GENETIC PARAMETERS IN A COMMERCIAL ATLANTIC COD (*Gadus morhua*) BREEDING PROGRAM

THANH VU NGUYEN

Norwegian University of Life Sciences
Department of animal and aquaculture sciences
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Master thesis by THANH VU NGUYEN

Supervisor: Professor Hans Magnus Gjøen

DEPARTMENT OF ANIMAL AND AQUACULTURAL SCIENCES (IHA)
05/2013, 1432 – Ås, Norway

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ABSTRACT

Despite many quantitative genetic studies on Atlantic cod (*Gadus morhua*) over the last two decades, the magnitude of heritabilities and genetic correlations for some economic important traits (growth rate, carcass quality traits) as well as genotype by environment (G×E) interactions, to some extent, still remain ambiguous. Therefore, this study estimated the genetic parameter using a dataset from a commercial cod breeding program (CodFarmers AS) in Norway for 3 generations, from 2002 to 2008, to ascertain that. Univariate and bivariate models were used to obtain (co)variance components. The estimated heritabilities were from moderate to extremely high for body weight at nine rearing locations, ranging from 0.11 – 0.86. Heritabilities for harvest body weight were estimated for three generations (2002, 2005, and 2008), and were medium to high, 0.54±0.15, 0.29±0.04 and 0.22±0.04, respectively. For generation 2005, all traits other than harvest body weight were recorded, and estimates of heritability were medium for most trait (harvest body weight, gutted body weight, fillet weight, loin weight and liver weight), ranging from 0.18 to 0.28. Some traits had high heritability such as body length and gonad weight (0.43 for both), but very low heritability estimate was obtained for head weight (only 0.06). No G×E was found among different reared locations in generation of 2002 and of 2005. There were some mild G×Es found for some reared locations in generation 2008. The strong and significant genetic correlation (r_g=0.99) between some traits (such as fillet weight, loin weight, gutted weight and harvest weight) indicated that they are genetically the same trait, and that estimation of genetic parameters for one trait can give good predictions for others.

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1. INTRODUCTION

Atlantic cod (*Gadus morhua*) has emerged as a new aquaculture species in European countries, especially in Norway. Norway is leading in cod farming worldwide. Atlantic cod is among the most important farmed gadoid (Bekkevold *et al.*, 2006; Rosenlund and Skretting, 2006), and is predicted to be the second most economic important marine finfish species in Europe, after Atlantic salmon (*Salmo salar*) (Jørstad *et al.*, 2006). Farmed cod realized good reputation in most market today, and is traditionally sold with gutted and head-off. However, more farmed cods are being processed for fillet and especially for loins (Conference, 2011). Unlike halibut and flatfish, Atlantic cod can use the same equipment as well as knowledge from Atlantic salmon farming, which are well-known and have successfully been applied (Bekkevold *et al.*, 2006; Rosenlund and Skretting, 2006). Technical supports for cod production and rearing systems are well documented (Gamble, 1981; Øiestad *et al.*, 1985; Brown *et al.*, 2003). According to Rosenlund and Skretting (2006), more companies are involved in cod farming, making bigger integrated firms that will contribute to a rapid growth of cod farming industry. The authors believed that production of Atlantic cod can reach the level similar to that of farmed salmon within the next 15 – 20 years.

However, for cod farming in Norway, there are still a lot of disadvantages for farming and marketing cod products recently. The largest cod production company (CodFarmers) has experienced serious financial problems and was almost bankrupt in 2013 (CodFarmers reports at www.codfarmers.no). Early sexual maturation is still probably a great problem for the industry despite light treatment (Karlsen *et al.*, 2006; Kolstad *et al.*, 2006b; Kolstad *et al.*, 2006a; Cowan *et al.*, 2011; Mikkelsen and Seppola, 2013). Finally, having a good and stable price is difficult, because of very large catches of wild Northeast Arctic cod in recent years (Conference, 2011).

Genetic stock improvement based on quantitative traits record has been successful reported many years ago, especially in livestock (Gjedrem, 2005). Compared with livestock genetics, application of quantitative genetics principles to fish breeding has limited until recently. In Norway, selective breeding program have been applied successfully in salmon farming (Gjedrem, 2005). Accompany with *Salmonid* as main species reared in Norway, production based on genetic improvement in aquaculture has been summarized and described previously by Gjedrem and Baranski (2009). Atlantic cod breeding program have been started in some countries but still underway, program has been set up from 2002 in Norway and then

in other countries such as Iceland (2003) and Canada (2005) for economic important traits like growth rate, delay early sexual maturation, etc. (Conference, 2011). Iceland and Canada are involved much for using genomic selection. In Canada, the program called "Atlantic Cod Genomics and Broodstock Development" has been started in 2005 with the purposes of developing tools for identify superior traits for commercial importance (Jørstad *et al.*, 2006).

In most aquaculture breeding programs, growth rate is the single most important trait, because it increases production turnover, and that fast growing fish will reach higher body weight before onset of sexual maturation (Gjedrem, 2005). For best operational of the breeding program, genetic parameters of economic important traits need to be estimated. Variance components including additive genetic variation and reliable heritability play an important role, and it is essential to know the magnitude of genetic correlations among those traits in order to optimize selection and to control possible adverse correlated genetic responses (Gjedrem and Baranski, 2009).

