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Genotype-by-environment interaction of growth traits in rainbow trout (*Oncorhynchus mykiss*): A continental scale study[1]

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ABSTRACT: Rainbow trout is a globally important fish species for aquaculture. However, fish for most farms worldwide are produced by only a few breeding companies. Selection based solely on fish performance recorded at a nucleus may lead to lower-than-expected genetic gains in other production environments when genotype-by-environment (G × E) interaction exists. The aim was to quantify the magnitude of G × E interaction of growth traits (tagging weight; BWT, harvest weight; BWH, and growth rate; TGC) measured across 4 environments, located in 3 different continents, by estimating genetic correlations between environments. A total of 100 families, of at least 25 in size, were produced from the mating 58 sires and 100 dams. In total, 13,806 offspring were reared at the nucleus (selection environment) in Washington State (NUC) and in 3 other environments: a recirculating aquaculture system in Freshwater Institute (FI), West Virginia; a high-altitude farm in Peru (PE), and a cold-water farm in Germany (GER). To account for selection bias due to selective mortality, a multitrait multienvironment animal mixed model was applied to analyze the performance data in different environments as different traits. Genetic correlation (r_g) of a trait measured in different environments and r_g of different traits measured in different environments were estimated. The results show that heterogeneity of additive genetic variances was mainly found for BWH measured in FI and PE. Additive genetic coefficient of variation for BWH in NUC, FI, PE, and GER were 7.63, 8.36, 8.64, and 9.75, respectively. Genetic correlations between the same trait in different environments were low, indicating strong reranking (BWT: r_g = 0.15 to 0.37, BWH: r_g = 0.19 to 0.48, TGC: r_g = 0.31 to 0.36) across environments. The r_g between BWT in NUC and BWH in both FI (0.31) and GER (0.36) were positive, which was also found between BWT in NUC and TGC in both FI (0.10) and GER (0.20). However, r_g were negative between BWT in NUC and both BWH (–0.06) and TGC (–0.20) in PE. Correction for selection bias resulted in higher additive genetic variances. In conclusion, strong G × E interaction was found for BWT, BWH, and TGC. Accounting for G × E interaction in the breeding program, either by using sib information from testing stations or environment-specific breeding programs, would increase genetic gains for environments that differ significantly from NUC.

Key words: heterogeneous genetic variance, multitrait multienvironment, reranking, scaling effect, selection bias, thermal growth coefficient

INTRODUCTION

Rainbow trout is a globally important species for aquaculture. It is produced under very diverse production conditions, such as different altitudes, water qualities, and farm management systems. In addition, the market size differs across production systems, e.g., from 300-g portion-sized fish to 2- to 3-kg large trout.

However, a breeding company may distribute trout from a single breeding program to these diverse production and market conditions. Selection at a single nucleus station may lead to lower-than-expected genetic gains in other production environments when genotype-by-environment (G × E) interaction exists (Mulder and Bijma, 2005). The G × E interaction has different forms: reranking across environments and heterogeneity of genetic variances (Falconer and Mackay, 1996; Lynch and Walsh, 1998). In addition, genetic correlations between pairs of different traits within environment may differ between environments due to G × E (Calus, 2006; Mulder, 2007). Finally, genetic correlations between the 2 traits, measured in different environments, can change, e.g., when 2-stage selection is practiced.

A survey among rainbow trout farmers revealed that growth was the most preferred trait among 13 traits (Sae-Lim et al., 2012). Body weight and thermal growth coefficient (**TGC**) are 2 complementary traits for improving growth rate. In rainbow trout, weak to moderate G × E interaction has been found for BW and TGC (Fishback et al., 2002; Kause et al., 2003, 2006; Le Boucher et al., 2011; Pierce et al., 2008). However, production systems located in different continents can differ greatly in temperature, altitude, photoperiod, and feeding, which may result in stronger G × E interaction. In this study, the aim was to quantify the magnitude of G × E interaction of growth traits in the forms of reranking, heterogeneity of genetic variances, heritabilities, and correlations between traits across 4 different production environments, located in 3 continents.

MATERIALS AND METHODS

Procedures for the ethical treatment of animals at Troutlodge, Inc. followed the U.S. and/or State guidelines for animal care and use including those outlined by "Guidelines for Use of Fishes in Field Research" established by the American Fisheries Society (AFS), the American Society of Ichthyologists and Herpetologists (ASIH), and the American Institute of Fisheries Research Biologists (AIFRB).

G × E Experiment

The fish used in this study were all female offspring supplied from the breeding program at Troutlodge, Inc., Washington State. The same standard was applied for all animals in the study. Troutlodge, Inc. ships salmonid eggs to >60 countries around the world with large differences in rearing environments. In August 2009, a total of 58 gender-reversed XX sires and 100 dams were mated to produce 100 full-sib families. Each sire was mated to 1 to 3 dams (average = 1.7) and each

dam was mated to 1 sire. Production of families took place over a period of 4 wk. Fertilized eggs from each of the 4 spawning wk were incubated using different water temperatures, resulting in all groups hatching at approximately the same time. Fertilized eggs were incubated in 100 incubators (1 for each family) until the eyed-egg stage.

