., 2006. Available fresh water sources for future production of smolts of Atlantic salmon and trout. AKVAFORSK report, p. 123.

Kolstad, K., Thorland, I., Refstie, T., Gjerde, B., 2006. Genetic variation and genotype by location interaction in body weight, spinal deformity and sexual maturity in Atlantic cod (Gadus morhua) reared at different locations off Norway. Aquaculture 259, 66–73.

Kråkenes,R., Hansen, T., Stefansson, S.O.,. Taranger, G.L., 1991. Continuous light increases growth of Atlantic salmon (Salmo salar) postsmolts in seacages. Aquaculture 95, 281–287.

L'Abe´e-Lund, J.H., Vøllestad, L.A., Beldring, S., 2004. Spatial and temporal variation in the grilse proportion of Atlantic salmon in Norwegian rivers. Trans Am Fish Soc 133, 743–761.

Lillehammer, M., Ødegård, J., Madsen, P., Gjerde, B., Refstie, T., Rye, M., 2013. Survival, growth and sexual maturation in Atlantic salmon exposed to infectious pancreatic necrosis: a multi-variate mixture model approach. Genetics Selection Evolution 45, 8.

Lynch, M., Walsh, B., 1998. Genetics and Analysis of Quantitative Traits. Sinauer Associates, Inc., U.S.A.

Martinez, V., Kause, A., Mäntysaari, E., Mäki-Tanila, A., 2006. The use of alternative breeding schemes to enhance genetic improvement in rainbow trout: II. Two-stage selection. Aquaculture 254,195–202.

McClure, C.A., Hammell K.L., Moore M., Dohoo I.R. & Burnley H. (2007) Risk factors for early sexual maturation in Atlantic salmon in seawater farms in New Brunswick and Nova Scotia, Canada. Aquaculture 272, 370–379.

Mulder, H.A., Bijma, P., 2005. Effects of genotype x environment interaction on genetic gain in breeding programs. Journal of Animal Science 83, 49 - 61.

Naevdal, G., 1983. Genetic factors in connection with age at maturation. Aquaculture 33, 97-106.

Naevdal, G., Holm, M., Ingerbrigtsen, O., Moller, D., 1978. Variation in age at first spawning in Atlantic salmon *(Salmo saint.).* J. Fish. Res. Board Can.35: 145-147.

Oppedal, F., Taranger, G.L., Juell, J.E., Fosseidengen, J.E., Hansen, T., 1997. Light intensity affects growth and sexual maturation of Atlantic salmon (Salmo salar) postsmolt in sea cages. Aquatic Living Resources 10, 351 – 357.

Piggins, D.J., 1974. The results of selective breeding from known grilse and salmon parents. Annu. Rep. Salm. Res. Trust Ireland, 18: 35-39.

Porter, M.J.R., Duncan, N.J., Mitchell, D., Bromage, N.R., 1999. The use of cage lighting to reduce plasma melatonin in Atlantic salmon (Salmo salar) and its effects on the inhibition of grilsing Aquaculture, 176, 237–244.

Randall, R. G., Thorpe, J. E. , Gibson, *R. J.* , Reddin, D. G., 1986. Biological factors affecting age at maturity in Atlantic salmon *(Salmo salar.),* p. 90-96. *In* D. J. Meerburg [cd.] Salmonid age at maturity. Can. Spec. Publ. Fish. Agnat. Sci. 89.

Ritter, JA. 1975. Lower ocean survival rates for hatchery-reared Atlantic salmon (*Salmo salar*) stocks released in rivers other than their native streams. ICES CM 1975/M:26, 10.

Ritter, J.A., Newbould, K., 1977. Relationships of parentage and smolt age to age at first maturity of Atlantic salmon *(Salmo salar).* ICES C.M. 1977/M:32, 5 pp.

Ritter, J.A., Farmer, G. J., Misra, R. K., Goff, T. R., Bailey, J. K., Baum, E. T., 1986. Parental influences and smolt size and sex ratio effects on sea age at first maturity of Atlantic salmon *(Salmo salar),* Can. Spec. Publ. Fish. Aquat. Sci. 89, 30-38.

Robertson, A., 1959. The sampling variance of the genetic correlation coefficient. Biometrics 15, 469-485.

Rowe, D.K., Thorpe, J.E. ,Shanks, A.M., 1991:Role of fat stores in the maturation of male Atlantic salmon (*Salmo salar*) parr Canadian Journal of Fisheries and Aquatic Sciences 48, 405–413.

Rowe, D.K., Thorpe, J.E., 1990. Suppression of maturation in male Atlantic salmon (*Salmo salar* L.) parr by reduction in feeding and growth during spring months. Aquaculture 86, 291–313.

Sae-Lim, P., Komen, H., Kause, A., 2010. Bias and precision of estimates of genotype-by-environment interaction: A simulation study. Aquaculture 310, 66-73.

