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RESEARCH ARTICLE

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The relationship between feed efficiency, growth and group dominance dynamics in turbot (*Scophthalmus maximus*)

Luis Gomez-Raya[1], Wendy M. Rauw[1], Santiago Cabaleiro[2], Rubén Caamaño[2], L. Alberto Garcia-Cortes[1] and Antti Kause[3]

[1]Instituto Nacional de Investigación y Tecnología Agraria y Alimentaria (INIA), Dept. Mejora Genética Animal, 28040 Madrid, Spain [2]Cluster de la Acuicultura de Galicia (CETGA), 15965 Aguiño (A Coruña), Spain [3]Natural Resources Institute Finland (LUKE), Dept. of Biometrical Genetics, Jokioinen, 31600, Finland

Abstract

Variation among families of turbot (Scophthalmus maximus) in growth, feed efficiency, and body weight variation was investigated. A total of 672 turbot (Scophthalmus maximus) originating from eight families (84 full-sibs per family) were used in this experiment. Body weight (BW) was recorded individually four times between approximately 250 and 370 days of age. Feed intake was measured for each tank during the three corresponding time periods. Feed efficiency was estimated for each tank based on the calculations of residual feed intake (RFI) and feed conversion ratio (FCR). The within-tank coefficient of variation in body weight (CV-BW) and residual body weight variation (RBWV) were calculated to evaluate group dominance dynamics. Components of variation attributable to families were estimated from linear and quadratic random regression orthogonal polynomials. The random quadratic family component explained 14% (RFI), 22% (FCR), 76% (BW), 50% (CV-BW), and 45% (RBWV) of the total variance. The family components were significant for BW, CV-BW and RBWV (p<0.001), and was very close to significance for FCR (p=0.052). The correlation between the intercept (grand mean) of RFI and FCR was highly significant (r=0.94). Intercepts of RFI and FCR were positively correlated with CV-BW and RBWV (r=0.09 to 0.12), however, the correlations were not significant. The results indicate differences between families in FCR, which may be used in selection programs aimed at improving feed efficiency.

Additional keywords: aquaculture, fish.

Abbreviations used: AIC (Akaike information criterion); BW (body weight); BWG (body weight gain); CETGA (Centro Tecnológico Gallego de Acuicultura); CV-BW (coefficient of variation of body weight); FCR (feed conversion ratio); FI (feed intake); LRT (likelihood ratio test); PVAR-FAM (variation between families); RBWV (residual body weight variation); RFI (residual feed intake); SDBW (standard deviation of body weight).

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Correspondence should be addressed to Luis Gomez Raya: gomez.luis@inia.es

Introduction

The six main cultured finfish species in Europe, accounting for 97% of the total aquaculture production, are Atlantic salmon (*Salmo salar*), rainbow trout (*Oncorhynchus mykiss)*, gilthead seabream (*Sparus aurata*), European seabass (*Dicentrarchus labrax*), common carp (*Cyprinus carpio*) and turbot (*Scophthalmus maximus*) (Janssen *et al.*, 2017). Gjedrem *et al.* (2012) estimated that about 10% of global aquaculture production is based on genetically improved stocks. According to Janssen *et al.* (2017), today about 80-83% of the European aquaculture production originates from selective breeding resulting in an annual gain in harvest weight of 3%. This increase is mainly explained by the dominance of European salmon farming. Turbot, which is mainly produced in Spain, is one of the most recently selected species, with about five generations of selection for the oldest program (Chavanne *et al.*, 2016). Traits of high economic importance in fish production are growth rate, feed conversion ratio (FCR), resistance to disease, fillet percentage, meat quality, and age at maturation (Gjedrem, 1983; Kankainen *et al.*, 2016).

Growth-related traits, which have medium to high heritabilities, are the main targets of turbot breeding programs applied by the main companies in Europe (Bouza *et al.*, 2014). Cumulative genetic gain in growth performance is about 25% for turbot (Janssen *et al.*, 2017).

In farmed fish species, feed accounts for at least 50% of production costs. In addition, feed production has been identified as a major contributor to potential climate change and acidification impacts, and feed waste is responsible for a substantial part of environmental loading (Aubin *et al.*, 2009; Grima *et al.*, 2010). Because measurement of feed intake (FI) in aquaculture species requires advanced methods, individual FI measurements are generally not available in fish reared in groups. As a result, in contrast with many terrestrial livestock species, knowledge about FCR in fish is limited (Kause *et al.*, 2006a,b). However, alternatively, FI can be recorded using tank as the unit of measurement. Tank means can be used for identifying and selecting entire families with superior feed efficiency performance.

When social hierarchies occur, feed is not equally divided among all members of the group. In fish, FI of an individual in a group is closely related to the individual's position in the hierarchy (McCarthy *et al.*, 1993). Dominant fish will first secure access to resources, limiting access by subordinate fish. In addition, resource-demanding stress resulting from aggressive behaviors in social hierarchies may affect the individual's efficiency to convert feed to growth. Since competitively superior, dominant fish may have better possibilities to grow fast. Consequently, dominance hierarchies may lead to large differences in body size. As a result, measurement of body weight (BW) variation may provide additional information on differences in group dynamics between families (Jobling, 1993).

