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Genotype by environment interactions for growth in European seabass (*Dicentrarchus labrax*) are large when growth rate rather than weight is considered

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Abstract:

Two hundred fifty three full-sib families from 33 males and 23 females of European seabass were produced in a partly factorial mating design. All fish were reared in the same tank for 14 months until reaching mean weight of 35 g, then 7000 of them were individually tagged and weighed, and dispatched to four farms in different locations (France, Israel, Italy and Portugal) representing a wide variety of environmental conditions. Around mean weight of 400 g, 1177 to 1667 fish at each site were weighed. Daily growth coefficient (DGC) was calculated. Pedigrees were successfully redrawn for 99.2% of fish using microsatellite markers. Genetic correlations between sites were high for body weight (> 0.80 in all cases but one, i.e., five cases over six), but only moderate for DGC (0.21–0.61), with one exception. This indicates significant G × E interactions for growth rate, which were not revealed when studying body weight due to shared common environment of the fish prior to separation to the different rearing environments.

Keywords: *Dicentrarchus labrax*; Seabass; Growth; Daily growth coefficient; Heritability; G × E interactions; Aquaculture

1. Introduction

European seabass is a major aquaculture species in the Mediterranean region and in the southern part of the north east Atlantic Ocean (Portugal, Canary Islands). Its domestication began in the 1980s, and while some breeding programs are starting (France, Greece, Israel), some hatcheries still use wild broodstock. Breeding programs are expected to provide important increases in productivity, as in all fish species (Gjedrem and Thodesen, 2005), especially because heritabilities of growth traits range from medium to high in this species (Dupont-Nivet et al., 2008; Saillant et al., 2006). High selection response (+23-42 % per generation) for weight at commercial harvest size was obtained in an individual selection experiment in a recirculating system (Vandeputte et al., 2009). However, hatcheries can provide fingerlings to a wide range of fish farms with very different culture conditions, thus efficient selective breeding for growth requires the knowledge of any GxE interactions. They are efficiently approached by calculating genetic correlations using a common family structure under different environmental conditions, and considering the traits at each site as separate traits. We previously published estimates of GxE interactions for weight at commercial size (Dupont-Nivet et al, 2008), and showed that they were small in most cases (genetic correlation r_A between sites >0.84), while it was moderate (r_A=0.70) between the two extreme sites in terms of rearing systems, especially regarding temperature. Fish in the experiment reported in this previous paper were tagged at a mean weight of 35g and harvested around 400g, and this relatively late tagging leaves the possibility that final weight performance was significantly influenced by weight at tagging (where all fish were in the same environment), thus reducing the possibilities to see GxE interactions. Thus, using the same dataset, we report in the present paper an additional analysis: GxE interactions for growth rate expressed as Daily Growth Coefficient (DGC).

2. Material and methods

2.1. Animals

Details regarding the production of experimental animals were given in Dupont-Nivet et al. (2008). Briefly, 253 full-sib families from 33 males and 23 females were produced according to a partly factorial mating design, and all families were reared as a single batch, starting at 48h post-fertilization. They were all kept in the same tank (Panittica Pugliese, Torre Canne di Fasano, Italy) until they reached 134 days post-fertilization (dpf), where a random sample of 16,000 fish was sent to the Ifremer station in Palavas (France) and pre-grown in a 5 m^3 tank. At 156 dpf, the batch of fish was split at random into four 5 m^3 tanks to lower stocking density. At 370 dpf, fish were 35 g (mean weight) and 7000 were randomly selected, individually PIT-tagged and fin-clipped (fin clips were kept in 90% ethanol for further DNA analyses). Four batches of 1750 fish each were distributed to four different farms.
The four farms were chosen for their varying growing or rearing conditions (Table 1), including a recirculating system (Palavas, France, Site A), a concrete raceway with well water (Torre Canne di Fasano, Italy, site B), semi-intensive estuarine earthen ponds (Vila Nova de Milfontes, Portugal, site C) and tropical seawater cages (Eilat, Israel, site D). These farms differed in many factors other than rearing system, such as water temperature (mean and variation), fish density, feed composition, feeding practices, associated pathogens and water quality. All these factors, and others not identified, may have contributed to GxE interactions. It must be noted that due to logistical problems, the batch of fish for site D remained at site B from 423 to 510 dpf, and they stayed at site D from 513 to 734 dpf. Each site used its own rearing procedures and feeds, the only restriction being that the fish had to be kept as one batch and should not at any time be sorted.