For predicting the additive genetics in farming of the specie, heritabilities were estimated for growth (Gjerde *et al.*, 2004; Kolstad *et al.*, 2006b; Kolstad *et al.*, 2006a; Kettunen and Fjalestad, 2007; Garber *et al.*, 2010; Ødegård *et al.*, 2010; Bangera *et al.*, 2011; Kristjánsson, 2011; Tosh *et al.*, 2011), disease resistance (Kettunen and Fjalestad, 2006; Garber *et al.*, 2010; Bangera *et al.*, 2011; Mikkelsen and Seppola, 2013), delay early maturation (Kolstad *et al.*, 2006b; Kolstad *et al.*, 2006a), and spinal deformity (Kolstad *et al.*, 2006b; Kolstad *et al.*, 2006a; Kettunen and Fjalestad, 2007). Most of the genetic parameters were reported for 2 year-old-fish. Estimates of heritability in previous studies were mainly for growth rate, sexual maturation and disease resistance that were varied widely (0.15 – 0.64). However, few studies estimated heritability for carcass traits such as liver weight, loin weight, gutted weight, and fillet yields (Garber *et al.*, 2010; Kristjánsson, 2011).

Genotype by environment (G×E) interaction will be considered if significant, and if accounts for a relatively large proportion of the total variance that could reduce response to selection; therefore it might be desirable to develop strains for different environments (Gjedrem, 2005). The performance of G×E tests on farming of cod were carried out on different geographical strains of South and North of Iceland (Kristjánsson, 2013), of North East Arctic Cod and Coastal Cod (Kolstad *et al.*, 2006b; Kolstad *et al.*, 2006a) in different locations along Norwegian coast. According to Kolstad (Kolstad *et al.*, 2006b; Kolstad *et al.*, 2006a), there were no significant differences for environmental sensitivity in cod farming to

various geographical strains they were reared at different locations for body weight and body deformity. Therefore, it was not necessary to develop different breeding programs. Nevertheless, G×E may be important for selection of disease resistance while information on full- and half-sib families are needed (Franco, 2007).

For estimating genetic correlations, there were many studies on genetic correlations between growth rate with sexual maturation (Kolstad *et al.*, 2006b; Kolstad *et al.*, 2006a), survival (Garber *et al.*, 2010), spiny deformity (Kolstad *et al.*, 2006b; Kolstad *et al.*, 2006a), and with disease resistance (Kettunen and Fjalestad, 2006; Garber *et al.*, 2010; Ødegård *et al.*, 2010; Bangera *et al.*, 2011). Few studies reported G×E between growth rate and carcass traits (Kettunen and Fjalestad, 2007; Garber *et al.*, 2010; Kristjánsson, 2011), only vaguely for fillet gutted body weight, loin weight, liver weight, and standard body length. Early estimations of genetic correlations between repeated measurements of body weight were high (0.64–0.76) (Kettunen and Fjalestad, 2007). According to Garber *et al.* (2010) there were strong genetic correlations between harvest weight and standard length, bled weight, carcass weight, loin, and liver weight, ranging from 0.87 – 0.98. Gonad weigh showed less genetic correlation with harvest weight (0.56) (Garber *et al.*, 2010). Kristjánsson (2011) estimated also high genetic correlations between some traits observed, for instance, between harvest weight and gutted weight (0.99), liver weight (0.67), and fillet yields (0.89).

This study aims to estimate genetic parameters (heritability and genetic correlation) for body weight at harvest (HBW) in a commercial cod farming company (CodFarmers AS). The same estimates were carried out for body length (BL), gutted body weight (GBW), fillet weight (FW), head weight (HW), loin weight (LoW), liver weight (LiW), and gonad weight (GW). All traits were recorded at harvest/slaughter. This would give estimates of the genetic parameters for many traits in the current breeding program.

2. MATERIALS AND METHODS

2.1. Data collection and description

The dataset used in this study was partly described by Kolstad *et al.* (2006b) and Kolstad *et al.* (2006a). Briefly, all data were previously collected by MarineBreed AS in a cod breeding program for growth from 2000 to 2008. The base population consisted of 103 individuals (35 males and 68 females) that were paired mating to produce full- and half-sib families. The best animals in each generation were selected and produced the subsequent generations at nine rearing locations namely Averøy (4 locations), Tromsø (1 location), Gildeskål (2 locations), and CodFarmers (2 locations) (*Table 2.1*). Averøy was chosen as the location for slaughter traits, while at other locations live weight at tagging and harvest were recorded. Fish age at recording varied between generations, average age for harvest was approximately 3.0, 2.0, and 1.5 years old for generations 2002, 2005, and 2008 respectively. Number of families and recordings for each trait are presented in *Table 2.1*.

