# 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 ± 0.14 to 0.44 ± 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 ± 0.10 to 0.99 ± 0.05. Genetic correlations between weight or length and K were not similar in the different sites.

**Keywords:** *Dicentrarchus labrax*; Seabass; Growth; Heritability; GxE interactions; Microsatellites

## Introduction

Domestication of sea bass Dicentrarchus labrax began in the 1980's 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

1     productivity. However, to optimise breeding programs, reliable estimates of genetic

2     parameters in a wide range of rearing systems are needed. Some heritability

3     estimates for growth traits exist for marine fish, but mainly for species other than

4     seabass, for example turbot <u>Scophthalmus maximus</u> (Gjerde et al., 1997), Atlantic

5     cod <u>Gadus morua</u> (Gjerde et al., 2004 ; Kolstad et al., 2006), black bream

6     <u>Acanthopagrus butcheri</u> (Doupé and Lymbery, 2005) and gilthead seabream <u>Sparus</u>

7     <u>aurata</u> (Knibb et al., 1997). Concerning seabass, heritability estimates were

8     published by Saillant et al. (2006), but based on a small design (3 dams X 10 sires).

9     One major constraint for estimating genetic parameters in fish is the inability to tag

10     hatchlings, and consequently the need to separately rear the families until tagging

11     size. This limits the number of families that can be used, and may bias family means

12     by tank effects, thus biasing (full-sibs designs) or reducing the precision of (half-sibs

13     designs) the estimated genetic parameters. An interesting alternative to separate

14     rearing of families is the use of mixed rearing of progenies with *a posteriori*

15     reconstruction of pedigrees using highly variable markers such as microsatellites.

16     This was first proposed more than ten years ago (Herbinger et al*.,* 1995; Estoup et

17     al., 1998) but it is only recently that mating designs of a size permitting reliable

18     estimations of genetic parameters are being used (Norris and Cunningham, 2004 ;

19     Vandeputte et al., 2004). The major benefits of this methodology are the absence of

20     between families environmental effects, and the possibility to use factorial designs

21     which allow precise estimation of additive, maternal and dominance effects

22     (Vandeputte et al., 2001). Most of the previously cited heritability estimates in marine

23     fish were obtained using the separate rearing method.

24     Seabass farming takes place in very different system managements, and thus

25     genetic and environment correlations of the same trait in different environments are

1 also needed to set up optimised breeding programs. Indeed, it is a key point to know

2 if a genetically improved strain in one environment would express superiority in other

3 environments. This issue has been seldom studied in marine fish and never in

4 seabass except by Saillant et al. (2006) but with a small design.

5 The present work reports results from a large scale experiment involving 253 full sib

6 families, communally reared, originating from 33 males and 23 females and

7 distributed to four contrasted environments (France, Portugal, Italy and Israel). In this

8 paper, we focus on growth traits (weight, length and condition factor) which are traits

9 of high economical interest. The large design allows precise estimates of maternal

10 and additive genetics effects as well as correlations between traits and genetic

11 correlations between growth traits in each environment (genotype environment

12 interactions)

13

14 **2. Material and methods**

15 2.1. Animals

16 The parents of the studied animals were wild fish of Atlantic origin collected by

17 Panittica Pugliese (Italy) on the Northern coast of Brittany (France). Sperm was

18 collected before the crossing and cryopreserved in 250 ml straws according to the

19 method described in Fauvel et al. (1998). Further reproduction operations took place

20 at Panittica Pugliese farm. Eggs were obtained by manual stripping following

21 hormonal induction of ovulation. For all parents a fin clip was collected and kept in 90

22 % ethanol for DNA analyses and parentage assignment.

23 253 full-sib families from 33 males and 23 females were produced according to a

24 partly factorial mating design. Crosses were conducted with three sets of different

25 parents: 11 males X 9 females, 11 males X 7 females and 11 males X 7 females.

1    Within each set a full factorial crossing was accomplished. All crosses were made by

2    individual fertilization of identical volumes of eggs, and five minutes after fertilisation,

3    eggs from the same female were mixed for further incubation.