2.2. Data collection

At each farm, fish were measured at commercial size (average 400 g), varying from 338 g (farm B) to 487 g (farm D). Number of fish measured, mean weight, age and DGC (defined below) are reported in Table 2. Each fish was measured (weight, length) and individually identified with its tag. At farms B, C and D, internal deformities (defined below) were scored after opening each fish. At farm A, fish were put back in the tanks after measurements, reared until 1 kg and were slaughtered at this stage. Internal deformities then were noted at this later stage. Sex was determined by examination of the gonads. Parentage assignment was performed by Landcatch Natural Selection (Scotland) using six microsatellite markers organised in a single PCR multiplex. The assignments were recovered with a home-made program (see details in Dupont-Nivet et al, 2008). Parentage assignment yielded 99.2% unique assignments.

2.3. Statistical analyses

To account for the growth rate of the fish in the different sites, we used the daily growth coefficient [DGC = 100 × (final individual weight$^{1/3}$ − initial individual weight$^{1/3}$)/days], which was chosen because it is much more independent of initial body weight than weight gain and specific growth rate (Cho, 1992), and its use for estimating growth rate in aquaculture is therefore recommended (Bureau et al, 2000). We also analysed the weight at tagging and the final weight (*ie* body weight at commercial size) of fish at the different sites. To test the potential significance of fixed effects on DGC, initial body weight (IBW) and final body weight (FBW) data were first analysed using proc GLM of the SAS ® System. Tank (prior to tagging) and sex were significant effects (P <0.05) for all traits. Deformities (coded 1 for deformed fish, 0 for undeformed) were significant for FBW (P <0.05) but not for other traits. A deformity effect was then kept as a fixed effect in the analysis model.

A very high proportion of the fish suffered from spinal deformities (65% of all examined fish had one or more kinds of deformities), mostly lordosis and scoliosis (43% and 30%, respectively). These probably were generated by forced swimming due to inappropriate hydrodynamics in the 5m^3 tanks in Palavas in the early phases of the experiment (from 3 to 35 g mean weight - Bardon et al., 2009). Because, in our previous paper (Dupont-Nivet et al, 2008), where we analyzed body weight, length and condition factor, as these traits, especially length and condition factor were affected by deformities, we chose to work on a reduced dataset in order to avoid potential effects of imperfect correction by a fixed effect. As seen before, there was no impact of deformities on DGC and IBW, and only moderate impact on FBW. Heritability and genetic correlations involving FBW were similar when including or not deformed fish, but standard errors of genetic correlations were larger when deformed fish were removed. Then, for this paper, we used the full dataset, including data from deformed and undeformed fish, in order to increase the precision and relevance of estimates.

Heritabilities and non-genetic maternal effect were first analyzed for all data using VCE6 (Groeneveld et al., 2008). A multi-trait animal model with maternal effect (model 1 shown below) or without maternal effect (model 2) was used:

$$Y = X\beta + Z_1u + Z_2m + e \qquad \text{(model 1)}$$

where Y is the vector of observations, β is the vector of fixed effects (overall mean, initial tank, sex, deformity – for final weight only –, site when data from all sites are treated as a single trait), u is the vector of random additive genetic effects, m is the vector of random maternal effects, and e is the vector of random residual effects. X, Z_1, and Z_2 are known incidence matrices.

Genotype-by-environment (GxE) interactions were estimated through genetic correlations between the trait of interest in environment 1 and the same trait in environment 2, considered as two different traits in the analysis, using model 1. The correlation of residuals between sites was zero, as one individual is present at only one site. GxE interaction is measured by

the difference between 1 and the genetic correlation; thus, the closer the genetic correlation to 1, the smaller the GE interaction.