In September 2009, groups of 25 eyed-eggs from each family were randomly sampled and pooled into 1 batch. For the 3 production environments, 5 batches, each containing 100 families of 25 full-sibs, were produced (total of 12,500 eyed-eggs). The number of families and family size were based on guidelines of a simulation study (Sae-Lim et al., 2010). Batch number 1 was shipped to the Freshwater Institute, West Virginia (**FI**), and grown in a recirculating aquaculture system. Batch numbers 2, 3, and 4 were shipped to Pasiri and Huancayo farms, Lake Titicaca, in Peru (**PE**). Batch number 4 served as a back-up in case of excessive mortality and was equally divided over the 2 farms. In total, Pasiri received 3,743 eggs and Huancayo received 3,757 eggs. Batch number 5 was shipped to Forellenzucht Trostadt in Germany (**GER**), a farm characterized by year-round low water temperatures.

For the breeding environment, 25 fish per family were randomly sampled as experimental fish at Troutlodge's Eastern Washington facility (**NUC**). In addition, we included performance at tagging of selection candidates in the NUC data set (~40 fish per family; 32 females and 8 males).

Numbers of fish surviving at tagging are given in Table 1. Due to flooding in November 2009, all fish at Huancayo farm were lost. The number of fish that hatched and survived up to tagging was 14,286 (Table 1).

Environmental conditions of the 4 farms are given in Table 1. The farms had been selected to represent extremes in rearing conditions. In brief, the German farm was chosen as an example of a low temperature farm; the Peru farm was chosen for its location at 3,812 m above sea level, and the Freshwater Institute was chosen as being representative for a recirculating aquaculture system.

Pedigree Reconstruction

The fish were tagged using passive integrated transponders (PIT tag; Allflex USA, Inc. for NUC, FI, and PE; and DORSET Identification b.v., the Netherlands, for GER) and the PIT tag scanned (scanner SF2001ISO: Destron Fearing, USA; for NUC, FI, and PE, and GR250: DORSET Identification b.v., the Netherlands; for GER) at the average size of 26.3 to 33.2g (5 to 7 mo of age; Table 2). Before tagging, fish were anesthetized using MS222 (150 mg/l) in NUC,

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Table 1. Environmental parameters measured during the genotype-by-environment interaction experiment

Environmental parameter	NUC[1]	FI	PE	GER
No. fish at tagging	2,496[2] + 4,010[3]	2,245	3,300	2,235
No. fish at harvest	2,372	2,243	2,890	1,992
Age at tagging (dph[4])	118 to 120	118 to 120	162 to 166	193 to 195
Age at harvest (dph)	280 to 295	294 to 296	357 to 359	445 to 446
Avg. dissolved oxygen[5] (mg/l)	7.3	10.2	6.63	10
Avg. water temperature (°C)	13.4	11.8	13.4	9.9
Feeding (% BW)	7.3 to 1.2%	11.2 to 1.2%	3.61 to 0.5%	2.5 to 0.5%
Protein %[6]	44 to 53%	42 to 55%	42 to 50%	42 to 64%
Fat %[6]	16 to 25%	15 to 16%	13 to 15%	11 to 30%
Photoperiod (min)[7]	223.1	163.3	-53.1	292.9
Altitude (above sea level; m)[8]	25	129	3812	361
Recirculation (%)[9]	0%	85%	0%	65%
Rearing environment	2 flow-through raceways	2 circular tanks in RAS	net pen submerged in Titicaca Lake	outside pond

[1]NUC = nucleus; FI = recirculating aquaculture system; PE = high elevated farm; GER = low temperature farming. Eyed eggs hatched during September to October 2009. Fish were tagged in January (NUC and FI), March (PE), and April (GER) of 2010. Fish were harvested in June (NUC), July (NUC and FI), September (PE), and December (GER) of 2010.

[2]Experimental fish at tagging.

[3]Information from selection candidates at tagging.

[4]Day post hatch.

[5]Average.

[6]Protein % and fat % were provided by feed manufacturers.

[7]Photoperiod was calculated from the difference between the highest day length (min) and average day length from overall rearing period. Day length was calculated from the difference between sunrise and sunset in minutes. The sunrise and sunset data (option: actual time) were assessed from: www.wunderground.com/history/. The negative sign indicates different directions of the change in day length.

[8]Altitude of each location was obtained from: www.daftlogic.com/sandbox-google-maps-find-altitude.htm.

[9]Recirculation aquaculture system in FI and reused water system in GER.

FI, and PE, and clove oil (10 mg/l) in GER. Fin clips were collected from all 158 broodstock fish and from fish at tagging from FI, PE, and GER for DNA extraction. In NUC, fish were kept in separated family tanks until tagging, allowing pedigree reconstruction based on physical tags; therefore, fin clips were not collected in NUC.

