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Genetic parameters and genotype by environment interaction for production traits and organ weights of gilthead seabream (*Sparus aurata*) reared in sea cages

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ABSTRACT

Gilthead seabream is a key fish species for farming in the Mediterranean region and is farmed in a large geographical area under various production circumstances. However, more than 80% of the genetically improved fingerlings originate from a single country, Greece, which poses a potential risk for genotype by environment interaction (GxE). Therefore, the objective of this study was to quantify GxE for several traits of gilthead seabream in two distinct commercial production sites, one in south of Greece (Galaxidi Marine Farm) and another in southeast of Spain (Cudomar). For this GxE experiment, a population of juveniles was produced by mass spawning of 33 males and 20 females on a single day. These juveniles were stocked in sea cages in both locations when they reached stocking size (~3 g) and grown under commercial conditions. Management conditions during the grow-out period were kept the same between the production sites, while the fish were subject to naturally occurring differences such as water temperature, dissolved oxygen, and salinity. Phenotypes were recorded when the fish reached commercial harvest size (~400 g). Genetic parameters were estimated by using a genomic relationship matrix that was built by using ~30 k SNP. All traits studied had higher genetic variation and heritabilities in Cudomar. For instance, the heritability of harvest weight was 0.37 ± 0.05 in Galaxidi and 0.55 ± 0.05 in Cudomar. GxE was estimated as genetic correlations between the same trait measured on different fish in the two environments. Moderate GxE was found for harvest weight (0.45 ± 0.11), growth (0.43 ± 0.11), fillet weight (0.49 ± 0.12), liver weight (0.61 ± 0.11), and viscera weight (0.62 ± 0.10). Weak GxE was found for fillet fat (0.87 ± 0.06), heart weight (0.76 ± 0.11), cardiosomatic index (0.93 ± 0.14), viscerosomatic index (0.90 ± 0.05), and hepatosomatic index (0.79 ± 0.09). In conclusion, moderate GxE estimates for growth traits indicate that with a single breeding program, performance data from both environments should be included, or that two separate breeding programs may be needed for the two environments. The higher genetic variances observed in Cudomar suggest that this environment is a more suitable test environment for selective breeding.

1. Introduction

Animal breeding strives to create populations that will perform well under commercial production circumstances. The performance of genotypes changes in response to varying environmental conditions. Genotype by environment interaction (GxE) occurs when different genotypes respond differently to variation in environmental conditions (Falconer and Mackay, 1996). If GxE leads to reranking of genotypes, the genetically improved animals that perform well in one environment may not perform as expected in another, which implies that the information collected in one environment is of limited value to another environment.

A significant GxE interaction between sites will reduce the effectiveness of a breeding program. The actual production performance of the genetically improved stock will differ from the expected performance that is based on data from the selection environment. Significant GxE was reported in various production systems, for example, in *Penaeus monodon* culture between indoor recirculating aquaculture systems and outdoor ponds (Van Sang et al., 2020), in rainbow trout (*Oncorhynchus mykiss*) culture between fresh and brackish water environments (Sae-Lim et al., 2013), and in Nile tilapia (*Oreochromis niloticus*) culture

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between cage and pond environments (Khaw et al., 2012). Significant GxE was also reported in response to differences in environmental conditions in the same production systems, such as, dissolved oxygen levels (Mengistu et al., 2020a), different nutrition conditions (Romana-Eguia and Doyle, 1992), and salinity levels (Domingos et al., 2021). The issue of GxE attracts more attention when breeding companies start to distribute genetically improved stock internationally (Mulder and Bijma, 2005), in which case the genetically improved animals are expected to perform well in different locations with different production conditions. In aquaculture, one of the species whose genetically improved fingerlings are distributed internationally is gilthead seabream (*Sparus aurata*).

Gilthead seabream is a key fish species for farming in the Mediterranean region. The total production of gilthead seabream increased by 90% between 2009 and 2019 to approximately 260,000 tons, making it the second most produced fish species in 2019 in the Mediterranean region (FAO, 2021). In 2019, gilthead seabream was farmed in 23 countries and the leading producers were Turkey, Greece, and Egypt (FAO, 2021). Gilthead seabream is farmed both semi-extensively in ponds and intensively in sea cages or indoor tanks (Elalfy et al., 2021; Lee-Montero et al., 2015). The production of gilthead seabream is spread over large distances from around the Canary Islands in the North Atlantic Ocean (Urbieta and Ginés, 2000) to the shores of the Red Sea in the Arabian Peninsula (FAO, 2017). Although gilthead seabream is farmed in a large geographical area and under various production circumstances, more than 80% of the genetically improved fingerlings originate from a single country, Greece (Janssen et al., 2015), which poses a potential risk for GxE interaction.

