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Fluctuations in growth are heritable and a potential indicator of resilience in Nile tilapia (*Oreochromis niloticus*)

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ABSTRACT

Resilience can be defined as the capacity of an animal to be minimally affected by perturbations or to quickly recover to the state it had before the perturbation. When applied to production animals, resilience is defined as consistency in production over time. This consistency can be quantified by the variance of deviations from the expected trait level measured at multiple time points. The objectives of this study were to estimate genetic parameters for resilience in Nile tilapia, measured as consistency in growth. We used log-transformed variance of deviations (LnVar) of body weight measured five times during grow-out in either an aerated or a non-aerated pond. The hypothesis was that fish grown in non-aerated ponds are more challenged by environmental conditions, such that heritable variation in LnVar of body weight is more expressed showing larger differences between more and less resilient fish. The heritability for LnVar was 0.10 in aerated pond and 0.12 in the non-aerated pond. In aerated ponds the genetic correlation (r_g) of LnVar with harvest weight (HW) was 0.36 ± 0.26, and with thermal growth coefficient (TGC) it was 0.47 ± 0.21. In the non-aerated pond, the r_g with HW and TGC were close to zero (−0.01 ± 0.29 and − 0.08 ± 0.22). The genetic correlation for LnVar between both environments was 0.80. These estimates suggest that selection for HW or TGC in aerated ponds will increase LnVar in both environments. Increased LnVar may decrease resilience and this will be detrimental to performance. Selecting for more resilient fish would lead to more constant growth rates, which makes biomass estimation more accurate and could therefore result in more optimal feeding regimes and less feed waste. This would have a favorable effect on the feed efficiency in production units and on the environmental impact of fish farming. To improve resilience together with growth we recommend that fish breeding programs collect repeated records on body weight, preferably in challenging environments.

1. Introduction

Resilience can be defined as the capacity of an animal to be minimally affected by perturbations or to quickly recover to the state it had before the perturbation (Colditz and Hine, 2016). When applied to production animals, resilience can also be defined as consistency of production over time. Resilience indicators are then based on all production deviations due to unknown disturbances during a production cycle (Scheffer et al., 2018; Berghof et al., 2019b). In animal production, there can be many perturbing factors, for example competition for feed, physical or environmental stressors, disease pressure, and hypoxia (in aquaculture). It is assumed that animals that show consistency in their production are less affected by these perturbation factors compared to animals that show less consistency in their production (Berghof et al., 2019a).

The genetic parameters of resilience can be analyzed from repeated or longitudinal records of a trait over time per individual (Friggens et al., 2017). Possible resilience indicators that can be calculated from these records are variance of deviations from the mean, autocorrelations between measurements, skewness of deviations or a slope of reaction norm

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(Berghof et al., 2019b). Only a few studies investigated resilience over time, using repeated records (summarized in Table 1, see also review by Iung et al. (2020). Of these, natural-log-transformed variance of deviations from the mean (LnVar) appears to be the most promising, given the observed heritabilities (range: 0.10–0.24) and GCV's (range: 0.23–0.34). LnVar can easily be calculated from longitudinal records on body weight that represent growth. More resilient animals are expected to show lower values for LnVar compared to less resilient animals. In chicken, (Berghof et al., 2019a) found a heritability of 0.10 and a substantial genetic coefficient of variation (0.30) for LnVar based on seven body weight records, measured every 4 weeks.

There are no known estimates of LnVar in aquaculture species. In this study, we investigated the genetic parameters of LnVar for growth in Nile tilapia (*Oreochromis niloticus*). Nile tilapia is the most widely cultured tropical fish species, with annual production exceeding 4.5 million tons globally in 2018 (FAO, 2020). Tilapia are cultured in a wide range of environments ranging from ponds to cages, and several strains have been developed and selected for increased growth rate for >15 generations (i.e. GIFT, Bentsen et al., 2017). This makes the study of resilience for growth based on repeated body weight measurements of particular interest for Nile tilapia.

In addition to obtaining repeated records per animal over time, it is important to choose the environment under which resilience is investigated. In Nile tilapia, oxygen availability is one of the major factors determining growth, health and survival, especially in non-aerated ponds (Mengistu et al., 2020b). Under optimal conditions (i.e. in aerated ponds) Nile tilapia are able to fully express their genetic potential for growth. However, without aeration, ponds show diurnal hypoxia which creates a challenging environment (Mengistu et al., 2020a). In such challenging environments more resilient tilapia may grow better and show better survival. We hypothesize that less resilient fish grown in non-aerated ponds are more challenged by environmental conditions and will show higher log-transformed variances of deviances (LnVar) for body weight. Therefore, the objectives of this study were: 1) to estimate genetic parameters of resilience using LnVar of body weight measured at five time points in aerated and non-aerated ponds, and 2) to estimate genetic correlations (r_g) between resilience and growth rate in both environments.

2. Material and methods

The production, raising, and harvesting of fish is described in detail in (Mengistu et al., 2020a), and is summarized below.

