Genetic variance for uniformity of body weight in lumpfish (*Cyclopterus lumpus*) used a double hierarchical generalized linear model

Panya Sae-Lim[a,1], Hooi Ling Khaw[a,*], Hanne Marie Nielsen[a,2], Velmurugu Puvanendran[b], Øyvind Hansen[b], Atle Mortensen[b]

[a] *Breeding and Genetics, Nofima, P.O. Box 210, N-1431 Ås, Norway*
[b] *Production Biology, Nofima, P.O. Box 6122, Tromsø NO-9291, Norway*

ABSTRACT

Lumpfish (*Cyclopterus lumpus*) is the most widely use biological pest control agent to delouse sea lice on Atlantic salmon (*Salmo salar*). From 2012 to 2017, the production of lumpfish has increased from less than two million individuals to more than 30 million individuals in Norway alone. To meet the increasing market demand for lumpfish and to ensure sustainable production in the future, we need to domesticate the wild stocks and establish a breeding program for lumpfish. One of the most important traits in lumpfish, the genetic property for uniformity of body weight was investigated. In 2015, wild broodstock of lumpfish were collected from Southern and Northern coastal regions of Norway. A total of 68 full-sib families were produced and 7588 lumpfish juvenile were measured for body weight at tagging. A sire-dam double hierarchical generalized linear model was used to estimate the genetic parameters for body weight and its uniformity. Body weight was transformed by standardized and log scales. The heritabilities for uniformity of body weight in both scales, were low at 0.014 and 0.021 for the standardized and log scales, respectively. However, the genetic coefficient of variation for uniformity were relatively high, 45.8% and 63.5% (for standardized and log transformation), indicating that uniformity of body weight for lumpfish are substantially under genetic control. The genetic correlation between body weight and its uniformity was estimated. For the standardized transformation, the genetic correlation was -0.055 ± 0.252 (close to zero), and for the log transformation, the estimate was -0.813 ± 0.114. Both genetic correlations suggest that it is possible to simultaneously select for body weight and uniformity of body weight without a trade-off in genetic gain. In conclusion, there is substantial genetic variation for uniformity of body weight in lumpfish and the potential to select on this trait is promising.

1. Introduction

Cleaner fish as biological pest control agent for sea lice on Atlantic salmon (*Salmo salar*) has become one of the best alternatives to medicinal solution (Imsland et al., 2016a). Currently, lumpfish (*Cyclopterus lumpus*), the most suitable cleaner fish, is the third most valuable species in Norway, after Atlantic salmon (*Salmo salar*) and rainbow trout (*Oncorhynchus mykiss*) (Holmyard, 2018). In Norway, in terms of sale to Atlantic salmon and rainbow trout sea farms, lumpfish production has increased from 0.4 million individuals in 2012 to 30.3 million individuals in 2017 (Norway Directorate of Fisheries, 2018). With the increasing demand, domestication of wild stocks and establishing a breeding program for lumpfish are top priorities. These will allow the

wild stocks to adapt to rearing environments, make it possible to select for economically important traits, and to minimize rate of inbreeding. However, before establishing a breeding program, information about important production traits and their genetic variations need to be understood.

The variation in growth rate for commercially produced lumpfish is usually large. Generally, the deployment size of lumpfish to commercial sea-cages is around 20 g (Imsland et al., 2016a). Imsland et al. (2016a, 2016b) showed that lice eating ability in lumpfish decreases with increasing size of lumpfish. In accordance with this, it is a common view among salmon farmers that lumpfish above 400 g are inefficient lice eaters. Thus, it is important to produce more uniform stocks of lumpfish before deploying to Atlantic salmon cages. Large variation in body size

among individuals may also increase competitive interactions, contributing to dominant behavior and stress in subordinate fish, consequently reducing animal welfare (Ahvenharju and Ruohonen, 2007; Dou et al., 2004; Nielsen et al., 2014). From a selective breeding point of view, optimal growth (not too fast growth nor too slow growth) may improve sea-lice eating activity of lumpfish in Atlantic salmon cages.