If the magnitude of GxE between different production sites is quantified, breeding programs may adjust their selection criteria to reach a balanced performance in many locations rather than a high performance in a single location (Sae-Lim, 2013). However, studies that quantify GxE for commercially important traits in gilthead seabream are limited (Elalfy et al., 2021; Lee-Montero et al., 2015; Navarro et al., 2009a, 2009b). The objective of this study was to quantify GxE for production traits and organ weights of gilthead seabream in two distinct commercial production sites, one in south of Greece and the other in southeast of Spain. The production sites were monitored for changes in water temperature, dissolved oxygen, and salinity. The traits analyzed were harvest weight, growth, fillet weight, fillet percentage, fillet fat percentage, viscera weight, viscerosomatic index, heart weight, cardiosomatic index, liver weight, and hepatosomatic index.

2. Materials & methods

2.1. Production sites, production of experimental fish, and grow-out management

Two distinct commercial production sites of gilthead seabream were selected to perform this GxE experiment. One production site is located in south of Greece in The Gulf of Corinth (Galaxidi Marine Farm S.A., Galaxidi, Greece) (GPS location: 38°21′06.6″N 22°23′18.8″E) and the other production site is located in southeast of Spain at open sea 3.1 km from shore near El Campello, Alicante (Cudomar SL, El Campello, Alicante, Spain) (GPS location: 38°25′12″N 0°20′51″W). For this GxE experiment, a population of juveniles was produced by mass spawning of 33 males and 20 females on a single day at Galaxidi Marine Farm. Juvenile fish were raised as a single group to avoid introduction of common environmental effects. When fish reached an average weight of 3 g, one batch of 99,000 juveniles was stocked in a sea cage at Galaxidi at a density of 0.13 kg/m^3 and another batch of 84,605 juveniles was stocked in a sea cage at Cudomar at a density of 0.42 kg/m^3. The fish in both locations were fed with the same commercial diet after reaching an average weight of 100 g. The feed was provided once a day. The amount of feed given per kilogram of biomass was recorded throughout the grow-out period (Table 1).

Table 1
Feed given daily (g) per kg of biomass for different size classes.

Average weight of the fish (g)	Feed given (g) per kg of biomass	
	Galaxidi	Cudomar
<100	25.6	29.7
100–200	8.9	6.8
200–300	10.1	12.1
300–400	12.2	10.9

The management conditions during the grow-out period were kept as consistent and similar as possible between the production sites by having meetings between the production managers of the two sites and the researchers before the start of the project. Consensus decisions were made on stocking density based on the availability of sea cages at the time of stocking and on feeding rates based on the effects of water temperature on feeding level throughout the experiment. The environmental conditions of water temperature, dissolved oxygen, and salinity were measured regularly at both locations (Table 2). The dissolved oxygen was measured inside the sea cages in Galaxidi and outside of the sea cages in Cudomar.

The minimum temperature required for gilthead seabream to grow is 12 °C (Hernández et al., 2003). Therefore, the effective daily temperatures were calculated by subtracting 12 °C from observed daily temperatures. The cumulative degree days during the grow-out period were calculated by summing all the effective daily temperatures (Fig. 1).

2.2. Phenotypic data collection

Data on production traits and organ weights were collected from the commercially produced fish that were harvested after a grow-out period of 465 days in Galaxidi and 500 days in Cudomar. Both locations comply with local regulations to produce and harvest seabream in their facilities. In total, 998 fish in Galaxidi and 945 fish in Cudomar were sampled for data collection. The data were collected over 7 days in Galaxidi (daily 100–170 fish) and 5 days in Cudomar (daily 150–200 fish). A random sample of fish were harvested every morning from the same cage into an oxygenated tank. Before processing, a small batch of fish received a mortal dose of clove oil (0.03 mL/L). This process was repeated until all the harvested fish was measured for all the traits.

After the fish was killed, body weight was measured with a scale sensitive to 0.5 g. Fillet fat measurements were taken on whole fish from eight points (four on each side of the fish) by using Distell Fish Fat meter equipment (Distell Inc., West Lothian, Scotland). The fillet fat percentage for each fish was calculated by taking the average of eight measurements on the same fish. The fish were then gutted, and viscera weight was recorded with a scale sensitive to 0.5 g. Viscera included all the internal organs and abdominal fat. Liver and heart were subsequently separated from the viscera and weighed by a scale sensitive to 0.001 g. The gutted fish were then filleted and fillet weight (one side)

Table 2
Average environmental and management conditions in Galaxidi and Cudomar.

