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Genotype by diet interactions in European sea bass (*Dicentrarchus labrax, L.*) in case of a nutritional challenge on totally plant-based diets[1]

R. Le Boucher[a, b, c, *], M. Vandeputte[a, b], M. Dupont-Nivet[a], E. Quillet[a], F. Ruelle[b], A. Vergnet[b], S. Kaushik[d], J. M. Allamellou[e], F. Médale[d] and B. Chatain[b]

[a] INRA, UMR1313 Génétique Animale et Biologie Intégrative, F-78350 Jouy-en-Josas, France
[b] Ifremer, UMR110 Intrepid, Chemin de Maguelone, F-34250 Palavas-les-Flots, France
[c] AgroParisTech, UMR1313 Génétique Animale et Biologie Intégrative, F-75231 Paris 05
[d] INRA, UMR1067, Nutrition, Métabolisme, Aquaculture, F-64310 St Pée-sur-Nivelle, France
[e] LABOGENA, Domaine de Vilvert, 78352 Jouy-en-Josas, France

*: Corresponding author : Richard

Abstract:

Aquaculture of carnivorous species has strongly relied on fish meal and fish oil for feed formulation and higher and higher replacement by terrestrial plant-based products is occurring now. This rapid change in dietary environment has been a major evolution and has to be taken into consideration in breeding programs. The present study analyzed potential consequences of this tendency for selective breeding, by estimating genetic parameters of body weight and growth rates estimated by TGC (Thermal Growth Coefficient) over different periods with extremely contrasted diets. European sea bass (*Dicentrarchus labrax* L.) issued from a factorial cross (1,526 fish) between 25 sires and 9 dams were used to estimate heritabilities and genotype by diet interaction. Starting 87 days after fertilization (2.5 g), half of them were fed a diet containing marine products (M) and the other half was fed a totally plant-based (PB) diet (without any fishmeal and any fish oil). They were individually tagged, reared in a recirculated system and genotyped at13 microsatellites to rebuild parentage of individuals. Body weight and TGC were measured during 335 days until fish fed M diet reached 108.3 g. These traits were significantly lower in fish fed the PB diet ($P < 0.05$) in the very first stages following the dietary shift but the difference in TGC between diets rapidly disappeared ($P > 0.1$). Survival was significantly lower in fish fed the PB diet (PB: 64.7% M: 93.7% after 418 days, $P<0.05$). This work evidenced moderate heritabilities (0.18 to 0.46) for body weight (*BW*) with both diets and high genetic correlations between diets (0.78 to 0.93) meaning low genotype by diet interactions, although diets were extremely contrasted. Heritabilities of TGC (0.11 to 0.3) were lower than for *BW* as well as genetic correlations between diets (0.43 to 0.64). Using such extremely contrasted diets, predicted gains in different scenarii indicated that selecting fish for growth on a marine diet should be the most efficient way to increase growth on plant-based diets, meaning that in this case indirect selection should be more efficient than direct selection.

Keywords: European sea bass ; genetic correlation ; genotype by diet interaction ; genotype by environment interaction ; plant based diet

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1. Introduction

Following the decline of fisheries worldwide, aquaculture now supplies an increasing proportion of aquatic products for human consumption. Farmed fish are supposed to cover the increase in demand in the next 20 years (FAO, 2008) when fisheries will not be able to meet it (Tacon and Metian, 2008; Naylor et al., 2009). Carnivorous species, like the European sea bass, were pointed out for their high use of fishmeal (FM) and fish oil (FO) issued from small pelagic species. The pressure to reduce dependency on such marine resources is high (Naylor et al., 2009) and higher and higher substitution rates with plant-based products have been tested in the diets (Powell, 2003).

In the late 1990's, the first breeding programs started on European sea bass and strong progress for growth (+ 23 to 42 %per generation) was demonstrated to be feasible (Vandeputte et al., 2009) as heritability estimates (h^2) were estimated to be medium to high (Dupont-Nivet et al., 2008 ; Saillant et al., 2006). However, recent trials showed that genotype by environment interactions could impact growth when fish were reared in different culture conditions (Dupont-Nivet et al., 2010). By extension, diet composition is projected to be highly variable and estimates of genotype by diet interactions are now needed to know how fingerlings will perform in different dietary environments. Most published results on this issue have been obtained in salmonids. Some found high genetic correlation between diets (0.97 ± 0.21, Quinton et al.,

2007a, b) and did not evidence significant genotype by environment interactions (Palti et al., 2006; Quinton et al., 2007a, b). Some others found moderate genetic correlation between diets (0.73 ± 0.13, Pierce et al., 2008) and concluded to significant interactions (Pierce et al., 2008; Dupont-Nivet et al, 2009). Starting at early stages (2.5 g), we assessed heritabilities of growth traits and genetic correlations between and within diets comparing a totally plant-based diet and a diet containing marine products.

The objective of the present study was to assess the potential efficiency of a breeding program when fish had been selected using a given diet (containing FM and FO or not) and transferred in a different dietary environment.

2 Material and methods

Experimental diets

Two experimental diets were formulated by INRA to be isoproteic, isolipidic and isoenergetic. Plant-based (PB) and marine (M) diets were extremely contrasted regarding the proportion of marine products. The M diet contained both fish meal and fish oil when the PB diet was totally devoid of marine products (Table 1). Both diets contained minerals and vitamins premix to meet European sea bass nutritional requirements according to NRC (1993). A first batch was processed in INRA facilities (Donzacq, France) and distributed until 344 days of age and a second batch was processed by Biomar (Denmark) and distributed until the end of the trial. Analytical compositions were identical (Table 1). Pellet size was adjusted according to mean

body weight of fish and rations based on estimated biomass (1-2 % of the biomass) were distributed using self-feeders.

Fish

This study was conducted in the Ifremer aquaculture station (Palavas-les-Flots, France) with wild-caught West Mediterranean European sea bass broodstock. A factorial cross between 9 dams and 25 sires was done in order to obtain 225 families. Sperm had been collected one year earlier and cryopreserved. After hormonal induction of ovulation (10 $\mu g.kg^{-1}$ luteinizing releasing hormone, Sigma D-TRP6LHRH), females were manually stripped and same volume of eggs from each female was collected, mixed and divided into 25 aliquots of 40 ml. Each aliquot of eggs was then fertilized by thawed sperm from a single male to avoid sperm competition. All fertilizations were performed within 30 minutes. After anaesthesia (phenoxyethanol, 300 ppm), fin clips were collected on the parents and stored in ethanol pending DNA extraction. In this experiment, the age of the fish is expressed in days post-fertilization. Until 68 days, larvae were all kept in the same tank and the temperature rose from 14°C to 20°C (Chatain, 1994). Fish were fed on *Artemia* nauplii for 40 days then weaned on a commercial diet that contained both marine ingredients and plant products (Marin Start, Le Gouessant, Lamballe, France). A high sensitivity of sea bass juvenile to plant-based products has been evidenced in preliminary trials and little is known about the origin of this sensitivity. This is the reason why it was preferred to use a commercial diet rather than 1:1 mixture of experimental diets prior to the beginning of trial, which would have been another possible option. At 83 days, 9,600 fish (2.5 g) were distributed in 6 conical-bottom 1.5 m^3 tanks (3 per diet). Recirculated water with regulated temperature (mean ± SD; 20.8 ± 1.1°C, range; 16.9-25.3) was supplied, a temperature below the optimum

temperature for the maximal growth of European sea bass which is about 27°C (Lemarié, pers. comm.). Experimental diets were loaded in self-feeders (87 days) and active feeding for both diets started 3 days later. When they reached approximately 20 g (mean ± SD; M (224 days): 23.3 ± 8.1 g; PB (266 days): 17.9 ± 7.6 g), fish were individually tagged with passive integrative transponders (AEG-Id, Germany). After anaesthesia (phenoxyethanol, 300 ppm), all fish were transferred (360 days, mean ± SD; M: 70.3 ± 1.6 g and PB: 36.6 ± 2.06 g) to 6 tanks (5 m^3) in order to keep the same batches and maintain low fish densities (< 20 kg/m^3). During the transfer, fin samples were collected from each fish after anesthesia (phenoxyethanol, 300 ppm) and kept into absolute ethanol.