Turbot (*Scophthalmus maximus*) is a highly-valued scaleless carnivorous flatfish that is naturally distributed in European sea waters. Turbot aquaculture first started in Scotland in the 1970s, expanded in Galicia in the 1980s, and with technological development of juvenile production in the 1990s further expanded across numerous European countries (Danancher & Garcia-Vazquez, 2007; Polanco & Bjorndal, 2013). In Europe, the farmed turbot production reached over 11,000 tons in 2014. A total of 7,808 tons were produced in Spain with a sale price of €58.6 million euro; Galicia accounted for 99% of the total Spanish production (FIS, 2015).

The objective of this study was to investigate differences between families of turbot in tank-based feed efficiency, growth, and in group dominance dynamics as approximated by the within-tank coefficient of variation in body weight and by the residual body weight variation (RBWV). Feed efficiency is measured as residual feed intake (RFI), a measure of efficiency that is independent of metabolic body weight and growth, and which is widely used as a selection criterion in genetic selection programs of terrestrial livestock animals. Low RFI values indicate high efficiency of feed utilization (Koch *et al.*, 1963; Rauw, 2012). We investigated the correlation between two measures of feed efficiency (RFI and FCR), and whether faster growing fish are also more efficient. In addition, we investigated whether more stable group dynamics as approximated by a lower variation in body weight within a family-tank is related to faster growth and more feed efficient fish. The results are used to evaluate the feasibility of performing between-family selection for feed efficiency and for low within-tank variation.

Material and methods

Mating and experimental design

A total of 672 turbot originating from eight families (84 fullsibs per family) located at the facilities of the Centro Tecnológico Gallego de Acuicultura (CETGA; NW Spain) were used in this experiment. Families were generated as follows: sperm was gently extracted from eight unrelated males and eggs were gently extracted from eight unrelated females. Eggs of each female were fertilized by mixing them with the sperm of one male after which salt water was added for activation. After a few minutes, the fertilized eggs were placed in an incubation tank. At a water temperature of 14 to 15°C, eggs hatched after 5 to 6 days. At one day of age (after hatching), fish were relocated to hatchery tanks, where they were fed rotifers between 2 and 18 days of age, artemia between 7 and 45 days of age, and dry fish feed after 30 days of age. At 45 days of age, fish were relocated to tanks for the fattening period.

The members of each family were randomly allocated to three tanks, *i.e.*, 28 fullsibs per tank. Fish were kept in tanks with a capacity of 400L. Each tank had an individual open-circuit inflow of sea water. The fish in each of the 24 tanks were maintained under the same conditions in the same room at an average water temperature (± SD) of 13.6 (± 1.5 °C; range 11.1 - 17.4 °C). The CETGA Committee on Bioethics has approved the protocols for this experiment.

This study particularly aims at investigating the part of the trait variation that is accounted for by differences between families. These differences, in addition to additive genetic effects, may be due to dominance genetic effects, non-genetic effects and maternal effects.

Trait recording

Two days after the fish were allocated to the experimental tanks, body weight (BW) was measured individually (day 0), and subsequently at day 47, 83 and 119 of the experiment. At day 0, fish were 274, 267, 277, 253, 263, 263, 246, and 240 d of age for families 1 through 8, respectively. The normal age at which turbot is marketed in Spain is around 24 to 30 months of age. Fish were hand fed to satiation and FI was measured for each tank for period 1 (day 0 to 47), period 2 (day 47 to 83), and period 3 (day 83 to 119). In order to ensure that all fish had access to the feed, feed was given manually in access until the technician observes that fish do not eat any longer. In a previous experiment at CETGA, it was determined that this feeding method results in feed wastage of around 3% (unpublished data). Fish were fed two to three times a day with a mix of Efico Sigma 870 4.5mm and Efico Sigma 870 6.5 mm feed which consisted of, respectively, 54 and 54% crude protein, 18 and 20% crude lipids, 11.7 and 9.3% carbohydrates, 0.3 and 0.2% crude cellulose, 9.7 and 10.8% ash, 1.4 and 1.5% phosphor, and 21.7 and 22 MJ/kg crude energy (Biomar Iberia SA). The amount of times that fish are fed at the facilities of the CETGA depends both on the fish species and their age. When fish get older, they need to be fed less often. If they are fed too often, they will not eat all feed, therefore the amount of feed wastage increases. In turbot, fish are fed four times per day when they are very young; this is reduced to two times per day when they get older.