Variable	Galaxidi	Cudomar
Overall water temperature (°C) [A]	20.5	21.4
Summer water temperature (°C) [A]	25.1	26.1
Autumn water temperature (°C) [A]	20.0	21.7
Winter water temperature (°C) [A]	14.3	15.2
Spring water temperature (°C) [A]	16.5	17.7
Total degree days from stocking until harvest (°C)	3830	4630
Dissolved oxygen (mg/L) [A]	5.58[*]	8.19[*]
Salinity (‰)	39.0[B]	37.3[A]

[A] Average daily values.
[B] Based on historic steady values.
[*] Dissolved oxygen measurements were made inside of the sea cages in Galaxidi, outside of the sea cages in Cudomar.

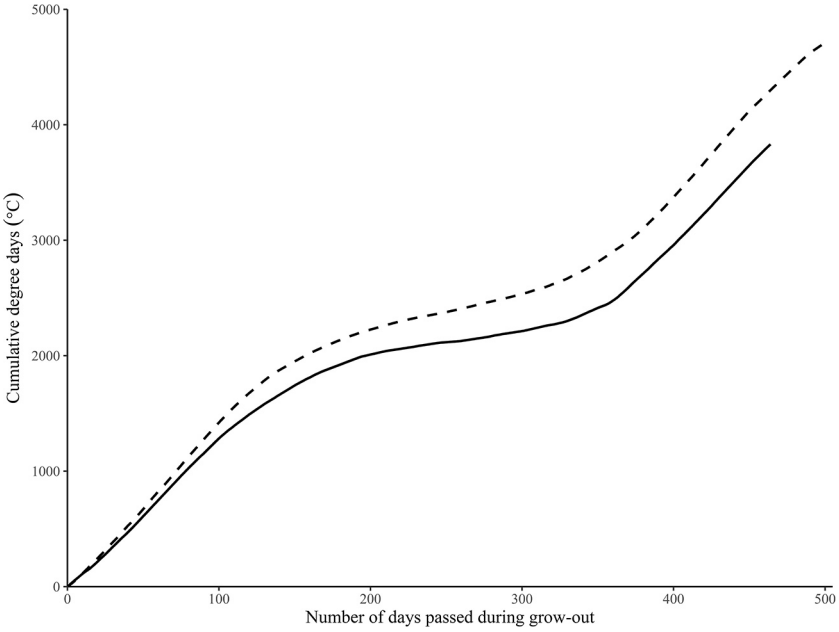

Fig. 1. Cumulative degree days (°C) in Galaxidi (——) and Cudomar (- - - -) from stocking to harvest.

was recorded. The recorded fillet weight was multiplied by two to calculate the total fillet weight. Measurements were standardized between the two sites, except fillet weight which was skin-off, trimmed in Galaxidi and skin-on, not-trimmed in Cudomar. Measurements taken in a single day were performed by the same person for each trait.

Editing of the data was performed by using R software and the "tidyverse" package collection in R (R Core Team, 2020; Wickham et al., 2019). Fillet percentage was calculated as (*fillet weight/body weight*) *x* 100. The viscerosomatic index was calculated as (*viscera weight/body weight*) *x* 100, the cardiosomatic index was calculated as (*heart weight/body weight*) *x* 100, and the hepatosomatic index was calculated as (*liver weight/body weight*) *x* 100.

Thermal growth coefficient (TGC) is a standardized growth rate that accounts for initial body weight and the sum of daily effective temperatures until harvest. Thermal growth coefficient was calculated as $TGC = \left[\left(W_t^{2/3} - W_0^{2/3}\right)/(T\,x\,t)\right]\,x\,1000$, where W_t is harvest weight, W_0 is stocking weight, T is the average effective temperature in °C, t is the number of days during grow-out period (Mayer et al., 2012). Stocking weight was on average 2.73 g in Galaxidi and 3 g in Cudomar. Because stocking weight was not individually measured, it was set to 2.73 g and 3 g for every fish in Galaxidi and Cudomar, respectively.

2.3. DNA extraction and genomic relationship matrix

DNA was isolated from fin clips by IdentiGEN (Dublin, Ireland). The genotyping was performed by using the ~30 k "MedFish" SNP array (Peñaloza et al., 2020). After removing 18 duplicate and 24 missing samples, 963 and 939 fish were available for genetic analyses from Galaxidi and Cudomar, respectively.