Table 2.1. *Number of recordings for harvest body weight and other traits by generations and locations*

Location of rearing	Generation	# of family	# of records							
			HBW (g)	BL (g)	GBW (g)	HW (g)	FW (g)	LoW (g)	LiW (g)	GW (g)
Averøy	2002	55	1549	360	360	360	0	360	0	360
Tromsø	2002	55	366	366	366	0	0	0	0	0
Averøy1	2005	86	4759	3605	460	460	460	460	460	460
Averøy2	2005	86	4748	3625	410	410	410	410	410	410
Gildeskål	2005	86	4722	1697	1697	0	0	0	0	0
Averøy	2008	72	967	650	650	650	650	650	0	650
CodFarmers1	2008	72	1676	781	0	0	0	0	0	0
CodFarmers2	2008	72	640	406	0	0	0	0	0	0
Gildeskål	2008	72	2548	1897	0	0	0	0	0	0

HBW=harvest body weight, BL=body length, GBW=gutted body weight, HW=head weight, FW=fillet weight, LoW=loin weight, LiW=liver weight and GW=gonad weight

Furthermore, the weight at tagging and fish age at different time-points of life were also recorded (*Table 3.1*).

The pedigree consisted of 15,548 animals that belong to 3 generations from 2000 to 2008. The population in the year 2000 was regarded as the base population. Collected data included animal identity, generation, sex, family, location of rearing and the real variables were recorded for age, weigh of whole body, gutted, head, fillet, loin, liver, and gonad. All slaughter traits measurements and harvest body weights of different locations and in different generations were scaled by dividing for the standard deviation itself, in order to obtain similar variance. The levels of class variables are as follows: two levels of sex (male, female); three generations (2002, 2005, and 2008); two hundred and thirteen families involved; and nine farming locations (*Table 2.1*).

2.2. Statistical analysis

DMU-package (Madsen and Jensen, 2002) uses mixed model equation (MME) base on Average Information Restricted Maximum Likelihood (AI-REML) with Crash Recovery. The methods for computing here are combined between EM (Expectation Maximization) and AI (Average Information).

For body weightat harvesting, estimates of the fixed effects and variance components for the random effects were obtained using linear mixed animal model in DMU. The best fitted models were chosen after testing the significant levels of all effects. Random effects such as generation, location, sire, dam and family were tested by comparing the log likelihood of the full-model (with the tested effect included) and the reduced model (without the tested effect) at 95% confidence.

In matrix notation, the model can be written: $\mathbf{y=Xb+Z_1a+Z_2f+e}$ (model 1)

Where:**y** is the vector of individual body weight, **b** is a vector of fixed effects, i.e., sex and (co)variable age for rearing at cages and weight at tagging, **a** is the vector of random additive genetic effect of individual animals, **f** is the vector of random effects common to full-sibs caused by factors other than additive genetics (i.e., environmental effect caused by the separate rearing of each full-sib family until tagging (tank effect), maternal effects and possible dominance effect; and **e** is the vector of individual random error effects. $\mathbf{X}$, $\mathbf{Z}_1$, and $\mathbf{Z_2}$ are known design matrices assigning observations to levels of **b**, **a** and **f**, respectively.

The full-sib families were assumed to be unrelated but the additive genetic relationship matrix among offspring such as full- and half-sib relations were accounted for in the model.

Heritability was estimated by univariate models (model 1) and genetic correlations between traits are using bivariate models (model 2). Model 2 is the same as model 1 but without the random effect of families. Model 2 was also used to estimate G×E for body weight in each generation. Since trait was recorded in different locations on different animals, there is no phenotypic correlation among locations. The (co)variances of residuals are set to non-existence in the model directive DMU file (Appendix B) in order to run G×E.

The (co)variance components, phenotypic correlation (r_p), genetic correlations (r_g), and their standard errors (*SE*) are calculated by DMU. Additionally, output files from DMU contain estimated (co)variance components that are needed to calculate these parameters.

According to Falconer and Mackay (1996), generally, heritability (h^2) for harvest body weight in different locations and for other traits is calculated as

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

Where σ_a^2 is additive genetic variance, σ_c^2 is common variance and σ_e^2 is the residual variance

Genetic correlation between trait a and b ($r_{a,b}$) is calculated by

$$r_{a,b} = \frac{\sigma_{ab}^2}{\sigma_a . \sigma_b}$$

Where σ_{ab}^2 is covariance between trait *a* and *b,* σ_a *and* σ_b are standard deviation of additive genetic *a* and *b*, respectively

Genotype by environment (G×E) interaction was calculated as

$$r_g = \frac{COV\ (A_{LOCATION\ 1}, A_{LOCATION\ 2})}{\sigma_{A_{LOCATION\ 1}} . \sigma_{A_{LOCATION\ 2}}}$$

Where A denotes additive genetic effects and σ_A denotes the corresponding standard deviation.

3. RESULTS

3.1. Descriptive statistics

Number of records, age and weight for each location and generation are presented in *Table 3.1, Table 3.2,* and *Table 3.3*. Some locations had limited number of records (<400 to < 1,000, *Table 3.1).* Age at tagging was quite similar among locations and generations, with an average of 209 days, at which fish weighed on average 26 g. However, age at harvest varied widely among locations, ranging from 1.5 to 3.0 years. More specific, ages at harvest for G1, G2 and G3 were approximately 3.0, 2.0 and 1.5 years, respectively. Accordingly, HBW was reduced from 2002 to 2008, from 2.2 to 1.5 and eventually 1.1 kg (*Table 3.1).* Therefore, the magnitudes of estimated heritability are expected to be varied among generations due to differences in age.