Phenotypic variability is explained by environmental variance which indicates presence of micro-environmental sensitivity. Micro-environmental sensitivity can be defined as a change in environmental variance due to sensitivity to unknown environmental factors (i.e. unidentifiable factors that cannot be quantified or categorized) and subtle development (i.e. internal abnormal development that cannot be observed externally and will not cause phenotypic variation), which contributes to increased phenotypic variation, leading to increased size variation within a population (Sae-Lim et al., 2016). If genetic heterogeneity of environmental variance exists, selection for lower environmental variance will enable us to increase uniformity in growth of the fish. Heterogeneity of environmental variance has not previously been estimated for growth in lumpfish. Hence, the aim of this study was to quantify genetic parameters for body weight and uniformity of body weight in lumpfish.

2. Materials and methods

2.1. Data

The data used in this study was generated from Center for Marine Aquaculture (CMAQ), Tromsø, Norway. In 2015, fertilized eggs from wild broodstocks were obtained from commercial lumpfish producers, Norsk Oppdrettservice AS and Akvaplan Niva. The broodfish used were caught by local fishermen from Southern (Flekkefjord, 58.2° N, 6.6° E) and Northern coastal regions (Sommarøy 69.3° N, 18.0° E) of Norway. A total of 23 sires and 60 dams were mated using a nested mating design to produce 68 full-sib families (Table 1). Out of these 68 full-sib families, 11 were paternal half-sib and seven maternal half-sib (no overlapping of paternal and maternal half-sib families). The number of progeny produced by each full-sib family were ranged from 90 to 140 fish. After hatching, lumpfish fingerlings from the same full-sib family were separately reared in 125 l circular tanks using standard rearing protocols implemented at CMAQ until they reached the taggable size, which is at a mean body weight of approximately 20 g. Each lumpfish juvenile was tagged using passive integrated transponder (PIT) and was individually weighed using electronic balance Sartorius QC7DCE-S. The phenotypic data comprised 7588 records of individual lumpfish juvenile body weight at tagging.

2.2. Statistical analysis

For many morphological traits, a positive correlation between mean and variance, also known as scale effect, is expected. Previous studies indicated that data transformation, for example log-transformation, results in a trait variation that does not depend on the scale effect (Lande, 1977; Sonesson et al., 2013). Thus, in this study, body weight at tagging was transformed in two different ways, which were

Table 1
Population structure of lumpfish.

Population parameter	Value
Sire	23
Dam	60
Full-sib family	68
Paternal half-sib	11
Maternal half-sib	7
Average progeny per full-sib family	111.6
Total number of progeny	7588

standardization and log transformation. In standardization (STDWT), individual body weight at tagging were standardized to a mean of 0 and variance of 1 to rescale the original data, which facilitates convergence (Sae-Lim et al., 2015). In the second transformation, individual body weight at tagging were log-transformed (LOGWT) to reduce dependency of variance on mean or the scale effect.

To estimate (co) variance components for body weight and its uniformity, a double hierarchical generalized linear model (DHGLM) was used (Rönnegård et al., 2010). Both STDWT and LOGWT data were modelled using the sire-dam DHGLM in ASReml (Felleki et al., 2012; Gilmour et al., 2009):

$$
\begin{bmatrix} \mathbf{y} \\ \mathbf{\Psi} \end{bmatrix}
= \begin{bmatrix} \mathbf{X} & \mathbf{0} \\ \mathbf{0} & \mathbf{X}_v \end{bmatrix} \begin{bmatrix} \mathbf{b} \\ \mathbf{b}_v \end{bmatrix} + \begin{bmatrix} (\mathbf{Z}_s + \mathbf{Z}_d) & \mathbf{0} \\ \mathbf{0} & (\mathbf{Z}_s + \mathbf{Z}_d)_v \end{bmatrix} \begin{bmatrix} \mathbf{u} \\ \mathbf{u}_v \end{bmatrix} + \begin{bmatrix} \mathbf{Q} & \mathbf{0} \\ \mathbf{0} & \mathbf{Q}_v \end{bmatrix}
$$
$$
\begin{bmatrix} \mathbf{c} \\ \mathbf{c}_v \end{bmatrix} + \begin{bmatrix} \mathbf{e} \\ \mathbf{e}_v \end{bmatrix}
$$