Data collection

To estimate early growth (before tagging), random samples of 50 fish per tank were measured at 4 dates (83 days, 116 days, 151 days and 224 days) for body weight (*BW*, in grams) and standard length (*SL*, in millimeters). After tagging, *BW* and *SL* were individually measured monthly (266, 298, 326, 361, 389, 418 days) and survival was monitored daily. Fish shape was characterized by computing Fulton's condition factor ($K = (BW/ SL^3)*100$). Between the second and the third measurement (300 days), a technical problem in the oxygen circuit led to massive mortality in one tank of the PB batch without involving the other tanks. Consequently, only 2 PB tanks were further considered for analyses. At the end of the trial (418 days), DNA samples of 1,526 randomly chosen fish (3 x 272 in M and 2 x 355 in PB) were analyzed for parentage assignment and the corresponding fish were slaughtered and dissected to determine their sex. The trial ended

when M fish reached approximately 100 g, which is one third of their commercial size (300-450g).

Thermal-unit growth coefficient (*TGC*) was chosen as a standardized measure of growth (Dumas et al., 2007) that is assumed to be unaffected by body weight, time interval and water temperature (Iwama and Tautz, 1981), as long as temperature is below the optimum temperature for growth, which is the case in the present study. For a period starting on day n and ending on day m, it is calculated as following

$$TGC_{nm} = 1000 * \frac{BW_m^{(1/3)} - BW_n^{(1/3)}}{\sum_{i=n}^{m} (T_i - 10)}$$

Where BW_n and BW_m were fish body weight (g) on day n and m, T_i (°C) was the daily temperature.

Parentage assignment

Parents and offspring were assayed at 13 microsatellite loci described in Chistiakov et al. (2006) and García De Leon et al. (1995). Rapid DNA extraction and genotyping were done by LABOGENA (Jouy-en-Josas, France). Parentage assignment was performed by exclusion allowing a maximum of 2 allelic mismatches using VITASSIGN (Vandeputte et al., 2006). At the end of this process, 98.7% of the fish sampled had been successfully and unambiguously assigned to their parents. Some families were poorly represented and only half-sib families containing more than 10 individuals per diet were kept for the analyses, meaning that the

offspring analyzed in both diets were finally issued from the same factorial cross between 9 dams and 22 sires. Similar sizes of half-sib families were obtained in the M diet (mean ± SD; 37.1 ± 22.0 for sire half-sib families; range: 12, 95, 90.8 ± 78.0 for dam half-sib families; range: 25, 247) and the PB diet (33.2 ± 19.5 for sire half-sib families; range: 13, 85, 81.1 ± 75.5 for dam half-sib families; range: 21, 248). In the same way, half-sib families were also evenly distributed among tanks.

Statistical analyses

For measurements collected before individual tagging, the significance of diet and tank effects was tested with the following model in the MIXED procedure of SAS (SAS Institute Inc., Cary, NC) using the REPEATED command (SAS Institute Inc., 2008) to account for variance heterogeneity between diets:

$$Y_{ijk} = \mu + Diet_i + \text{tank}(diet)_{j(i)} + e_{ijk} \quad (1)$$

Where Y_{ijk} is the individual performance, μ is the overall mean, $Diet_i$ is the fixed effect of the diet (i = 1, 2), $tank_{j(i)}$ is the random effect of the tank j (j = 1, 2, 3 for M batch and 1, 2 for PB batch) nested within diet i and e_{ijk} is the random residual. At this stage, fish were not yet identified and sex, dam and sire were not known. Containment method was used to define the degrees of freedom as denominator.

For measurements collected after tagging, the significance of diet, sex, tank, sire and dam effects as well as sire-diet and dam-diet interactions were tested with the following model in the

MIXED procedure of SAS (SAS Institute Inc., Cary, NC) using the REPEATED command (SAS Institute Inc., 2008) to account for variance heterogeneity between diets:

$$Y_{ijklmn} = \mu + Diet_i + \text{tank}(diet)_{j(i)} + Sex_k + sire_l + dam_m + sire*Diet_{il} + dam*Diet_{im} + e_{ijklmn} \quad (2)$$

Where Y_{ijklmn} is the performance of individual n, Sex_k is the fixed effect of sex k (1 = male, 2 = female), $sire_l$ is the random effect of sire l, dam_m is the random effect of dam m, sire*$diet_{il}$ the random interaction between sire l and diet i, dam*$diet_{in}$ the random interaction between dam n and diet i and e_{ijklmn} is the random residual. Containment method was used to define the degrees of freedom as denominator. Preliminary analyses indicated that the sire-dam interaction was never significant for any trait and it was therefore not included in the models. Preliminary analyses also showed that *K* was influenced by *BW* which could lead to biased estimates when comparing fish fed different diets. Body weight was tested as a covariate, but as there was a significant interaction between *BW* as covariate and diet (heterogeneous slopes), log (*BW*) for which slopes were homogeneous was preferred and added as a covariate in model, so that the comparison of K between diets was corrected for the phenotypic effect of BW.

Coefficient of variation (standard deviation/mean in %, *CV*), skewness (*Skew*) and kurtosis (*Kurt*) were calculated for each tank within each diet using SAS MIXED procedure (SAS Institute Inc., 2008). Skewness and kurtosis were considered significantly different from 0 when their absolute value was higher than twice the standard errors [$\sqrt{(6/N)}$ for skewness and $\sqrt{(24/N)}$ for kurtosis].

The effect of diet on *BW* variance was studied by comparing models with homogeneous (MIXED procedure of SAS Institute Inc., Cary, NC) or heterogeneous (REPEATED command in MIXED procedure) variances in each diet. Chi-square tests (1 df, $P < 0.05$) were computed between Akaike's Information Criterion (AIC) of both models to determine when heterogeneous variances were useful to describe the model. When it was the case, *CV* of *BW* were considered to be different in each diet. To analyze the diet effect on the survival, numbers of live and dead individuals were computed in a generalized linear mixed model setting conditional distribution of the data as binomial. Lmer procedure with family set to binomial (Vazquez et al., 2010) was used in the R software (Ihaka and Gentleman, 1996) and its lme4 library (Bates and Sarkar, 2006).

ASREML (Gilmour et al., 2008) was used to estimate heritabilities (using univariate models) of the traits in both diets, as well as genetic correlations (using bivariate models) between and within diets according to the following model:

$$Y_{ijklmno} = Diet_{ij} + Sex_{ik} + Tank(diet)_{il(ij)} + an_{im} + dam_{in} + e_{ijklmno} \quad (3)$$

Where i is the trait, Y_{ijklmo} is the i performance of individual m (i = 1 for univariate models and i = 1,2 for bivariate models), $Diet_{ij}$ is the fixed effect of diet j on trait I, Sex_{ik} is the fixed effect of sex k (1 = male, 2 = female) on trait i, $Tank_{il(ij)}$ is the fixed effect of tank l (l = 1, 2, ... , 5) nested within diet k on trait i, an_{im} is the random additive genetic effect of trait i on animal m, dam_{in} is

the random effect of dam n on trait i (accounting for non-genetic maternal effect) and $e_{ijklmno}$ is the random residual error for trait i.