Genotypic data was filtered by excluding SNPs that had missing call rates exceeding 10%, that were fixed, or had Hardy-Weinberg equilibrium exact test *p*-value below 1e-10. We computed a genomic relationship matrix (GRM) based on the remaining 28,164 SNPs by using calc_grm software (Calus and Vandenplas, 2019). The calculation of the GRM was based on the "vanraden" option (VanRaden, 2008), in which the GRM is computed as $= \frac{zz'}{2\sum_{p_i}\,p_i\,(1-p_i)}$. To use this option, marker genotypes were coded as "0", "1", or "2". Z is a matrix that contains marker genotypes for all loci, which is corrected for the allele frequency per locus. p_i is the frequency of the less frequent allele and was calculated by using all the fish in both locations. In total, 18 animals were genotyped in duplicate. The GRM was recomputed after removing these animals from the dataset. The inverse of the GRM matrix was obtained directly from calc_grm by using "giv" function. Genotypes of the parents were not available, which prevented the reconstruction of family relationships from parentage analysis.

2.4. Estimation of heritabilities and correlations

The magnitude of the GxE was estimated for each trait as the genetic correlation (r_g) of the same trait measured on different animals in the two environments by using a bivariate animal model in ASReml version 4.1 (Gilmour et al., 2015). In the bivariate models, the same traits measured on different fish in the two locations were treated as different traits. Heritabilities of the trait in both environments were estimated by using the same bivariate animal model.

The bivariate animal model is $y = X\beta + Zu + e$, where y is a vector of phenotypes for the same trait in two environments, β is the vector of fixed effect "sampling day", u is the vector of random animal additive genetic effects $\sim \left(\begin{bmatrix}0\\0\end{bmatrix}, G\begin{bmatrix}\sigma^2_{a,T_G} & r_{a,T_{G,C}}\sigma_{a,T_G}\sigma_{a,T_C}\\ r_{a,T_{G,C}}\sigma_{a,T_G}\sigma_{a,T_C} & \sigma^2_{a,T_C}\end{bmatrix}\right)$, where G is the genomic relationship matrix and $\sigma_{a,\ T_G}{}^2$ is the additive genetic variance of trait measured in Galaxidi, $\sigma_{a,\ T_C}{}^2$ is the additive genetic variance of trait measured in Cudomar, $r_{a,\ T_{G,\ C}}$ is the additive genetic correlation between the same trait measured in Galaxidi and Cudomar and e is the vector of random residual effects $\sim \left(\begin{bmatrix}0\\0\end{bmatrix}, I\begin{bmatrix}\sigma^2_{e,T_G} & 0\\ 0 & \sigma^2_{e,T_C}\end{bmatrix}\right)$, where I is an identity matrix, $\sigma_{e,\ T_G}{}^2$ is the residual variance of trait measured in Galaxidi, and $\sigma_{e,\ T_C}{}^2$ is the residual variance of trait measured in Cudomar. The residual covariance between the two environments was set to zero because no individual was measured both in Galaxidi and Cudomar. X and Z are design matrices, that relate observations to the fixed effect and additive genetic effect of animals, respectively. The fixed effect "sampling day" was a categorical variable with one category for each measurement day (7 days in Galaxidi and 5 days in Cudomar). Gilthead seabream is a protandrous fish (Loukovitis et al., 2011) and all individuals were males during harvest. Therefore, "sex" was not included as a fixed effect in this study. The expectation of

$cov(u,e)$ is zero. Heritability (h^2) of each trait was calculated as $h^2 = \frac{\sigma_a^2}{\sigma_a^2+\sigma_e^2}$. After fitting the bivariate animal models for each trait by using all 963 and 939 phenotypic records in Galaxidi and Cudomar, residuals that were more than 3.5 standard deviations in magnitude were identified and the corresponding phenotypic records were removed. Table 3 shows the number of fish used in the analysis of each trait.