where, $\mathbf{y}$ is the vector of either STDWT or LOGWT for the ith individual; $\mathbf{\Psi}$ is the vector of response variables for the residual variance, where $\psi_i = \log(\hat{\sigma}_{e_i}^2) + \frac{\frac{\hat{e}_i^2}{1-h_i} - \hat{\sigma}_{e_i}^2}{\hat{\sigma}_{e_i}^2}$, which was linearized using a Taylor series approximation in ASReml (Felleki et al., 2012), $\hat{e}_i^2$ is the squared residual of the ith STDWT, h_i is the diagonal element in the hat-matrix of $\mathbf{y}$ (predicted value matrix) (Hoaglin and Welsch, 1978), and $\hat{\sigma}_{e_i}^2$ is the predicted residual variance of the ith observation in the previous iteration of ASReml; $\mathbf{X}$ and $\mathbf{X}_v$ are incidence matrices of the fixed effect (covariate of age at tagging) for the trait mean and its uniformity, respectively; $\mathbf{b}$ ($\mathbf{b}_v$) is the solution vector for the corresponding fixed effect; $\mathbf{Z}_s$ and $\mathbf{Z}_d$ are incidence matrices for the random sire (s) and dam (d) effects; $\mathbf{u}$ ($\mathbf{u}_v$) is the vector of additive genetic effects of sire-dam on either STDWT or LOGWT (uniformity), which was assumed to follow a normal distribution:

$$
\begin{bmatrix} u \\ u_v \end{bmatrix} \sim N \left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \frac{1}{4} \begin{bmatrix} \sigma_a^2 & \sigma_{a,a_v,exp} \\ \sigma_{a,a_v,exp} & \sigma_{a_v,exp}^2 \end{bmatrix} \otimes A \right)
$$

where the 1/4 accounts for the fact that the sire and dam each explain only a quarter of the additive genetic variance for growth ($\sigma2_a$) and its uniformity on the exponential scale ($\sigma2_{a_v, exp}$). The $\sigma_{a, a_v, exp}$ is the additive genetic covariance between growth and its uniformity; $\mathbf{Q}$ ($\mathbf{Q}_v$) is the incidence matrix for the random common effects to full-sibs; $\mathbf{c}$ ($\mathbf{c}_v$) is the vector of common effects to full-sibs:

$$
\begin{bmatrix} c \\ c_v \end{bmatrix} \sim N \left(\begin{bmatrix} 0 \\ 0 \end{bmatrix}, \begin{bmatrix} \sigma_c^2 & \sigma_{c,c_v,exp} \\ \sigma_{c,c_v,exp} & \sigma_{c_v,exp}^2 \end{bmatrix} \otimes I \right)
$$

where σ^2_c and $\sigma^2_{c_v, exp}$ are common environmental variances for growth and its uniformity and $\sigma_{c, c_v, exp}$ is the common environmental covariance. The residuals of $\mathbf{y}(\mathbf{e})$ and $\mathbf{\Psi}(\mathbf{e}_v)$ were assumed to be independently normally distributed as follows:

$$
\begin{bmatrix} e \\ e_v \end{bmatrix} \sim N \left(\begin{bmatrix} \mathbf{0} \\ \mathbf{0} \end{bmatrix}, \begin{bmatrix} \mathbf{W}^{-1}\sigma_e^2 & \mathbf{0} \\ \mathbf{0} & \mathbf{W}_v^{-1}\sigma_{e_v}^2 \end{bmatrix} \right), \quad \text{where} \quad \mathbf{W} = \text{diag}(\hat{\mathbf{\Psi}}^{-1}) \quad \text{and}
$$

$\mathbf{W}_v = \text{diag}\left(\frac{1-\mathbf{h}}{2}\right)$, and σ^2_e ($\sigma^2_{e_v}$) is a scaled variance that was expected to be 1. The sire-dam DHGLM was fitted iteratively to update ψ, diag($\mathbf{W}$) and diag($\mathbf{W}_v$) until the log-likelihood converged (Felleki et al., 2012).

2.3. Calculation of genetic parameters

Estimates of $\sigma2_{u_v, exp}$ and $\sigma2_{c_v, exp}$ for uniformity of body weight were on the exponential scale (exp) and were converted to an additive scale ($\sigma^2_{u_v}$ and $\sigma2_{c_v}$) using the extension of the equations of Mulder et al. (2007), as derived by Sae-Lim et al. (2015). To reduce steps of calculations, the converting equations:

$$\sigma_{a_v}^2 + \sigma_{c_v}^2 = \sigma_{e,exp}^4 \exp(2\sigma_{a_v,exp}^2) \exp(2\sigma_{c_v,exp}^2) - \sigma_E^4$$