4    Eggs were incubated (one female per incubator) for 48 hours after which two

5    milliliters of floating eggs from each female were sampled and mixed to constitute a

6    single batch of eggs that hatched in a 0.5 m$^3$ incubator four days after the fertilization.

7    They were all kept in the same tank for larval rearing until day 64. After which, they

8    were transferred to a concrete raceway until they reached day 130. During larval

9    rearing, the temperature gradually increased from 13 (at hatching) to 18℃ (at day

10    15) after which it stabilised at the latter temperature. Fish were fed on artemia for 40

11    days, then weaned on dry food (Nippay, Hendrix). Food was first distributed manually

12    to satiation, then, starting from day 66, one or two automatic feeders were used.

13    During the pregrowing phase, the water temperature and salinity varied from 14.2 to

14    19.3℃ and from 19.5 to 37.5 ‰, respectively.

15    At 134 days post hatch (about 4g), a random sample of 16000 fish was sent to

16    Ifremer station in Palavas (France) and pregrown in a 5 m3 tank in a recirculating

17    system (10-30% renewal/day, 18℃, 34 ‰ average sali nity). At 156 days, the batch

18    of fish was split at random into four 5 m3 tanks to lower the density. At 238 days,

19    their weight was higher than scheduled, so the temperature was lowered to 14℃

20    (0.5℃ per day).

21    At 370 days, fish had reached a mean weight of 35 g and 7000 were randomly

22    selected, individually PIT-tagged and fin-clipped (kept in 90% ethanol for further DNA

23    analyses). Four batches of 1750 fish each (on average, 6.9 per fullsib family) were

24    constituted and each one was kept in a 5m3 tank prior to distribution to four different

25    farms.

1    The four farms were chosen for their varying growing or rearing conditions. Main

2    rearing conditions are reported in Table 1. One batch was kept at the Ifremer station

3    in France (Farm A) in tanks where the density was maintained below 30 kg/m$^3$. The

4    temperature was raised progressively from 14℃ and  maintained throughout the

5    whole experiment at 20-22℃.

6    A second batch arrived at 423 days at Panittica Pugliese in Italy (Farm B) where it

7    was reared in a 12 m$^3$ concrete raceway supplied with 19℃ (constant temp erature)

8    borehole water. A third one arrived at Viveiro Villanova in Portugal (Farm C) at 420

9    days and was first reared in an 8m$^3$ tank. Then, they were transferred to a semi-

10   intensive estuarine pond at 588 days. The last batch of fish was reared from day 513

11   in a 216 m$^3$ sea-cage in tropical conditions at Ardag in Israel (Farm D). This batch

12   was kept in the farm B from day 423 to day 510, due to transportation problems.

13

14   <u>2.2. Data collection.</u>

15   In each farm, fish were measured at commercial size (average 400 g), varying from

16   338 g (farm B) to 487 g (farm D). Number of fish measured, mean weight and age

17   are reported in Table 2. Fish were starved 3 days prior to harvest. On harvest day, all

18   fish were euthanized in an excess dose of 2-phenoxyethanol (0.6 ml.l$^{-1}$) or eugenol

19   (0.1 ml.l$^{-1}$, farm B). In farm A, the fish were not euthanized but only anaesthetized

20   (0.3 ml.l$^{-1}$ phenoxyethanol).

21   Each fish was weighed (to the nearest 0.1g) and its length measured (to the nearest

22   1 mm) and its tag read to determine and record its parentage. The condition factor

23   (K) was calculated. In farms B, C and D, internal deformities were scored after

24   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.

1

2  To determine the potential significant fixed effects, data were first analysed using

3  proc GLM of the SAS [®] System. Tank effect was not significant ($\underline{P} > 0.1$) for all traits

4  but sex effect was kept in further models ($\underline{P} < 0.05$). A farm effect ($\underline{P}<0.05$) was also

5  included when all data were analyzed together. Interactions were not significant.

6  A model with the deformity as a fixed effect was also tested to make decisions about

7  including or not deformed fish in the analysis (see Results section).