Two traits were used to evaluate feed utilization: feed conversion ratio (FCR) and residual feed intake (RFI). FCR is defined as the ratio of feed intake to weight gain. RFI is defined as the difference between the actual FI and that predicted from a linear multiple regression of FI on maintenance (metabolic body weight) and growth, and is therefore phenotypically independent of body weight gain (BWG) and body weight (size) (Koch *et al.*, 1963). Total average FI in each tank was calculated separately for each period. Following Rauw *et al.* (2016), the equation used to estimate RFI for each tank was based on the following multiple linear regression of average total FI on average metabolic body weight and average BWG in each tank, including all measurements of each tank in periods 1, 2, and 3 (a total of 72 observations, i.e., eight families × three tanks × three observations):

$$FI_i = b_0 + (b_1 \times BW_i^{0.80}) + (b_2 \times BWG_i) + e_i, \quad (1)$$

where FI_i is the average feed intake of an individual in tank i (kg); $BWi^{0.80}$ is the average metabolic body weight of an individual in tank i ($kg^{0.80}$); BWG_i is the average BWG of an individual in tank i (kg); b_0 is the population intercept; b_1, b_2 are the partial regression coefficients representing maintenance requirements per metabolic body weight and feed requirements for BWG, respectively; and e_i is the error term, which represents the RFI of an average individual in tank i. Metabolic body weight was estimated by averaging the body weight of an average individual at the beginning and at the end of each period and raising it to the power 0.80 (Grima *et al.*, 2010). Negative tank-means for RFI imply higher efficiency than the average of the population, whereas those with a positive RFI are less efficient. FCR was calculated for each period for an average fish in each tank as FCR = FI / BWG.

To use variation in body weight as a measure of dominance group dynamics (Jobling, 1995), the coefficient of variation of individual body weight records within a tank was calculated from the individual observations of BW as CV-BW = [SDBW/mean] × 100%, where SDBW is the standard deviation of body weight. In addition, RBWV was used as a measure of the variation. This is a novel trait estimated as the residual of the regression $SDBW_i = \mu + BW_i + e_i$. The benefit of using this trait is that it does not depend on mean BW and that it is easy to interpret. Positive values represent a higher variation than that expected for the average tank given their average BW, whereas negative values represent a lower variation that that expected for the average tank.

Statistical analysis

Because the dataset included multiple observations over time (age at recording) for each family, a linear and a quadratic random regression model were used. The quadratic model was included to account for the observed lack of linearity in most of the traits. The following linear and quadratic random regression models were fitted using ASReml (Gilmour *et al.*, 2009):

$$y_{ij:t} = \beta_0 + S_0 X_t + (\beta_i + S_i X_t) + (\beta_T + S_T X_t) + e_{ij:t}, \text{ and} \quad (2)$$

$$y_{ij:t} = \beta_0 + S_0 X_t + T X_t^2 + (\beta_i + S_i X_t + T_i X_t^2) + (\beta_T + S_T X_t + T_T X_t^2) + e_{ij:t}, \quad (3)$$

where $y_{ij:t}$ is the dependent variable (RFI, FCR, CV-BW and RBWV) for the *j-th* tank within the *i-th* family at age X_t; β_0, S_0, and T_0 are the fixed effects intercept, slope, and second order coefficient, respectively; β_i, S_i, and T_i are the random effects intercept, slope, and second order coefficient for the *i-th* family, respectively; β_T, S_T, and T_T are the random effects intercept, slope, and second order coefficient for the *j-th* tank, respectively; $e_{ij:t}$ is the residual at age *t*. The intercept of the orthogonal polynomials represents the grand mean for each trait. The linear regression coefficient represents a linear increase (positive) or decrease (negative) of the change over time. The quadratic regression coefficients characterize the curvature of the trend: positive quadratic coefficients are associated with U-shaped curves whereas negative quadratic coefficients are associated with inverted U-shaped curves. Thus, a positive quadratic coefficient causes the ends of the parabola to point upwards, whereas a negative quadratic coefficient causes the ends of the parabola to point downwards. The smaller the quadratic coefficient, the wider the parabola. The Akaike information criterion (AIC) fit statistic was used for model evaluation.

The function "pol" from ASReml was used to fit orthogonal polynomials. Orthogonal polynomials avoid high correlations between estimates of the polynomial coefficients, which can cause estimation problems. It was also assumed that all coefficients within each of the regressions (family or tank) were identically distributed and uncorrelated because of the otherwise large number of parameters to be estimated relative to the low number of observations typical in aquaculture experiments. Therefore, models (2) and (3) provide estimates of the components of variance for the random regression coefficients attributable to tank and to family. We present the proportion of the variance attributable to variation between families (PVAR-FAM). Hypothesis testing of the family component was carried out using a Likelihood Ratio Test (LRT):

$$\text{LRT} = 2[\ln L(Fam, Tank) - \ln L(Tank)], \quad (4)$$

where $\ln L(Fam, Tank)$ is the natural logarithm of the likelihood of the full model with both Family and Tank random factors, and $\ln L(Tank)$ is the natural logarithm of the likelihood of the reduced model excluding the Family factor. LRT is distributed as a χ^2 with 1 degree of freedom. The fixed part of the regression of models (2) and (3) represents the overall trend of the traits in all tanks.

