# Heritabilities and GxE interactions for growth in the European sea bass (*Dicentrarchus labrax* L.) using a marker-based pedigree

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## Abstract

253 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 during 14 months, then 7000 of them were dispatched in four farms to different locations (France, Israel, Italy, Portugal) representing a wide variety of environmental conditions. Around 400 g mean weight, 1177 to 1667 fish in each site were weighed and length was measured. Condition factor (K) was calculated. Pedigrees were redrawn *a posteriori* using microsatellites markers: parental origin could be retraced for 99.2% of fish. Due to a high incidence of deformities, the useful sample size was reduced to 491–670 fish per site.

Maternal effects were small. Using a simple animal model, heritability of weight ranged from $0.38 \pm 0.14$ to $0.44 \pm 0.14$ in the different sites. Length was highly correlated to weight, with similar heritabilities. GxE interaction, estimated through genetic correlations of weight across the different environments ranged from $0.70 \pm 0.10$ to $0.99 \pm 0.05$. Genetic correlations between weight or length and K were not similar in the different sites.

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## 1. Introduction

Domestication of sea bass *Dicentrarchus labrax* began in the 1980s and some breeding programs already exist for the species (Italy, Greece, France …). However this is still the very beginning and some hatcheries still use wild broodstock. As in any animal production, breeding programs are expected to provide important increases in productivity. However, to optimise breeding programs, reliable estimates of genetic parameters in a wide range of rearing systems are needed. Some heritability estimates for growth traits exist for marine fish, but mainly for species other than seabass, for example turbot *Scophthalmus maximus* (Gjerde et al., 1997), Atlantic cod (Gjerde et al., 2004; Kolstad et al., 2006), black bream *Acanthopagrus butcheri* (Doupé and Lymbery, 2005) and gilthead seabream *Sparus aurata* (Knibb et al., 1997). Concerning seabass, heritability estimates were published by Saillant et al. (2006), but based on a small design (3 dams × 10 sires).

One major constraint for estimating genetic parameters in fish is the inability to tag hatchlings, and consequently the need to separately rear the families until tagging size. This limits the number of families that can be used, and may bias family means by tank effects, thus biasing (full-sibs designs) or reducing the precision of (half-sibs designs) the estimated genetic parameters. An interesting alternative to separate rearing of families is the use of mixed rearing of progenies with *a posteriori* reconstruction of pedigrees using highly variable markers such as microsatellites. This was first proposed more than 10 years ago (Herbinger et al., 1995; Estoup et al., 1998) but it is only recently that mating designs of a size permitting reliable estimations of genetic parameters are being used (Norris and

Table 1
Growing conditions in the four rearing sites

|  | Rearing period (days) | Rearing system | Temperature (°C) | Volume (m³) | Rearing density (kg/m³) |
|---|---|---|---|---|---|
| Farm A | 420–714 | Semi-closed recirculation system | 20–22 | 5 (×4) | <30 |
| Farm B | 423–795 | Concrete tank with borehole water | 19–20 | 12 | <46 |
| Farm C | 420–873 | Semi-intensive estuarine | 9–25 | 400 | <2 |
| Farm D* | 513–734* | Floating cage in tropical waters | 22–27 | 216 | <4 |

*Fish of farm D were reared in farm B during the period 423–510 days post hatching.

Cunningham, 2004; Vandeputte et al., 2004). The major benefits of this methodology are the absence of between families environmental effects, and the possibility to use factorial designs which allow precise estimation of additive, maternal and dominance effects (Vandeputte et al., 2001). Most of the previously cited heritability estimates in marine fish were obtained using the separate rearing method.

Seabass farming takes place in very different system managements, and thus genetic and environment correlations of the same trait in different environments are also needed to set up optimised breeding programs. Indeed, it is a key point to know if a genetically improved strain in one environment would express superiority in other environments. This issue has been seldom studied in marine fish and never in seabass except by Saillant et al. (2006) but with a small design.

The present work reports results from a large scale experiment involving 253 full sib families, communally reared, originating from 33 males and 23 females and distributed to four contrasted environments (France, Portugal, Italy and Israel). In this paper, we focus on growth traits (weight, length and condition factor) which are traits of high economical interest. The large design allows precise estimates of maternal and additive genetics effects as well as correlations between traits and genetic correlations between growth traits in each environment (genotype–environment interactions).