8

9  Heritabilities, non genetic maternal effect and dominance were first analyzed for all

10  data using Asreml (Gilmour et al., 2002). An animal model with dominance and

11  maternal effect (model 1) or without dominance effect (model 2) or without

12  dominance nor maternal effect (model 3) was used.

13

14          $Y = X\beta + Z_1u + Z_2m + Z_3fs + e$          (model 1)

15  where Y is the vector of observations, $\beta$ is the vector of fixed effects (overall mean,

16  sex and farm), u is the vector of random additive genetic effects, m is the vector of

17  random maternal effects, fs is the random vector of fullsib family effect *ie* accounts

18  for dominance and e is the vector of random residual effects. X, $Z_1$, $Z_2$ and $Z_3$ are

19  known incidence matrices. Dominance effect was very low (see Results section) and

20  was removed for further analyses.

21  Then genetic parameters were also estimated for each site using model 2 (without

22  dominance effect) without farm effect.

23  Genetic by environment interactions (GxE interactions) were estimated through

24  genetic correlations between the trait of interest in environment 1 and the same trait

25  in environment 2, considered as two different traits in the analysis. GxE interactions

1    is the difference between 1 and the genetic correlation, and the closer the genetic

2    correlation is to 1, the smaller is the interaction.

3

4    **3. Results**

5    Parental origin could be traced for 99.2% of the fish. The full-sibs family sizes were

6    variable (from 0 to 66), but only 37 families (15%) had less than half the number of

7    expected offspring and only one family had zero offspring.

8    The number of fish remaining at the final slaughtering and their age are given in

9    Table 2. The survival during the ongrowing phase was satisfactory in all sites,

10   ranging from 67 to 95%. Sex ratio was similar in all sites, ranging from 17 to 19.4% of

11   females. Weight of females was 24% higher.

12   The growth rate was different among sites, as expected, and the differences between

13   sites were largely due to temperature differences. The proportion of deformed fish

14   (from the scoring of internal deformities) reached 83, 60, 55 and 58% in farm A, B, C

15   D, respectively. The main type of deformity was lordosis often associated with

16   scoliosis, while a few fusions and cyphosis were also observed.

17   Estimates of heritabilities of weight, length and K in farm C are presented in Table 3

18   for all fish, normal + mildly deformed fish or normal fish only. A correction by

19   introducing a fixed effect of deformity was also tested. Results are presented only for

20   farm C but the conclusions were the same for other farms. Deformities seem to have

21   almost no effect on the estimation of the heritability of weight. However, one can see

22   that the precision of the estimation is not better when using the full data set,

23   compared to the normal fish only, despite the 2 to 2.5 fold increase of the number of

24   fish. This is probably due to a decrease of precision in the estimation of additive

25   genetic values when deformed fish are integrated in the analysis. Deformities have

1  an important effect on estimations for length and even more for K. This was

2  expected, as deformities have an obvious impact on length and thus on the length-

3  weight relationship. Despite this high impact of deformities, the correction with a fixed

4  effect was not really efficient in most cases: heritability estimates remain lower with

5  correction than when considering only normal fish. Thus, we have chosen to use only

6  normal fish in the rest of our analysis.

7  This considerably reduces the size of the available datasets: from 1177-1675 to 250-

8  648 animals. For farm A, there were only 250 normal animals and we considered that

9  this number was too low relative to the number of families. Thus we have added

10  mildly deformed fish to reach a sample size of 610, for the sake of models stability.

11  Moreover, as the deformities were scored at a later age in farm A, it is quite likely that

12  fish scored as mildly deformed there could have been scored as normal if they had

13  been slaughtered at 400g like in the other sites. In Table 4, sample size and means

14  of the reduced data set are given for each trait.

15

16  Estimations of heritabilities for all farms together and according to models 1, 2 and 3

17  are given in Table 5. For all three traits, dominance effect is clearly non significant

18  and can be removed from the model. According to differences of –2LogL between

19  models, maternal effect is not significant for the three traits. However for weight and

20  especially for length, maternal effect is not negligible and even (for length) at border

21  of significance if we consider S.E. Moreover, if maternal effect is removed, heritability

22  estimates are highly increased.