To analyze family rankings evolution over time within each diet, genetic correlations between different measurements were estimated (one per measurement pair). The closer to 1 the correlation, the more consistent the family rankings. To analyze the genotype by diet interaction, genetic correlations between a trait in the M batch and the same trait in PB batch were estimated. In this case, Diet effect was removed and environmental covariance was set to 0. The closer to 1 the correlation, the smaller the genotype-by-diet interaction. To know how genotype by diet interaction evolved with time, these correlations were also computed between non simultaneous dates (for instance between *BW* in M fish at 265 days and *BW* in PB fish at 361 days).

Heritabilities and genetic correlations of *BW* and *TGC* were used to predict the potential relative gain (% of *BW*, *TGC*) for one generation of individual selection (Falconer, 1952). Direct response expected for *BW* on diet X was given by:

$$R_X = i_X h_X^2 \sigma_X$$

Where R_X is the direct response when fish were fed a diet X for an i_x intensity of selection, h^2_X is the heritability of *BW* in diet X and σ_X is the phenotypic standard deviation of *BW* fed diet X. The correlated response expected for *BW* on diet Y when selection pressure was applied on individuals fed a diet X was given by:

$$RC_Y = i_X h_X h_Y r_A \sigma_Y$$

Where RC_Y is the correlated response on body weight (g) for fish fed a diet Y, for a selection intensity i_x applied on candidates fed a diet X, h_X is the square root of the heritability of *BW* with diet X, h_Y is the square root of heritability of *BW* with diet Y, r_A is the genetic correlation of *BW* between the diets X and Y, and σ_Y is the phenotypic standard deviation of *BW* with diet Y.

Under farming conditions, fish are usually reared until an expected weight, thus correlated response was estimated for similar weights instead of similar ages. To be consistent with this choice, corresponding heritabilities and genetic correlations estimates were used. For example, assuming that mean *BW* of fish fed M diet at date 3 is similar to *BW* of fish fed PB diet at date 6, the correlated response of *BW* on plant-based diet after a selection on marine diet was given by:

$$RC_{PB_6} = ih_{M_3} h_{PB_6} r_{3-6} \sigma_{PB_6}$$

Where RC_{PB6} is the correlated response of *BW* in fish fed a PB diet (based on their weight at date 6) for a selection intensity i applied when fed a M diet at date 3, h_{M3} is the square root of heritability of *BW* with M diet (date 3), h_{PB6} is the square root of heritability of *BW* with PB diet at date 6, $r_{3\text{-}6}$ is the genetic correlation of *BW* between the M diet at date 3 and PB diet at date 6, σ_{PB6} is the phenotypic standard deviation of *BW* on PB diet at date 6.

3 Results

Diet effect

Survival was lower (Table 1, $P < 0.01$) in fish fed the PB diet (83.9%) than in fish fed the M diet (99.3%) at 224 days and this difference was stronger at the end of the trial (418 days), when survival were 64.7% with the PB diet and 93.7% with the M diet (Table 3).

Before the first feeding with experimental diets, *BW* ls-means were similar ($P = 0.66$) in both the M and the PB samples (Table 2). As early as the second measurement (116 days), fish fed the M diet were significantly heavier ($P < 0.001$) and longer ($P < 0.01$) than fish fed the PB diet and these differences remained significant all along the trial ($P < 0.01$). When considering *TGC* (Table 2), the PB fish grew less than the M fish in the first 2 periods ($P < 0.05$) but the difference disappeared after 151 days (except between 266 days and 298 days). The diet effect was important on shape (Table 4) and fish fed the M diet were thinner than fish fed the PB diet after 266 days. *CV* of *BW* (Table 4) were almost always significantly higher in the PB diet (43.3% to 34.7%) than in the M diet (34.5% to 30.5%) as the model to analyze *BW* with heterogeneous variances had a lower AIC ($P < 0.05$, Chi-square tests, $df = 1$) than the model with homogeneous variances. Higher kurtosis of *BW* distribution in fish fed the PB diet indicated that population shape had a sharper peak than in fish fed M diet. Higher skewness (Table 4) showed that smaller fish were proportionally more present in the PB batch.

Genetic parameters

Heritability estimates were moderate (between 0.18 and 0.46) for *BW*, stable over time in M fish, and tending to decrease in PB fish (Figure 1). They were higher in M fish at each measurement but the difference between diets was never significant (less than 2 standard errors). The genetic correlation for *BW* calculated between simultaneous measurements (Figure 1) in both diets was a

little less than 1 for the first measurement and slightly decreased during the trial to finally stabilize around 0.8.

Figure 2.A shows genetic correlations for *BW* between diets with a time dimension. For synchronous measurements (on the diagonal), the estimates are the same as those presented in Figure 1. For asynchronous measurements, genetic correlations decreased with time interval. On both sides of the diagonal, correlations were slightly unbalanced and evolution can be considered as similar in both diets. Lower diagonal (Figure 2.A, dotted line) indicates measurement when *BW* in each diet were similar (Table 2), genetic correlation were then between 0.8 and 0.9 in this case. Within-diet genetic correlations were high (Figure 2.B and 2.C) showing a strong consistence for family structures within diets.

Heritabilities and genetic correlations for *TGC* are shown in Table 3. When focusing on the longest period (152 days between 266 and 418 days), heritability estimates were low in both diets and significantly lower in fish fed the PB diet than in fish fed the M diet (more than 2 standard errors). For shorter periods (60 days between 266 and 326 days and 92 days between 326 and 418 days), heritability estimates were similar in both diets. Genetic correlations between diets were moderate, ranging from 0.43 for the shortest period to 0.64 for the longest one (Table 3).

Expected genetic gains

Heritability and genetic correlation estimates of *BW* were used to predict the expected genetic gain by individual selection on BW, with a proportion of selected animals of 5 % (Figure 3). In a

first scenario, selection response was estimated for fish fed the PB diet and selected when they reach approximately 37g. If progenies were fed PB diet, a 18.3% gain in *BW* per generation could be expected. If these progenies were fed M diet, the expected gain would be reduced to 14.9%. However, there would not be any difference between these strategies if fish were selected around 46g (+ 13.4% vs +13.1%) or 52g (+ 11.8% vs +11.2%).

In a second scenario, if fish were fed the M diet and selected when they approximately reach 35 g, a 26.3% gain in *BW* per generation could be expected if progenies were fed the same M diet. If these progenies were fed the PB diet, the expected gain would be reduced to 21.5%. Similar differences between these 2 strategies were observed if fish were selected around 46 g (+ 23.7% *vs.* +16.7%) or 54 g (+22.9% *vs.* 17.8%). Comparing the 2 scenarios, selected fish fed the PB diet would always give lower gains in BW than selecting fish fed the M diet (Figure 3), whatever the diet given to progenies.

