



Short communication

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.

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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 G×E 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 G×E 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 35 g and harvested around 400 g, 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 G×E interactions. Thus, using the same dataset, we report in the present paper an additional analysis: G×E 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

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mating design, and all families were reared as a single batch, starting at 48 h 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 m³ tank. At 156 dpf, the batch of fish was split at random into four 5 m³ 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 G×E 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

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 (×4)	<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

estimating growth rate in aquaculture is therefore recommended (Bureau et al., 2000). We also analysed the weight at tagging and the final weight (i.e., 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 5 m³ 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:

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

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 (G×E) 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. G×E interaction is measured by the difference between 1 and the genetic correlation; thus, the closer the genetic correlation to 1, the smaller the G×E 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

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