Table 3.1. *Age and body weight of animals (±SD) at tagging and harvesting at different locations in different generations*

Location	Generation	# of records	AAT (day)	AAH (day)	TW (g)	Age (year)	HBW (g)
Averøy	2002	1,549	202±9.3	778±10.5	26 ± 10.5	2.7	2,406±614
Tromsø	2002	366	203±9.3	905±10.6	29±10.5	3.0	1,873±459
Averøy 1	2005	3,606	214±6.5	572±61.7	25± 07.3	2.2	1,570±351
Averøy 2	2005	3,625	214±6.5	574± 58.4	25± 07.3	2.2	1,561±343
Gildeskål	2005	1,698	214±6.5	457± 09.6	24± 07.6	1.8	1,275±323
Averøy	2008	967	199±8.3	435±0 3.7	27± 08.2	1.7	1,381±319
CodFarmers1	2008	782	199±8.8	332± 03.7	27± 08.4	1.5	874±256
CodFarmers 2	2008	407	200±8.1	332± 03.8	27± 07.7	1.5	912±256
Gildeskål	2008	2,548	199±8.2	339± 04.8	28± 08.7	1.5	1,035±302
Sum/average		15,548	209	512	26	2.0	1,418

AAT=age at tagging, AAH=age at harvest, TW=tag weight, HBW=harvest body weight.

The rearing stage in tanks (before tagging) realised slow growth rate, that is, it took nearly 7 months for the fish to reach the size for tagging (26 g). After that, when fish were transferred to the cages, faster growth was obtained. Fish reached 1.4 kg after 14 months, 1.6 kg after 20 months and 2.4 kg after 25 months in cages for Averøy. In 2002, fish reared in Averøy realised the best growth rate, that is, 2.4 kg after 2.7 years. In contrast, fish reared in Tromsø was on average 1.9 kg after 3 years. This could probably due to the higher temperature and longer day-light in a year at Averøy.

Table 3.2. *Age and body weight (±SD) in different locations and generations, by sex.*

Sex	Generation	# of records	AAT (day)	AAH (day)	TW (g)	HBW (g)
Male	2002	321	202.0±9.9	834.0±64.0	28.0±10.4	2,326±600
Female	2002	242	203.0±8.1	811.0±57.1	28.0±11.9	2,180±585
Unknown	2002	163	204.0±8.2	905.0±13.6	30.0±09.9	1,695±376
Male	2005	460	214.0±6.5	419.0±34.0	25.0±07.3	1,222±267
Female	2005	837	213.0±6.4	449.0±53.9	24.0±07.5	1,255±274
Unknown	2005	7,630	213.0±6.6	570.0±54.3	25.0±07.4	1,560± 359
Male	2008	416	199.0±8.6	416.0±38.0	28.0±8.1	1,394±329
Female	2008	658	199.0±8.5	385.0±47.6	29.0±8.1	1,242±267
Unknown	2008	533	199.0±8.5	341.0±13.4	31.0±8.5	1,242±254

AAT=age at tagging, AAH=age at harvest, TW=tag weight, HBW=harvest body weight

The average HBW of male was slightly greater than that of female in the same generation, except for the generation 2005, where HBW of females was 33g heavier than that of males. There was a large number of fish with unknown sex in 3 generation, but their HBW was not much smaller than that of the males or females (*Table 3.2*). Most noticeable was in 2005, with 7,630 animals had their sexes undetermined, accounting for approximately 80% of all records. This, of course, increased the error term when sex was fitted into the models used.

Table 3.3. *Average weight and body length and other traits (±SD) in 3 generations, recorded only in Averøy.*

Generation	HBW (g)	GBW (g)	BL(cm)	FW (g)	HW (g)	LoW (g)	LiW (g)	GW (g)
G1-2002	2,413±604.0	1,860±444.7	54±4.0	1,192±321.3	NA	NA	288±101.6	NA
G2-2005	1,390±248.7	1,084±165.5	45±2.9	615±131.3	201±34.2	265±63.9	151±37.7	109±23.7
G3-2008	1.246±310.1	975±231.1	47±3.0	547±145.2	183±40.4	NA	131±47.0	99±51.2

NA=not available, HBW=harvest body weight, GBW=gutted body weight, BL=body length, HW=head weight, LoW=loin weight, LiW=liver weight and GW=gonad weight.