2.1. Family production and nursery

The experiment was carried out in the Aquaculture Extension Centre, Department of Fisheries, Jitra, Kedah State, Malaysia. The fish used in this experiment were mass produced from generation 15 of the GIFT breeding program as follows: The male and female breeders were conditioned for two weeks separately in cages in an earthen pond before stocking them in mating hapas. Mating was done in four hapas (each 30m^2) in a 500 m^2 earthen pond, which was aerated by a paddlewheel. Eighteen males and 50 female breeders were stocked for 15 days in each of the mating hapas. In total 72 males and 200 females were used.

On the sixteenth day the breeders were removed, and the fry were kept in the same hapas for nursing for a duration of 60 days. The fry were fed commercial feed with 43% crude protein and 5% crude fat at a daily rate of 10–15% of body weight. The feed was divided into three portions and the fry were fed three times a day.

2.2. Grow-out and pond management

After 60 days of nursery, the fingerlings from the same hapa were transferred into one of four aerated tanks and conditioned for three days before tagging. Feeding was stopped one day before tagging. From each

Table 1
Summary of studies that investigated resilience based on repeated trait measurements.

Species	Measurement Method	heritability	GCV	Remark	References
Dairy cattle	Absolute change in daily milk yield (dMY), residual absolute change in dMY and standard deviation in DMY	0.10 to 0.20	–	5 to 200 days in milk records were used	Moncur et al. (2021)
Dairy cattle	Log-transformed variances of deviations (LnVar) of three periods of the first lactation and the first three full lactations	0.12 to 0.20	–	Data and data preparation were the same as Poppe et al. (2020)	(Poppe et al., 2021)
	Lag-1 autocorrelation of deviations from lactation curve	0.05 to 0.08	–		
	Average daily milk yield	0.32 to 0.45	–		
Sheep	Natural logarithm of daily coefficient of variation of daily feed intake (DFI)	0.08 to 0.14	–	951 lambs tested, 51,832 DFI records	(Garcia-Baccino et al., 2021)
Dairy cattle	Milk yield	0.20 to 0.24	0.23 to 0.25	Cows with at least 95% daily milk yield records were included, The first 350 days milk record were included	Poppe et al. (2020)
	Log-transformed variances based on quantile regression curve autocorrelation	0.08 to 0.10	0.07 to 0.17	330 to 350 daily milk yield records per individual	
	Milk yield, skewedness of deviations from lactation curve	0.01 to 0.02	0.05 to 0.10		
Pigs	LnVar of litter size in different parities	0.02	0.16–0.17		Dobrzański et al. (2020)
Pigs	Root mean square error of prediction (RMSEP) of daily feed intake and feed duration	0.15 to 0.26	–	RMSEP is closely related to the variance of deviations	Putz et al. (2019)
Chicken	Log-transformed variances of body weight	0.10	0.30	Seven body weight records over time per individual	Berghof et al. (2019a)
	Skewness of deviations within an individual	0.09	1.56		
	Lag-one autocorrelation of deviations within an individual	0.11	0.52		
Dairy cattle	Milk yield Log-transformed variance within cow	0.10	–	Cows with at least 21 consecutive daily milk yield records, and up to 355 days record were included	Elgersma et al. (2018)
Nile tilapia (*Oreochromis niloticus*)	Log-transformed variances	0.10 to 0.12	0.30 to 0.34	Five body weight records per individual over time	This study

tank a random sample of fingerlings was anesthetised using clove oil and individually tagged using Passive Integrated Transponder (PIT) tags. At tagging, a 1 cm^2 fin clip sample was collected and PIT tag number and body weight (BW) were recorded. The fin clip samples were preserved in 95% ethanol. The tagging, weight recording, fin clip sample collection and photographing was done in four consecutive days. A random sample of an equal number of individually tagged fingerlings from each nursery hapa was stocked in two earthen ponds. Totally 1570 fish were stocked in each pond with a stocking density of 3 fish/m^2.

The size of each of the ponds was 511m^2 with a water depth of 1.0 to 1.2 m. One of the ponds was aerated using a paddle wheel aerator and air blower to create a normoxic environment. The second pond was without aerator resulting in diurnal dissolved oxygen (DO) fluctuations.

During the grow-out period fish were initially fed commercial feed with 30% crude protein and 5% crude fat at a daily rate of 5% of body weight. After 2 months feeding rate was reduced to 3% of body weight. The feeding rate was adjusted approximately every three weeks based on the weight of a sample of ~100 fish. It was also adjusted based on total biomass and number of fish recorded at each time point when body weight was recorded. The feed was divided into two portions and fed in the morning from 9:00 to 10:00 and afternoon from 15:00 to 16:00. Some mornings feeding was skipped due to cloudy weather conditions that made the DO level in the non-aerated pond drop to below 2 mg/L. At these concentrations, it was observed that fish no longer fed.

2.3. Records

Body weight of each fish was recorded, using a digital scale, at stocking, at 55/56 days, 104/105 days, 167/168 days after stocking, and at harvest, which was after 217 and 218 days of grow-out in the non-aerated pond and aerated pond, respectively. Thermal growth coefficient (TGC) (Jobling, 2003) was computed as:

$$TGC = [(\sqrt[3]{(W_t)} - \sqrt[3]{(W_0)})/(T \times t)] \times 1000 \quad (1)$$

where W_t is harvest weight, W_0 is stocking weight, T is temperature in °C and t is time in days.