The analyses were univariate because of a lack of convergence in multi-trait analyses due to the small number of observations. In order to gain information about the relationships between RFI, FCR, CV-BW, and RBWV, correlations were calculated between the estimates of the intercept, and linear and quadratic regression coefficients based on tank measurements estimated with model (3). In addition, phenotypic correlations are presented between RFI, FCR, BWG, CV-BW, and RBWV based on values of RFI, FCR, BWG, CV-BW, and RBWV fitted with model (3).

Results

Feed utilization

Feed intake of each family was positively correlated with metabolic body weight and with BWG, indicating that animals of larger size (Fig. 1a) and those that grew faster (Fig. 1b) ate more feed. The R^2 of equation (1) indicated that 71% of the variation observed in FI could be attributed to variation in metabolic body weight and BWG.

Comparison of linear and quadratic random regression models

Table 1 shows the main results of the random regression analyses for both linear and quadratic models for all traits. For RFI and BW, the Akaike information criterion (AIC) was lower for the quadratic models than for the linear models, indicating a better

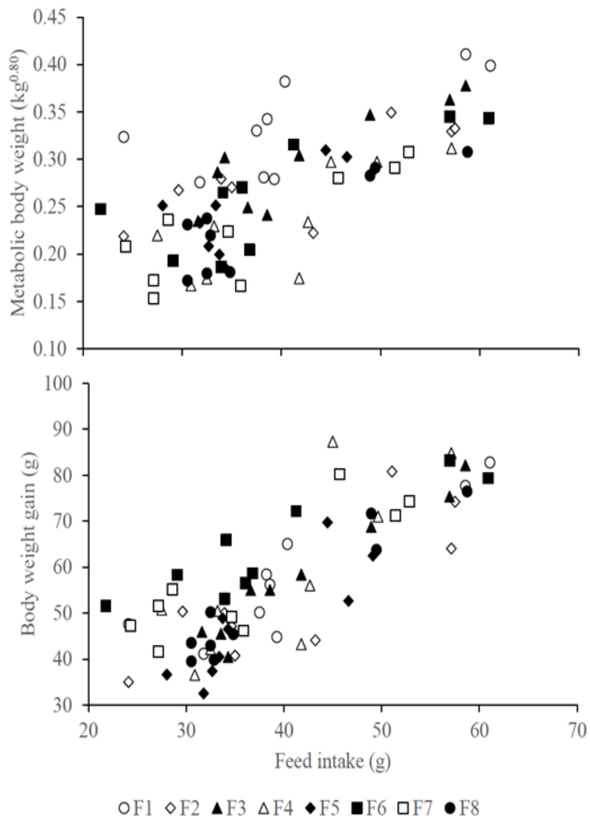

Figure 1. Relationship between tank means of feed intake, and metabolic body weight (a) and body weight gain (b) for families 1 to 8 in periods 1, 2, and 3.

Table 1. Amount of variance explained by family of estimates of the fixed and random components of both linear and quadratic random regression models of residual feed intake (RFI), feed conversion ratio (FCR), body weight gain (BW), the coefficient of variation of body weight (CV-BW), and the residual body weight variation (RBWV).

	RFI	FCR	BW	CV-BW	RBWV
Linear					
PVAR - FAM	0.010	0.192	0.528	0.469	0.480
LRT	0.013	2.746	28.080	10.854	10.640
p-value LRT	0.909	0.097	<0.001	<0.001	0.001
AIC	-186.71	-226.69	646.81	247.38	364.35
p-value of fixed regression	0.783	0.489	<0.001	0.875	0.330
Quadratic					
PVAR - FAM	0.138	0.223	0.759	0.500	0.4511
LRT	0.990	3.764	46.416	17.692	13.904
p-value LRT	0.320	0.052	<0.001	<0.001	<0.001
AIC	-192.49	-221.47	541.08	253.99	383.70
p-value of fixed regression	0.002	0.278	<0.001	0.991	0.439

PVAR-FAM: Proportion of the variance wxplained by families. LRT: Value of the χ^2 statistics for the Likelihood Ratio Test. AIC: Akaike Information Criterion.

fit of the quadratic model. On the contrary, the linear models had a better fit than the quadratic models for FCR, CV-BW, and RBWV. To facilitate the discussion of the relationships between traits, only estimates from the quadratic models applied to all traits (which include both a linear and a quadratic component) will be presented. The *p*-value of the fixed regression indicates whether there is a common overall linear *vs*. quadratic trend for all tanks of all families in the experiment. However, lack of significance of the fixed regression does not necessarily imply that trends are absent within families: the *p*-value of the LRT indicates whether linear or quadratic trends differ between families.

Relationships between RFI and FCR

Trends over time in both feed efficiency traits across families and tanks were rather variable (Figs. 2 and 3). The variance in the linear regression explained by the family component (PVAR-FAM) was 1% and 19% for RFI and FCR, respectively (Table 1). This was a trend only for FCR (p=0.097). The variance in the quadratic regression coefficient explained by the family component was 14% and 22% for RFI and FCR, respectively; this was close to significance for FCR (p=0.052) but was not for RFI (Table 1). This could be attributed to the observed large variation within families.