The DNA were isolated from fin clips to reconstruct the pedigree. Genotyping of the DNA samples was done in 3 laboratories: National Center for Cool and Cold Water Aquaculture, USDA; Troutlodge, Inc.; and Animal Breeding and Genomics Centre, Wageningen University. The protocols for DNA isolation and genotyping were synchronized across the labs. In brief, the

Table 2. Mean and its SD, phenotypic (V_p), genetic (V_A), and residual (V_R) variance estimates, phenotypic (CV_p), genetic (CV_A), and residual (CV_R) coefficients of variance, h^2, common environmental effect (c^2), and their SE for growth traits in each production environment (estimates from bivariate analysis)

Trait[1]	Environment[2]	No.	Mean	SD	V_P	V_A	V_R	CV_P	CV_A	CV_R	h^2	SE (h^2)	c^2	SE (c^2)
BWT	NUC	6,448	33.15	5.96	36.70	14.65	19.23	18.27	11.55	13.23	0.40	0.15	**0.08**[3]	0.05
	FI	2,138	26.26	6.20	40.51	17.63	20.62	24.24	15.99	17.29	0.44	0.15	0.06	0.05
	PE	3,179	29.15	5.81	33.88	13.56	19.72	19.97	12.63	15.24	0.40	0.13	0.02	0.04
	GER	2,041	27.06	6.62	44.57	11.98	29.27	24.67	12.79	20.00	0.27	0.13	**0.07**	0.05
BWH	NUC	2,364	546.82	94.70	9,035.40	1,742.67	6,749.19	17.38	7.63	15.02	0.19	0.10	**0.06**	0.03
	FI	1,893	395.15	75.84	6,127.50	1,092.29	4,589.94	19.81	8.36	17.15	0.18	0.11	**0.07**	0.04
	PE	2,795	524.28	105.17	11,212.00	2,054.06	8,682.51	20.20	8.64	17.77	0.18	0.09	0.04	0.03
	GER	1,819	376.39	81.72	6,148.90	1,345.45	4,715.37	20.83	9.75	18.24	0.22	0.09	0.01	0.03
TGC	NUC	2,364	2.07	0.18	0.03	0.009	0.022	8.37	4.47	7.14	0.27	0.12	0.04	0.04
	FI	1,891	1.73	0.16	0.03	0.003	0.022	10.01	2.96	8.48	0.10	0.08	**0.07**	0.03
	PE	2,790	1.75	0.20	0.04	0.002	0.034	11.43	2.79	10.58	0.06	0.06	**0.05**	0.03
	GER	1,818	1.43	0.19	0.04	0.008	0.029	13.99	6.35	11.84	0.22	0.09	0.01	0.03

[1]BWT = BW at tagging; BWH = harvest BW; TGC = thermal growth coefficient with Mallet correction.

[2]NUC = nucleus; FI = recirculating aquaculture system; PE = high elevated farm; GER = low temperature farming.

[3]Bold letter indicates significant effect when using likelihood ratio test (**LRT**) ~χ^2 with mixture of degrees of freedom (50:50) between 0 and 1, α = 0.05.

DNA isolation was done using NucleoSpin 96 Tissue Core Kit (Macherey-Nagel GmbH and Co, Duren, Germany). Multiplex PCR amplification was done as described by Johnson et al. (2007). Fragment analysis of the PCR products was done by setting the fragment sizes relatively to Genescan LIZ 500 size standard (Applied Biosystems, Foster City, CA). Output data were analyzed using Genemapper software version 4 (Applied Biosystem; Sae-Lim et al., 2013).

Parental allocation was performed using PAPA software (Duchesne et al., 2002). To ensure maximum accuracy of parental assignments and avoid bias in (co)variance estimation, the known mating data were used (Sae-Lim et al., 2013) as it is an available option in PAPA (Duchesne et al., 2002). In total, 2,142 out of 2,243 fish sampled in FI, 3,106 out of 3,236 fish sampled in PE, and 2,104 out of 2,235 fish sampled in GER were successfully allocated to the 100 full-sib families. Fish that were not successfully allocated to families were removed from the data set.

In total, 6 generations of pedigree information used in the genetic analysis were from the DNA reconstructed pedigree and from the 5 previous generations of pedigree information.

Trait Measurement

After tagging, fish in all environments were measured for body weight (**BWT**, in grams). All surviving fish were measured for body weight at harvest (**BWH**, in grams), which is the round weight prior to any processing. The age at harvest ranged from 9 mo in NUC to 14 mo in GER (Table 1).

Thermal growth coefficient from tagging to harvest (**TGC**) was calculated as

$$\left[\frac{(\sqrt[3]{BWH}-\sqrt[3]{BWT})}{T \times t}\right] \times 1,000$$

where T = average water temperature (°C) and t = rearing period in days. To correct for the nonlinear relationship between growth rate and water temperature (Jobling, 2003), formula TGC was modified to

$$\left[\frac{(\sqrt[3]{BWH}-\sqrt[3]{BWT})}{k \times t}\right] \times 1,000$$

by substituting T with k calculated from the model used by Mallet et al. (1999):

$$k = \frac{T_{opt}(T-T_{min})(T-T_{max})}{(T-T_{min})(T-T_{max})-(T-T_{opt})^2}$$

where k = new temperature, corrected for the concave relationship between growth rate and temperature. The optimal water temperature (T_{opt}) was set to 14.8°C, which was calculated as the average optimal water temperature for salmonid growth (Austreng et al., 1987; Hokanson et al., 1977; FAO, 2011). Daily water temperature: T was from the daily measurement at a farm. The limits for the lower and upper thermal tolerance: T_{min} = 0°C and T_{max} = 23°C, respectively, were taken from the literature (Hokanson et al., 1977; Matthews and Berg, 1997; Ojolick et al., 1995).