2.4. Genomic relationship matrix

DNA extraction and genotyping are described in Mengistu et al. (2020a). In total, records from 1686 genotyped fish were available for the analyses. We computed a genomic relationship matrix (GRM) based on 11,293 SNPs using calc_grm program (Calus and Vandenplas, 2016) using the vanraden2 option. The resulting GRM was adjusted using the number of non-missing alleles per individual for self-relatedness (diagonal elements) and using the non-missing alleles found on the two individuals for the off-diagonal elements, as follows:

$$k_{ij} = \frac{N_{SNP_{all}}}{N_{SNP_{all}} - N_{SNP_{missing}}} \quad (2)$$

And

$$G_{2_{ij}} = k_{ij} G_{ij} \quad (3)$$

where N_{SNPall} is the total number SNP-loci used (11,293 SNPs) and $N_{SNPmissing}$ is the number of SNP-loci missing in a particular individual for diagonal elements of GRM. For off-diagonal elements of the GRM (i.e. the genomic relationship between two animals), $N_{SNP\_missing}$ was the number of SNP loci missing in at least one of the two individuals; $N_{SNP\_all} - N_{SNP\_missing}$ was therefore the number of SNP-loci with genotypes for both individuals. Finally, G_2 was multiplied with an extra adjustment factor to make the average of the diagonal elements equal to 1 (Mengistu et al., 2020a):

$$G_{3_{ij}} = \frac{1}{0.842} G_{2ij} \quad (4)$$

2.5. Calculation of log-transformed variance of the standardized deviation: LnVar

First, mean body weight ($\overline{Wt}$) and standard deviation (SD) of body weight for the fish belonging to the same nursery hapa, sex and grow-out pond (cohort) was calculated, for each measurement t separately. Standardized deviations of body weight were calculated as:

$(Wt, i - \overline{Wt, i})$ / SD, with t the measurement number (1–5), and i = cohort.

Next, for each fish, the mean and variance of the resulting 5 standardized deviations was calculated (Berghof et al., 2019a). Finally, this variance ("Var-dev") was log-transformed using the natural logarithm to obtain LnVar, which is the commonly used scale to express genetic variation in environmental/residual variance or uniformity in other studies (Hill and Mulder, 2010; Iung et al., 2020).

2.6. Genetic parameter estimation

Phenotypic and genetic variances were estimated using ASReml version 4.1 (Gilmour et al., 2015) fitting an animal model with a genomic relationship matrix. Phenotypic (r_p) and genetic (r_g) correlations between LnVar and, harvest weight (HW) and TGC within aerated and non-aerated ponds; and r_g for LnVar between the aerated and non-aerated ponds were estimated from fitting bivariate linear models. The linear mixed models were:

$$\mathbf{y} = \mathbf{Xb} + \mathbf{Za} + \mathbf{e} \quad (5)$$

where, **y** is the vector of one of the traits LnVar, HW or TGC for the univariate models or two of those traits for the bivariate models, **b** is the vector of fixed effects which were nursery hapa (1–4), sex (female, male, and not determined) and stocking weight (fitted only for HW), **a** is the vector of random additive genetic effects, **e** is the vector of residual effects. The **X** and **Z** are design matrices assigning phenotypic values to the levels of fixed effects and additive genetic effects respectively. The additive genetic effects were normally distributed as $N\left([\mathbf{0}], \mathbf{A} \otimes \begin{bmatrix} \sigma^2_{a,T1} & r_{a,T12}\sigma_{a,T1}\sigma_{a,T2} \\ r_{a,T12}\sigma_{a,T1}\sigma_{a,T2} & \sigma^2_{a,T2} \end{bmatrix}\right)$ with $\sigma^2_{a,\ T1}$ ($\sigma^2_{a,\ T2}$) being the additive genetic variance of trait 1 (trait 2) and $r_{a,\ T12}$ the additive genetic correlation between trait 1 and 2.

Heritability of each trait was computed as the ratio of genetic variance and phenotypic variance, $h^2 = \frac{\sigma^2_a}{\sigma^2_p}$, where h^2 is heritability, σ^2_a is additive genetic variance and σ^2_p is phenotypic variance. The approximate standard errors (SE) were derived from the average information matrix (Fischer et al., 2004). The 95% confidence interval for the heritabilities were calculated as $h^2 \pm 1.96 * SE$. The significance of heritabilities were tested using loglikelihood ratio test with one degree of freedom (Lynch and Walsh, 1997) comparing the model with random additive genetic effect against a model without the additive genetic effect. The significance of the genetic correlations were tested using loglikelihood ratio test with one degree of freedom (Lynch and Walsh, 1997) comparing a model without constraining the covariance against a model where the covariance was constrained to zero. Genetic coefficient of variation (GCV) for LnVar was calculated as: $GCV = \sqrt{\sigma^2_{a-LnVar}}$ because the log transformation implicitly assumes an exponential model which makes $\sigma^2_{a-LnVar}$ unitless (Mulder et al., 2007). For the other traits GCV was calculated as: $GCV = \sqrt{\sigma^2_a}/\mu$, where μ is the phenotypic mean of the population (Hill and Mulder, 2010). The residual effects were normally distributed as $N(\mathbf{0}, \mathbf{I}\sigma^2_e)$ for the univariate models. For the bivariate models between traits within ponds, the residual effects were