Table 3.3 shows mean values of other measurements on slaughter fish (only recorded at Averøy). Traits such as HBW, GBW and LoW are now the most economic important breeding goal in a cod breeding program. Ratios between other traits with HBW give insights into their proportion compared to the whole body weight. For example, for 3 year-old-fish, GBW accounted for 77%, and FW 49% of whole body weight. For generation 2005, the

numbers were 78% and 44%; while for generation 2008, the numbers were 78% and 44%. The trend was similar among 3 generations for other ratios, for instance, LiW accounted for 11 – 12% of whole body weight, while LoW and HW proportion accounted for 19% and 14.5% of total fish weight respectively. Gonad weight was depends on the maturation of the fish, and in general it accounted for 8% of whole body weight (*Table 3.3).*

3.2. Heritability and genotype by environment (G×E) interaction among locations of rearing in each generation for body weight

Table 3.4, Table 3.5, and *Table 3.6* presented estimate for heritability (h^2) on the diagonal, genetic correlations (r_g) below the diagonal with their corresponding standard error (±*SE*) for harvest body weight in 3 generations. The estimates of heritability in every generation were used all generation data with presence of location as a random effect in the mixed model.

Table 3.4. *Genetic parameters estimated (on the diagonal: heritability, below diagonal: genetic correlation between two locations) for G1-2002.*

Locations	Averøy	Tromsø
Averøy	**0.86±0.47**	
Tromsø	0.95±0.10	**0.14±0.05**

For G2-2002, there was the large different in estimated h^2 in Averøy (0.86) and Tromsø (0.14). Estimation of heritability in Averøy had large *SE* (0.47), probably indicated a large variation among individuals. The genetic correlation (r_g) was high (0.95), indicating no genotype by environment (G×E) interaction between 2 locations for HBW (*Table 3.4*). When combining data from 2 locations, heritability estimate was very high as well (0.54±0.15), accounting for nearly 28% of the total variance.

Table 3.5. *Genetic parameters estimated (on the diagonal: heritability, below diagonal: genetic correlations among locations) for G2-2005.*

Locations	Averøy1	Averøy2	Gildeskål
Averøy1	**0.34±0.11**		
Averøy2	0.99±0.01	**0.48±0.11**	
Gildeskål	0.87±0.05	0.81±0.06	**0.11±0.06**

Heritability estimates in 3 locations were from 0.11 to 0.48. Gildeskål had lowest h^2 (0.11), while Averøy2 revealed the highest h^2 (0.48). Heritability estimate for G3-2008 (data from 3 locations combined) was high (0.29±0.04). Genetic correlations between locations were high (0.81 – 0.99) with small *SE* (0.01 – 0.06). The genetic correlation between Averøy1 and Averøy2 was very high (0.99±0.01), indicating no G×E.

Table 3.6. *Genetic parameters estimated (on the diagonal: heritability, below diagonal: genetic correlations among locations) for G3-2008.*

Locations	Averøy	CodFarmers1	CodFamers2	Gildeskål
Averøy	**0.24±0.13**			
CodFarmers1	0.79±0.11	**0.36±0.15**		
CodFarmers2	0.87±0.13	0.95±0.09	**0.25±0.10**	
Gildeskål	0.58±0.16	0.72±0.12	0.64±0.17	**0.29±0.11**

For G3-2008, the genetic correlation was medium to high (0.58 – 0.95). The range were, however, wider compared to the two previous generations, with high SE (0.06 – 0.17) among locations. Genetic correlation between CodFamers1 and Codfarmers2 was highest (0.95), and genetic correlations among these locations with Averøy were also high, 0.79 and 0.87 respectively. Genetic correlations for Gildeskål and CodFamers1 & CodFamers2 were moderate to high (0.64 and 0.72), except for Averøy with medium r_g (0.58) (*Table 3.6*). When combined all data, heritability estimate was 0.22±0.04, while heritability estimates for the locations separately ranged from 0.24 to 0.36 with small *SE* (0.06 – 0.08) (*Table 3.6*).

3.3. Genetic parameters estimation for other traits in generation 2005

For generation G2-2005, several traits were measured on the same animal, allowing estimations of genetic and phenotypic correlation among more traits to be generated (*Table 3.7*).

Table 3.7. *Heritability (on the diagonal), phenotypic correlation (above diagonal) and genetic correlation with ±SE for other traits (below diagonal) for G2-2005.*

Traits	HBW	GBW	BL	FW	HW	LoW	LiW	GW
HBW	**0.18±0.20**	0.990	0.847	0.979	0.899	0.875	0.898	0.470
GBW	0.993±0.002	**0.21±0.19**	0.860	0.989	0.889	0.889	0.866	0.398
BL	0.893±0.032	0.91±0.030	**0.43±0.17**	0.829	0.825	0.748	0.688	0.305
FW	0.991± .003	0.997±0.001	0.895±0.032	**0.23±0.19**	0.856	0.924	0.870	0.404
HW	0.909±0.026	0.905±0.027	0.844±0.043	0.876±0.035	**0.06±0.18**	0.741	0.707	0.292
LoW	0.981±0.012	0.981±0.011	0.876±0.042	0.995±0.005	0.815±0.055	**0.20±0.17**	0.773	0.356
LiW	0.873±0.035	0.836±0.044	0.710±0.074	0.851±0.041	0.691±0.076	0.857±0.046	**0.28±0.21**	0.426
GW	0.536±0.110	0.505±0.117	0.350±0.134	0.523±0.115	0.328±0.137	0.569±0.114	0.437±0.124	**0.43±0.20**

HBW=harvest body weight, GBW=gutted body weight, BL=body length, HW=head weight, LoW=loin weight, LiW=liver weight and GW=gonad weight

Phenotypic correlations (r_p) among traits were from moderate to very high, ranging from 0.69 to 0.99, except for GW (<0.47). The highest r_p were found to be among HBW and GBW, GW and FW, LoW and FW. LiW revealed high r_p (>0.71) with other traits, except with GW (0.36). Genetic correlations were slightly higher than corresponding phenotypic correlations. For example, r_g versus r_p for HBW and GBW, HBW and BL, FW, and HBW were 0.993>0.990, 0.893>8847, and 0.991>0.979 respectively.