Genetic Analysis

Data records were combined with the reconstructed pedigree and duplicate observations and measurement errors were removed. In total, 13,806 records were available for the data analysis (Table 2; BWT). Heritability, common environmental effect for full-sibs (**c²**), and phenotypic (**r_p**) and genetic (**r_g**) correlations were estimated, using restricted maximum likelihood in an animal mixed model in ASReml v. 3.0 (Gilmour et al., 2009).

Heritability. Significant fixed effects were tested in SAS Version 9.2, using PROC GLM (SAS Inst. Inc., Cary, NC). The fixed effects tested were different across environments due to different data structure. Thus, the final model for different environments varied and included only the significant effects.

In NUC, each trait was modeled as:

$$y_{ijklm} = \mu + Gender_i + \beta*AGE_j + FERT_k + a_l + FS_m + e_{ijklm}, \tag{1}$$

In FI, each trait was modeled as:

$$y_{jklmn} = \mu + \beta*AGE_j + FERT_k + Tank_n + a_l + FS_m + e_{jklmn}, \tag{2}$$

In PE and GER, each trait was modeled as:

$$y_{jklm} = \mu + \beta*AGE_j + FERT_k + a_l + FS_m + e_{jklm}, \tag{3}$$

where y is the observation of the lth individual from the mth full-sib family, μ is the overall mean, Gender is a fixed effect of observation (i = 1: male, 2: female, 9: unknown). The Gender effect was only modeled in NUC for BW at tagging, as we included BWT of the selection candidates in the data set. Otherwise, this effect was omitted. Fixed regression of performance on AGE_j was included in the model to correct for different measurement dates within environment and corrected for rearing periods from hatching to the day of trait measurement (Table 2). For TGC, AGE was not included in the model

because TGC is already corrected for the rearing period. The Tank is the fixed effect for BWT due to the 2 circular tanks used in FI for stocking fish from fingerling up to tagging ($j = 1, 2$). The FERT is the fixed effect corrected for fertilization period of 4 wk ($k = 1, 2, 3,$ or 4) due to different groups of available fertile dams. The a_l is the random additive genetic effect, $a \sim N(0, \mathbf{A}\sigma^2_a)$ of the lth animal, where $\mathbf{A}$ is the additive genetic relationship matrix and σ^2_a is the additive genetic variance. The FS_m is the random full-sib common environmental effect, $FS \sim N(0, \mathbf{I}\sigma^2_{FS})$, and e is the random error term, $e \sim N(0, \mathbf{I}\sigma^2_e)$, where $\mathbf{I}$ is the identity matrix, σ^2_{FS} is the common environmental variance, and σ^2_e is the residual variance. The full-sib effect was included in the model to account for effects common to full-sibs, for example, incubator effects, environmental maternal effects, and a quarter of the dominance variance.

Univariate analysis was performed for each trait to test for the significance of common environmental effect. The models with and without the full-sib effect were compared using likelihood ratio test (**LRT**). The LRT = $-2[\ln(L)_r - \ln(L)_f]$, where $\ln(L)_r$ and $\ln(L)_f$ are natural logarithm of likelihood from the reduced model (without full-sib effect) and the full model (with full-sib effect), respectively (Lynch and Walsh, 1998). The asymptotic distribution of likelihood ratio follows Chi-square (χ^2) distribution with a mixture (50:50) of degrees of freedom between 0 and 1 (Stram and Lee, 1994). The 5% significance level was $\chi^2 = 2.706$.

After LRT, h^2 and c^2 were estimated using a bivariate model. Selection bias (Henderson, 1984; Pollak et al., 1984; Ouweltjes et al., 1988) due to selective mortality was accounted for by always including BWT of each environment as a reference trait in the bivariate model (Kause et al., 2011). Full-sib effect was always included in the bivariate model to avoid overestimated h^2. Heritability from the model with full-sib effect was quantified as $h^2 = V_A/(V_A + V_{FS} + V_R)$, where V_A, V_{FS}, and V_R are estimated additive genetic, estimated full-sib, and estimated residual variances. The common environmental effect was calculated as $c^2 = V_{FS}/(V_A + V_{FS} + V_R)$. In addition, variation across environments was compared by estimating phenotypic ($[CV_P = (SD_P/\overline{X}) \times 100]$, genetic $[CV_A = (SD_A/\overline{X}) \times 100]$, and residual ($[CV_R = (SD_R/\overline{X}) \times 100]$, coefficients of variation. The SD_P, SD_A, and SD_R are phenotypic, genetic, and residual standard deviations, respectively. The following parameters were obtained from the models 1 to 3. The $\overline{X}$ is phenotypic trait mean. The V_A and CV_A were used to quantify the degree of heterogeneous genetic variation across environments.