distributed as $N\left(\begin{bmatrix}\mathbf{0}\\ \mathbf{0}\end{bmatrix}, \mathbf{I}\otimes\begin{bmatrix}\sigma^2_{e,T1} & r_{e,T12}\sigma_{e,T1}\sigma_{e,T2}\\ r_{e,T12}\sigma_{e,T1}\sigma_{e,T2} & \sigma^2_{e,T2}\end{bmatrix}\right)$ where $\sigma^2_{e,\,T1}$ ($\sigma^2_{e,\,T2}$) is the residual variance for trait 1 (trait 2) and $r_{e,\,T12}$ is the residual correlation between trait 1 and trait 2. For bivariate models between traits in different ponds, the residual effects were distributed as $N = \left(\begin{bmatrix}\mathbf{0}\\ \mathbf{0}\end{bmatrix}, I\otimes\begin{bmatrix}\sigma^2_{e,T1} & 0\\ 0 & \sigma^2_{e,T2}\end{bmatrix}\right)$. The residual correlations between traits in different ponds were set to zero because each individual was reared in either an aerated pond or a non-aerated pond and therefore the residual correlation is non-existing.

3. Results

3.1. Descriptive statistics

Average body weights at each of the five body weight measurements are presented in Table 2 and Fig. 1. The average body weight was similar at stocking but started to diverge after 55 and 56 days of grow-out in non-aerated and aerated ponds, respectively. Fig. 2 shows body weight and standardized body weight at each of the five time points for the ten fish with the lowest and ten fish with the highest estimated breeding values (EBV) for LnVar in aerated ponds. Fish with the lowest EBV for LnVar showed more consistency of growth and more consistent standardized body weight at the five time points compared to fish with high EBV for LnVar. A similar, but more extreme, pattern was seen for fish from the non-aerated pond (Fig. 3). Mean values for LnVar were similar for both ponds but the range in LnVar values was larger in non-aerated pond compared to aerated pond (Table 3).

3.2. Genetic and phenotypic parameters within ponds

Variances and heritabilities from univariate models for LnVar, HW and TGC are presented in Table 4. The additive genetic variance for LnVar was substantial in both the aerated and non-aerated pond. The heritability estimate for LnVar was slightly higher in non-aerated pond (0.12 ± 0.04) compared to in the aerated pond (0.10 ± 0.05). The heritability estimates in the aerated pond and in the non-aerated pond were significantly different from zero ($P < 0.05$). However, these heritabilities were not significantly different from each other with 95% confidence interval in the non-aerated pond of [0.022, 0.218] and in the aerated pond of [0.002, 0.198]. The coefficient of variation for LnVar was higher in non-aerated pond than the aerated pond. Contrary to the trend observed for LnVar, the GCVs for both HW and TGC were higher in aerated than in non-aerated ponds. Both the genetic and phenotypic variances for HW and TGC were higher in aerated ponds.

3.3. Genetic correlation

In the aerated pond we estimated a moderate and positive genetic correlation between LnVar and HW (0.36 ± 0.26) and between LnVar and TGC (0.47 ± 0.21) (Table 5). In the non-aerated pond however, close to zero genetic correlations between LnVar and HW (−0.01 ± 0.29) and between LnVar and TGC (−0.08 ± 0.22) were estimated. The genetic correlation estimates were not significantly different from zero ($p > 0.05$) except for the genetic correlation between LnVar and TGC in aerated pond ($p < 0.05$). The genetic correlation between environments for LnVar was 0.80 ± 0.17. The genetic correlation estimate was not significantly different from one. These results show that LnVar is genetically similar in both environments with limited GxE.

4. Discussion

In this study, our heritability estimates for LnVar in a non-aerated pond (0.12 ± 0.05) and in an aerated pond (0.10 ± 0.05) were significantly different from zero and not significantly different from each other. Our heritability estimates for LnVar were considerably higher than heritability estimates reported for uniformity (Table 6). These estimates for LnVar are in line with other heritability estimates based on multiple records per individual (Table 1). Berghof et al. (2019a) also used body weight records, seven per individual chicken, and estimated LnVar heritability at 0.10.

The high genetic correlation (0.8) between LnVar in both environment was significantly different from zero and not different from 1.0, suggesting it is roughly the same trait in both environments. Nevertheless, the GCV for LnVar in non-aerated pond (Table 4) may indicate that the genetic variation in LnVar is more expressed in the more challenging non-aerated pond. This higher expression in the non-aerated pond is in contrast with production traits, where challenging environments are expected to suppress the expression of the genetic potential. We did indeed observe lower GCVs for production traits HW and TGC in the non-aerated pond compared to the aerated pond. With the genetic correlation of 0.80 for LnVar between aerated and non-aerated ponds, a response in LnVar in non-aerated production environments is possible from data collected in aerated ponds, e.g. in a nucleus breeding station. However given the 0.80 genetic correlation between the aerated and non-aerated ponds and higher GCV for LnVar in the non-aerated pond the use of sib testing with genomic selection could further increase selection response for LnVar (Mulder, 2016).