Sae-Lim, P., Kause, A., Mulder, H., Martin. K., Barfoot, A., Parsons, J., *et al., 2*013. Genotype-by-environment interaction of growth traits in rainbow trout (*Oncorhynchus mykiss*): a continental scale study. Journal of Animal Science 91, 5572 - 5581.

Saunder, R.L., Henderson, E.B., Glebe, B.D., 1982. Precocious sexual maturation and smoltification in male Atlantic salmon *(Salmo salar).*Aquaculture 28, 211-229.

Salte, R., Norberg, K., Ódegaard, O.R., 1995. Evidence of ongoing coagulation and fibrinolysis in early-maturing Atlantic salmon, *Salmo salar* L. J. Fish Dis. 18, 623–626.

Silverstein, J.T., Shearer, K.D., Dickhoff, W.W., and E.M. Plisetskaya. (1998). Effects of growth and fatness on sexual development of chinook salmon (Oncorhynchus tshawytscha) parr. Canadian Journal of Fisheries and Aquatic Sciences 55, 2376-2382.

Standal, M., Gjerde, B., 1987. Genetic variation in survival of Atlantic salmon during the sea-rearing period. Aquaculture 66, 197–207.

Stram, D. O., Lee, J. W., 1994. Variance components testing in the longitudinal mixed effects model. Biometrics 50, 1171–1177.

St-Hilaire, S., Ribble, C., Whitaker, D.J., Kent, M., 1998. Prevalence of Kudoa thyrsites in sexually mature and immature pen-reared Atlantic salmon (*Salmo salar*) in British Columbia, Canada. Aquaculture 162, 69–77.

Taranger, G.L., Haux, C., Stefansson, S.O., Björnsson, B.T., Walther, B.T., Hansen, T., 1998. Abrupt changes in photoperiod affect age at maturity, timing of ovulation and plasma testosterone and oestradiol-17ß profiles in Atlantic salmon, Salmo salar. Aquaculture 162, 85–98.

Taranger, G.L., Haux, C., Hansen, T., Stefansson, S.O., Björnsson, B.T., Walter, B.T., Kryvi, H., 1999. Mechanisms underlying photoperiodic effects on age at sexual maturity in Atlantic salmon, Salmo salar. Aquaculture 177, 47–60.

Taranger, G.L., Carrillo, M., Schulz, R.W., Fontaine, P., Zanuy, S., Felip, A., Weltzien, F.A., Dufour, S., Karlsen, O., Norberg, B., Andersson, E., Hausen, T., 2010. Control of puberty in farmed fish. General and Comparative Endocrinology 165, 483–515.

Traxler, G.S., Roome, J.R., Lauda, K.A., LaPatra, S., 1997. Appearance of infectious haematopoietic necrosis virus (IHNV) and neutralizing antibodies in sockeye salmon Oncorhynchus nerka during their migration and maturation period. Dis. Aquat. Org. 28, 31–38.

Thorpe, J.E., Morgan, R.I.G., 1980. Growth-rate and smolting-rate of progeny of male Atlantic salmon parr, Salmo salarL. J. Fish Biol., 17, pp. 451–460.

Thorpe, J.E. , 1994. Reproductive strategies in Atlantic salmon, Salmo salar L. Aquacult. Fish. Manage., 25, 77–87.

Whalen, K. G., and D. L. Parrish. 1999. Effect of maturation on parr growth and smolt recruitment of Atlantic salmon. Canadian Journal of Fisheries and Aquatic Sciences 56, 79–86.

Wild, V., Simianer, H., Gjøen, H.M., Gjerde, B., 1994. Genetic parameters and genotype environment interaction for early sexual maturity in Atlantic salmon (*Salmo salar*). Aquaculture 128, 51-65.

Winkelman, A.M., Peterson, R.G., 1994. Heritabilities, dominance variation, common environmental effects and genotype by environment interactions for weight and length in chinook salmon. Aquaculture 125, 17–30.

Wolters, W.R., 2010. Sources of phenotypic and genetic variation for seawater growth in five North American Atlantic salmon stocks. Journal of the World Aquaculture Society 41, 421–429.

Appendix I: Selection differential for body weight and sexual maturity

AKVA GEN was selected broodstock for manufacturing year-class 1987 from families of teay-class 1883. Genetic selection differential for slaughter weight and early sexual maturity from previous report and estimated breeding value of full-sibs families for early sexual maturity from present study. And the numbers of male and female fish were selected from each family. Family number 1-62 from year-class 1983, family number 63-69 from year-class 1982.