Genetic and phenotypic correlations among the traits within the same environment were also estimated by using bivariate animal models. In this case, u is the vector of random animal additive genetic effects $\sim \left(\begin{bmatrix}0\\0\end{bmatrix}, G\begin{bmatrix}\sigma^2_{a,T_1} & r_{a,T_{1,2}}\sigma_{a,T_1}\sigma_{a,T_2}\\ r_{a,T_{1,2}}\sigma_{a,T_1}\sigma_{a,T_2} & \sigma^2_{a,T_2}\end{bmatrix}\right)$, where $\sigma_{a,\ T_1}{}^2$ is the additive genetic variance of trait 1, $\sigma_{a,\ T_2}{}^2$ is the additive genetic variance of trait 2, $r_{a,\ T_{1,\ 2}}$ is the additive genetic correlation between trait 1 and 2. Also, e is the vector of random residual effects $\sim \left(\begin{bmatrix}0\\0\end{bmatrix}, I\begin{bmatrix}\sigma^2_{e,T_1} & r_{e,T_{1,2}}\sigma_{e,T_1}\sigma_{e,T_2}\\ r_{e,T_{1,2}}\sigma_{e,T_1}\sigma_{e,T_2} & \sigma^2_{e,T_2}\end{bmatrix}\right)$, where I is an identity matrix, $\sigma_{e,\ T_1}{}^2$ is the residual variance of trait 1, and $\sigma_{e,\ T_2}{}^2$ is the residual variance of trait 2, and, $r_{e,\ T_{1,\ 2}}$ is the residual correlation between trait 1 and trait 2.

3. Results

3.1. Descriptive statistics

Descriptive statistics of body weight at harvest, thermal growth coefficient, fillet weight, fillet percentage, fillet fat percentage, viscera weight, viscerosomatic index, liver weight, hepatosomatic index, heart weight, and cardiosomatic index were calculated (Table 3).

The harvested fish in Cudomar were on average 40.1 g heavier than in Galaxidi; however, the coefficients of variation were virtually the same. TGC was higher in Galaxidi. The average fillet weight of harvested fish in Cudomar was on average 63.2 g higher than in Galaxidi; however, this is mainly because the fillet was skin-on and not trimmed in Cudomar, while it was skin-off and trimmed in Galaxidi. The coefficients of variation of fillet weight were very similar. The viscera weights of harvested fish in the two environments were very similar despite the difference of 40.1 g in harvest weights. The liver of harvested fish in Cudomar was on average more than 70% heavier than in Galaxidi, which was also reflected in the large difference in hepatosomatic indices. Liver and heart weights, and corresponding indices had high coefficients of variation in both environments. The mean fillet fat percentages of harvested fish in the two environments were almost identical; however, the coefficient of variation was somewhat higher in Cudomar.

Table 3
The number of fish (N) used for analyses, and means and coefficients of variation (CV) of all traits in the two production environments.

Trait	Galaxidi			Cudomar		
	N	Mean*	CV	N	Mean*	CV
Harvest weight (g)	957	372.1	17.0	938	412.2	17.0
TGC ($g^{2/3}$ x $°C^{-1}$ × 1000)	955	12.8	11.9	936	11.4	11.9
Fillet weight (g)	960	116.6	19.6	933	179.8	19.8
Fillet percentage (%)	946	31.4	8.1	929	43.6	7.1
Fillet fat (%)	950	12.7	18.1	932	12.8	21.6
Viscera weight (g)	963	27.2	27.0	935	29.3	23.1
Viscerosomatic index (%)	961	7.3	16.8	934	7.1	13.9
Liver weight (g)	947	3.9	29.1	930	6.8	31.4
Hepatosomatic index (%)	945	1.0	21.2	933	1.6	23.4
Heart weight (g)	963	0.38	25.6	933	0.48	21.4
Cardiosomatic index (%)	954	0.10	21.6	927	0.12	13.4

* All trait means were significantly different between sites ($p < .001$) except for fillet fat (%).

3.2. Genetic parameters

The only fixed effect in our dataset, "sampling day", was significant in the analysis of all traits ($p < .05$) except for harvest and viscera weight in Galaxidi. The estimates of genetic variance, environmental variance, and heritability were obtained from bivariate models for each trait (Table 4).

The heritability estimates were higher for all traits in Cudomar than in Galaxidi, although the differences were significant only for fillet weight and hepatosomatic index ($p < .05$). The heritability estimates of harvest weight were moderate to high. The heritability estimates of TGC were almost identical to the heritability estimates of harvest weight. Heritability estimates of fillet percentage were low in both environments. In comparison, the heritabilities of viscerosomatic, hepatosomatic, and cardiosomatic indices were higher than fillet percentage in both environments, with higher values in Cudomar. The heritability estimates for liver and heart weight were moderate to high in both environments. The heritability for cardiosomatic index was lower than the one for heart weight, but the difference was not as big as between fillet weight and fillet percentage.