The genetic correlations between LnVar and HW (−0.01), and between LnVar and TGC (−0.08) in non-aerated pond and between LnVar and HW (0.36) in aerated pond were not significantly different from zero. The genetic correlations between LnVar and TGC (0.47) in aerated pond was moderate and significantly different from zero. The genetic correlations had high standard errors and so caution is needed when interpreting these results. The SE of heritability and correlation were estimated (Fischer et al., 2004) by ASReml. No bias is expected in these SE estimates from ASReml, as shown in simulation by comparison to the standard deviation of repeated estimates (Lozano-Jaramillo et al., 2020). These low to moderate genetic correlations indicate that LnVar is a trait that is not strongly correlated to HW and TGC. LnVar does not discriminate between positive and negative standardized deviations (Berghof et al., 2019b), which means that fish with constant growth can have either higher or lower than average weight. Therefore, with near

Table 2
Descriptive statistics of body weight at stocking, at three interval measurements and at harvest, and thermal growth coefficient (TGC)* in aerated and non-aerated ponds.

	Aerated			Non-aerated		
	N	Mean (sd)	Range	N	Mean (sd)	Range
Stocking	1026	25.4 (13.2)	2.9–77.1	1037	24.8 (13.2)	3.6–77.0
1	1026	159.0 (63.2)	30.2–394.3	1037	144.3 (54.7)	26–328.0
2	941	289.2 (92.7)	63.3–650.5	907	266.1 (73.2)	70.5–498.3
3	903	533.4 (177.4)	68.2–1079.1	887	426.4 (118.8)	117.0–805.0
Harvest	885	781.0 (256.6)	185.7–1588.6	801	579.9 (154.6)	135.5–1003.4
TGC	885	1.01 (0.17)	0.47–1.46	801	0.85 (0.13)	0.41–1.18

* $TGC = [(\sqrt[3]{(W_t)} - \sqrt[3]{(W_0)}) / (T \times t)] \times 1000$, where W_t is harvest weight, W_0 is stocking weight, T is temperature in °C and t is time in days.

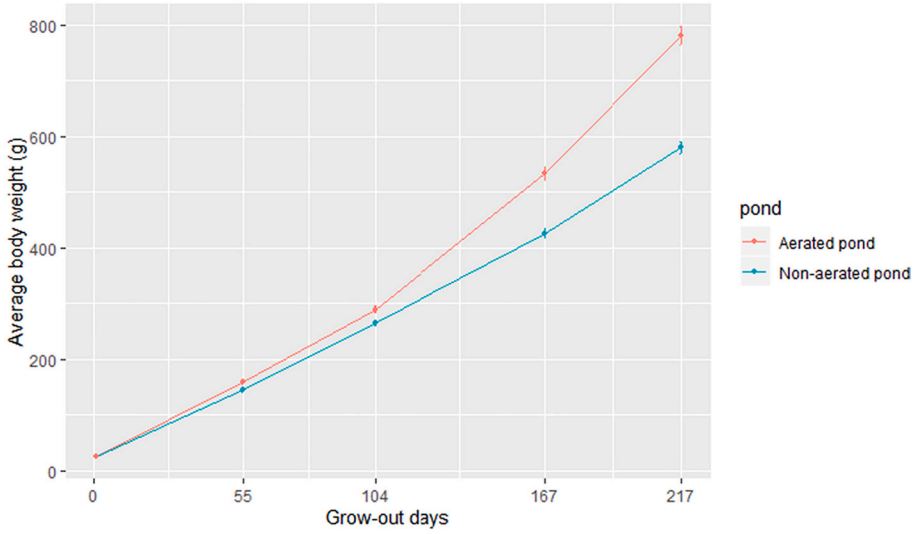

Fig. 1. Mean body weight with 95% confidence interval at stocking, three interval measurements and at harvest.