$$\sigma_{a_v}^2 = (\sigma_{a_v}^2 + \sigma_{c_v}^2) \frac{\sigma_{a_v,exp}^2}{\sigma_{a_v,exp}^2 + \sigma_{c_v,exp}^2}$$

$$\sigma_{a_v}^2 = (\sigma_{a_v}^2 + \sigma_{c_v}^2) \frac{\sigma_{c_v,exp}^2}{\sigma_{a_v,exp}^2 + \sigma_{c_v,exp}^2}$$

where, $\sigma4_E$ is the square residual variance ($\sigma_E^2 = \sigma_e^2 - 2\sigma_u^2$) from the animal model. The $\sigma2_e$ is the residual variance of body weight from a sire-dam model. For the sire-dam DHGLM, the estimated genetic variance for sire-dam ($\sigma2_u$) was equal to a quarter of additive genetic variance. Therefore, the additive genetic variance for body weight ($\sigma2_a$) and its uniformity ($\sigma2_{a_v}$) were calculated as $4\sigma_u^2$ and $4\sigma_{u_v}^2$, respectively. Phenotypic variance ($\sigma2_P$) of body weight was equal to $2\sigma_u^2 + \sigma_c^2 + \sigma2_e$, where $\sigma2_c$ is the variance component for the effect common to full-sibs. Heritability estimate for body weight (h^2) was calculated as $\sigma_a^2/\sigma2_P$ while heritability estimate for uniformity of body weight (h_v^2) on the additive scale was calculated as $\frac{\sigma_{a_v}^2}{2\sigma_P^4 + 3(\sigma_{a_v}^2 + \sigma_{c_v}^2)}$ (Felleki and Lundeheim, 2013; Sae-Lim et al., 2015). Similarly, the common environmental effect was calculated as $c^2 = \sigma_c^2/\sigma2_P$ for body weight and as $c_v^2 = \frac{\sigma_{c_v}^2}{2\sigma_P^4 + 3(\sigma_{a_v}^2 + \sigma_{c_v}^2)}$ for uniformity of body weight (Sae-Lim et al., 2015). The genetic coefficient of variation for uniformity of body weight (GCV) was calculated as $\sqrt{\sigma_{a_v,exp}^2}$. The GCV is the indicator of evolvability (a population's ability to response to natural or artificial selection; Houle, 1992), which expresses the biological opportunity for response to selection, relative to the mean of phenotype. Standard errors of h_v^2 and GCV were approximated using the equations derived and presented by Mulder et al. (2016). The genetic correlation (r_g) between STDWT or LOGWT and its uniformity was calculated as $\sigma_{a, a_v, exp}$ divided by the product of the two corresponding additive genetic standard deviations. Likewise, the common environmental correlation (r_c) was calculated as $\sigma_{c, c_v, exp}$ divided by the product of the two corresponding common environmental standard deviations.

3. Results

3.1. Descriptive statistics

The descriptive statistics of the traits is presented in Table 2. The average age at tagging was 163.3 days (minimum of 149 days and maximum of 185 days). The mean of body weight at tagging was 24.12 g with standard deviation of 8.96. The body weight at tagging by family is presented in boxplot as showed in Fig. 1, which has corrected for the differences in age at tagging.

3.2. Genetic variation of body weight and its uniformity

For STDWT, the σ_a^2 and $\sigma2_c$ were 0.514 and 0.045, respectively (Table 3). For LOGWT, the σ_a^2 and $\sigma2_c$ were reduced to 0.072 and 0.007, respectively. The h^2 estimate for STDWT was relatively high, 0.596 and with rather low c^2, 0.050. The estimated h^2 and c^2 for LOGWT were almost the same as those for STDWT, which were 0.607

Table 2
Number of observations (N), simple mean (μ), minimum, maximum, standard deviation (SD) and coefficient variation (CV, %) of age at tagging (days), body weight at tagging (g) in original, standardized (STDWT) and log-transformed (LOGWT) scales.

Trait	N	μ	Min	Max	SD	CV
Age at tagging	7528	163.32	149	185	11.65	7.14
Body weight at tagging	7588	24.12	7.30	105.00	8.96	37.14
STDWT	7588	0.00	−1.88	9.03	1.00	–
LOGWT	7588	3.12	1.99	4.65	0.34	11.02

and 0.059, respectively.