23  Heritabilities estimated in each site using model 2 are reported in Table 6.

24  Heritabilities were all medium to high. They are little higher in farm C, but in this latter

1    farm the CV of weight within sex was lower (18.9% versus 24-26% in other sites). For

2    length and K, heritability seems lower in farm D.

3    Phenotypic correlations and genetic correlations estimated with model 2 are gathered

4    in Table 7 for all farms and for each farm. Correlation between weight and length is

5    always very high (> 0.9). Genetic correlations between weight or length and K can

6    change widely from one site to another.

7    Genetic correlations for weight between different farms are summarized in Table 8.

8    They are especially high (thus very small interaction) between farm A, B and D. They

9    are lower between farm C and other farms (<0.9), especially farm D (0.70) which

10   suggests higher genotype-environment interactions.

11

12   **4- Discussion**

13   <u>4.1. Deformities</u>

14   The cause of the deformities was apparently not to be sought during larval rearing,

15   as the fish that were kept by farm B for its breeding program, which were produced

16   from the same parents on the same day and reared in the same conditions, did not

17   suffer (at least externally) from such deformities. The most probable cause is the

18   rearing conditions in farm A, prior to tagging. Indeed, the small fish that arrived from

19   farm B (134 days, 3.6 g mean weight) were reared in 5m3 circular tanks, where a

20   strong circular water current induced tank self-cleaning. However, it is known that the

21   intensive swimming provoked by such water current is not suitable for this size of fish

22   that have not completed their bone calcification (Chatain, 1994).

23   As the fish were chosen at random to constitute the different farm batches, we can

24   make the hypothesis that the rate of deformities was initially the same in all batches.

25   The differences observed at slaughter then should come from environmental effects

1    of the rearing systems, allowing the fish to recover or not, or at least worsening or not

2    the initial deformities. The much higher proportion of deformed fish in farm A is

3    probably also accounted for by the bigger size (1 kg) at which the scoring was done.

4    We cannot exclude a bias on estimates of genetic parameters even with removal of

5    deformed fish. However this should lead to a decrease of estimates unless heritability

6    of deformities is very high which is not the case ($h^2$ = 0.16-0.29 on the underlying

7    scale).

8

9    <u>4.2. Maternal effect</u>

10    With our results, it is still difficult to conclude on maternal effects in growth of

11    seabass. Statistics show that they are not significant. Considering the small egg size

12    in seabass, the absence of maternal effects in large fish is not surprising. Similar

13    results were found by Saillant et al. (2006). More generally maternal effects have

14    been often described in different marine fish but only on early life history traits such

15    as larvae weight or yolk-sac volume [see for example, Bang et al. (2006) in Atlantic

16    herring, Saillant et al. (2001) in seabass]. For later stages, to our knowledge,

17    maternal effects in marine fish are not very well documented. In Atlantic cod, Gjerde

18    et al. (2004) found 0.03 to 0.12 as an estimation of common full-sibs effect for body

19    weight at 25 g. This effect contains maternal effect but also tank effects and

20    dominance, and maternal effect was thus probably low in this experiment. Doupé and

21    Lymbery (2005) in black bream found that maternal effect decrease gradually with

22    age from 9.4 % (75 days old, 0.6 g) to 1.8% (180 days old, 17.2 g). In salmonid fish

23    for which egg size is much larger and maternal effects are high in early stages, they

24    are also known to decrease with age (for example, Mc Kay et al., 1986; Crandell and

25    Gall, 1993).

1 However, in our experiment, a systematic increase of heritability is observed when

2 maternal effect is removed. This could be due to the introduction in the model of a

3 non significant - and thus difficult to estimate - maternal effect than to a real maternal

4 effect. But, the higher is the estimate of maternal effect, the higher is the increase of

5 heritability estimate. Maternal effects are probably at the border of significance in our

6 dataset and thus we cannot reject their existence. It is not impossible that egg quality

7 can be the origin of a small but real maternal effect. We finally choose a conservative

8 attitude, and kept the maternal effect in further models. Since it leads to lower

9 heritabilities, we prefer this choice which leaves room for more genetic progress than

10 expected. However introduction of maternal effect in the model mainly affects

11 heritability estimates: estimations of genetic correlations between traits are not

12 changed and genotype by environment interactions little affected.