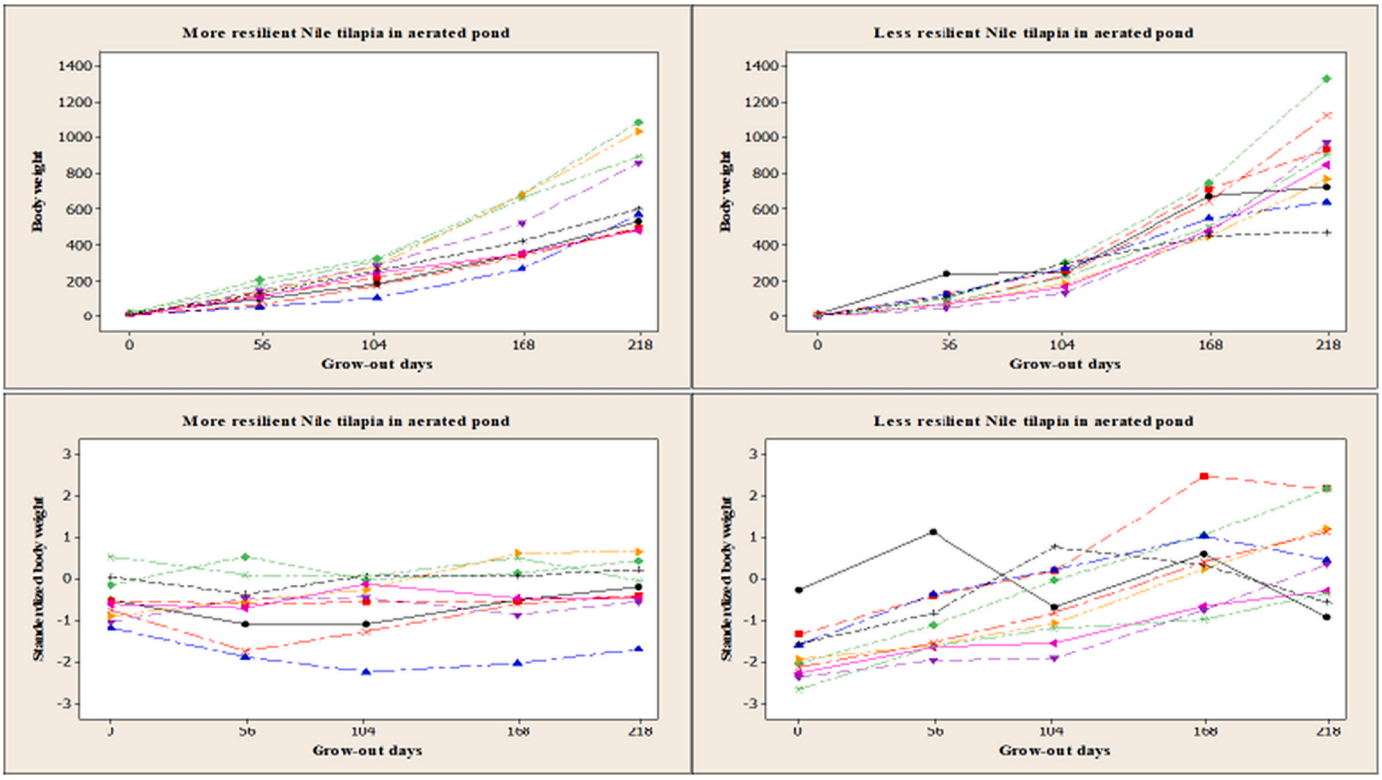

Fig. 2. Body weight and standardized body weight of ten most resilient and ten least resilient fish from aerated pond, based on genomic estimated breeding values (GEBV) for log-transformed variances (LnVar). Top panels: body weight of ten most resilient fish (left) and ten least resilient fish (right). Bottom panels: standardized weight of ten most resilient fish (left) and ten least resilient fish (right).

zero to moderately positive genetic correlations the genetic improvement of both growth and resilience would be very well possible which could benefit performance, especially in non-aerated ponds.

Fish with low LnVar may have a better capacity to cope with disturbances and maintain their performance. A low LnVar could identify animals with less sensitivity to stressors that results in improved production, improved welfare and reduced therapeutic cost (Pottinger, 2000). Fish with lower LnVar are also expected to have a better disease resistance and better survival than fish with higher LnVar, but this needs to be confirmed by further investigation. In dairy cattle LnVar was found indicative of health traits and survival (Elgersma et al., 2018; Poppe et al., 2020). In layer chicken, a lower estimated breeding value for LnVar was predictive for lower lesion scores after avian pathogenic *Escherichia coli* inoculation (Berghof et al., 2019a). Lower LnVar could be indicative of the animals' ability to cope with disturbances and be less affected by stressors.

A number of studies have investigated measures of uniformity in fish with a single observation on each individual (Table 6). These measures are called uniformity, inherited variability, residual variance, or genetic heterogeneity of environmental variance. Measures for uniformity,