Similar strategies were then tested for a selection on *TGC* calculated on the largest period (152 days between 266 and 418 days of age) (Figure 4). If fish were fed the M diet and selected at 418 days for their *TGC*, the expected gain of their progenies could be +9% if they were fed the same diet. However, if the progenies were fed the PB diet, the expected gain would be only +3%. In a second scenario, selection response was estimated for fish selected when they were fed the PB diet. The expected growth gain for their progenies would be very similar whatever the diet they would be fed (+3 to 4%).

4 Discussion

Diet effect on health

Total replacement of FM and FO by plant-based products led to an important diet effect on survival with a high final difference between diets (PB: 64.7%, M: 93.7%). Effects of fish oil replacement with plant-based oil on fish health have been reviewed by Montero and Izquidero (2010) and included stress response, immune status, disease resistance and physiological mechanisms. However, the same review concluded that evaluation of these effects is a complex subject as that it is "very much dependant on the type of both FO and vegetal oil, level of FO substitution, duration of feeding, fish species, fish size and stage in the life cycle, presence and availability of other nutrients and environmental conditions, mainly temperature". In European sea bass, only few studies focused on the health effect of substitution. Parpoura and Alexis (2001) observed a higher sensibility to pathological symptoms when sea bass are fed with plant-based oil. Piedecausa et al. (2007) concluded to lower survival due to sudden post-sampling mortality in sharpsnout sea bream (*Diplodus puntazzo*) fed a diet containing linseed oil. Immune system disturbance associated with plant-based products are partly due to n-3 highly unsaturated fatty acids deficiencies (Montero and Izquidero, 2010), but more work is needed on marine fish to understand the link with pathogen sensitivity.

Diet effect on growth

In previous studies, partial replacement of FO with plant-based oils (characterized by the Fish Oil replacement ratio FOr = plant-based oils/total oils) produced uneven consequences on

growth. Some studies showed similar growth in European sea bass for FOr: 100% (Parpoura and Alexis, 2001), FOr: 60% (Izquidero et al., 2003), FOr: 60% (Mourente et al., 2005), FOr: 83% (Martins et al., 2006) whereas some other studies found lower growth for FOr: 60% to 80% (Montero et al., 2005), FOr: 80% (sea bream, *Sparus aurata* L., Izquidero et al., 2005,). A review by Turchini et al. (2009) concluded that FO can be totally replaced by plant-based oils when essential fatty acids (EFA) requirements are met. Regarding fish meal replacement rate (FMr = plant-based meal/total meal), some studies evidenced lower growth in marine fish for FMr: 43% (Dias et al., 2005), FMr: 100% (sea bream, Gomez-Requeni et al., 2004), FMr: 100% (Montero et al., 2005) when other studies proved that replacement with plant-based meals could be done without any impact on growth for FMr: 40% (sea bream, Robaina et al., 1995,), FMr: 95% (Kaushik et al. 2004), FMr: 69% (Adamidou et al., 2009), FMr: 65% (Olivia-Teles et al., 2001) and FMr: 70% (Ballestrazzi et al., 1994). Our choice of extremely contrasted diets aimed at facilitating the observation of contrasted genetic abilities to cope with marine or plant-based diets, and replacement rates were respectively FOr: 100% and FMr: 100%. It led to significant impact on *BW* and *SL* since the first days following the dietary transition.

TGC were lower in the PB diet only for the first 151 days after starting experimental diets. After this date, no more difference was visible confirming that the first stages of such a dietary transition induced a delay in growth which remains visible in the final body weight difference, as seen in older sea bass by Le Boucher et al. (2011). The initial lower growth after the dietary transition could be due to a lower feed intake or lower feed efficiency and it would be interesting to know more about these traits when fish are faced to a new diet. Deficiencies for some essential fatty acids (Navarro et al., 1997), especially for totally plant-based diet (Geay et al., 2010) have also been evidenced as a source of potential lower growth. Effects of PB diet in

this study could be a combination of confounding factors and more studies are needed to precise respective importance of feeding behavior, diet palatability, digestibility, nutritional value (Glencrosss et al., 2007) or genetic abilities to cope with these effects especially in the early stage.

Population size distribution was also impacted, as fish fed the plant-based diet showed a more heterogeneous repartition of *BW*. Coefficient of variation has been suggested as an indicator of welfare (Jobling, 1995. North et al., 2006) and high heterogeneity is known to facilitate cannibalism (Baras, 1999; Fessehaye et al., 2004). In our case, higher CV and skewness confirmed that the cohort of fish fed the PB diet faced challenging environmental conditions. When temperature, salinity, zootechnical conditions are the usual suspects for environment variability, composition of the feed should clearly be considered as one of the main parameter of this environment.

In the present trial, it is difficult to distinguish the diet effect from the diet-switch effect at the beginning of the trial. Both batches received a commercial diet containing marine products and plant products prior to the beginning of the trial and the diet-switch shock may explain an important part of the observed diet effect. More information is needed to understand the effect of plant-based diets on European sea bass juveniles.

Genetic parameters for body weight

Genetic variability estimates for the ability to grow on plant-based diet are needed to know whether genetic improvement on growth can be made using specifically plant-based diets. Most of the previous results have been obtained on salmonids. Palti et al. (2006) concluded that

genetic variability for growth and body weight exists in rainbow trout (*Oncorhynchus mykiss* W.) in case of partial substitution (FOr: 11.4%, FMr: 87%). Pierce et al. (2008) and Quinton et al. (2007a) found moderate heritabilities both for growth (0.31±0.07) in rainbow trout (FOr: 37.2%, FMr: 93.7%) and for individual daily gain (0.32±0.14) in European whitefish (*Coregonus larvaretus* L., FOr: 0%, FMr: 73.3%). In the present study, heritabilities of *BW* when fish were fed M diet were very similar (Saillant et al., 2006; Dupont-Nivet et al., 2010) or slightly lower (Dupont-Nivet et al., 2008) to those previously found in European sea bass. The differences between M and PB were never significant but lower heritabilities for fish fed the PB diet was a tendency that has also been suggested in a previous work (Le Boucher et al., 2011). It nevertheless proved that genetic gains for growth are still possible in fish fed the PB diet (h^2 between 0.18 and 0.36).

Genotype by diet interactions could impact the efficiency of breeding programs initially conducted on mainly marine diets but previous results are variable. Comparing diets with different proportions of plant-based products, Blanc (2002) and Palti et al. (2006) found non significant interactions for *BW* in rainbow trout (respectively FOr: 0%, FMr: 47.6% and FOr: 11.4%, FMr: 87%). In 2007, 2 studies with European whitefish recorded non significant re-ranking of family performances for whole body lipid, protein percentages (Quinton et al., 2007 a) and growth, feed intake, feed efficiency (Quinton et al., 2007b, FOr: 0%, FMr: 73.3%) and evidenced high genetic correlations between diets for these traits (0.89-1.00). At the opposite, significant re-ranking of the families for growth (Pierce et al, 2008, Dupont-Nivet et al, 2009, FOr: 0%, FMr: 100%) as well as feed intake and feed efficiency (Dupont-Nivet et al., 2009) were found in rainbow trout and in this case genetic correlation was moderate between diets

(0.73 ± 0.13, Pierce et al., 2008). In European sea bass, total substitution rate was recently tested with older fish, starting at 192 g mean weight (FOr: 100%, FMr: 100%) and low genotype by diet interactions were evidenced for lipid content of the filet and late body weight (Le Boucher et al., 2011) as the genetic correlations between diets were never significantly different from 1.