NO.	Sire	Dam	WI	MI	EMI	No.sire	No.dam
1	790052063	790051011	95.2	115.8	124.1		1
2	790052004	790051014	104.7	114.3	121.2		1
3	790052027	790051085	101.8	112.4	119.5	1	1
4	790052027	790051087	-	-	119.4		1
5	790052015	790051051	103	114.2	118.1		1
6	790052036	790051153	99	110.1	118.1	2	1
7	790052023	790051173	90.4	106.9	115.9		1
8	790052001	790051159	111.9	108.3	115.4		1
9	790052027	790051151	98.1	107.5	114.5		1
10	790052002	790051005	96.1	107.7	113.5		1
11	790052025	790051083	105.3	110.1	113.1		2
12	790052031	790051100	96.2	109	111.7		1
13	790052008	790051122	104.3	108.6	111.4	1	
14	790052027	790051149	100.4	103.7	110.7		1
15	790052013	790051043	91.4	106.7	110.6		1
16	790052013	790051042	96.3	104.8	109.5	1	2
17	790052001	790051002	120.7	101.8	108.2	4	2
18	790052031	790051102	97.2	101.8	107.5		1
19	790052037	790051143	102.7	110.1	107.4		4
20	790052001	790051158	105.2	99	107.3		1
21	790052011	790051036	99.5	108.3	107.3		4
22	790052020	790051154	95.6	108.1	107.2		1
23	790052007	790051132	108.9	106	106.1		1
24	790052010	790051139	105.9	107.1	106.0		1
25	790052011	790051035	111.6	102.3	102.8	4	1
26	790052010	790051138	97.7	101.8	102.4		2

NO.	Sire	Dam	WI	MI	EMI	No.sire	No.dam
27	790052011	790051034	97.5	100.5	102.0		1
28	790052037	790051145	95.9	104.7	101.7		3
29	790052011	790051109	107.9	101.9	101.7		5
30	790052002	790051006	106.8	99.1	101.5		3
31	790052028	790051089	101.7	98	101.4		2
32	790052011	790051110	94.5	94.9	101.1		2
33	790052010	790051062	101.1	99.5	101.1	1	2
34	790052038	790051141	103.4	94	100.6		1
35	790052015	790051049	107.3	97.5	100.2		5
36	790052028	790051090	99.2	102	99.2		1
37	790052018	790051059	89.1	99.4	98.4		1
38	790052009	790051030	116.2	98.7	98.4		2
39	790052008	790051121	100.5	92.1	98.3		2
40	790052011	790051111	99.7	96.5	97.9		1
41	790052010	790051063	107.4	100.3	97.8		1
42	790052009	790051028	104.5	97.5	97.7		3
43	790052007	790051133	99.7	99.3	97.6	1	1
44	790052020	790051071	111.5	101.1	97.3	1	2
45	790052004	790051015	113.1	97.2	97.1		2
46	790052037	790051118	91.9	97.9	96.4		1
47	790052020	790051065	111.5	99.2	95.7		5
48	790052029	790051176	107	93.6	95.3	1	
49	790052034	790051107	103.9	96.2	94.3		1
50	790052020	790051156	102.8	90.4	92.6		3
51	790052037	790051144	97.4	92.3	91.8		1
52	790052037	790051117	107.3	89	91.7		1
53	790052009	790051124	100.2	93.9	91.7		1
54	790052020	790051072	98.3	93.1	91.2		3
55	790052038	790051140	105.4	72.3	91.0		1
56	790052028	790051160	116.6	86.4	88.6	4	2
57	790052037	790051116	89.4	84.4	88.3		1
58	790052010	790051033	127	83.3	87.4	2	6
59	790052017	790051057	99.9	87.6	87.3		1
60	790052020	790051155	113.4	82	87.3		4
61	790052010	790051031	97.4	84.8	85.4		3
62	790052020	790051066	110.7	75	80.7		2
63	780052011	780051031			118.6		1
64	780052015	780051095	114.2	97.4	117.7		1

NO.	Sire	Dam	WI	MI	EMI	No.sire	No.dam
65	780052012	780051012	108.3	98.6	106.7		1
66	780052005	780051124			105.0		1
67	780052005	780051015	104.4	109.8	98.9		1
67	780052005	780051015	104.4	109.8	98.9		1
68	780052005	780051125	114.7	99	94.8		1
69	780052026	780051118	108.8	101.7	94.6		1

NO.= family number;

WI = body weight index from previous report;

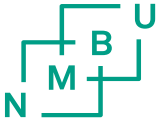
MI=sexual maturity index from previous report;

EMI = full-sib families breeding value for early sexual maturity estimate from present study;

No.sire = numbers of sires selected from year-class 1983 for next generation (year-class 1987);

No.dam = numbers of sires selected from year-class 1983 for next generation (year-class 1987);

"-" not available.



Norwegian University
of Life Sciences

Postboks 5003
NO-1432 Ås, Norway
+47 67 23 00 00
www.nmbu.no