3. Results and discussion

The estimated heritability and maternal effects of DGC, IBW and FBW at each site and across all sites are given in Table 3. Maternal effects were not significant, but not taking them into account caused inflated heritability estimates, so they were kept for further analyses. Heritability of initial body weight was very high (0.61±0.14), while the values were more moderate for final body weight (0.29-0.45 among the different sites) and for DGC (0.16-0.34). Interestingly, the heritability estimate across sites for DGC (0.12±0.04) was lower than the estimates at individual sites. So, even if heritability of growth rate within site is relatively high, family re-rankings between sites may cause both smaller between-family variance and higher within-family variance when all sites are considered, lowering heritability across all sites.

Genetic correlations of DGC and FBW between sites are given in Table 4. Results for FBW were a little different, but consistent with results on the reduced dataset (without data from deformed fish) (Dupont-Nivet et al, 2008). Genetic correlations of FBW were high (>0.80), revealing little GxE interaction, except between sites C and D (0.75). A very high value (0.93) was reached between site B and site D, where fish shared a longer common rearing period in site B, as noted above. In contrast, genetic correlations of DGCs between sites were much lower: although sites B and D were still close to each other (r_A=0.78), the other values ranged from 0.21 to 0.61. As the standard errors were moderate (0.08 to 0.16), the genetic correlations clearly differ from 1, and then reveal significant GxE interactions. Existence of GxE interactions is further confirmed by the observation that the value of heritability across sites for DGC was lower than the individual values estimated within site, as noted above.

Compared to our previous results, this genetic analysis of DGC between sites reveals a higher level of GxE interactions than previously expected based on commercial weight. We primarily focused on commercial weight, as it is the most important trait that generates income to the farmers. However, growth rate is also important, because in many cases the on-grower buys its fingerlings from a hatchery or a breeding company, fast growth rate during on-growing is of major interest as it shortens the production cycle. Also, a faster growth rate is expected to generate improved feed conversion ratio (Kause et al., 2006; Quinton et al., 2007; Thodesen et al., 1999), and thus lower production costs.

The GxE interactions estimated in this paper for DGC are similar to those observed by Saillant et al. (2006) on log (weight) in sea bass, who observed genetic correlations mostly in the 0.40-0.50 range. The major difference is that the environments tested by Saillant et al. (2006) were generated by manipulation of rearing parameters within the same facility (temperature, density), while the environments we tested were distinct, constrasting on-growing environments. Also, in Saillant et al. (2006), the range of conditions were applied since the early phases of rearing, making final weight a surrogate estimation of growth rate. In the present experiment, because our fish were tagged and separated between the environments relatively late, at 35g mean weight, it allowed the initial common rearing phase to have more impact on the final weight observed. This is reinforced by the very high heritability of weight at 35 g (0.61), which effectively makes divergences in size-at-tagging have a strong genetic component. Thus, these differences will still be present, at least partly, at commercial size, even if DGCs of the different families rank differently across the different rearing sites.

In fish, genotype-environment interactions for growth traits have been studied in many species, but mostly as responses of geographic strains to contrasting environments. Studies at the family level investigating genetic correlations between environments are few, but quite consistently show GxE interactions, apart for Chinook salmon (Oncorhynchus tshawytscha) where no family re-rankings were apparent (Winkelman and Peterson, 1994). Genetic correlations between environments ranged from 0.58 to 0.86 for body weight of rainbow trout

across different systems and salinities up to 2-3 kg, starting from 1 year-old fish (Sylven et al., 1991). In the same species, different densities from start-of-feeding yielded genetic correlations in the range 0.32 - 0.90 for body weight (Bagley et al., 1994). For sea bream, genetic correlations for body weight at commercial size (360-480g) between cage and intensive tank rearing systems were 0.70±0.10, with fish tagged and separated at 4.8g mean weight (Navarro et al., 2009). These results, together with those of Saillant et al. (2006) and our present results, suggest that high genetic correlations (i.e. low GxE interactions) for body weight across different environments are more an exception than a rule, especially when fish are reared separately for the largest part of their growth period.