The h_v^2 estimates for uniformity either of STDWT or LOGWT were low, 0.014 and 0.021. Although, the $\sigma2_{a_v}$ for uniformity of LOGWT was lower than the estimate of STDWT, 0.001 vs 0.025, the GCV for uniformity of LOGWT was higher, 63.5%, than the GCV for uniformity of STDWT, 45.8%. The c_v^2 for both uniformities of STDWT and LOGWT were low, 0.007 and 0.003, respectively.

3.3. Genetic correlation between body weight and its uniformity

The estimate of r_g between STDWT and its uniformity was zero, −0.055 ± 0.252. However, the estimate of r_g between LOGWT and its uniformity was strongly negative, −0.813 ± 0.114 (Table 3).

4. Discussion

4.1. Genetic variation for uniformity of body weight

In this study, the estimated h_v^2 for uniformity of STDWT and LOGWT for lumpfish was relatively low (0.014 and 0.021). However, the magnitude of these estimates are in line with previous studies reported in Atlantic salmon (h_v^2 = 0.036 by Sae-Lim et al., 2017), rainbow trout (h_v^2 = 0.024 by Janhunen et al., 2012; h_v^2 = 0.011 by Sae-Lim et al., 2015) and in some of the livestock species ($\bar{h}_v^2$ = 0.028, or ranged from 0.006 to 0.047, as reviewed by Hill and Mulder, 2010). Based on our knowledge and reported studies, in livestock and aquaculture, the h_v^2 estimates are at the maximum of 5% (for example, Hill and Mulder, 2010; Janhunen et al., 2012; Sae-Lim et al., 2015; Sae-Lim et al., 2017).

The low magnitude of h_v^2 for both STDWT and LOGWT indicates that the accuracy of selection may be low, and large number of sibs is required to obtain sufficient accuracy of selection. In this study, the accuracy of sib selection with average h_v^2 (0.0175) and c_v^2 (0.005) calculated from estimates of STDWT and LOGWT is 0.440, using the average full-sib family size of 111 (Table 1). When full-sib family size approaches infinity, the maximum accuracy is 0.564. Due to high fecundity of lumpfish (Gregory and Daborn, 1982), it may be possible to increase accuracy by increasing family size. An alternative approach to increase accuracy is by using genomic selection, especially for the lowly heritable traits, such as uniformity of birth weight of piglet (Sell-Kubiak et al., 2015) and somatic cell score in dairy cattle (Mulder et al., 2013). Sae-Lim et al. (2017) reported that single-step genomic evaluation with an animal DHGLM can increase predictive ability of estimated genomic breeding values for uniformity (41% to 78%) compared to genetic evaluation based on numerator relationships. To our knowledge, there is no single nucleotide polymorphism (SNP) chip available for lumpfish. Thus, currently, to increase the accuracy of selection for lumpfish breeding program, we will have to increase the family size ().

Although, the h_v^2 for STDWT and LOGWT were low, the GCV was substantial (45.8% and 63.5%), which indicate a high genetic potential for selective breeding compared to the trait mean (Houle, 1992; Mulder et al., 2007). Both GCV estimates in our study were in the upper range compared to those GCV reported in Atlantic salmon (48% by Sae-Lim et al., 2017; 42% from untransformed data by Sonesson et al., 2013), rainbow trout (37% by Janhunen et al., 2012; 21% by Sae-Lim et al., 2015), and Nile tilapia (34% on variance scale by Khaw et al., 2016; 58% by Marjanovic et al., 2016).