## 2. Materials and methods

### 2.1. Animals

The parents of the studied animals were wild fish of Atlantic origin collected by Panittica Pugliese (Italy) on the Northern coast of Brittany (France). Sperm was collected before the crossing and cryopreserved in 250 ml straws according to the method described in Fauvel et al. (1998). Further reproduction operations took place at Panittica Pugliese farm. Eggs were obtained by manual stripping following hormonal induction of ovulation. For all parents a fin clip was collected and kept in 90% ethanol for DNA analyses and parentage assignment.

253 full-sib families from 33 males and 23 females were produced according to a partly factorial mating design. Crosses were conducted with three sets of different parents: 11 males × 9 females, 11 males × 7 females and 11 males × 7 females. Within each set a full factorial crossing was accomplished. All crosses were made by individual fertilization of identical volumes of eggs, and 5 min after fertilisation, eggs from the same female were mixed for further incubation.

Eggs were incubated (one female per incubator) for 48 h after which 2 ml of floating eggs from each female were sampled and mixed to constitute a single batch of eggs that hatched in a 0.5 m³ incubator 4 days after the fertilization. They were all kept in the same tank for larval rearing until day 64. After which, they were transferred to a concrete raceway until they reached day 130. During larval rearing, the temperature gradually increased from 13 (at hatching) to 18 °C (at day 15) after which it stabilised at the latter temperature. Fish were fed on artemia for 40 days, then weaned on dry food (Nippay, Hendrix). Food was first distributed manually to satiation, then, starting from day 66, one or two automatic feeders were used. During the pregrowing phase, the water temperature and salinity varied from 14.2 to 19.3 °C and from 19.5 to 37.5‰, respectively.

At 134 days post hatch (about 4 g), a random sample of 16,000 fish was sent to Ifremer station in Palavas (France) and pregrown in a 5 m³ tank in a recirculating system (10–30% renewal/day, 18 °C, 34‰ average salinity). At 156 days, the batch of fish was split at random into four 5 m³ tanks to lower the density. At 238 days, their weight was higher than scheduled, so the temperature was lowered to 14 °C (0.5 °C per day).

At 370 days, fish had reached a mean weight of 35 g and 7000 were randomly selected, individually PIT-tagged and fin-clipped (kept in 90% ethanol for further DNA analyses). Four batches of 1750 fish each (on average, 6.9 per full-sib family) were constituted and each one was kept in a 5 m³ tank prior to distribution to four different farms.

The four farms were chosen for their varying growing or rearing conditions. Main rearing conditions are reported in Table 1. One batch was kept at the Ifremer station in France (Farm A) in tanks where the density was maintained below 30 kg/m³. The temperature was raised progressively from 14 °C and maintained throughout the whole experiment at 20–22 °C.

A second batch arrived at 423 days at Panittica Pugliese in Italy (Farm B) where it was reared in a 12 m³ concrete raceway supplied with 19 °C (constant temperature) borehole water. A third one arrived at Viveiro Villanova in Portugal (Farm C) at 420 days and was first reared in an 8 m³ tank. Then, they were transferred to a semi-intensive estuarine pond at 588 days. The last batch of fish was reared from day 513 in a 216 m³ sea-cage in tropical conditions at Ardag in Israel (Farm D). This batch was kept in the farm B from day 423 to day 510, due to transportation problems.

### 2.2. Data collection

In 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 and age are reported in Table 2. Fish were starved 3 days prior to harvest. On harvest day, all fish were euthanized in an excess dose of 2-phenoxyethanol (0.6 ml.l⁻¹) or eugenol (0.1 ml.l⁻¹, farm B). In farm A, the fish were not euthanized but only anaesthetized (0.3 ml.l⁻¹ phenoxyethanol).