When fish were compared at the same weight, which could be the classical selection conditions, the genetic correlation between diets observed in the present study was around 0.7-0.8. Standard errors are still too high to observe significant evolution over time but highest genetic correlation was found at the first individual measurement (266 days). It would tend to indicate that family rankings were not modified in the early stages following dietary transition, but this would have to be ascertained using individual tagging of smaller fish.

In the absence of studies about optimal design for genotype by environment interactions, we chose to use a relatively low number of sires in order to increase the mean half-sib family size and avoid the risk of having very unbalanced offspring numbers for the same family in both diets (due to a-posteriori assignment and potential differential mortalities), which we anticipated would lower the quality of GxE estimates. In the course of the present study, the publication by Sae-Lim et al (2010) of an optimal design simulation study for GxE estimation, proposed that 200 families with 10 individuals per family would be appropriate for a trait of moderate heritability. This is not far from our figures in terms of full-sib families. However the structure they use was a nested design, which implies the use of more sires and dams for the same number of families, and hence reasonably suggests that the number of parents that we used was below the optimum, and may lower the precision of our estimates.

In the present study, high genetic correlations (0.8 to 0.9) were observed between diets for synchronous measurements of *BW*. It confirmed that total substitution of fish meal and fish

oil would not deeply impact family rankings for *BW*. As a comparison, genotype-by-environment interactions for *BW* have been studied in contrasted rearing conditions and production systems in European sea bass (Dupont-Nivet et al. 2008). They concluded that genetic correlation for *BW* was (mean ± SE) 0.84 ± 0.08 comparing a semi-closed recirculation system (30 kg/m^3, 20 to 22°C) and a semi-intensive estuarine system (2 kg/m^3, 9 to 25°C). In the same work, genetic correlation for *BW* was 0.70 ± 0.10 comparing a semi-intensive estuarine system (2 kg/m^3, 9 to 25°C) and a floating cage in tropical waters system (4 kg/m^3, 22 to 27°C). This confirms that dietary environments could impact *BW* performance in the same range as culture conditions.

Genetic parameters for growth rate

Individual tagging was only possible at 224 days for fish fed M diet and 266 days for fish fed PB diet (respectively 135 and 177 days after dietary transition), when BW was already strongly influenced by the diet. The first *BW* measurement was also influenced by the commercial diet given until 87 days, which was not linked with the experimental diets. Then, consequences of the dietary challenge are indirectly estimated by *BW* and *TGC* gave a more realistic performance estimate than final *BW* as it is not dependant on the initial *BW*. Dupont-Nivet et al. (2010) evidenced higher genotype-by-environment interactions for daily growth rate than for *BW* comparing rearing conditions and production systems. In our experiment, the genetic correlation between *TGC* (266 dpf to 418 dpf) in each diet was lower (0.64) than those found for *BW* at any date (0.74 to 0.93). It confirmed that the genotype by diet interaction was more important on this trait, thus that families showed different abilities to grow depending on the diet.

Expected genetic gains

High gains for *BW* would be possible in European sea bass (18.3% for a 5% selection pressure) if selected breeders and their progenies were fed with PB diet. If progenies issued from this strategy were fed the M diet, the gain in BW would similar. It means that selecting fish for their ability to grow on PB diet would lead to high genetic gains whatever the diet (M or PB) given to the progenies (Figure 3). The reason is that the higher genetic variation we evidenced with the M diet would compensate for the lower accuracy of selection with the PB diet and the lower than unity genetic correlation between diets.

Higher gains for *BW* would be possible (26.3% for a 5% selection pressure) if selected breeders and their progenies were fed with M diet, due to a higher accuracy of selection. If progenies issued from this strategy were fed a PB diet, the gain in *BW* would be lower (21.5%). In order to anticipate a transition from M to PB diet and maximize the genetic gains on BW, it would be more interesting to go on with a selection using M diet. Expected genetic gains from selection for *TGC* would lead to similar genetic gains (3 %) in progenies fed PB diet whatever the diet used during selection (Figure 4). The cumulative effect of a medium genetic correlation (0.64) and a low genetic variance for *TGC* ($h^2 = 0.11$) in fish fed PB diet rendered the strategy to select on M diet less efficient for *TGC* than for *BW*.

Expected indirect gains were estimated comparing fish fed M or PB diet with similar *BW* rather than at the same age. The objective was to remain closed to the commercial conditions where fish are harvested at a (market-driven) fixed mean *BW*.

We also made the choice to compare non commercial but extremely contrasted diets, so conclusions can only be used as boundaries to address the current challenges of breeding

programs. For instance, the strong effect of a totally plant-based diet on phenotypic traits may have hindered the expression of essential adaptation mechanisms and created metabolism bottlenecks. The low heritability estimates on the PB diet may partly reflect a lower health status of fish fed the PB diet and should be considered as a consequence of our extreme choice in diet composition.

In a similar way, the impact of totally plant-based diet on global survival may also have biased genetic parameters estimates and more studies are needed to orient breeding strategies in their adaptation to dietary transition in European sea bass.

Fish farming faces rapid diversification of rearing environments and proofs of genotype sensitivity to environment exist as fish are extremely sensitive to temperature, salinity, stocking density (Jackson et al., 1998; Streelman and Kocher, 2002; Dupont-Nivet et al., 2010). However, dietary environment whether it concerns feed composition, access to rations or feeding rhythms has only recently been considered as a potential source of interaction with genotypes. This is the reason why it seemed very important to have a better knowledge of the effect of these parameters on breeding values to improve on-site efficiency of breeding programs. Our estimation of predicted gains tends to prove that a totally plant-based compared with a marine diet would have a negative impact on breeding program efficiency. We showed that selecting European sea bass on their ability to grow on the experimental PB diet would not be more efficient than pursuing a breeding program using the experimental marine diet, even if commercial fish are grown on a PB diet. This is consistent with the beneficial selection in alternative environment described by Falconer (1952). As summarized in Kause et al. (2006), it could be beneficial to select in an environment which is not the production one when the heritability of the trait in this environment and genetic correlation between environments are high. Extreme choice in diet ingredients

allowed estimating genotype by diet interactions in a worst case scenario but more studies are needed to understand how intermediate substitution rates and products quality would impact selective breeding of sea bass.

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Table 1. Formulae and analytical composition of the experimental diets (M: fish meal and fish oil diet, PB: all fish meal and fish oil replaced by plant products)

Diets	**M**	**PB**
Ingredients ($g.kg^{-1}$)		
Fishmeal	380	0
Corn gluten meal	180	200
Soybean meal	0	182
Wheat gluten	72	20
Extruded wheat	253	72
White lupin	0	140
Fish oil	85	0
Linseed oil	0	94
Soy lecithin	0	10
L-Lysine	0	27
$CaHPO_4$, $2H_20$	0	30
Binder (Sodium alginate)	10	10
Attractant Mix[1]	0	15
Min. Premix[2]	10	10
Vit. Premix[2]	10	10
Chemicals composition		
DM, %	92.3	93.7
Crude protein, % DM	50.6	49.6
Crude fat, % DM	15.3	14.3
Nitrogen free extract (NFE)[3], %DM	23.0.1	19.3
Energy, kj/g DM	23.0	23.3

[1]Attractant mix contained (g/kg feed) taurine (3), betaine (3), glycine (2), alanine (2) and glucosamine (5)
[2]As in Guillaume et al. (2001).
[3]NFE = Dry matter-Crude protein-crude fat-Ash

Table 2. Least square means (Mean), standard errors (SE) for traits on 2 diets, and statistical tests for diet effect