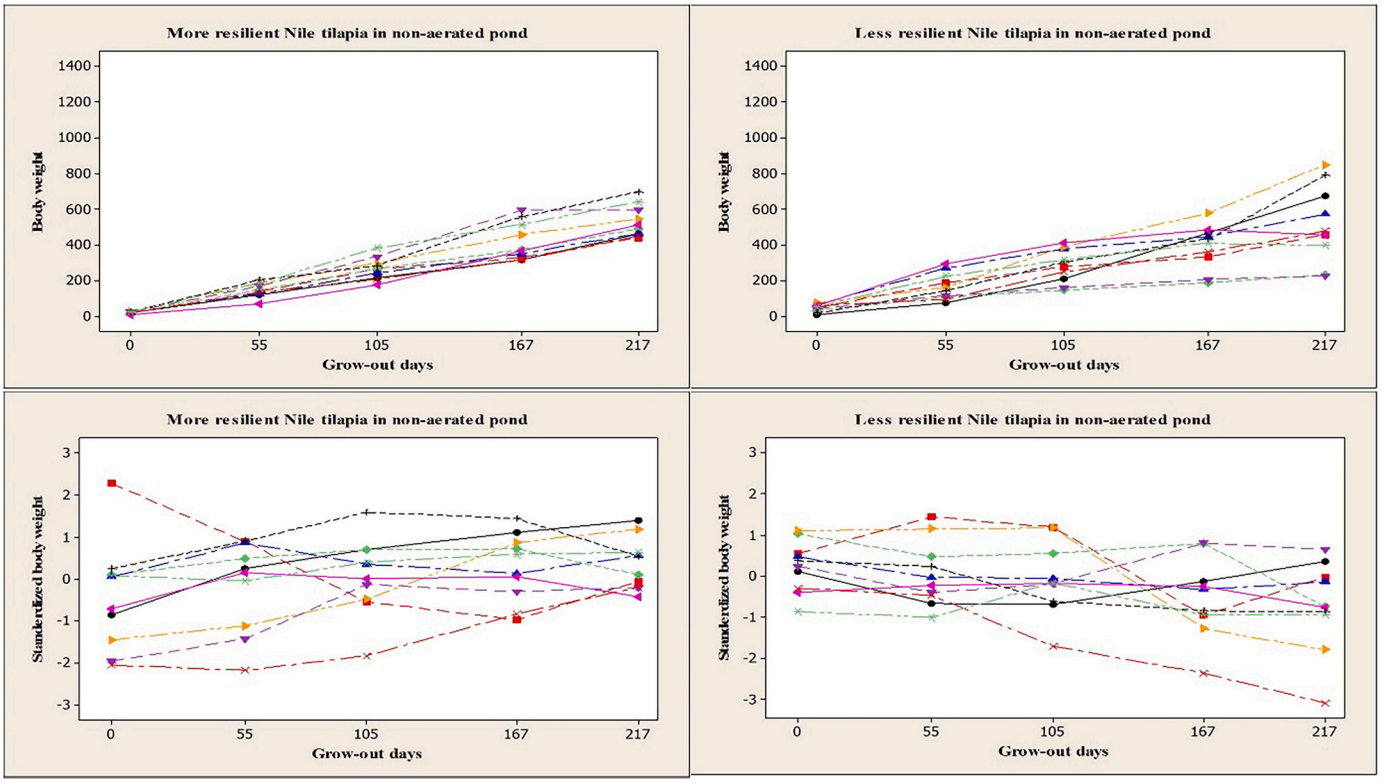

Fig. 3. Body weight and standardized body weight of ten most resilient and ten least resilient fish from non-aerated pond, based on genomic estimated breeding values (GEBV) for log-transformed variances (LnVar). Top panels: body weight of ten most resilient fish (left) and ten least resilient fish (right). Bottom panels: standardized weight of ten most resilient fish (left) and ten least resilient fish (right).

Table 3
Descriptive statistics of variance of deviances (Var-dev), log transformed variance (LnVar), and thermal growth coefficient (TGC) in aerated and non-aerated ponds.

Trait*	Aerated pond			Non-Aerated pond		
	Mean (sd)	Min	Max	Mean (sd)	min	max
Var-dev	0.5 (0.47)	0.00	3.84	0.47 (0.56)	0.01	8.84
LnVar	−1.09 (0.98)	−5.68	1.35	−1.23 (1.03)	−5.27	2.18
TGC	1.01 (0.17)	0.47	1.46	0.85 (0.13)	0.41	1.18

Trait values were calculated for 885 fish from the aerated pond and 801 fish from the non-aerated pond that had five individual body weight records.

based on single observations of e.g. harvest weight do not capture transient disturbances during the growth trajectory and generally have low heritability estimates ranging from 0.01 to 0.06. The GCVs of uniformity measures range from 17% to 64%, indicating that there is potential for improving uniformity by selective breeding (Janhunen et al., 2012; Sae-Lim et al., 2015; Marjanovic et al., 2016; Sae-Lim et al., 2017). However, the low heritability estimates indicate the necessity of large datasets to accurately estimate heritabilities and low accuracy to select on uniformity indicators (Hill and Mulder, 2010).

The optimal frequency of measurements to estimate LnVar needs to be determined but this probably varies with the trait that is measured. In our study, we used five body weight records per individual. Measuring body weight at five time points was found sufficient to capture the disturbances during the growth trajectory of Nile tilapia. Elgersma et al. (2018) and Poppe et al. (2020) estimated LnVar heritabilities based on 21 to 335 daily milk yield records and 50 to 350 daily milk yield records per individual, respectively. To measure LnVar, more frequent records may be required for traits that respond fast to disturbances than for traits that require some time to show a response. For a trait like milk yield daily measurements may be required because milk yield can respond

Table 5
Genetic and phenotypic correlation between log transformed variance (LnVar) and harvest weight (HW) and thermal growth coefficient (TGC) in aerated pond (A) and non-aerated pond (NA).

LnVar with -	Genetic correlation (r_g)		Phenotypic correlation (r_p)	
	A	NA	A	NA
HW	0.36 ± 0.26	−0.01 ± 0.29	0.10 ± 0.04	0.04 ± 0.04
TGC	0.47 ± 0.21	−0.08 ± 0.22	0.09 ± 0.04	−0.01 ± 0.04

Table 4
Additive genetic and phenotypic variances*, genetic coefficient of variation (GCV) and heritability of log transformed variance based (LnVar), harvest weight (HW) and thermal growth coefficient (TGC) within aerated and non-aerated pond.