13

14 <u>4.3. Heritability estimates</u>

15 Our results show moderate to high heritabilities. These results are in the range of

16 those obtained by Saillant et al. (2006). These authors published the first heritability

17 estimates in seabass, however our paper gives much more reliable estimates,

18 obtained in different rearing conditions, with a large number of families and a design

19 which prevents biases by dominance, maternal or other common environment

20 effects. In other marine fish, medium to high heritabilities have also been found: 0.45-

21 0.70 for body weight of turbot (Gjerde et al., 1997), but probably overestimated

22 because of the mating design (sires nested within dams)), $0.29 \pm 0.27$ to $0.52 \pm 0.26$

23 for body weight at 25 g for Atlantic cod (Gjerde et al., 2004) and $0.51 \pm 0.10$ for body

24 weight at two years in Atlantic cod (Kolstad et al., 2006). However in black bream

1    with a small design (five dams mated to six sires), Doupé and Lymbery (2005) found

2    moderate heritability of growth traits in juvenile stages.

3

4    Therefore, comparing to classically selected fish species, like salmonids, the

5    heritability of growth seems a little larger in seabass. Indeed, in salmonids, estimates

6    generally range between 0.2 and 0.4 (for a review, see Gjerde, 1986). The fact that

7    seabass is not domesticated (here, all parents were caught from the wild) could be

8    one explanation.

9    These heritability values are promising for genetic progress, at least in the short term.

10   As an example, for weight, the expected genetic gain for a mass selection with a

11   pressure of 5% should range between 16 and 25% of the mean per generation. But

12   this has to be confirmed by selection experiments as many examples in litterature

13   show unsuccessful selection experiments in fish (for example, Moav and Wohlfarth,

14   1976; Hulata et al., 1986; Huang and Liao, 1990; Gjedrem, 1998, for a review).

15

16   4.4. Genotype by environment interactions

17   Low interaction between farm B and D is not surprising knowing the long common life

18   of both batches. The highest interactions are seen between Farm C and other farms.

19   It is plausible that the semi-intensive nature of the Farm C rearing system, together

20   with its low temperature in winter, leads to different rankings of the families,

21   compared with the other sites which are all warmer and more intensive (the warmest

22   being Farm A and Farm D).

23   For seabass aquaculture, these results show that in most cases there would be

24   similar response on weight if fish selected in one site would be reared in another site,

25   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 multiplication 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 (Romania-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), *ie* 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. (1986) found significant family x 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.

1 In farms A, B and D, the genetic correlation between length and K is close to zero, so

2 selection on length would have no impact on K, but the positive genetic correlation

3 between weight and K would lead to the selection of "fatter" fish if weight was used

4 as a selection criterion. In this case, selection on length should be preferred. On the

5 opposite, in farm C, the genetic correlation between weight and K is close to zero so

6 that selecting on weight would have no impact on the global shape of the fish.

7 However, the genetic correlation between length and K is negative, so selection on

8 length would lead to leaner, though heavier, fish. This kind of fish is generally

9 appreciated as it looks more like a wild fish, and finally selection on length will

10 probably be preferred again. In other sites, a specific selection on K would be

11 necessary to obtain leaner fish.

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1    Table 1- Growing conditions in the four rearing sites.

|  | Rearing period (days) | Rearing system | Temperature (°C) | Volume (m$^3$) | Rearing density (kg/m$^3$) |
|---|---|---|---|---|---|
| Farm A | 420-714 | semi-closed recirculation system | 20-22 | 5 (x4) | < 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 |

2    *: fish of farm D were reared in farm B during the period 423-510 days post hatching.