Phenotypic and Genetic Correlations. Three types of genetic correlations were estimated: a) genetic correlations of different traits within an environment, b) ge-netic correlation of a trait measured in different environments (measure of genotype reranking), and c) genetic correlations of different traits in different environments.

To estimate all types of genetic correlations simultaneously, we performed a multitrait multienvironment (**MTME**) analysis using a multivariate animal mixed model. The first MTME model contained 3 traits measured in 4 environments, but ASREML had difficulty in estimating the parameters. Therefore, the size of a single MTME model was reduced to 2 traits and 4 environments (total of 8 traits). The full-sib effect was excluded from the model because, in many cases, the full-sib effect captured all (co)variance of the traits (Maluwa et al., 2006). Residual (co)variances of the same trait and different traits, measured in different environments, were set to zero:

$$\text{VAR (e)} = \begin{array}{cccc} R_{T1,E1} & & \cdots & \\ R_{T12,E1} & R_{T2,E1} & & \text{Symmetry} \\ \vdots & & \ddots & \vdots \\ 0 & 0 & & R_{T1,E4} \\ 0 & 0 & \cdots & R_{T12,E4} \quad R_{T2,E4} \end{array}$$

where $R_{T1,E1}$ is the residual variance of trait: T_1 measured in environment: E_1. $R_{T12,E1}$ is the residual covariance between T_1 and T_2, measured in E_1. Therefore, phenotypic correlations (r_p) were only calculated between traits measured within the same environment.

After estimating all variance components, phenotypic and genetic correlation matrices were bended to be positive definite (Hayes and Hill, 1981) in Octave computer software (A. Kause, MTT, Finland; personal communication). The bending induced only minor changes in phenotypic (range: 0 to 0.005) and genetic (range: −0.016 to 0.068) correlation estimates. The bended estimates were presented.

Effect of Selection Bias. To study the effect of selection bias on V_A and V_R estimates, a comparison of V_A and V_R from 2 models was made. These models were: i) multivariate model for BWH, measured in 4 environments, and ii) MTME model for BWT and BWH, measured in 4 environments. These models did not include the full-sib effect to enhance the comparison of models. Simultaneous estimation of V_A and V_{FS} typically creates discrepancy in V_A across the compared models because of the difficulty of accurately estimating the 2 at the same time.

RESULTS

Genotype-by-Environment Interaction

Heterogeneity of Genetic Variation. The V_A in BWT ranged from 11.98 to 17.63 (Table 2). In contrast, V_A of BWH in PE (2,054.06) was twice as high as V_A of BWH in FI (1092.29). However, the C_{VA} in BWH

Table 3. Phenotypic (r_p) and genetic (r_g) correlations and their SE between different traits measured within environment

Trait[1]	Environment[2]	$r_p \pm$ SE	$r_g \pm$ SE
BWT-BWH	NUC	0.56 ± 0.02	0.47 ± 0.09
	FI	0.64 ± 0.02	0.65 ± 0.07
	PE	0.50 ± 0.02	0.58 ± 0.08
	GER	0.36 ± 0.03	0.41 ± 0.12
BWT-TGC	NUC	0.13 ± 0.03	–0.15 ± 0.12
	FI	0.22 ± 0.03	0.13 ± 0.13
	PE	0.16 ± 0.02	0.20 ± 0.13
	GER	–0.09 ± 0.03	–0.14 ± 0.14
BWH–TGC	NUC	0.90 ± 0.01	0.71 ± 0.05
	FI	0.88 ± 0.01	0.72 ± 0.05
	PE	0.92 ± 0.00	0.81 ± 0.03
	GER	0.88 ± 0.01	0.75 ± 0.05

[1]BWT = BW at tagging; BWH = harvest BW; TGC = thermal growth coefficient with Mallet correction.

[2]NUC = nucleus; FI = recirculating aquaculture system; PE = high elevated farm; GER = low temperature farming.

Table 4. Genetic correlation and its ±SE for genotype-by-environment (G × E) interaction for growth traits

Trait[1]	Environment[2]	Environment		
		FI	PE	GER
BWT	NUC	0.34 ± 0.10	0.15 ± 0.11	0.37 ± 0.10
	FI		0.58 ± 0.08	0.65 ± 0.07
	PE			0.55 ± 0.09
BWH	NUC	0.41 ± 0.11	0.19 ± 0.13	0.48 ± 0.12
	FI		0.40 ± 0.12	0.51 ± 0.12
	PE			0.43 ± 0.12
TGC	NUC	0.35 ± 0.13	0.31 ± 0.13	0.36 ± 0.13
	FI		0.32 ± 0.14	0.42 ± 0.14
	PE			0.34 ± 0.14

[1]BWT = BW at tagging; BWH = harvest BW; TGC = thermal growth coefficient with Mallet correction.