			M		PB		Statistical test for diet effect		
Days	**Trait[1]**	**Unit**	**Mean**	**SE**	**Mean**	**SE**	**Df**	**F**	**P-value**
83	BW[2]	g	2.5	± 0.1	2.6	± 0.1	4	-0.5	0.6555
116	BW[2]	g	6.9	± 0.2	4.8	± 0.2	4	9.3	0.0007
151	BW[2]	g	11.4	± 0.4	6.6	± 0.4	4	7.9	0.0014
224	BW[2]	g	23.5	± 0.5	13.5	± 0.6	4	11.7	0.0003
266	BW[3]	g	36.1	± 1.8	20.5	± 1.9	3	8.0	0.0041
298	BW[3]	g	47.6	± 2.3	24.8	± 2.5	3	8.7	0.0032
326	BW[3]	g	55.9	± 2.2	29.5	± 2.3	3	12.0	0.0012
361	BW[3]	g	72.1	± 2.8	38.3	± 2.8	3	12.1	0.0012
389	BW[3]	g	85.3	± 2.8	48.4	± 2.7	3	14.7	0.0007
418	BW[3]	g	108.3	± 3.7	64.6	± 3.9	3	11.7	0.0013
83	SL[2]	mm	59.3	± 1.0	60.0	± 1.0	4	-0.5	0.6535
116	SL[2]	mm	78.9	± 0.8	71.7	± 0.7	4	6.8	0.0025
151	SL[2]	mm	97.5	± 1.4	83.0	± 1.4	4	7.3	0.0019
224	SL[2]	mm	126.5	± 1.5	105.0	± 1.6	4	9.7	0.0006
266	SL[3]	mm	148.7	± 2.6	120.2	± 2.8	3	11.6	0.0014
298	SL[3]	mm	n.e.	n.e.	n.e.	n.e.			
326	SL[3]	mm	173.4	± 2.7	134.8	± 2.8	3	16.2	0.0005
361	SL[3]	mm	191.4	± 2.5	148.8	± 2.6	3	20.0	0.0003
389	SL[3]	mm	197.5	± 2.5	154.4	± 2.6	3	18.3	0.0004
418	SL[3]	mm	207.8	± 2.6	167.3	± 2.7	3	15.6	0.0006
83	K[2]		1.17	± 0.02	1.15	± 0.02	4	0.6	0.5812
116	K[2]		1.37	± 0.02	1.26	± 0.02	4	3.8	0.0192
151	K[2]		1.18	± 0.01	1.10	± 0.01	4	4.4	0.0112
224	K[2]		1.12	± 0.01	1.10	± 0.01	4	0.8	0.4587
266	K[3]		1.0	± 0.01	1.12	± 0.01	3	-4.2	0.0244
298	K[3]		n.e.	n.e.	n.e.	n.e.			n.e.
326	K[3]		1.02	± 0.01	1.15	± 0.01	3	-16.7	0.0005
361	K[3]		0.97	± 0.01	1.12	± 0.01	3	-9.2	0.0027
389	K[3]		1.05	± 0.02	1.28	± 0.02	3	-10.8	0.0017
418	K[3]		1.15	± 0.01	1.35	± 0.01	3	-15.1	0.0006
83	TGC[2]								
116	TGC[2]		1.78	± 0.06	1.04	± 0.04	4	10.2	0.0005
151	TGC[2]		0.89	± 0.08	0.48	± 0.11	4	2.9	0.0424
224	TGC[2]		0.98	± 0.16	0.98	± 0.09	4	0.0	0.9919
266	TGC[3]		0.77	± 0.06	0.52	± 0.11	4	2.0	0.1121
298	TGC[3]		0.89	± 0.05	0.52	± 0.06	3	1.0	0.0202
326	TGC[3]		0.63	± 0.06	0.52	± 0.06	3	0.9	0.4187
361	TGC[3]		0.79	± 0.07	0.67	± 0.09	3	1.1	0.3502
389	TGC[3]		0.69	± 0.07	0.80	± 0.06	3	1.0	0.2582
418	TGC[3]		1.24	± 0.09	1.28	± 0.01	3	-0.3	0.7899

[1] BW = body weight, SL = standard length, K = condition factor, TGC = thermal growth rate calculated for the previous shortest period.

[2] Analyses were done with model (1), degrees of freedom (Df) are denominator.

[3] Analyses were done with model (2), degrees of freedom (Df) are denominator.

n.e. : non estimated

Table 3. Means, standard deviation (SE) for survival on 2 diets, and statistical tests for diet effect

			M		PB		Statistical test for diet effect		
Days	**Trait**	**Unit**	**Mean**	**SD**	**Mean**	**SD**	**Df[1]**	**F**	**P-value**
83	S	%	100.0	0.0	100.0	0.0	4		
116	S	%	99.9	0.1	97.9	0.7	4	4.9	0.0001
151	S	%	99.8	0.2	96.5	0.7	4	4.4	0.0001
224	S	%	99.3	0.5	83.9	7.5	4	2.8	0.0005
266	S	%	98.8	0.6	79.3	9.0	4	2.6	0.0009
298	S	%	98.1	1.4	72.9	9.6	4	2.3	0.0195
326	S	%	98.1	1.4	71.0	9.7	4	2.2	0.0260
361	S	%	93.8	1.5	68.0	9.5	4	2.5	0.0135
389	S	%	93.7	1.4	65.5	10.0	4	2.3	0.0229
418	S	%	93.7	1.4	64.7	9.9	4	2.2	0.0270

[1] Degrees of freedom (Df) are denominator.

Table 4. Coefficients of phenotypic variation (CV), kurtosis (Kurt), skewness (skew) of body weight, and statistical tests for diet effect

	M			PB			Statistical test for diet effect		
Days	CV	Kurt	Skew	CV	Kurt	Skew	CV[1]	Kurt[2]	Skew[2]
83	30.5	0.0	0.7	34.7	0.8	0.7	*	*	n.s.
116	30.9	0.4	0.7	29.0	1.6	0.8	*	*	n.s.
151	32.0	-0.3	0.3	38.9	2.2	1.1	*	*	*
224	34.5	0.4	0.7	41.4	0.9	1.0	*	*	n.s.
266	32.7	0.6	0.7	40.9	1.8	1.2	*	*	*
298	31.9	0.5	0.7	43.3	2.4	1.3	*	*	*
326	31.3	0.5	0.7	42.9	2.9	1.3	*	*	*
361	31.7	0.4	0.6	42.9	3.7	1.4	*	*	*
389	31.1	0.2	0.6	40.3	2.8	1.2	*	*	*
418	31.1	0.1	0.5	38.3	2.2	1.1	*	*	*

[1] Traits were considered significantly different (*) when AIC of a model with heterogeneous variances in each diet was lower ($P < 0.05$, Chi-square tests, df = 1) than AIC of a model with homogeneous variances in each diet for *BW* analyzes.

[2] Traits were considered significantly different (*) when they differed by more than 2 standard errors.