3.3. Genetic and phenotypic correlations

The genetic and phenotypic correlations between traits were estimated with fish grown in Galaxidi (Table 5) and in Cudomar (Table 6). The genetic correlation between harvest weight and TGC was close to unity in both environments, indicating these two traits are genetically same. The genetic correlation between harvest weight and fillet weight was also very close to unity, which means selecting for increased harvest weight will result in correlated favorable response in fillet weight. However, the genetic correlation between harvest weight and fillet percentage was negative in Galaxidi (although the correlation was weak and not significantly different from zero) and positive in Cudomar (with a large standard error). This indicates that selecting for increased harvest weight in Galaxidi will not result in correlated favorable response in fillet percentage; however, some correlated response is expected in

Table 4
Genetic variance (V_A), environmental variance (V_E), and heritability of the traits in the two production environments.

Trait	Galaxidi			Cudomar		
	V_A	V_E	h^2 (se)	V_A	V_E	h^2 (se)
Harvest weight	1474	2553	0.37 (0.05)	2863	2361	0.55 (0.05)
TGC	0.87	1.49	0.37 (0.05)	1.09	0.87	0.56 (0.05)
Fillet weight	34.60	82.7	0.30 (0.05)	156.32	156.10	0.50 (0.05)
Fillet percentage	0.09	1.21	0.07 (0.04)	0.21	1.49	0.13 (0.04)
Fillet fat (%)	2.24	2.64	0.46 (0.05)	3.54	2.94	0.55 (0.05)
Viscera weight	21.84	33.12	0.40 (0.05)	23.16	26.24	0.47 (0.05)
VSI	0.66	0.85	0.44 (0.05)	0.50	0.48	0.51 (0.05)
Liver weight	0.43	0.84	0.34 (0.05)	2.05	2.48	0.45 (0.05)
HSI	0.013	0.032	0.29 (0.05)	0.066	0.070	0.48 (0.05)
Heart weight	0.002	0.007	0.23 (0.05)	0.004	0.006	0.39 (0.05)
CSI	0.69	3.56	0.16 (0.04)	0.48	2.02	0.19 (0.05)

VSI = Viscerosomatic index, HSI = Hepatosomatix index, CSI = Cardiosomatic index.

Cudomar. Harvest weight was strongly and positively correlated with viscera and organ weights, which means that selecting for increased harvest weight will result in correlated response for increased organ weights; however, the genetic correlations between harvest weight and organ indices were not significantly different than zero, indicating that selecting for increased harvest weight will not result in correlated response for the increased proportion of organs to body weight.

Fillet fat percentage was positively correlated to viscera weight and viscerosomatic index, indicating that selecting for heavier viscera will result in correlated response for increased fillet fat. Fillet fat percentage was also positively correlated to liver weight and hepatosomatic index, which means that selecting for increased liver weight will result in correlated response for increased fillet fat.

3.4. Genotype by environment interaction between the production environments

Genotype by environment interactions were estimated as genetic correlations between the same traits in two production environments (Table 7).

TGC had the lowest genetic correlation between the two production environments, and therefore the strongest genotype by environment interaction. Harvest weight and TGC had very similar levels of genotype by environment interaction. The GxE interaction for fillet weight, liver weight, and viscera weight was moderate. On the other hand, the GxE interaction for fillet fat percentage, heart weight, cardiosomatic index, and viscerasomatic index was weak.

4. Discussion

The objective of this study was to quantify genotype by environment interaction for production traits and organ weights of gilthead seabream in two distinct production sites in the Mediterranean, one site in The Gulf of Corinth, Greece (Galaxidi Marine Farm) and the other site in open sea near El Campello, Spain (Cudomar). Estimates for heritabilities were higher in Cudomar. TGC, harvest weight and fillet percentage showed the strongest genotype by environment interaction, which are traits of economic importance and commonly included in fish breeding programs (Chavanne et al., 2016; Janssen et al., 2017). Fillet fat percentage, on the other hand, had weak genotype by environment interaction.