The correlations between the intercepts, linear slopes, and quadratic coefficients of the two feed efficiency measures RFI and FCR were very high and significant (Table 2). This indicates that animals with a high RFI also have a high FCR, both indicating low feed efficiency, and *vice versa.*

Relationships between BW, CV-BW, and RBWV

As expected, for BW, all tanks and families showed a linear increase over time (*i.e*., growth), which is also confirmed by the high significance of the fixed regression (Table 1). Fig. 4 shows that each tank within family has a similar pattern (intercept and slope). Trend

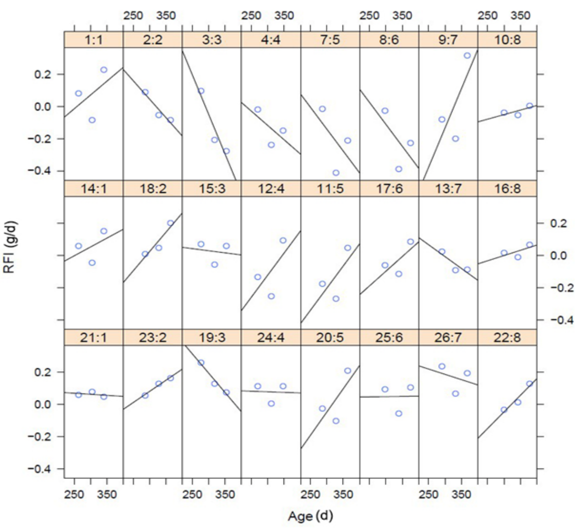

Figure 2. The trend of residual feed intake (RFI) for each tank and family over time. The annotation X:Y on top of the figure indicates the tank number (X) and the family (Y), therefore, each column corresponds to three tanks per family.

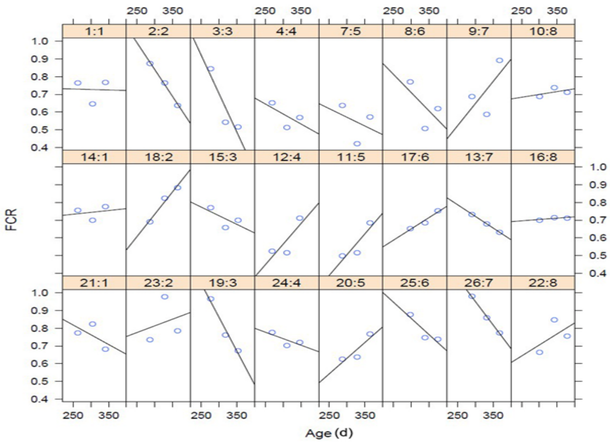

Figure 3. The trend of feed conversion ratio (FCR) for each tank and family over time. The annotation X:Y on top of the figure indicates the tank number (X) and the family (Y), therefore, each column corresponds to three tanks per family.

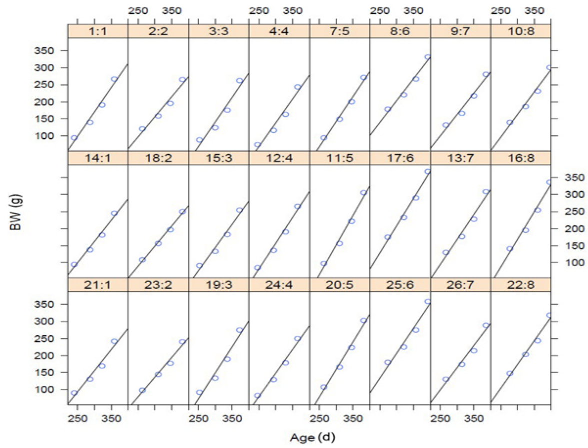

Figure 4. The trend of body weight (BW) for each tank and family over time. The annotation X:Y on top of the figure indicates the tank number (X) and the family (Y), therefore, each column corresponds to three tanks per family.

over time of CV-BW and RBWV across families and tanks was variable (Figs. 5 and 6).

The variance in the linear regression coefficient explained by the family component was 53%, 47% and 48% for BW, CV-BW, and RBWV, respectively, and the variance in the quadratic regression coefficient explained by the family component was 76%, 50%, and 45%, respectively. This was highly significant for all three traits and considerably higher than the variance explained by the family components for the feed efficiency traits (Table 1).

The correlations between the intercepts, linear slopes, and quadratic coefficients of the two measures of variation in BW were mostly high and significant (Table 2). Correlations between the regression coefficients of BW and the regression coefficients of the two measures of variation in BW (Table 2) were not significant.

Relationships between RFI and FCR, with BW, CV-BW, and RBWV

Correlations between the regression coefficients of RFI and FCR with the regression coefficients of BW, CV-BW, and RBWV were not significant, except for the linear component of FCR and the quadratic component of BW (Table 2). The intercept of RFI was not correlated with the linear component of BW; this is expected since RFI is phenotypically independent of growth. Generally, animals that grow faster have a lower FCR, however, the correlation between the intercept of

Table 2. Correlations between estimates of the intercept (I), linear slope (L) and quadratic coefficient (Q) in the quadratic random regression (model (3)) for residual feed intake (RFI), feed conversion ratio (FCR), body weight (BW), the coefficient of variation of body weight (CV-BW), and the residual body weight variation (RBWV).