Table 5. Heritabilities (h^2), common environment ratios (c^2), their SE, and variance components of genetic(σ_G), maternal (σ_m) and residual (σ_r) variance for TGC on 2 diets, genetic correlations for these traits between diets

	PB[4]							M[4]							Gen.Corr.	
	h^2	SE	c^2	SE	σ_G	σ_m	σ_r	h^2	SE	c^2	SE	σ_G	σ_m	σ_r	ρ	SE
TGC[1]	0.11	± 0.06	0.0	±0.0	0.5	0.0	2.4	0.33	±0.10	0.0	±0.0	0.7	0.0	1.9	0.64	±0.28
TGC[2]	0.20	± 0.08	0.0	±0.0	0.5	0.0	1.8	0.35	±0.13	0.0	±0.1	1.0	0.0	1.8	0.43	±0.27
TGC[3]	0.19	± 0.07	0.0	±0.0	0.2	0.0	1.4	0.31	±0.09	0.0	±0.0	0.6	0.0	1.3	0.56	±0.35

[1]TGC = thermal growth coefficients calculated for the longest period (152 days between 266 (date 5) and 418 days (date 10))

[2]TGC = thermal growth coefficients calculated for intermediary period (60 days between 266 (date 5) and 326 days (date 7)

[3]TGC = thermal growth coefficients calculated for intermediary period (92 days between 326 (date 7) and 418 days (date 10)).

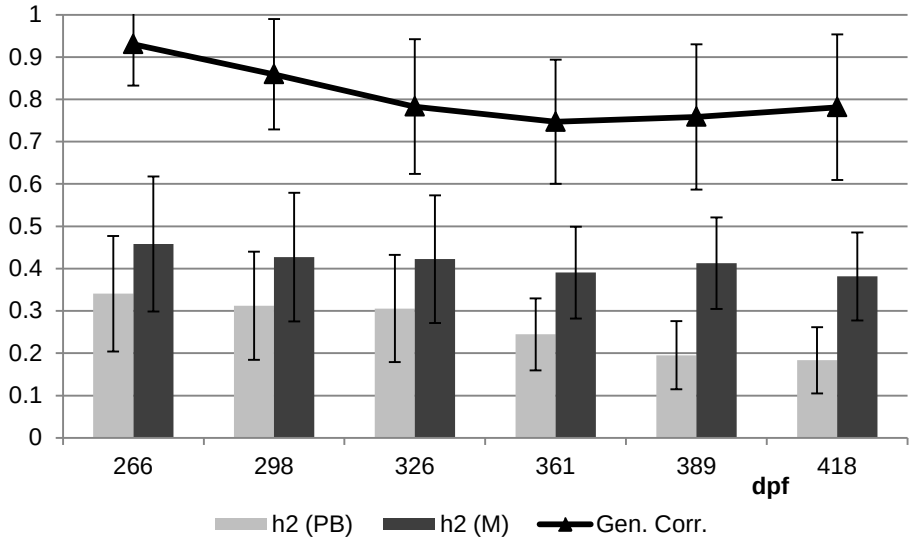

Figure 1. Heritabilities of Body Weight for both PB and M diet and genetic correlations for this trait between diets. Estimates are calculated for each measurement in days post fertilization (days) and vertical bars indicate standard errors.

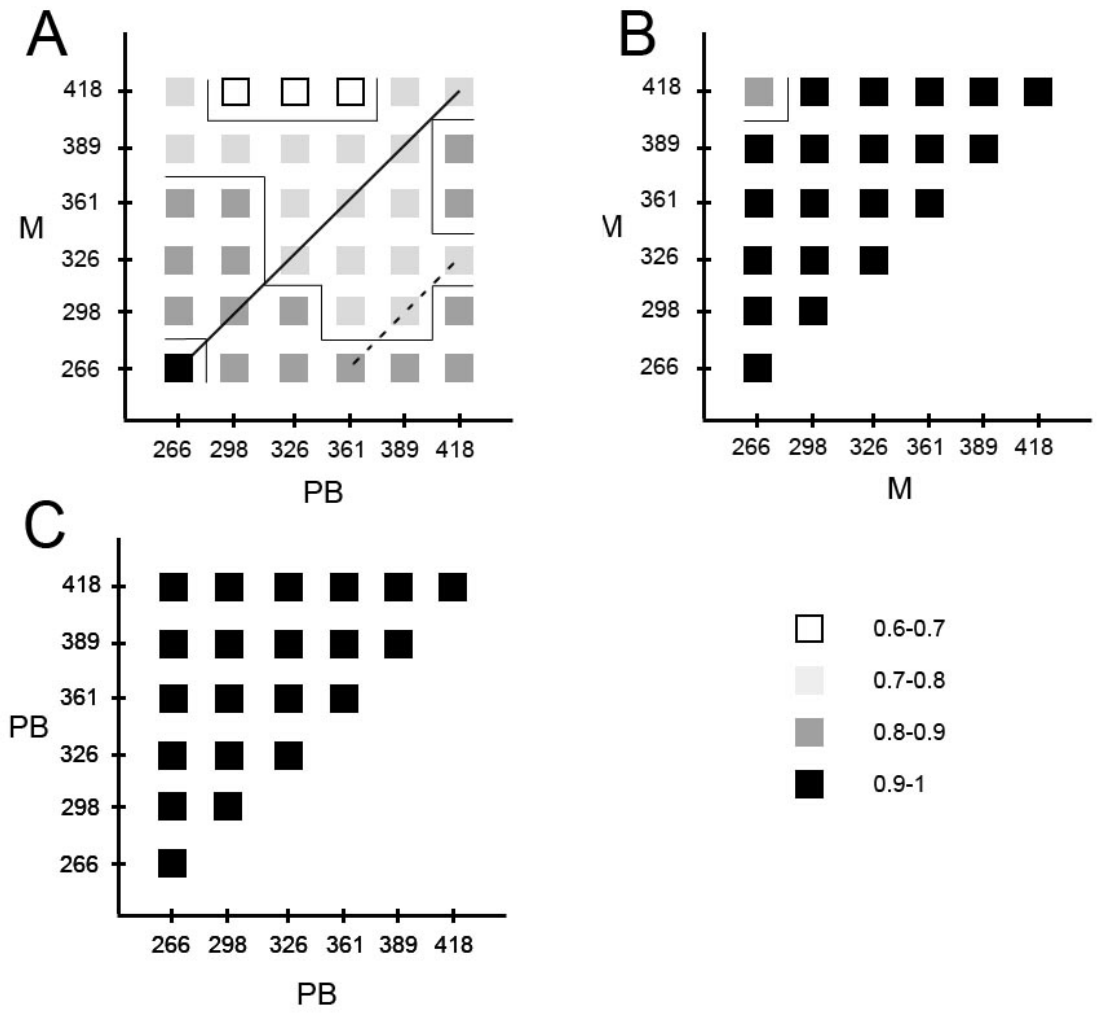

Figure 2. Genetic correlations for *BW* between fish fed M diet or PB diet (A), estimates are calculated for each pair of dates. Genetic correlations for *BW* within the PB batch (B) and within the M batch (C) were also estimated for each date pair of dates.