There were strong genetic correlations between HBW, GBW, FW and LoW, with value of over 0.8. Gonad weight revealed less correlations with the others (ranging from 0.44 to 0.54) while LiW, HW, BL had also high genetic relations with HBW, 0.87, 0.91 and 0.89, respectively.

The heritability estimates were very low for HW (0.06) with high *SE* (0.18) and quite high for BL and GW (0.43). In most traits, the medium h^2 were obtained, for example, HBW (0.18), GBW (0.21), FW (0.23), LoW (0.20), and LiW (0.28). However, most estimates had relatively high *SE*, and thus reduce reliability.

4. DISCUSSION

4.1. Statistical description and effect of fixes, random factors on harvest body weight

In generally, harvest body weight is the trait with highest number of records that obtained from 15,548 animals, are used for testing fix and random factors (Appendix A, *Table 1a*).There was a large difference in mean harvest body weight within and across generation, from 874 to 2,406 g (*Table 3.2*). This can be understood by different time of rearing as already mentioned here. The mean weight of male was relatively heavier than that of female, differed from results reported by Gjerde *et al.* (2004), Kolstad *et al.* (2006a) and Kolstad *et al.* (2006b).

Age and weight at tagging in nine locations were statistical significant difference (T-test for means, $p<0.001$). Thus, these parameters should take account into the model as covariate factors for correcting harvest body weight when calculating heritability and genetic correlation. Tests run by ASReml using the same model (results not shown) showed that sex, tagging weight and age of rearing were highly significance ($p<0.001$) on the models used.

The random effects included sire, dam, location, year-class, and family (*Table 1a*). In this study, the mating design was 1 dam × 2 sires, thus the effects of sire and family were expected to be similar, because the number of sires (195) was almost the same as the number of families (213 families). On the other hands, the effect of dam is expected to be larger. However, the log likelihood ratio test (LRT) for effect of sire and dam did not support this hypothesis (χ^2=0.8, df=2, $p=0.371$), while location and generation were highly significant ($p<0.001$) compare to effect of family ($p=0.03$) (*Table 1a*).

There were studies that tested the effects of 'dam' and 'family', but not for 'sire', in Atlantic cod. Family effect that consisted of maternal, sire and additive effect were used as an important effect when analysing recent data of cod breeding (Gjerde and Gjedrem, 1984; Gjerde *et al.*, 1994; Gjerde *et al.*, 2004; Kolstad *et al.*, 2006b; Kolstad *et al.*, 2006a; Garber *et al.*, 2010; Tosh *et al.*, 2011). Tosh *et al.* (2011) reported the effects of dam and family/tank on genetic variance of Atlantic cod at two years of age. According Tosh *et al.* (2011), there was a strong effect of dam on body weight at tagging, accounting for 15% of total variance. However, the effect of dam was not significant on body weight ($p=0.854$) at 2 years of age (3% of total genetic variance). Furthermore, the effect of family was significantly at every time-point (tagging and harvest) of the same study (Tosh *et al.*, 2011). This agreed with the results from the current study. In contrast, Gjerde *et al.* (2004) found no effect of environment

effect common to full-sibs (family) on body weight, but quite different when the region effect that included in the model. This caused by the possible confounding of the effects. The confounding effect always occurs when analysing data breeding program (Mrode, 2005). Likewise, in this study, dam and sire are confounded with family (tank), effective sorted out of these effects need adequate data and model structure (Tosh *et al.*, 2011) which was limited in this study.

4.2. Heritability for harvest body weight in three generation

There are a large variation of estimated heritability in this study by locations, ranging from 0.11 – 0.86 despite large *SE* (*Table 3.4*). It seemed the gain of h^2 will reduce over generation, very high in 2002 (0.54) and intermediate in 2005 (0.29) and slightly smaller than that in 2008 (0.24). These h^2 revealed here is somewhat inconsistence and larger than those cited in the literature, which is from 0.15 – 0.34. This may due to the model for calculating the proportion of additive genetic variance with absence of dam effect. According to Tosh *et al.* (2011), poor data structure or inadequate models can potentially lead to overstatement of heritability and thus also of the predicted selection response. For instance, omitting family or dam from the full model would inflate the h^2 although dam proved no significant effect (Tosh *et al.*, 2011)

Additive genetic variation was evident for growth of cod at different time-points in this study. Estimated of h^2 increases with time Tosh *et al.* (2011) agreed what were found here for G1, G2 and G3 as described above (*Table 3.4, Table 3.5 and Table 3.6).* However, most literature cited here calculated the heritability at almost two years of age (the same with G2 in the report). Kolstad *et al.* (2006a) suggested the weight at two years old may be used as a criterion for growth in Atlantic cod, with h^2 was quite high (0.64±0.12) at that time.