		FCR			BW			CV-BW			RBWV		
		I	L	Q	I	L	Q	I	L	Q	I	L	Q
RFI	I	0.94***	0.13	-0.46**	0.26	0.13	-0.14	0.12	0.08	0.06	0.11	0.15	0.10
	L	0.15	0.89***	-0.02	0.25	0.27	-0.33	0.12	-0.16	0.27	0.08	-0.05	0.23
	Q	-0.37	0.27	0.82***	-0.14	-0.09	-0.02	0.1	0.13	-0.03	0.12	0.16	0.10
FCR	I				0.13	-0.09	-0.12	0.09	0.18	0.01	0.10	0.21	0.08
	L				0.17	0.19	-0.49**	0.11	-0.22	0.23	0.07	-0.10	0.18
	Q				-0.11	0.02	0.07	0.22	0.18	-0.14	0.23	0.23	0.03
BW	I							0.13	-0.18	0.33	0.09	-0.03	0.29
	L							0.12	-0.23	-0.01	0.08	-0.08	0.00
	Q							-0.01	0.06	-0.31	0.02	0.03	-0.22
CV-BW	I										0.92***	0.71***	0.32
	L										0.78***	0.90***	0.46*
	Q										0.30	0.50*	0.88***

Standard errors ranged between 0.07 and 0.21. ***$p<0.001$, **$p<0.01$,*$p<0.05$.

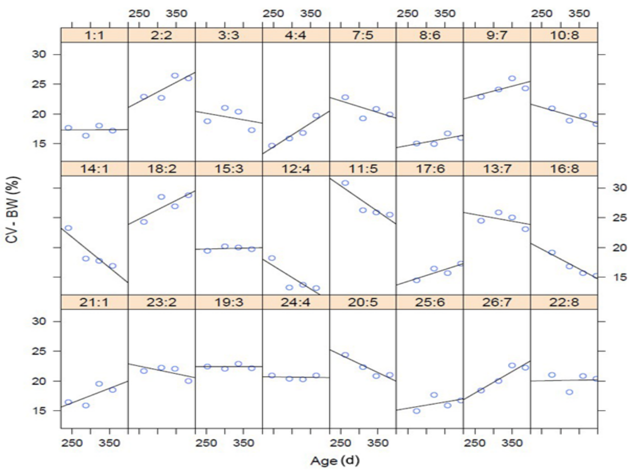

Figure 5. The trend of the coefficient of variation of body weight (CV-BW) for each tank and family over time. The annotation X:Y on top of the figure indicates the tank number (X) and the family (Y), therefore, each column corresponds to three tanks per family.

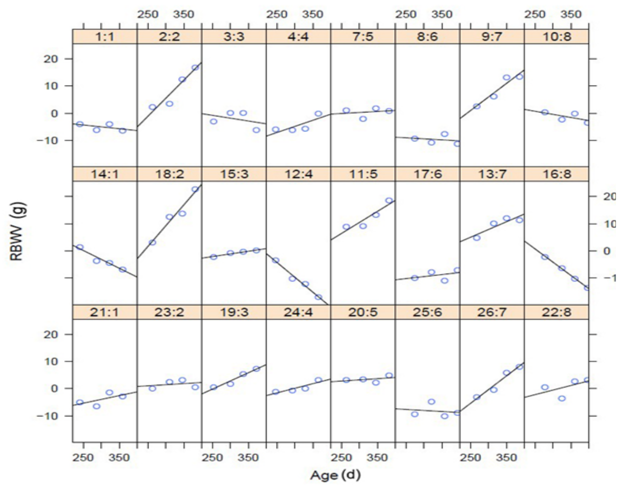

Figure 6. The trend of the residual body weight variation (RBWV) for each tank and family over time. The annotation X:Y on top of the figure indicates the tank number (X) and the family (Y), therefore, each column corresponds to three tanks per family.

FCR with the linear component of BW was negative but not significant.

Discussion

Differences between families in tank-based feed efficiency, growth, and in group dominance dynamics

The United Nations Population Division projects that the human population is likely to rise to 9.15 billion people by 2050 (Godfray *et al.*, 2010). Intensive animal production will contribute to the increase in production requirements, in addition, reliance on farmed fish production as an important source of protein will also increase (Naylor *et al.*, 2000). Since land, water, and energy resources are limited, a 70 to 100% increase in the projected need for human food must necessarily come from what is called "sustainable intensification", *i.e.*, improved levels of production in ways that are environmentally, socially and ethically sustainable (Godfray *et al.*, 2010). Improving feed efficiency in livestock and aquaculture species is a major goal towards sustainable intensification as FI relates directly to farm profit and losses of potential human-edible food (Rauw, 2012). In addition, since fish FI and metabolism directly relates to the release of solid and dissolved waste of dietary components, improving feed efficiency will aid in reducing environmental pollution (Bureau & Hua, 2010). Therefore, similar to terrestrial livestock species, in aquaculture, improving feed efficiency is a major production objective (Doupé & Lymbery, 2003; Grima *et al.*, 2010; Kankainen *et al.*, 2016).