Each fish was weighed (to the nearest 0.1 g) and its length measured (to the nearest 1 mm) and its tag read to determine and record its parentage. The

Table 2
Number, age and mean weight of measured animals in each site

|  | Age (days) | Number | Mean weight (g) | Proportion of deformed fish (%) | Survival rate (%) |
|---|---|---|---|---|---|
| Palavas (A) | 714 | 1473 | 398 | 83 | 84.2 |
| Panittica (B) | 795 | 1651 | 338 | 60 | 94.8 |
| Vila Nova (C) | 873 | 1177 | 358 | 55 | 67.3 |
| Ardag (D) | 734 | 1667 | 487 | 58 | 95.7 |

Table 3
Effects of deformities on heritability estimates ($h^2$) and their standard errors (s.e) at harvest size, for farm C (Vila Nova, Portugal), depending on the groups of fish kept for analysis and on the models used : with (corrected data) or without ( raw data) a fixed effect accounting for the occurrence of deformities

| Trait | Fish kept for analysis | Sample size | $h^2$ for raw data (±s.e.) | $h^2$ for corrected data (±s.e.) |
|---|---|---|---|---|
| Weight | All fish | 1151 | 0.62±0.06 | 0.62±0.06 |
| Weight | Normal+mildly deformed | 789 | 0.65±0.07 | 0.65±0.07 |
| Weight | Normal | 523 | 0.64±0.07 | – |
| Length | All fish | 1151 | 0.54±0.06 | 0.58±0.07 |
| Length | Normal+mildly deformed | 789 | 0.64±0.07 | 0.66±0.07 |
| Length | Normal | 523 | 0.70±0.08 | – |
| K | All fish | 1151 | 0.19±0.04 | 0.23±0.04 |
| K | Normal+mildly deformed | 789 | 0.40±0.06 | 0.49±0.07 |
| K | Normal | 523 | 0.53±0.07 | – |

condition factor ($K$) was calculated. In farms B, C and D, internal deformities were scored after opening each fish. In farm A, fish were then reared until 1 kg and were slaughtered at this stage. Internal deformities were then noted at this later stage. Sex was determined by examination of the gonads.

### 2.3. Parentage assignment

Parentage assignment was performed by Landcatch Natural Selection (Scotland) using six microsatellite markers organised in a single PCR multiplex.

Assignments were redrawn using software (written by Landcatch) for pedigree analysis. The software uses two separate algorithms for pedigree assignment: a Bayesian probabilistic calculation computes the most likely parents; and a simple text matching algorithm compares parental and offspring genotypes at each locus sequentially and excludes mismatches in turn. The two sets of results were then compared. There was almost perfect concordance between the two sets of assignments.

### 2.4. Statistical analyses

One major problem for data analysis was the high occurrence of spinal deformities (mainly lordosis). In most cases, even when accounted for by a fixed effect, deformities introduced uncontrolled variation in the models, and we preferred to work only on normal fish, as the increase of precision brought by the use of exclusively normal fish overcame or at least compensated the loss in precision due to the lower number of fish used when eliminating the deformed ones from analyses. An exception was done for farm A where the number of normal fish was so low that some slightly deformed fish were also used in the analysis. Occurrence of deformities and our method for accounting for them will be presented further in the Results section.

To determine the potential significant fixed effects, data were first analysed using proc GLM of the SAS ® System. Tank effect was not significant ($P>0.1$) for all traits but sex effect was kept in further models ($P<0.05$). A farm effect ($P<0.05$) was also included when all data were analyzed together. Interactions were not significant.

A model with the deformity as a fixed effect was also tested to make decisions about including or not deformed fish in the analysis (see Results section).

Heritabilities, non genetic maternal effect and dominance were first analyzed for all data using Asreml (Gilmour et al., 2002). An animal model with

dominance and maternal effect (model 1) or without dominance effect (model 2) or without dominance nor maternal effect (model 3) was used.

$$Y = X\beta + Z_1u + Z_2m + Z_3\text{fs} + e \qquad \text{(model 1)}$$

where $Y$ is the vector of observations, $\beta$ is the vector of fixed effects (overall mean, sex and farm), $u$ is the vector of random additive genetic effects, $m$ is the vector of random maternal effects, fs is the random vector of full-sib family effect i.e. accounts for dominance and $e$ is the vector of random residual effects. $X$, $Z_1$, $Z_2$ and $Z_3$ are known incidence matrices. Dominance effect was very low (see Results section) and was removed for further analyses.

Then genetic parameters were also estimated for each site using model 2 (without dominance effect) without farm effect.

Genetic by environment interactions (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. GxE interactions is the difference between 1 and the genetic correlation, and the closer the genetic correlation is to 1, the smaller is the interaction.

### 3. Results

Parental origin could be traced for 99.2% of the fish. The full-sibs family sizes were variable (from 0 to 66), but only 37 families (15%) had less than half the number of expected offspring and only one family had zero offspring.