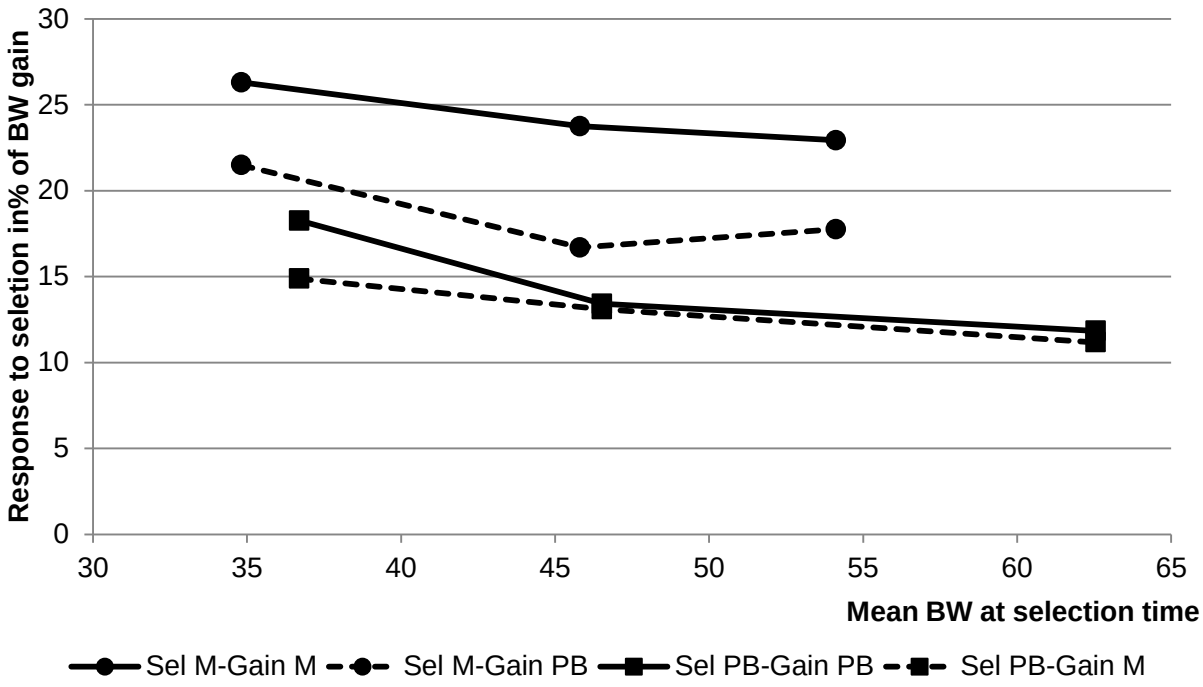

Figure 3. Direct and indirect gains (% of *BW*) in 4 selection strategies for 5% proportion of selected individuals: Offsprings of fish selected on the M diet are fed with the M diet (Sel M–Gain M). Offsprings of fish selected on the M diet are fed with the PB diet (Sel M–Gain PB). Offsprings of fish selected on the PB diet are fed with the PB diet (Sel PB–Gain PB). Offsprings of fish selected on the PB diet are fed with the M diet (Sel PB–Gain M). Abscissa axis indicates the mean population body weight at selection time.

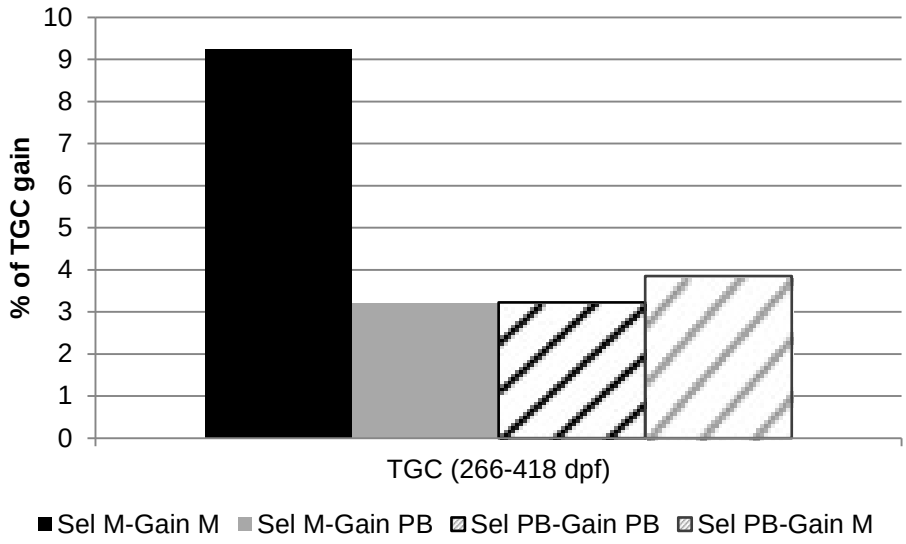

Figure 4. Direct and indirect gains (% of Thermal Growth Rate (*TGC*)) in 4 selection strategies for 5% proportion of selected individuals: Offsprings of fish selected on the M diet are fed with the M diet (Sel M–Gain M). Offsprings of fish selected on the M diet are fed with the PB diet (Sel M–Gain PB). Offsprings of fish selected on the PB diet are fed with the PB diet (Sel PB–Gain PB). Offsprings of fish selected on the PB diet are fed with the M diet (Sel PB–Gain M). Selection trait was *TGC* calculated on the largest period (152 days between 266 and 418 days).

Errata

doi:10.2527/jas2012-5311

The article "Genotype by diet interactions in European sea bass (*Dicentrarchus labrax* L.): Nutritional challenge with totally plant-based diets" (J. Anim. Sci. 2012.91:44−56) contains 2 equations ([1] and [2]) that printed incorrectly in the original version of the article. The corrected equations can be found below.

$$Y_{ijk} = \mu + Diet_i + tank(diet)_{j(i)} + e_{ijk}, \quad [1]$$

and

$$Y_{ijklmn} = \mu + Diet_i + tank(diet)_{j(i)} + Sex_k + sire_l + dam_m + sire \times Diet_{il} + dam \times Diet_{im} + e_{ijklmn}, \quad [2]$$

The following articles were published with the incorrect DOI. The correct DOI numbers are listed below for each article. The DOI numbers have been corrected in the online version of the articles.

"Companion Animal Symposium: Living beyond 20: Discoveries in geriatric companion animal biology" (J. Anim. Sci. 90:1650−1652). Correct DOI is as follows: doi.102527/jas.2012-5132.

"Response of the modern lactating sow and progeny to source and level of supplemental dietary fat during high ambient temperatures" (J. Anim. Sci. 90:2609−2619). Correct DOI is as follows: doi:10.2527/jas.2011-4242.

"Impact of weaning and an antioxidant blend on intestinal barrier function and antioxidant status in pigs" (J. Anim. Sci. 90:2581−2589). Correct DOI is as follows: doi:10.2527/jas.2011-4444

"Mineral concentrations of plasma and liver following injection with a trace mineral complex differ among Angus and Simmental cattle" (J. Anim. Sci. 90:2692−2698). Correct DOI is as follows: doi:10.2527/jas.2011-4482

"Boar sperm quality in lines of pigs selected for either ovulation rate or uterine capacity" (J. Anim. Sci. 90:2515−2523). Correct DOI is as follows: doi:10.2527/jas.2011-4723

"Bayesian genome wide association analyses of growth and yearling ultrasound measures of carcass traits in Brangus heifers" (J. Anim. Sci. 90:3398−3409). Correct DOI is as follows: doi:10.2527/jas.2011-4507

"Evaluation of standardized ileal digestible lysine requirement of nursery pigs from seven to fourteen kilograms" (J. Anim. Sci. 90:4380−4390). Correct DOI is as follows: doi:10.2527/jas.2012-5131

"Relationships between rumination time, metabolic conditions and health status in dairy cows during the transition period" (J. Anim. Sci. 90:4544−4554). Correct DOI is as follows: doi:10.2527/jas.2011-5064

"Dietary sulfur concentration affects rumen hydrogen sulfide concentrations in feedlot steers during transition and finishing" (J. Anim. Sci. 90:4478−4486). Correct DOI is as follows: doi:10.2527/jas.2011-5078