To be extend, in comparison with Atlantic salmon, the h^2 estimated for harvest body weight of Atlantic cod was higher than reported by Gjerde *et al.* (1994) from 0.10 – 0.32 for six traits observed, by Gjerde and Gjedrem (1984) from 0.38 – 0.44 for harvest body weight of Atlantic salmon and harvest weight of rainbow trout (0.19 – 0.32). The larger estimated for h^2 give good prospects for genetic improvement of growth rate in Atlantic cod.

4.3. Heritability and genetic correlation between body weight and other traits recorded

There are 870 animals of total 86 families were analysed to obtained heritability and genetic correlation for those traits (*Table 3.7).* A model 2 was used without family effect to obtained genetic correlations among traits due to the small number of observations and some families did not have enough recording. The genetic correlation between HBW, maturation and disease resistance have previous mentioned by many studies. Whereas, there is no estimate of such these traits on Atlantic cod are going to discuss here, especially for the carcass quality trait, FW, LiW and GW.

The resultant from *Table 3.7* showed that high genetic correlations (r_g>0.70) between HBW, GBW and FW with BL, HW and LoW. The strong and significant correlations were found for HBW, GBW and FW (r_g>0.97). Kristjánsson (2011) reported the estimates on his report on Atlantic cod for some trait such as GBW, LW and fillet yields. All r_g estimations here are slightly higher than of that study. For example, the estimate of genetic correlation (Kristjánsson, 2011) between LiW with HBW and GBW is 0.67 and 0.42 respectively. In this study, the corresponding values are 0.87 and 0.84. The genetic correlations between traits of this study were slightly bigger than what reported by Garber *et al.* (2010). For instance, high r_g were found between HBW versus BL, bled weight, carcass weight, LW and GW with 0.83; 0.98; 0.94; 0.91; and 0.56. In this study, the corresponding r_g were 0.89; 0.99; 0.99; 0.98; and 0.54. The strong and significant correlation between traits other than HBW indicated the good genetic links of those traits at two years of age. The correlation between BL and HBW is also high (nearly 0.9) while GW revealed less correlation with other traits, range 0.33 – 0.57. These resultants gave the basic and first glance at traits characteristic in Atlantic cod farming at two years old.

For harvest body weight, the h^2 showed here was low and high degree of *SE* (0.18±0.20) probably indicated the high variation for additive genetic among individuals. Heritability of other traits were low to mediate (0.06 – 0.43) with high *SE* if compare to proportion of additive genetic. According to Garber *et al.* (2010), estimates of heritability of most observed traits such as HBW, BL, bled weight, carcass weight, LiW, GW and total skin weight were high for Canadian cod populations (0.35 – 0.39), GW had low h^2(0.11) that was lower in the current study (0.43). The heritability of BL (0.43) is likely the same of estimated by Kettunen and Fjalestad (2007), from 0.31 – 0.48 and slightly bigger of Tosh *et al.* (2011)

report, with value of 0.31. The moderate heritabilities were found for GBW (0.21), FW (0.23), LoW (0.20) and LiW (0.28). Head weight showed a very low h^2 (0.06), whereas h^2 of GW was high (0.43). This result gave the information of such traits at the first time of calculation; however, more data is needed to confirm this further.

4.4. Genotype by environment (G×E) interaction for the trait body weight

Generally speaking, the r_g seemed bigger in older cod fish. According to (Tosh *et al.*, 2011), the genetic correlation between the time of tagging and harvesting is 0.95 and at 2 year of age and harvesting (0.89) by Kolstad *et al.* (2006a). A high genetic correlation (0.64 – 0.76) were found by Kettunen and Fjalestad (2007) between the weight at tagging, one year+ and two year+ and low genetic correlation between most distance measurements.

The genetic correlation between locations that presented in *Table 3.4*, *Table 3.5* and *Table 3.6* varied from 0.58 to 0.99 for nine locations in three generations. There were high genetic correlations between Averøy and Tromsø in 2002, with r_g=0.95 and between location at generation 2005, ranged from 0.81 to 0.99 with relatively low *SE*, indicating no genotype by location of rearing in the first two generations for HBW in the current breeding program. This also agreed with previous studies (Kolstad *et al.*, 2006b; Kolstad *et al.*, 2006a; Tosh *et al.*, 2011).

The generation 2008, however, presented much different from two previous generations (*Table 3.6*). No G×E has been found between CodFarmers2 and Averøy, CodFarmer2 and CF1, with r_g were 0.87 and 0.95 respectively. Otherwise, mild G×Es were obtained when fish reared at CodFarmers1 and Averoy, CodFarmers1 and Gildeskål, with value of r_g were 0.79 and 0.64, respectively. Fish reared at Gildeskål had low genetic correlation when comparing with Averøy and CodFarmers2 (0.58 and 0.64), indicated the existence of G×E to some extent. On the other hand, genetics correlations are very imprecise (Falconer, 1981) as the larger *SE* show (*Table 3.6*). These results in 3 generation also showed the magnitude of genetic variation by different age (1.5; 2.0; and 3.0 years of age).