4.1. Experimental design

The two commercial production locations were specifically chosen to analyze the effect of distinct temperature profiles on genotype by environment interaction with respect to production traits and organ weights. The historical sea surface temperature data indicate that the sea surface water in south of Greece is warmer than in southeast of Spain, which makes Greece the more favorable environment for growth (Besson et al., 2016; Llorente and Luna, 2013). Water temperatures recorded during this experiment however, revealed a different pattern (Fig. 1), which was mainly due to the specific location of Galaxidi, which is in The Gulf of Corinth. In this experiment, Cudomar was characterized by consistently higher daily average water temperatures during the first summer, which led to increasing differences in cumulative degree days in favor of Cudomar until the beginning of winter. Winter only fortified the divergence of cumulative degree days until the beginning of second summer, which did not cause further divergence in cumulative degree days. The 35 days gap in harvesting dates was also an influential factor on the final difference on cumulative degree days. Water temperature has a direct effect on the performance of fish. Fish that are subjected to higher temperatures grows faster (Green and Fisher, 2004); however, temperatures above certain limits inhibit the growth (Azaza et al., 2008). The water temperature in the Mediterranean has been increasing consistently over the last decades (Pastor et al., 2018). The temperature has increased at different levels in different parts of the Mediterranean. Therefore, increasing water temperature is likely to become a major factor contributing to genotype by environment interaction in fish farming in the future as temperature has a direct effect on physiological performance. In addition to water temperature, the two locations differed in the levels of dissolved oxygen and salinity (Table 1), which may also have contributed to genotype by environment interactions. Lower salinity was concluded to result in improved growth in various marine fish species including gilthead seabream (McKay and Gjerde, 1985; Morgan and Iwama, 1991; Tandler et al., 1995; Ytrestøyl et al., 2020). The underlying reason for this may be that higher salinity demands higher metabolic costs in order to maintain the osmotic pressure of the body fluids within acceptable ranges, therefore any saved energy due to lower salinity can be spent for growth (Morgan and Iwama, 1991; Tandler et al., 1995). Feed efficiency was detected to improve in lower salinity, which reflects that more of the feed is used for growth rather than for other metabolic processes (Imsland et al., 2001; Ytrestøyl et al., 2020). Higher dissolved oxygen concentrations were reported to improve growth and feed efficiency (Duan et al., 2011; Mengistu et al., 2020a, 2020b). Under hypoxia, the blood flow through the intestines is restricted (Axelsson and Fritsche, 1991), which can negatively affect the nutrient absorption and feed utilization. Taking these observations together, Cudomar appeared to be the more favorable environment for fish growth, which could explain why the estimates of genetic variation (Table 4) were higher in Cudomar compared to Galaxidi.

In this study, genotype by environment interaction was quantified as the genetic correlation between the same trait measured in the two production environments. The experimental fish were grown in commercial sea cages to commercial harvest size and they were subject to natural environmental conditions. In this study, no systematic manipulation of environmental conditions was applied, and the same commercial feed was given in both sites from an average weight of 100 g until the time of harvest.

The fish that were stocked in sea cages in Galaxidi and Cudomar resulted from a single mass spawning event. In mass spawning, it is not possible to control the mating and the contribution of the parents may be skewed (Loughnan et al., 2013). While mass spawning leads to unequal contribution of parents, which is a disadvantage for genetic parameter estimation, it also avoids introduction of common environmental effects that could obscure genetic differences between families. Unequal family sizes may create a slight bias on the estimations of genotype by environment interaction when the analyses are performed using the pedigree relationships (Sae-Lim et al., 2010); however, the genetic analyses were performed using genomic relationships in this study. The use of genomic relationships increases the accuracy of parameter estimates as compared to the use pedigree relationships (Veerkamp et al., 2011).

4.2. Heritability of the traits

In this study, the genetic variances of all the traits were higher in

Table 7
Genetic correlations between the production environments of Galaxidi and Cudomar for all traits.

Trait	Genetic correlation (se)
Harvest weight	0.45 (0.11)
TGC	0.43 (0.11)
Fillet weight	0.49 (0.12)
Fillet percentage	0.51 (0.30)
Fillet fat (%)	0.87 (0.06)
Viscera weight	0.62 (0.10)
Viscerosomatic index	0.90 (0.05)
Liver weight	0.61 (0.11)
Hepatosomatic index	0.79 (0.09)
Heart weight	0.76 (0.11)
Cardiosomatic index	0.93 (0.14)

Table 5
Genetic (below diagonal) and phenotypic (above diagonal) correlations among the traits measured at harvest in Galaxidi. HW (harvest weight), TGC (thermal growth coefficient), FW (fillet weight), FP (fillet percentage), FF% (fillet fat percentage), VW (viscera weight), VSI (viscerosomatic index), LW (liver weight), HSI (hepatosomatic index), HeW (heart weight), and CSI (cardiosomatic index).