The number of fish remaining at the final slaughtering and their age are given in Table 2. The survival during the on-growing phase was satisfactory in all sites, ranging from 67 to 95%. Sex ratio was similar in all sites, ranging from 17 to 19.4% of females. Weight of females was 24% higher.

Table 5
Estimates (±Standard Error) of heritabilities ($h^2$) and maternal effects ($m^2$) for growth traits at commercial size using model 1 (dominance and maternal effect), model 2 (without dominance) or model 3 (without dominance nor maternal effect) for all data

| Trait | Model | $h^2\pm$S.E | $M^2\pm$S.E | $d^2\pm$S.E | $-2$ Log L |
|---|---|---|---|---|---|
| Weight | Model 1 | 0.34±0.09 | 0.06±0.05 | 0.01±0.01 | 23,952.0 |
| | Model 2 | 0.35±0.09 | 0.06±0.05 | – | 23,953.8 |
| | Model 3 | 0.46±0.08 | – | – | 23,955.4 |
| Length | Model 1 | 0.24±0.07 | 0.10±0.05 | 0.02±0.01 | 17,208.14 |
| | Model 2 | 0.25±0.06 | 0.10±0.05 | – | 17,212.84 |
| | Model 3 | 0.43±0.07 | – | – | 17,217.46 |
| K | Model 1 | 0.34±0.09 | 0.01±0.04 | 0.00±0.01 | 16,366.22 |
| | Model 2 | 0.34±0.09 | 0.01±0.04 | – | 16,366.22 |
| | Model 3 | 0.36±0.06 | – | – | 16,366.32 |

The relative explanatory powers of models are accounted for by the differences in $-2$Log-Likelihood between both models.

Table 4
Sample size and means (±standard deviations) of growth traits in the reduced data sets used for estimation of heritability and genetic correlations at commercial size, in four different sites (A: Palavas, France; B: Panittica, Italy; C: Vila Nova, Portugal; D: Ardag, Israel)

| | Number | Weight (g) | Length (cm) | $K$ |
|---|---|---|---|---|
| Farm A | 610 | 415.4±119.2 | 25.9±2.2 | 2.33±0.24 |
| Farm B | 648 | 336.6±94.3 | 25.4±2.4 | 1.99±0.16 |
| Farm C | 491 | 358.5±71.7 | 26.4±1.7 | 1.93±0.13 |
| Farm D | 629 | 516.6±139.4 | 28.2±2.9 | 2.25±0.32 |

Table 6
Estimates (±Standard Error) of heritabilities ($h^2$) and maternal effects ($m^2$) for growth traits at commercial size using model 2 with maternal effect and no dominance effect, in four different sites (A: Palavas, France; B: Panittica, Italy; C: Vila Nova, Portugal; D: Ardag, Israel)

| Trait | Farm | $h^2 \pm$ S.E | $m^2 \pm$ S.E. |
|---|---|---|---|
| Weight | A | 0.40±0.14 | 0.07±0.07 |
| | B | 0.44±0.14 | 0.04±0.07 |
| | C | 0.39±0.14 | 0.13±0.08 |
| | D | 0.38±0.14 | 0.08±0.07 |
| Length | A | 0.41±0.15 | 0.07±0.07 |
| | B | 0.33±0.12 | 0.09±0.07 |
| | C | 0.34±0.13 | 0.19±0.09 |
| | D | 0.27±0.11 | 0.10±0.06 |
| $K$ | A | 0.46±0.15 | 0.05±0.07 |
| | B | 0.45±0.15 | 0.04±0.07 |
| | C | 0.51±0.18 | 0.03±0.08 |
| | D | 0.26±0.11 | 0.03±0.05 |

The growth rate was different among sites, as expected, and the differences between sites were largely due to temperature differences. The proportion of deformed fish (from the scoring of internal deformities) reached 83, 60, 55 and 58% in farm A, B, C D, respectively. The main type of deformity was lordosis often associated with scoliosis, while a few fusions and cyphosis were also observed.