Because in most cases, marine fishes (including sea bass) are sold as fingerlings at a small size (<10g), some practices should be adapted to avoid GxE interactions in order to allow expression of the potential of growth-selected fish. These practices should include rearing selected fish in conditions resembling those of production environment. Our data do not allow us to test specific hypotheses about the major factors (temperature mean and variation, density, feed composition and feeding practices, associated pathogens) generating GxE interactions, as we cannot tease at causes of the genetic correlations observed, except for the high correlation (0.78) between sites B and D, which can be explained by the long common life. Another unanswered question is the temporal stability of such interactions; *i.e.* would the respective families rank the same in different years at the same sites, or would there be genotype*year interactions within site? Further research is needed to understand the determinants of GxE interactions in sea bass before developing breeding programs adapted to the different type of rearing systems (cage, ponds, closed water system, raceway) used across the industry.

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Tables

Table 1- Growing conditions at the four rearing sites.

	Rearing period (dpf)	Rearing system	Temperature (°C)	Volume (m^3)	Rearing density (kg/m^3)
Farm A France	420-714	Semi-closed recirculation system	20-22	5 (x4)	< 30
Farm B Italy	423-795	Concrete tank with well water	19-20	12	< 46
Farm C Portugal	420-873	Semi-intensive estuarine pond	9-25	400	< 2
Farm D * Israël	513-734*	Floating cage in tropical waters	22-27	216	< 4

*: Fish of farm D were reared at farm B during the period 423-510 days post-hatching.

Table 2. Number, age, mean weight, mean daily growth coefficient (DGC), proportion of deformed fish and survival rate at each site.

		Age (days)	Number (N)	Mean weight (g)	Mean DGC	Proportion of deformed fish (%)	Survival rate (%)
Farm A France		714	1473	398	1.18	83	84.2
Farm B Italy		795	1651	338	0.86	60	94.8
Farm C Portugal		873	1177	358	0.76	55	67.3
Farm D Israel		734	1667	487	1.25	58	95.7

Table 3. Heritability (h^2) and maternal effects (m^2) estimates (± S.E.) for daily growth coefficient (DGC), initial body weight (IBW) and final body weight (FBW) at four sites and across all sites. Heritability estimates are given for models with (model 1) and without (model 2) maternal effects. Estimates for IBW are given only across all sites, as all fish were reared in a single site (site A) at that stage.

Trait	Parameter	Site A (France)	Site B (Italy)	Site C (Portugal)	Site D (Israël)	All Sites
DGC	h^2 model 1	0.19±0.07	0.32±0.07	0.34±0.10	0.16±0.06	0.12±0.04
	m^2 model 1	0.03±0.03	0.00±0.00	0.06±0.06	0.04±0.03	0.03±0.02
	h^2 model 2	0.25±0.06	0.32±0.06	0.45±0.08	0.23±0.05	0.17±0.03
FBW	h^2 model 1	0.44±0.12	0.45±0.12	0.44±0.11	0.29±0.09	0.28±0.07
	m^2 model 1	0.06±0.06	0.03±0.06	0.09±0.07	0.10±0.06	0.04±0.04
	h^2 model 2	0.54±0.09	0.51±0.08	0.62±0.09	0.48±0.08	0.36±0.06
IBW	h^2 model 1	-	-	-	-	0.61±0.14
	m^2 model 1	-	-	-	-	0.05±0.07
	h^2 model 2	-	-	-	-	0.70±0.09

Table 4. Genetic correlations between sites and heritabilities within site (bold, on the diagonal) for Daily Growth Coefficient (DGC) and final body weight (FBW). Estimates ± S.E.

trait		site A (France)	site B (Italy)	site C (Portugal)	site D (Israël)
DGC	site A	**0.19±0.04**	0.39±0.12	0.21±0.14	0.34±0.16
	site B		**0.26±0.05**	0.61±0.10	0.78±0.08
	site C			**0.35±0.06**	0.42±0.14
	site D				**0.16±0.04**
FBW	site A	**0.42±0.09**	0.81±0.06	0.81±0.06	0.86±0.06
	site B		**0.40±0.08**	0.81±0.06	0.93±0.04
	site C			**0.44±0.08**	0.75±0.09
	site D				**0.29±0.07**