[2]NUC = breeding environment; FI = recirculating aquaculture system; PE = high elevated farm; GER = low water temperature farming.

was very similar in PE (8.64) and FI (8.36), suggesting that the variances differed because of the differences in trait means. Similarly, V_A and CV_A of BWH in NUC was 1,742.67 and 7.63, whereas V_A and CV_A of BWH in GER was 1,345.45 and 9.75. For TGC, CV_A varied between environments—from 2.79 in PE to 6.35 in GER.

Heterogeneity of Heritabilities. Heritability for BWT was similar in NUC (0.40 ± 0.15), FI (0.44 ± 0.15), and PE (0.40 ± 0.13), but lower in GER (0.27 ± 0.13; Table 2). The lower estimate of h^2 in GER was due to lower V_A (11.98) and higher V_R (29.27), compared with the other environments. For BWH, h^2 ranged from 0.18 to 0.22. For TGC, h^2 was heterogeneous across environments (0.06 to 0.27). In addition, c^2 for TGC was significant in FI (0.07) and PE (0.05), indicating some effects common to full-sibs beyond additive genetic effects.

Heterogeneity of Within Environment Correlations. The r_g between BWT and BWH were heterogeneous, especially between FI (r_g = 0.65 ± 0.07) and GER (r_g = 0.41 ± 0.12), but less so between NUC (r_g = 0.47 ± 0.09) and PE (r_g = 0.58 ± 0.08; Table 3). Similarly, r_g between BWT and TGC showed heterogeneity on one hand, between FI (r_g = 0.13 ± 0.13) and PE (r_g = 0.20 ± 0.13), and on the other hand, between GER (r_g = –0.14 ± 0.14) and NUC (r_g = –0.15 ± 0.12). In contrast, r_g between BWH and TGC tended to be more homogeneous across environments, r_g ranged from 0.71 to 0.81.

Genetic Correlation for Same Trait across Environments. Genetic correlation of BWT measured in NUC and the 3 production environments ranged from 0.15 (PE) to 0.37 (GER; Table 4). Genetic correlation of BWH measured in NUC and the 3 production environments ranged from 0.19 (PE) to 0.48 (GER). Genetic correlation for TGC measured in NUC and the 3 production environments ranged from 0.31 ± 0.13 (PE) to 0.36 ± 0.13 (GER).

Moderate r_g of all traits was found among the production environments in FI, PE, and GER. The r_g of BWT ranged from 0.55 (PE vs. GER) to 0.65 (FI vs. GER). Lower r_g were found for BWH (0.40 to 0.51) and TGC (0.32 to 0.42). Overall, the results showed strong reranking across environments for BWT, BWH, and TGC.

Genetic Correlation between Different Traits Measured in Different Environments. Genetic correlations between BWH in NUC and TGC in FI (0.44), GER (0.36), and PE (0.19) were all positive, showing that single-trait selection for BWH in NUC will lead to a favorably correlated response for TGC across environments (Table 5).

Estimates of r_g between BWT in NUC and BWH in FI (0.31) and GER (0.36) were positive, but close to zero with BWH in PE (–0.06). Similarly, r_g between BWT in NUC and TGC in FI (0.10) and in GER (0.20) were positive but negative with TGC in PE (–0.20), indicating that selection on BWT in NUC may lead to different directions and size of correlated responses for BWH and TGC across environments.

Effect of Selection Bias

Overall, including BWT in the multitrait analysis resulted in higher estimates of V_A and V_R for BWH than that from multivariate model without BWT (Table 6). This suggested it is important to include BWT in multiple trait analysis to avoid selection bias in estimates for BWH.

Table 5. Genetic correlation and its ±SE between different traits measured in different environments

Environment[1]	Trait[2]	Environment BWT	BWH	TGC
		FI		
NUC	BWT	-	0.31 ± 0.11	0.10 ± 0.13
	BWH	0.21 ± 0.12	-	0.44 ± 0.13
	TGC	−0.04 ± 0.13	0.32 ± 0.13	-
		PE		
NUC	BWT	-	−0.06 ± 0.12	−0.20 ± 0.13
	BWH	0.14 ± 0.12	-	0.19 ± 0.14
	TGC	0.05 ± 0.13	0.27 ± 0.13	-
		GER		
NUC	BWT	-	0.36 ± 0.12	0.20 ± 0.13
	BWH	0.21 ± 0.12	-	0.36 ± 0.14
	TGC	−0.03 ± 0.13	0.33 ± 0.13	-

[1]NUC = nucleus; FI = recirculating aquaculture system; PE = high elevated farm; GER = low temperature farming.

[2]BWT = BW at tagging; BWH = harvest BW; TGC = thermal growth coefficient with Mallet correction.