Trait	Aerated				Non-aerated			
	σ_a^2	σ_p^2	$h^2 \pm se$	GCV	σ_a^2	σ_p^2	$h^2 \pm se$	GCV
LnVar	0.091	0.907	0.10 ± 0.05	30.2	0.118	0.988	0.12 ± 0.05	34.4
HW	8444.79	37,274	0.23 ± 0.06	11.8	2791.11	15,148	0.18 ± 0.06	9.1
TGC	0.004	0.016	0.26 ± 0.06	6.3	0.002	0.009	0.21 ± 0.06	5.3

* Results are from univariate model.

Table 6
Summary of studies that investigated heritability of uniformity in fish.

Species	Trait	method	heritability	GCV	Remark	References
Lumpfish (*Cyclopterus limpus*)	Uniformity of body weigh	standardized body weight and log-transformed body weight	0.01 to 0.02	0.46 to 0.64		Sae-Lim et al. (2020)
Nile tilapia (*Oreochromis niloticus*)	Uniformity of body weight	Square root transformed body weight	–	0.30 to 0.44	Information was incomplete to calculate heritability	Agha et al. (2018)
Atlantic salmon (*Salmo salar*)	Uniformity of growth.	Using log-transformed data and square root transformed	0.01 to 0.04	0.30 to 0.52		Sae-Lim et al. (2017)
Nile tilapia (*Oreochromis niloticus*)	Uniformity of body weight	Using Standard deviation of Box-Cox transformed body weight at family by group level	0.23	0.17	The trait was defined at the group level and not directly comparable with the other studies.	Khaw et al. (2016)
Nile tilapia (*Oreochromis niloticus*)	Uniformity of body weight.	Using Box-cox transformed body weight	0.03	0.58	Eight observation per family per group	Marjanovic et al. (2016)
Rainbow trout (*Oncorhynchus mykiss*)	Body weight uniformity	Using Standardized body weight and Log-transformed data	0.01 to 0.24	0.19 to 0.30		Sae-Lim et al. (2015)
Atlantic salmon (*Salmo salar*)	Genetic heterogeneity of body weight	Log-transformed, Square root transformed	0.06	0.34		Sonesson et al. (2013)
Rainbow trout (*Oncorhynchus mykiss*)	Micro-environmental sensitivity of body weight (residual variation of body weight)	Using Log-transformed squared residual values	0.02	0.37	Only sire families with at least 35 offspring were selected for the analysis	Janhunen et al. (2012)

quickly to disturbances and the impact may best be observed the next day. Body weight in Nile tilapia takes some time to respond to disturbances and monthly, bi-weekly or weekly measurements could be sufficient to capture disturbances.

While 5 measurements were sufficient for LnVar based on growth in Nile tilapia, this still required repeated phenotyping of individuals which is time consuming and can be stressful on the fish. Methods to perform automated phenotyping and image analysis are rapidly developing (Yang et al., 2021) which will make multiple measurements per individual over time easier. Automated phenotyping is non-invasive to fish and in time it may provide an automatic and effective size measurement (Li et al., 2020). Technological developments in automated phenotyping are expected to facilitate the application of resilience traits based on multiple measurements over time.

In aquaculture, constancy of growth leads to more uniformity in fish sizes which is important for biomass estimation, feeding decisions and to schedule harvesting. The heritabilities of 0.10 to 0.12 for LnVar show that constancy of growth could be improved by selective breeding. Improving uniformity in Nile tilapia by selection would bring economic benefits to the farmer, leads to less stress due to the reduced need of size grading and reduced competition among fish (Omasaki et al., 2017). More accurate biomass estimation from less variable growth rates also results in more optimal feeding regimes and less feed waste. At cohort/cage level, resilient fish may have more constant feed intake over time, waste less feed, and would therefore be more efficient. FE can vary widely in Nile tilapia production systems (Mengistu et al., 2020b), and the economic value of improving FCR by selection is considerable (0.41 US$/kg production/σa; Omasaki et al., 2017). Selecting for more resilient fish could therefore lead to a correlated response in FE and in that case improving resilience would also have a positive effect on the environmental impact of fish farming (Besson et al., 2016).

In conclusion, substantial additive genetic variance was found for LnVar in the aerated and non-aerated ponds and this can be exploited by selective breeding in Nile tilapia. Favorable genetic correlations of LnVar with health, survival and feed efficiency may be expected but this needs to be confirmed in further research. To improve resilience together with growth we recommend that fish breeding programs collect repeated records on body weight and use of sib testing in non-aerated pond with genomic selection.

Author contributions

SM: Writing- Original draft, Methodology, Investigation, Formal analysis, Interpretation of results.

HM: Writing - Review & Editing, Conceptualization, Methodology, Interpretation of results, Software, Supervision.

JWMB: Writing - Review & Editing, Methodology, Interpretation of results.

JB: Writing - Review & Editing, Interpretation of results, Supervision, Resources.

HLK: Writing - Review & Editing, Investigation, Interpretation of results, Resources.

TQT: Writing - Review & Editing, Investigation, Interpretation of results, Resources.

HK: Writing - Review & Editing, Conceptualization, Methodology, Interpretation of results, Funding acquisition, Supervision, Project administration.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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