However, because it is expensive and particularly difficult to record individual FI in fish, it is not usually included in the selection index (Gjedrem, 2000; Lymbery, 2000; Kause *et al.*, 2006a,b). Feed intake has been measured individually in fish research by housing fish individually (Silverstein *et al.*, 2005; Martins *et al.*, 2006) or by X-radiography (McCarthy *et al.*, 1993; Kause *et al.*, 2006ab). Alternatively, FI can be studied using the tank as a unit of measurement (Kolstad *et al.*, 2004; Mambrini *et al.*, 2004). Measurements of FI by tank have been used to estimate feed efficiency in trout in the study of Rauw *et al.* (2016). Although within-group information is lost when calculating a family or a tank mean, this method may be useful for selection of families that are superior for feed efficiency. Indeed, according to Kolstad *et al.* (2004), experience of breeding within Atlantic salmon suggests that feed efficiency may just as well be recorded on a family basis. For instance, many of the traits in the breeding goal for Atlantic salmon are improved by family selection and show satisfactory genetic gain (Kolstad *et al.*, 2004). Yet, sole family selection does not utilize within-family variation, *i.e.* the Mendelian sampling term, which accounts for half of the additive genetic variation available for selection.

Feed efficiency can be measured as feed conversion ratio (FCR), *i.e.*, the amount of FI per unit of growth. Árnason *et al.* (2009) showed that FCR in turbot was dependent on water temperature and body weight and ranged between 0.44 to 0.82. Alternatively, feed efficiency can be measured by calculation of residual feed intake (RFI). RFI is defined as the difference between the actual FI and that predicted from a multiple linear regression of FI on maintenance (metabolic body weight) and growth (*e.g.*, Rauw, 2012). The benefit of using measurements of RFI is that they do not show, as measurements of FCR could do, significant phenotypic correlations with FI, growth rate, and mature size. Moreover, when efficiency is included in the selection index, the outcome of selecting for a ratio such as FCR cannot be predicted. Selection for low FCR may result in increased growth rates, mature size, and presumably, maintenance requirements (Crews, 2005). For this reason, with a moderate heritability, RFI has been included in the breeding goal of several terrestrial livestock species (Herd, 2009). Herd & Bishop (2000) indicate that RFI is both phenotypically and genetically correlated with FCR in cattle. Indeed, in the present experiment, values fitted with (*i.e*., expected based on) model (3) of RFI and FCR were highly positively correlated.

The results of the present study support the existence of detectable variation in growth and, to a lesser extent (nearly significant at p=0.052), in FCR between families of turbot between approximately 250 and 370 days of age. The random family component explained considerably more variation in BW (76%) than in FCR (22%). The higher genetic variation for growth than for feed utilization is in line with previous studies recording individual FI in rainbow trout (Kause *et al.*, 2006b, 2016).

Our results indicate that the random family component explained more of the variation in FCR than in RFI (14%), therefore, FCR may respond better to selection. However, a high correlation between FCR and RFI indicates that RFI may be selected for if the goal is to improve feed efficiency but not to affect size and maintenance requirements. These results are supported by scarce literature on RFI in other fishes and ample literature on RFI in terrestrial livestock species, which indicates that a genetic component exists for both FCR and RFI, and that it is possible to select for these traits. For example, individual measurements of RFI in rainbow trout indicate genetic variation between six different genetic cross-types (Silverstein *et al.*, 2005). Grima *et al.* (2008) estimated RFI in group-housed rainbow trout clones and FI was measured individually with the X-ray method in a feed-restriction-refeeding experiment. They showed that genetic variation exists in RFI, confirming that genetic improvement is possible for this trait. Kause *et al.* (2016) estimated a heritability of 0.04-0.11 for RFI and FCR, while the heritability for daily weight gain was 0.28-0.29.

In our study, RFI was based on tank measurements only. Therefore, more work may be needed to further adapt the equation of RFI to accommodate tank production systems, for example by inclusion of a measure that can account for the social interaction of the group. When FI is measured at the tank level, accuracy of selection is reduced due to the lack of individual differences within a family tank. To increase accuracy of selection, a combination of family-based recording for FCR (or RFI) and individually recorded traits like growth and lipid deposition that are genetically correlated with FCR can be used (Quinton *et al.*, 2007; Kause *et al.*, 2016). This approach utilizes also the Mendelian sampling variance in selection.

From the point of view of the producer, the interest is to produce fish with low FCR or RFI from growth till slaughtering. However, selection procedures are generally based on phenotypic recording at an early age in the production cycle, after which it needs to be assumed that the measure is correlated with the entire growth period. Studies in terrestrial livestock indicate that feed efficiency measured over a limited time period may not be necessarily representative of a genotype's efficiency across the entire production system (*e.g*., Doupé & Lymbery, 2003; Rauw *et al.*, 2006), therefore, correlations with feed efficiency during other periods of the production cycle need to be investigated. Alternatively, fish with body weights more close to harvest weight could be tested for family-level feed efficiency.