DISCUSSION

Genotype-by-Environment Interaction

The G × E interaction can have different consequences: reranking of breeding values of genotypes across environments, heterogeneous genetic variation across environments (also known as scaling effect), heterogeneous heritabilities, and heterogeneous correlations between traits (measured within environment) across environments (Lynch and Walsh, 1998; Calus, 2006; Mulder, 2007). Statistically, reranking is absent when genetic correlation (r_g) of a trait measured in different environments does not differ from 1. However, in practice, the presence of reranking is commonly considered unimportant for a breeding program when $r_g \geq 0.8$ (Robertson, 1959). Reranking is more serious than heterogeneity of genetic variance because reranking means that a single genotype is not superior across all environments (Calus, 2006; Mulder, 2007). For example, in dairy cattle genetic evaluations, it is important to account for heterogeneity of genetic variance between farms to accurately estimate breeding values (**EBV**; e.g., Hill, 1984; Meuwissen et al., 1996). However, in fish, heterogeneity of genetic variance is less important because selection candidates are typically located in a single environment and performance of their sibs in other environments are treated as genetically different traits, automatically accounting for heterogeneity of variance between environments (e.g., Kause et al., 2003, 2005).

In our study, heterogeneity of additive genetic variance, heritabilities, and correlations across environments were also found. High reranking between NUC and other environments was found for all traits, but reranking was stronger for TGC than BWH, especially between NUC

Table 6. Additive genetic (V_A) and residual (V_R) variances of BW at harvest from 2 different models: multivariate model with 4 traits (BW at harvest measured in 4 environments) and multitrait multienvironment (MTME) model with 8 traits (BW at tagging and BW at harvest, measured in 4 environments)

Environment[1]	Multivariate V_A	V_R	MTME V_A	V_R
NUC	3,304.17	5,250.71	3,552.10	5,869.99
FI	2,404.87	3,687.04	2,525.57	3,896.43
PE	3,558.27	7,758.52	3,812.78	7,857.38
GER	1,637.63	4,537.64	1,654.06	4,563.28

[1]NUC = nucleus; FI = recirculating aquaculture system; PE = high elevated farm; GER = low temperature farming.

and FI, and between NUC and GER. The BWH differed between environments due to variation in age at harvest, which resulted from the differences in local market objectives. These differences in age at harvest have influenced r_g estimates between environments. The BWH is the cumulative result of growth from hatching to harvest and there is a common period between hatching to harvest across environments. In contrast, TGC is a more dynamic trait than BWH because TGC was calculated for a specific grow-out period, i.e., between BWT and BWH measured at different ages. Consequently, it is expected that reranking in time (Rutten et al., 2005; Sae-Lim et al., 2013) and between environments is higher in TGC than BWH. Higher reranking across environments in TGC is in agreement with a previous study in European seabass (*Dicentrarchus labrax*), in which daily gain coefficient (r_g = 0.21 to 0.61) showed more reranking than harvest BW (r_g > 0.80; Dupont-Nivet et al., 2010).

Reranking has been studied in different fish species for multiple environments. For different locations, in Atlantic cod, weak reranking (r_g = 0.82 to 0.94) for 2-yr BW measured in 3 different locations off the coast of Norway was found (Kolstad et al., 2006). In rainbow trout, moderate G × E exists (r_g = 0.61) between fresh and brackish water environments in BW measured at 2 yr of age (Kause et al., 2003). In tilapia (*Oreochromis shiranus*) grown at different altitudes, (Maluwa et al., 2006) weak reranking (r_g = 0.74) for BW measured between high and low altitudes has been reported. Reranking has also been studied in different livestock species for multiple environments. In contrast to tilapia, Colorado Angus cattle weaning weight, for example, measured at high, medium, and low altitude showed moderate to weak reranking (r_g = 0.47 to 0.83; Williams et al., 2012). Under a partially controlled environment, weak reranking was found in slow-growing chickens for 8-wk BW (r_g = 0.74 to 0.98) and BW at slaughter (r_g = 0.76 to 0.97). Initial specific growth rate in chickens (r_g = 0.83 to 0.99) was found when

measuring in different husbandry systems—cages, floor pens, and outdoor (N'Dri et al., 2007). Similarly, moderate to weak reranking (r_g = 0.67 to 0.96) was reported in BW of rainbow trout measured between 2 different diets (Kause et al., 2006; Le Boucher et al., 2011). The previous studies above do not show a consistent pattern of G × E interaction across livestock kept in different environments. However, most studies tend to show weak reranking across regions, locations, or countries.

The high reranking in this study may be due to the large diversity of commercial environments combined with differences in age at harvest. Differences in various macro-environmental parameters, such as altitude, dissolved oxygen, water temperature, photoperiod, water sources, feeding composition, and feeding levels, may have contributed to the strong G × E interaction observed. When environmental differences are more extreme, it is more likely to find strong G × E interaction. In this study the environments used reflect the current commercial conditions that have large differences. Consequences of G × E interaction may be reduced by changing environmental conditions to be more similar to the breeding environment. Identifying the environmental parameter explaining the G × E interaction will help develop a breeding scheme to meet the different environments.

In our study, the r_g among the 3 production environments are more similar and does not explicitly indicate which environment is the most different from the others. However, there is a tendency that r_g between PE and other environments are slightly lower for all traits. This suggests that PE is a slightly different environment than FI and GER.