5. CONCLUSION

Heritability were estimated for three generations (2002, 2005 and 2008), and for harvest body weight they were medium to high, 0.54±0.15, 0.29±0.04 and 0.22±0.04, respectively. Thus, there should be a good potential for improvement of growth rate by selection in the on-going breeding program.

Furthermore, heritability was also estimated for traits other than harvest body weight for generation G3-2005. Moderate heritability was obtained for gutted body weight (0.21±0.19), fillet weight (0.23±0.19), loin weight (0.20±0.17) and liver weight (0.28±0.21). Body length and gonad weight had high heritability, 0.43±0.17 and 0.43±0.20, respectively. The medium to high heritability in most recorded traits (except for head weight with 0.06±0.18) assure the potential of improvement for these traits in the breeding program as well.

When estimating the genetic correlation among all the investigated traits, we obtained extremely high genetic correlations (0.98 – 0.99) between harvest body weight with gutted body weight, fillet weight, and loin weight. In addition, genetic correlation between traits remained high (0.71 – 0.9). Gonad weight have lower genetic correlations with the other traits (0.29 – 0.47). The high genetic correlation among some of the traits indicated that they are genetically highly related, and that they are probably controlled by many of the same genes. Selection of one trait might thus improve other traits as well.

There were strong genetic correlations between performance at each location of rearing within each generation ($0.58<r_g<0.95$). Therefore, at the moment, there should be no need to separate the breeding program into different strains to meet the specific requirements of the different environment. Other assessment in subsequence generations may be necessary to further evaluate G×E.

It seemed that we obtained genetic parameters for the current breeding program over three generations with relatively high standard errors. That was probably caused by the limited number of records in each generation, locations and families, and it would be necessary to conduct more analysis with larger data set to get more accurate estimates.

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APPENDIX

Appendix A. Test results regard to the test of fix and random factors

Table 1a. *Likelihood ratio test for comparing significance random effects*

Model	Chi-square score	df	*P-value*
Full model			
Generation	173.7	1	<0.0001
Location	297.6	1	<0.0001
Sire	-0.00004	1	~ 1
Dam	0.80	1	0.370
Family	4.3	1	0.038
Sire+Dam	0.80	2	0.371

Appendix B. Four driver are used in running DMU for this report

Driver file 1

```
$COMMENT
Dmuai to estimate h2 of harvest body weight in Averøy, 2002.

$ANALYSE 1 1 0 0

$DATA ASCII (7,8,-9999) 2002

$VARIABLE
sex y-class location sire dam family ID
Age_tank age_cage tag_wt w_corrected Age_tank2 age_cage2 tag_wt2 w_corrected2

$MODEL

1
0
4 0 3 1 6 7
2 2 1
2 1 2
0

$VAR_STR 1 PED 2 ASCII ped1204

$DMUAI
10
1.0d-7
1.0d-6
1
0
0
```

Driver file 2

```
$COMMENT
DMUAI-estimate genetic correlation (to find G×E) for harvest body weight in Averøy and
Tromsø, 2002.

$ANALYSE 1 1 0 0

$DATA ASCII (7,8,-9999) 2002

$VARIABLE
sex y-class location sire dam family ID
Age_tank age_cage tag_wt w_corrected Age_tank2 age_cage2 tag_wt2 w_corrected2

$MODEL
2
0
0
4 0 2 1 7
8 0 2 1 7
1 1
1 1
2 1 2
2 5 6
1
1 2


$VAR_STR 1 PED 2 ASCII ped1204

$DMUAI
10
1.0d-7
1.0d-6
1
0
0
```

Driver file 3

```
$COMMENT
DMUAI-for estimate genetic correlation gutted body weight versus fillet weight for animal in
Averøy, 2005.

$ANALYSE 1 1 0 0

$DATA ASCII (5,12,-9999) 2005

$VARIABLE

Y-class sex location family ID
Age_tag Age-harv tag_wt har_len Har-def har_wt gut-wt head-wt fillet_wt Lo_wt liver_wt
gonad_wt


$MODEL
2
0
0
9 0 2 2 5
7 0 2 2 5
1 1
1 1
2 2 3
2 2 3
0
0

$VAR_STR 1 PED 2 ASCII ped1204


$DMUAI
10
1.0d-7
1.0d-6
1
0
0
```

Driver file 4

```
$COMMENT
DMUAI-estimate heritability for gutted body weight in Averøy 1 & 2 in 2005.

$ANALYSE 1 1 0 0

$DATA ASCII (5,12,-9999) 2005

$VARIABLE

Y-class  sex desti Fami ID
Age_tag Age-harv tag_wt har_len Har-def har_wt gut-wt head-wt fillet_wt Lo_wtliver_wt
gonad_wt

$MODEL

1
0
7 0 4 2 3 4 5
3 3 2 1
2 2 3
0
0

$VAR_STR 1 PED 2 ASCII ped1204

$DMUAI
10
1.0d-7
1.0d-6
1
0
0
```