To gain more understanding about the expected genetic change in uniformity of body weight, we calculated expected change using, $\Delta G = ir_{IH}GCV$ (as a percent of the trait mean). With 10% of selected animals (selection intensity, $i = -1.755$), the accuracy (r_{IH}) of sib selection of 0.440, and a GCV of 0.458, the expected genetic change in residual variance of body weight was −35.4% per generation. The genetic gain may be lower if the number of full-sibs is reduced to, for example, 20 fish per family (−21.2%). The predicted reduction in
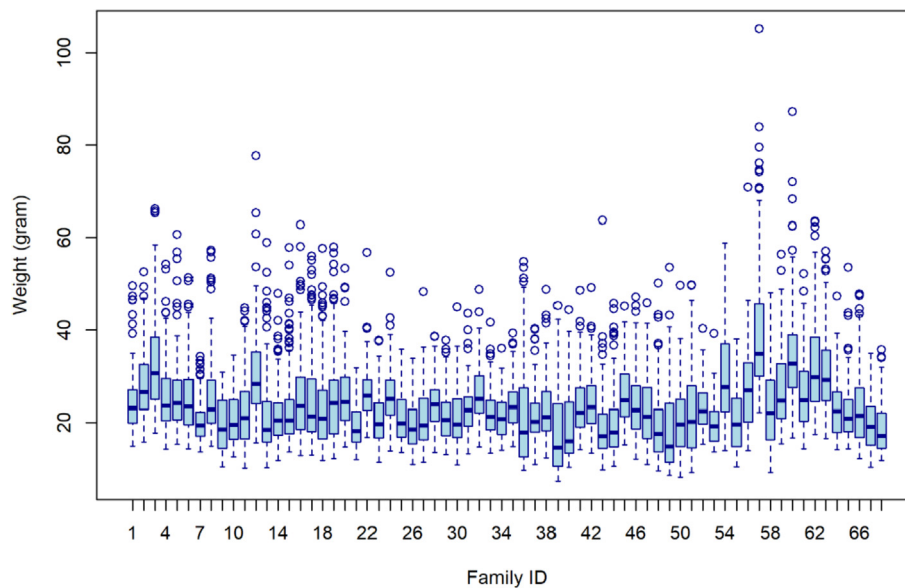
Fig. 1. Body weight at tagging (corrected for age at tagging) for each family in the lumpfish breeding program.

Table 3
Phenotypic and genetic parameters with their standard errors (in parenthesis) for body weight at tagging and its uniformity, under standardization and logarithm transformation.

Parameters	REML estimate	
	Standardization	Logarithm
Body weight (bw)		
σ^2_p	0.903	0.118
σ^2_a	0.514	0.072
σ^2_c	0.045	0.007
h^2	0.569 (0.100)	0.607 (0.148)
c^2	0.050 (0.023)	0.059 (0.044)
Variability of body weight (bw_v)		
$\sigma^2_{a_v, exp}$	0.183 (0.093)	0.330 (0.134)
$\sigma^2_{c_v, exp}$	0.092 (0.035)	0.055 (0.038)
$\sigma^2_{a_v}$	0.025	0.001
$\sigma^2_{c_v}$	0.013	0.000
GCV	0.458	0.635
h^2_v	0.014 (0.009)	0.021 (0.021)
c^2_v	0.007	0.003
$r_{g_{bw, bwv}}$	−0.055 (0.252)	−0.813 (0.114)
$r_{c_{bw, bwv}}$	0.999 (NA)	0.033 (0.630)

residual variance in lumpfish is higher than the predicted reduction in rainbow trout (Sae-Lim et al., 2015), which could be mainly due to higher *GCV* reported in this study.

4.2. Data transformation

The $\sigma^2_{a_v}$ for uniformity of LOGWT (which has accounted for the scale effect) was more than 50% lower than the $\sigma^2_{a_v}$ for uniformity of STDWT (0.001 vs 0.025). However, the h^2_v for uniformity of LOGWT was slightly higher than the h^2_v for uniformity of STDWT. Our finding is in agreement with the rainbow trout study by Sae-Lim et al. (2015). Authors reported a slightly higher h^2_v (0.024) estimated from log-transformed body weight in rainbow trout compared to the h^2_v estimate of non-transformed body weight (0.011). On the other hand, there are studies reported reduction in h_v^2 after data transformation (e.g. Sae-Lim et al., 2017). The pattern of higher h^2_v after data transformation was observed at the breeding environment, while the opposite pattern was observed in the production environment (Sae-Lim et al., 2015). Hence, different environments may result in different direction of change of h^2_v

after accounting for the scale effect.

The *GCV* presented in this study also correspond to the direction of change of h^2_v. It can be concluded that the potential for selective breeding is beyond the scale effects.

4.3. Genetic correlation between body weight and its uniformity

The estimated genetic correlation between body weight and its uniformity, under standardization scale, in lumpfish (−0.055) is lower than the estimates in Nile tilapia (0.60; Marjanovic et al., 2016), Atlantic salmon (0.952; Sae-Lim et al., 2017), and rainbow trout (0.79 and 0.30; Sae-Lim et al., 2015). The genetic correlation between body weight and its uniformity was influenced by the scaling effect drastically. The genetic correlation between body weight and its uniformity was close to zero (−0.055). However, after log-transformation, the genetic correlation was strongly negative (−0.813). The change in magnitude of genetic correlation after data transformation is in line with the previous studies in aquaculture and livestock species (Yang et al., 2011). In Atlantic salmon, Sonesson et al. (2013) found that Pearson correlation between estimated breeding values of body weight and its uniformity changed from 0.42 to −0.17 after log-transformation. Similarly, the genetic correlation between body weight and its uniformity reduced from 0.952 to −0.093 after log-transformation in Atlantic salmon (Sae-Lim et al., 2017). In rainbow trout, Sae-Lim et al. (2015) reported changes in genetic correlations between body weight and its uniformity after data transformation in the same direction as in this study, which were from 0.30 to −0.83 in breeding environment, and from 0.79 to −0.62 in production environment.