Estimates of heritabilities of weight, length and $K$ in farm C are presented in Table 3 for all fish, normal+mildly deformed fish or normal fish only. A correction by introducing a fixed effect of deformity was also tested. Results are presented only for farm C but the conclusions were the same for other farms. Deformities seem to have almost no effect on the estimation of the heritability of weight. However, one can see that the precision of the estimation is not better when using the full data set, compared to the normal fish only, despite the 2 to 2.5 fold increase of the number of fish. This is probably due to a decrease of precision in the estimation of additive genetic values when

Table 7
Phenotypic (above diagonal) and genetic correlations (±S.E. below diagonal) between weight, length and $K$ at commercial size in seabass for all farms, and in each of the four farms (A: Palavas, France; B: Panittica, Italy; C: Vila Nova, Portugal; D: Ardag, Israel)

| | Weight | Length | $K$ |
|---|---|---|---|
| All farms | | | |
| Weight | | 0.87 | 0.47 |
| Length | 0.95±0.02 | | 0.08 |
| $K$ | 0.27±0.15 | −0.05±0.16 | |
| Farm A | | | |
| Weight | | 0.91 | 0.39 |
| Length | 0.91±0.01 | | 0.01 |
| $K$ | 0.34±0.11 | −0.07±0.12 | |
| Farm B | | | |
| Weight | | 0.95 | 0.01 |
| Length | 0.96±0.01 | | 0.03 |
| $K$ | 0.23±0.11 | −0.05±0.12 | |
| Farm C | | | |
| Weight | | 0.88 | 0.13 |
| Length | 0.94±0.01 | | −0.32 |
| $K$ | 0.02±0.12 | −0.32±0.11 | |
| Farm D | | | |
| Weight | | 0.93 | 0.44 |
| Length | 0.95±0.01 | | 0.15 |
| $K$ | 0.35±0.11 | 0.05±0.13 | |

Table 8
Estimations of genetic correlations for weight at commercial size measured in different environments (A: Palavas, France; B: Panittica, Italy; C: Vila Nova, Portugal; D: Ardag, Israel)

| | Farm A | Farm B | Farm C |
|---|---|---|---|
| Farm B | 0.99±0.05 | | |
| Farm C | 0.84±0.08 | 0.88±0.07 | |
| Farm D | 0.97±0.03 | 0.96±0.04 | 0.70±0.10 |

deformed fish are integrated in the analysis. Deformities have an important effect on estimations for length and even more for $K$. This was expected, as deformities have an obvious impact on length and thus on the length–weight relationship. Despite this high impact of deformities, the correction with a fixed effect was not really efficient in most cases: heritability estimates remain lower with correction than when considering only normal fish. Thus, we have chosen to use only normal fish in the rest of our analysis.

This considerably reduces the size of the available datasets: from 1177–1675 to 250–648 animals. For farm A, there were only 250 normal animals and we considered that this number was too low relative to the number of families. Thus we have added mildly deformed fish to reach a sample size of 610, for the sake of models stability. Moreover, as the deformities were scored at a later age in farm A, it is quite likely that fish scored as mildly deformed there could have been scored as normal if they had been slaughtered at 400 g like in the other sites. In Table 4, sample size and means of the reduced data set are given for each trait.

Estimations of heritabilities for all farms together and according to models 1, 2 and 3 are given in Table 5. For all three traits, dominance effect is clearly non significant and can be removed from the model. According to differences of −2LogL between models, maternal effect is not significant for the three traits. However for weight and especially for length, maternal effect is not negligible and even (for length) at border of significance if we consider S.E. Moreover, if maternal effect is removed, heritability estimates are highly increased.

Heritabilities estimated in each site using model 2 are reported in Table 6. Heritabilities were all medium to high. They are little higher in farm C, but in this latter farm the CV of weight within sex was lower (18.9% versus 24–26% in other sites). For length and $K$, heritability seems lower in farm D.

Phenotypic correlations and genetic correlations estimated with model 2 are gathered in Table 7 for all farms and for each farm. Correlation between weight and length is always very high (>0.9). Genetic correlations between weight or length and $K$ can change widely from one site to another.

Genetic correlations for weight between different farms are summarized in Table 8. They are especially high (thus very small interaction) between farm A, B and D. They are lower between farm C and other farms (<0.9), especially farm D (0.70) which suggests higher genotype–environment interactions.