In all production environments, we collected information at a single location. Caution should, therefore, be taken in generalizing our results. To confirm the current result, we recommend additional experiments, using multiple farms.

Trait Selection at Nucleus

In trout breeding, 2-stage selection (Cunningham, 1975) is sometimes used to enhance genetic gain; for instance, in Finland (Kause et al., 2005; Martinez et al., 2006), and by Troutlodge. Two-stage selection can be implemented by tagging only the biggest fingerlings, typically within families in the first stage, and the final selection among tagged individuals based on EBV for all traits of interest (Martinez et al., 2006). To implement 2-stage selection efficiently in trout across multiple environments, a positive r_g between trait used in the first stage (BWT) and traits in the breeding goal (BWH and/or TGC across environments) are needed.

Our study revealed that preselection for BWT in NUC will yield favorable correlated genetic responses in both BWH and TGC in FI and GER. Therefore, 2-stage selection can be efficiently implemented for FI and GER. In contrast, preselection for higher BWT in NUC may indirectly contribute to lower-than-expected genetic gain (due to G × E interaction) of BWH and TGC in PE. Postponing preselection may improve the efficiency of 2-stage selection and enhance genetic gain in PE (Sae-Lim et al., 2013).

Method and Selection Bias

In this study, an MTME model was used and by including BWT, we accounted for selection bias due to selective mortality (Henderson, 1984; Pollak et al., 1984; Ouweltjes et al., 1988). This resulted in higher additive genetic and residual variances for BWH. The explanation could be that mortality related to low BW resulted in reduced variance among the surviving fish. Tagging weight is recorded on all fish and hence BWH of culled fish can be predicted when both BWT and BWH are included in the model, returning the variance closer to its original value. In European whitefish, the impact of selection bias due to preselection was accounted for by using multitrait analysis (Kause et al., 2011). In dairy cattle, an approximate multitrait model was used to account for selection bias, which resulted in higher accuracy of EBV (Lassen et al., 2007). In Dutch Warmblood horse, bivariate model accounting for selection bias due to preselection increased h^2 for dressage competition from 0.15 to 0.21 (Ducro, 2010).

Implications for Breeding

Where G × E interaction is present, optimization of a breeding program allows genetic gains in all environments to be maximized. There are several strategies of optimization to be used, as described by Mulder et al. (2006). First, adjusting farming management to be similar to breeding environment may reduce G × E interaction. This certainly holds for harvest weight. Differences in harvest weight between environments can be accommodated better by collecting multiple weights in the nucleus. However, not all environmental conditions can be controlled. Second, sibs' performance information collected in different production environments can be incorporated into EBV for selection candidates in the nucleus. Using sib information, it is possible to select breeding candidates in the nucleus that have high EBV for performance in another environment (Mulder and Bijma, 2005). Third, environment-specific breeding programs can be implemented. To make a decision from a genetic point of view, whether or not a single breeding

program should be divided into 2 environment-specific breeding programs, "break-even correlation" can be used as a criterion under the assumption that costs of running 2 smaller breeding programs is equal to the cost of 1 single breeding program (Mulder et al., 2006). The break-even correlation is defined as the intersection of genetic correlations when the genetic gain of different breeding strategies is equal. When the genetic correlation across environments is lower than the break-even correlation, separate breeding programs are recommended. The estimated break-even correlation in a dairy cattle breeding program ranges from 0.61 (Mulder et al., 2006) to 0.70 (James, 1961). In fish breeding, the break-even correlation is expected to be higher, i.e., ≥0.70, due to sib testing, which puts more emphasis on own performance than progeny testing and due to higher selection intensity compared with cattle, which is related to properties of normal distribution (Mulder et al., 2006).

In our study, we found that r_g of a trait measured in different environments is <0.7. This suggests that from a strictly genetic point of view, separate breeding programs for different environments seem to lead to a higher genetic gain than a single breeding program. However, it is very costly to organize environment-specific breeding programs. Opportunities to exploit sib information to overcome the disadvantage of G × E interaction needs to be further explored in combination with recording weight over different periods in the nucleus. Apart from the break-even correlation, decision on optimization of a breeding program for G × E interaction may depend on cost-benefit analysis, including extra cost for additional testing or environment-specific breeding program, and potential added benefit to the breeding program. Moreover, for example in dairy cattle, a single breeding program with progeny testing of all bulls in 2 environments (OJ-2 strategy; Mulder et al., 2006) resulted in lower genetic gain in an overall objective than in 2 separate breeding programs (TE-1 strategy). However, overall genetic gain from OJ-2 is not severely less than TE-1, even though r_g is lower than the break-even correlation of 0.61.

In conclusion, strong G × E interaction was found in BWT, BWH, and even stronger G × E interaction in growth rate. Preselection in nucleus may indirectly contribute to lower-than-expected genetic gain in Peru, due to G × E interaction. This study calls for further research on optimization of breeding schemes that meets the different environments. A better understanding of the causes of the G × E interaction will help to design the most optimal breeding scheme from not only a genetic but also an economic point of view.

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