The uniformity of body weight may combine the micro-environmental sensitivity and scale effect while the uniformity of log-transformed body weight may consider only micro-environmental sensitivity. The definition of uniformity before and after data transformation has been discussed in previous studies (Sae-Lim et al., 2015; Sae-Lim et al., 2017). For fish breeding programs, the major goal is to increase body weight and reduce micro-environmental sensitivity resulting in more uniformity fish. In other word, genetic control of observed residual variance is more relevant for selection on more uniform growth. The reason is the uniformity on the observed scale has a direct interpretation to an actual range of body sizes which are processed by aquaculture industries. Hence, the uniformity of observed body weight should be considered as a breeding goal trait. The decision whether the uniformity of log-transformed body weight may be included in the

selection index may depend on the genetic correlation between uniformity of observed and log-transformed weights.

5. Conclusion

Our study shows that the genetic potential for response to selection for uniformity of body weight in lumpfish is substantial, but the accuracy of selection may be low due to low heritability for uniformity. A larger number of relatives may be required to obtain sufficient accuracy of selection if the breeding goal is to select for more uniform lumpfish in term of body weight. The genetic correlations which were close to zero and strongly negative after log-transformation suggests that selection for both body weight and its uniformity should be possible without trade-off in genetic gains when including both traits into a selection index.

Declaration of Competing Interest

None.

References

Ahvenharju, T., Ruohonen, K., 2007. Agonistic behaviour of signal crayfish (*Pacifastacus leniusculus* Dana) in different social environments: effect of size heterogeneity on growth and food intake. Aquaculture 271, 307–318.

Dou, S.-Z., Masuda, R., Tanaka, M., Tsukamoto, K., 2004. Size hierarchies affecting the social interactions and growth of juvenile Japanese flounder, *Paralichthys olivaceus*. Aquaculture 233, 237–249.

Felleki, M., Lundeheim, N., 2013. Genetic control of residual variance for teat number in pigs. In: 20th Association for the Advancement of Animal Breeding and Genetics Conference, Napier, New Zealand, 20 to 23 October. 2013. pp. 538–541.

Felleki, M., Lee, D., Lee, Y., Gilmour, A.R., Rönnegård, L., 2012. Estimation of breeding values for mean and dispersion, their variance and correlation using double hierarchical generalized linear models. Genet. Res. 94, 307–317.

Gilmour, A.R., Gogel, B., Cullis, B., Thompson, R., 2009. VSN International Ltd: Hemel Hempstead.

Gregory, R.S., Daborn, G.R., 1982. Notes on adult lumpfish *Cyclopterus lumpus* L. from the Bay of Fundy. Proc. N.S. Inst. Sci. 32, 321–326.

Hill, W.G., Mulder, H.A., 2010. Genetic analysis of environmental variation. Genet. Res. (Camb) 92, 381–395.

Hoaglin, D., Welsch, R., 1978. The hat matrix in regression and ANOVA. Am. Stat. 32, 17–22.

Holmyard, N., 2018. Lumpfish production becoming big business in Norway. In: SeafoodSource, . https://www.seafoodsource.com/news/aquaculture/lumpfish-production-becoming-big-business-in-norway (Accessed on 05 February 2019).

Houle, D., 1992. Comparing evolvability and variability of quantitative traits. Genetics 130, 195–204.

Imsland, A.K., Reynolds, P., Nytrø, A.V., Eliassen, G., Hangstad, T.A., Jónsdóttir, Ó.D.B., Emaus, P.-A., Elvegård, T.A., Lemmens, S.C.A., Rydland, R., Jonassen, T.M., 2016a. Effects of lumpfish size on foraging behaviour and co-existence with sea lice infected Atlantic salmon in sea cages. Aquaculture 465, 19–27.