## 4. Discussion

### 4.1. Deformities

The cause of the deformities was apparently not to be sought during larval rearing, as the fish that were kept by farm B for its breeding program, which were produced from the same parents on the same day and reared in the same conditions, did not suffer (at least externally) from such deformities. The most

probable cause is the rearing conditions in farm A, prior to tagging. Indeed, the small fish that arrived from farm B (134 days, 3.6 g mean weight) were reared in 5 m$^3$ circular tanks, where a strong circular water current induced tank self-cleaning. However, it is known that the intensive swimming provoked by such water current is not suitable for this size of fish that have not completed their bone calcification (Chatain, 1994).

As the fish were chosen at random to constitute the different farm batches, we can make the hypothesis that the rate of deformities was initially the same in all batches. The differences observed at slaughter then should come from environmental effects of the rearing systems, allowing the fish to recover or not, or at least worsening or not the initial deformities. The much higher proportion of deformed fish in farm A is probably also accounted for by the bigger size (1 kg) at which the scoring was done.

We cannot exclude a bias on estimates of genetic parameters even with removal of deformed fish. However this should lead to a decrease of estimates unless heritability of deformities is very high which is not the case ($h^2 = 0.16$–$0.29$ on the underlying scale).

### 4.2. Maternal effect

With our results, it is still difficult to conclude on maternal effects in growth of seabass. Statistics show that they are not significant. Considering the small egg size in seabass, the absence of maternal effects in large fish is not surprising. Similar results were found by Saillant et al. (2006). More generally maternal effects have been often described in different marine fish but only on early life history traits such as larvae weight or yolk-sac volume [see for example, Bang et al. (2006) in Atlantic herring, Saillant et al. (2001) in seabass]. For later stages, to our knowledge, maternal effects in marine fish are not very well documented. In Atlantic cod, Gjerde et al. (2004) found 0.03 to 0.12 as an estimation of common full-sibs effect for body weight at 25 g. This effect contains maternal effect but also tank effects and dominance, and maternal effect was thus probably low in this experiment. Doupé and Lymbery (2005) in black bream found that maternal effect decrease gradually with age from 9.4% (75 days old, 0.6 g) to 1.8% (180 days old, 17.2 g). In salmonid fish for which egg size is much larger and maternal effects are high in early stages, they are also known to decrease with age (for example, McKay et al., 1986; Crandell and Gall, 1993).

However, in our experiment, a systematic increase of heritability is observed when maternal effect is removed. This could be due to the introduction in the model of a non significant- and thus difficult to estimate- maternal effect than to a real maternal effect. But, the higher is the estimate of maternal effect, the higher is the increase of heritability estimate. Maternal effects are probably at the border of significance in our dataset and thus we cannot reject their existence. It is not impossible that egg quality can be the origin of a small but real maternal effect. We finally choose a conservative attitude, and kept the maternal effect in further models. Since it leads to lower heritabilities, we prefer this choice which leaves room for more

genetic progress than expected. However introduction of maternal effect in the model mainly affects heritability estimates: estimations of genetic correlations between traits are not changed and genotype by environment interactions little affected.

### 4.3. Heritability estimates

Our results show moderate to high heritabilities. These results are in the range of those obtained by Saillant et al. (2006). These authors published the first heritability estimates in seabass, however our paper gives much more reliable estimates, obtained in different rearing conditions, with a large number of families and a design which prevents biases by dominance, maternal or other common environment effects. In other marine fish, medium to high heritabilities have also been found: 0.45–0.70 for body weight of turbot (Gjerde et al., 1997), but probably overestimated because of the mating design (sires nested within dams)), $0.29 \pm 0.27$ to $0.52 \pm 0.26$ for body weight at 25 g for Atlantic cod (Gjerde et al., 2004) and $0.51 \pm 0.10$ for body weight at 2 years in Atlantic cod (Kolstad et al., 2006). However in black bream with a small design (five dams mated to six sires), Doupé and Lymbery (2005) found moderate heritability of growth traits in juvenile stages.

Therefore, comparing to classically selected fish species, like salmonids, the heritability of growth seems a little larger in seabass. Indeed, in salmonids, estimates generally range between 0.2 and 0.4 (for a review, see Gjerde, 1986). The fact that seabass is not domesticated (here, all parents were caught from the wild) could be one explanation.

These heritability values are promising for genetic progress, at least in the short term. As an example, for weight, the expected genetic gain for a mass selection with a pressure of 5% should range between 16 and 25% of the mean per generation. But this has to be confirmed by selection experiments as many examples in literature show unsuccessful selection experiments in fish (for example, Moav and Wohlfarth, 1976; Hulata et al., 1986; Huang and Liao, 1990; Gjedrem, 1998, for a review).