3

4

5    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 |

6

1 Table 3. Effects of deformities on heritability estimates (h²) and their standard errors

2 (s.e) at harvest size, for farm C (Vila Nova, Portugal), depending on the groups of

3 fish kept for analysis and on the models used : with (corrected data) or without ( raw

4 data) a fixed effect accounting for the occurrence of deformities.

5

| Trait | Fish kept for analysis | Sample size | h² for raw data (± s.e.) | h² 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 | - |

6

1

2 Table 4. Sample size and means (± standard deviations) of growth traits in the

3 reduced data sets used for estimation of heritability and genetic correlations at

4 commercial size, in four different sites (A: Palavas, France; B: Panittica, Italy; C: Vila

5 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 |

6

7

1    Table 5. Estimates ($\pm$ Standard Error) of heritabilities (h²) and maternal effects (m²)

2    for growth traits at commercial size using model 1 (dominance and maternal effect),

3    model 2 (without dominance) or model 3 (without dominance nor maternal effect) for

4    all data. The relative explanatory powers of models are accounted for by the

5    differences in -2Log-Likelihood between both models.

6

| Trait | Model | h² $\pm$ S.E | m² $\pm$ S.E | d² $\pm$ S.E | - 2 Log L |
|---|---|---|---|---|---|
| Weight | Model 1 | 0.34 $\pm$ 0.09 | 0.06 $\pm$ 0.05 | 0.01 $\pm$ 0.01 | 23952.0 |
| | Model 2 | 0.35 $\pm$ 0.09 | 0.06 $\pm$ 0.05 | - | 23953.8 |
| | Model 3 | 0.46 $\pm$ 0.08 | - | - | 23955.4 |
| Length | Model 1 | 0.24 $\pm$ 0.07 | 0.10 $\pm$ 0.05 | 0.02 $\pm$ 0.01 | 17208.14 |
| | Model 2 | 0.25 $\pm$ 0.06 | 0.10 $\pm$ 0.05 | - | 17212.84 |
| | Model 3 | 0.43 $\pm$ 0.07 | - | - | 17217.46 |
| K | Model 1 | 0.34 $\pm$ 0.09 | 0.01 $\pm$ 0.04 | 0.00 $\pm$ 0.01 | 16366.22 |
| | Model 2 | 0.34 $\pm$ 0.09 | 0.01 $\pm$ 0.04 | - | 16366.22 |
| | Model 3 | 0.36 $\pm$ 0.06 | - | - | 16366.32 |

7

1   Table 6. Estimates (± Standard Error) of heritabilities (h²) and maternal effects (m²)

2   for growth traits at commercial size using model 2 with maternal effect and no

3   dominance effect, in four different sites (A: Palavas, France; B: Panittica, Italy; C: Vila

4   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 |

5

6

Table 7. Phenotypic (above diagonal) and genetic correlations ($\pm$ 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 | $0.95 \pm 0.02$ | | 0.08 |
| K | $0.27 \pm 0.15$ | $-0.05 \pm 0.16$ | |
| **Farm A** | | | |
| Weight | | 0.91 | 0.39 |
| Length | $0.91 \pm 0.01$ | | 0.01 |
| K | $0.34 \pm 0.11$ | $-0.07 \pm 0.12$ | |
| **Farm B** | | | |
| Weight | | 0.95 | 0.01 |
| Length | $0.96 \pm 0.01$ | | 0.03 |
| K | $0.23 \pm 0.11$ | $-0.05 \pm 0.12$ | |
| **Farm C** | | | |
| Weight | | 0.88 | 0.13 |
| Length | $0.94 \pm 0.01$ | | -0.32 |
| K | $0.02 \pm 0.12$ | $-0.32 \pm 0.11$ | |
| **Farm D** | | | |
| Weight | | 0.93 | 0.44 |
| Length | $0.95 \pm 0.01$ | | 0.15 |
| K | $0.35 \pm 0.11$ | $0.05 \pm 0.13$ | |

1

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)

5

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

6

7