Imsland, A.K., Reynolds, P., Eliassen, G., Mortensen, A., Hansen, Ø., Puvanendran, V., Hangstad, T.A., Jónsdóttir, Ó.B., Emaus, P.-A., Elvegård, T.A., Lemmens, S.C.A., Rydland, R., Nytrø, A.V., Jonassen, T.M., 2016b. Is cleaning behaviour in lumpfish (*Cyclopterus lumpus*) parentally controlled? Aquaculture 459, 156–165.

Janhunen, M., Kause, A., Vehvilainen, H., Jarvisalo, O., 2012. Genetics of micro-environmental sensitivity of body weight in rainbow trout (*Oncorhynchus mykiss*) selected for improved growth. PLoS One 7, e38766.

Khaw, H.L., Ponzoni, R.W., Yee, H.Y., Aziz, M.A., Mulder, H.A., Marjanovic, J., Bijma, P., 2016. Genetic variance for uniformity of harvest weight in Nile tilapia (*Oreochromis niloticus*). Aquaculture 451, 113–120.

Lande, R., 1977. On comparing coefficients of variation. Syst. Zool. 26, 214–217.

Marjanovic, J., Mulder, H.A., Khaw, H.L., Bijma, P., 2016. Genetic parameters for uniformity of harvest weight and body size traits in the GIFT strain of Nile tilapia. Genet. Sel. Evol. 48, 41.

Mulder, H.A., Bijma, P., Hill, W., 2007. Prediction of breeding values and selection response with genetic heterogeneity of environmental variance. Genetics 175, 1895–1910.

Mulder, H.A., Crump, R.E., Calus, M.P.L., Veerkamp, R.F., 2013. Unraveling the genetic architecture of environmental variance of somatic cell score using high-density single nucleotide polymorphism and cow data from experimental farms. J. Dairy Sci. 96, 7306–7317.

Mulder, H.A., Visscher, J., Fablet, J., 2016. Estimating the purebred–crossbred genetic correlation for uniformity of eggshell color in laying hens. Genet. Sel. Evol. 48, 39.

Nielsen, H.M., Monsen, B.B., Ødegård, J., Bijma, P., Damsgård, B., Toften, H., Olesen, I., 2014. Direct and social genetic parameters for growth and fin damage traits in Atlantic cod (*Gadus morhua*). Genet. Sel. Evol. 46, 5.

Norway Directorate of Fisheries, 2018. Cleanerfish (Lumpfish and Wrasse). Accessed on 05 February 2019. https://www.fiskeridir.no/English/Aquaculture/Statistics/Cleanerfish-Lumpfish-and-Wrasse.

Rönnegård, L., Felleki, M., Fikse, F., Mulder, H.A., Strandberg, E., 2010. Genetic heterogeneity of residual variance-estimation of variance components using double hierarchical generalized linear models. Genet. Sel. Evol. 42, 8.

Sae-Lim, P., Kause, A., Janhunen, M., Vehviläinen, H., Koskinen, H., Gjerde, B., Lillehammer, M., Mulder, H.A., 2015. Genetic (co) variance of rainbow trout (*Oncorhynchus mykiss*) body weight and its uniformity across production environments. Genet. Sel. Evol. 47, 46.

Sae-Lim, P., Gjerde, B., Nielsen, H.M., Mulder, H., Kause, A., 2016. A review of genotype-by-environment interaction and micro-environmental sensitivity in aquaculture species. Rev. Aquac. 8, 369–393.

Sae-Lim, P., Kause, A., Lillehammer, M., Mulder, H.A., 2017. Estimation of breeding values for uniformity of growth in Atlantic salmon (*Salmo salar*) using pedigree relationships or single-step genomic evaluation. Genet. Sel. Evol. 49, 33.

Sell-Kubiak, E., Wang, S., Knol, E.F., Mulder, H.A., 2015. Genetic analysis of within-litter variation in piglets' birth weight using genomic or pedigree relationship matrices. J. Anim. Sci. 93, 1471–1480.

Sonesson, A., Ødegård, J., Rönnegård, L., 2013. Genetic heterogeneity of within-family variance of body weight in Atlantic salmon (*Salmo salar*). Genet. Sel. Evol. 45, 41.

Yang, Y., Christensen, O.F., Sorensen, D., 2011. Analysis of a genetically structured variance heterogeneity model using the Box-Cox transformation. Genet. Res. 93, 33–46.