### 4.4. Genotype by environment interactions

Low interaction between farm B and D is not surprising knowing the long common life of both batches. The highest interactions are seen between Farm C and other farms. It is plausible that the semi-intensive nature of the Farm C rearing system, together with its low temperature in winter, leads to different rankings of the families, compared with the other sites which are all warmer and more intensive (the warmest being Farm A and Farm D).

For seabass aquaculture, these results show that in most cases there would be similar response on weight if fish selected in one site would be reared in another site, except with highly divergent systems. This leaves open both the possibility to undertake a single breeding program and the possibility to set up site-specific breeding programs. Another possibility would be a single breeding program with multisite testing and site-specific multi-plication according to the best ranking families in each site. The

choice is open for each farm, according to its characteristics and objectives. We must also underline that in the present work, all fish are reared in a common environment before being sent to the various rearing sites (farms), thus limiting the possible GxE interaction effects to the only on-growing period.

The genotype–environment interactions obtained here are much lower than those already reported in seabass by Saillant et al. (2006). In Saillant et al. (2006), each experimental group was exposed to the different environmental conditions from fertilization time, thus extending the interaction action from the early larval stages. Therefore, it should be really interesting to test genotype–environment interactions in the early stage in a larger design. Moreover, the significantly lower precision of estimates reported in the latter experiment reduces the accuracy of results.

In fish, genotype–environment interactions for growth traits have been studied mainly in salmonid, catfish, carp and tilapia species. They have been estimated through reaction norms or, as in this paper, through genetic correlations of a trait measured in different environments and considered as different traits, or through selection response in different environments. Most papers indeed studied GxE interactions through reaction norms: different strains or genotypes reared in different environments. Significant genotype–environment (environments were generally characterised by different temperature/photoperiod/nutritional environment/density) for growth was found in many fish species: carp (Wohlfarth et al., 1983), catfish (Dunham et al., 1990), tilapia (Romana-Eguia and Doyle, 1992), Rainbow trout (Iwamoto et al., 1986) and in marine fish: turbot (Imsland et al., 2000), Atlantic halibut (Jonassen et al., 2000) and Atlantic cod (Imsland et al., 2005). Papers estimating genetic correlations between the same trait in different environments are less numerous and results highly variable. In rainbow trout, Sylven et al. (1991) found genetic correlations ranging from 0.58 to 0.86 between slaughter weight in freshwater (Sweden), brackish water (Sweden) and salt water (Norway), i.e. higher interactions than in our experiment. Still, in rainbow trout, Bagley et al. (1994) found genetic correlations ranging from 0.32 to 0.9 for different stocking densities. Again in rainbow trout, Palti et al. (2006) found similar family rankings reared under a classical fishmeal diet or a gluten-based diet. In Atlantic salmon, Hanke et al (1989) found similar family rankings for different photoperiods while Stefansson et al. (1990) found significant family × photoperiod interactions. In tilapia, Ponzoni et al. (2005) show small interactions for weight of selected fish (GIFT strain) in cages or ponds and concluded that 'selection response was being achieved in both environments and that there was not enough evidence to justify the conduct of separate genetic improvement programs'.

Generally speaking, GxE interactions depend on the traits, populations and environments studied and are still difficult to predict. It is however a key point when setting up a breeding program in species with wide range of environments and large geographical area like in seabass.

### 4.5. Correlations between growth traits

As the genetic correlation is high and heritabilities of both traits are also similar, selection on weight or length should yield the same results on weight. However, because of the correlations with $K$, selecting on weight or on length is not equivalent.

In farms A, B and D, the genetic correlation between length and $K$ is close to zero, so selection on length would have no impact on $K$, but the positive genetic correlation between weight and $K$ would lead to the selection of "fatter" fish if weight was used as a selection criterion. In this case, selection on length should be preferred. On the opposite, in farm C, the genetic correlation between weight and $K$ is close to zero so that selecting on weight would have no impact on the global shape of the fish. However, the genetic correlation between length and $K$ is negative, so selection on length would lead to leaner, though heavier, fish. This kind of fish is generally appreciated as it looks more like a wild fish, and finally selection on length will probably be preferred again. In other sites, a specific selection on $K$ would be necessary to obtain leaner fish.

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