Relationship between feed efficiency, growth and group dominance dynamics

Variation in RFI can be explained by variation in partial efficiencies for maintenance and growth, and by variation in metabolic feed demanding processes not included in the model, such as activity, response to pathogens and response to stress (Rauw, 2012). Individual fish within a tank inevitably deal with stress depending on the social state of the individual and the stability of the social tank community (Fox *et al.*, 1997). Generally, dominant fish are more active and aggressive and gain a larger share of the available feed typically resulting in high growth rates, whereas fish lower in the hierarchy show behavioral inhibition, reduced activity and FI and reduced growth rates (Gilmour *et al.*, 2005). For example, Irwin *et al.* (2002) showed that dominant turbot within feeding hierarchies that are consistently able to feed to satiation have higher growth rates than subordinate individuals that feed on the remaining share. The measurement of FI of an average fish in the tank, such as used in the present experiment for the calculation of tank feed efficiency, will not be able to capture such dynamics. However, since dominant fish in a group may grow faster and more efficiently than the rest of the population, the variance of growth rate, consumption rate and growth efficiency tend to increase with population dynamics. For example, Li &

Brocksen (1977) indicated that the variance of growth rate, consumption rate and growth efficiency tended to increase with population density resulting from an increase in intraspecific competition. Also Jobling (1995) suggests that rapid and homogeneous growth rates, a more favorable feed efficiency, and uniform body weights at harvest, must result from a social environment that is favorable, whereas the opposite holds when inter-individual competition increases. Its estimation requires measurements of individual body weights over time.

The results of the present study indicate that about half of the variation in CV-BW and RBWV could be explained by the family effect, which may suggest underlying differences in behavioral dynamics that may have a genetic component. This is consistent with previous work in fish, e.g., in rainbow trout the within-family variation has been shown to exhibit additive genetic variation (Janhunen *et al.*, 2012; Sae-Lim *et al.*, 2015, and references therein). Variation attributable to differences between families may suggest that competition for feed exists and that the establishment of dominance-subordinate relationships may have a family component. Yet, to prove that within-family variation is due to social behavior, a separate test should be conducted. In addition, results obtained in other fish species will need to be verified in turbot. In the present experiment, the correlation between CV-BW and RBWV with BWG was close to zero and non-significant. This is similar to previous observations on rainbow trout (Janhunen *et al.*, 2012). In our study, the correlations of CV-BW and RBWV with BWG were positively, but non-significantly, related to feed efficiency. The latter may be due to the low number of families and tanks used in this study as discussed before. In addition, although the results are equivocal, theoretical frameworks exist that suggest that competitive intensity reduces where related individuals interact (Ward *et al.*, 2006). In theory, self-restraint evolves when genetic relatedness is high, reducing competition among group members and increasing average group success through improved efficiency of resource utilization (Frank, 1995). In the present study, relatedness may have affected group competition within families. Also Martins *et al.* (2005) did not observe a relationship between size distribution and growth performance in sibling fish, suggesting that differences in weight observed seemed not to be a direct consequence of social hierarchies. In addition, variation in body weight may result from behavioral or metabolic factors that are not directly related to dominance relationships and feed competition. More work including more families may be needed to conclude whether social interaction for feed competition affects family feed efficiency.

The use of random regression models for analyzing longitudinal traits in aquaculture

A general situation in aquaculture experiments is that i) traits are expressed over time (*e.g.*, growth and feed efficiency), ii) traits do not necessary follow linear trajectories, and iii) the number of experimental units (tanks) is very limited. The use of linear and/or nonlinear random regression models can account for the effects described in the two first points. Random regression models using orthogonal polynomials have been widely used in terrestrial species (*e.g.*, Jamrozik & Schaeffer, 1997; Jamrozik *et al.*, 1997) and also in aquaculture species (*e.g.*, Rutten *et al.*, 2005). A reduced number of observations may lead to large correlations between estimated coefficients in random regression models. Orthogonal polynomials have the advantage of reducing correlations among the estimated coefficients (Schaeffer, 2004). In this study, the limitations in the experimental testing facilities were mitigated by the use of orthogonal polynomials but more work with more tanks is necessary to corroborate our findings.

Conclusions and recommendations

Although BWG was very similar across tanks within families, there were large differences between tanks and families for feed efficiency and for within-tank variation in body weight. Our results show that detectable variation in growth, CV-BW and RBWV exist between families of turbot between approximately 250 and 370 days of age. Differences between families suggest that a genetic component may exist and that it may be possible to select for these traits. The results also indicate significant differences between families in FCR, which may be used in selection programs aimed at improving feed efficiency.

Selection of families based on group-means is particularly interesting for economically important traits that are not easily measured individually, such as feed efficiency. Based on the results of the present study, it can be recommended to select families with the lowest FCR as estimated from the random regression analyses. In the future, within-family genomic selection methods may further improve genetic gain (Sonesson & Meuwissen, 2009)

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