	HW	TGC	FW	FP	FF%	VW	VSI	LW	HSI	HeW	CSI
HW		>0.99 (<0.01)	0.90 (0.01)	0.05 (0.04)	0.32 (0.04)	0.79 (0.02)	0.28 (0.04)	0.69 (0.02)	0.18 (0.04)	0.56 (0.03)	−0.16 (0.04)
TGC	>0.99 (<0.01)		0.91 (0.01)	0.09 (0.04)	0.38 (0.04)	0.80 (0.02)	0.31 (0.04)	0.70 (0.02)	0.21 (0.04)	0.57 (0.03)	−0.18 (0.04)
FW	0.98 (0.01)	0.98 (0.01)		0.46 (0.03)	0.41 (0.03)	0.73 (0.02)	0.28 (0.04)	0.67 (0.02)	0.23 (0.04)	0.52 (0.03)	−0.16 (0.04)
FP	−0.15 (0.22)	−0.10 (0.25)	0.11 (0.25)		0.26 (0.03)	0.06 (0.04)	0.06 (0.04)	0.11 (0.04)	0.13 (0.04)	0.05 (0.03)	0.13 (0.04)
FF%	0.16 (0.13)	0.17 (0.13)	0.24 (0.13)	0.38 (0.19)		0.34 (0.04)	0.23 (0.04)	0.48 (0.03)	0.43 (0.03)	0.11 (0.04)	−0.19 (0.04)
VW	0.75 (0.05)	0.77 (0.05)	0.75 (0.06)	−0.04 (0.24)	0.26 (0.12)		0.80 (0.01)	0.70 (0.02)	0.35 (0.03)	0.43 (0.03)	−0.16 (0.04)
VSI	0.24 (0.11)	0.27 (0.11)	0.26 (0.12)	0.01 (0.22)	0.29 (0.11)	0.82 (0.04)		0.42 (0.03)	0.37 (0.04)	0.14 (0.04)	0.01 (0.04)
LW	0.73 (0.07)	0.76 (0.06)	0.77 (0.07)	−0.02 (0.25)	0.50 (0.10)	0.67 (0.07)	0.35 (0.11)		0.83 (0.01)	0.36 (0.03)	−0.17 (0.04)
HSI	0.25 (0.13)	0.27 (0.13)	0.29 (0.14)	0.05 (0.26)	0.64 (0.09)	0.36 (0.12)	0.28 (0.12)	0.83 (0.04)		0.06 (0.04)	−0.11 (0.04)
HeW	0.81 (0.07)	0.81 (0.07)	0.75 (0.09)	−0.28 (0.27)	−0.08 (0.15)	0.46 (0.12)	−0.04 (0.14)	0.48 (0.13)	−0.02 (0.17)		0.69 (0.02)
CSI	−0.11 (0.18)	−0.11 (0.19)	−0.17 (0.19)	0.05 (0.26)	−0.35 (0.16)	−0.34 (0.16)	−0.16 (0.16)	−0.35 (0.18)	−0.41 (0.18)	0.50 (0.14)	

Table 6
Genetic (below diagonal) and phenotypic (above diagonal) correlations among the traits measured at harvest in Cudomar. HW (harvest weight), TGC (thermal growth coefficient), FW (fillet weight), FP (fillet percentage), FF% (fillet fat percentage), VW (viscera weight), VSI (viscerosomatic index), LW (liver weight), HSI (hepatosomatic index), HeW (heart weight), and CSI (cardiosomatic index).

	HW	TGC	FW	FP	FF%	VW	VSI	LW	HSI	HeW	CSI
HW		>0.99 (<0.01)	0.95 (0.01)	0.20 (0.04)	0.28 (0.04)	0.81 (0.02)	0.18 (0.04)	0.71 (0.02)	0.25 (0.04)	0.77 (0.02)	−0.06 (0.04)
TGC	>0.99 (<0.01)		0.95 (0.01)	0.21 (0.04)	0.30 (0.05)	0.81 (0.02)	0.19 (0.04)	0.71 (0.02)	0.26 (0.04)	0.77 (0.02)	−0.06 (0.04)
FW	0.99 (0.01)	0.99 (0.01)		0.48 (0.03)	0.33 (0.04)	0.76 (0.02)	0.15 (0.04)	0.69 (0.02)	0.28 (0.04)	0.74 (0.02)	−0.04 (0.04)
FP	0.39 (0.15)	0.39 (0.15)	0.50 (0.13)		0.28 (0.03)	0.14 (0.04)	−0.01 (0.04)	0.23 (0.17)	0.19 (0.04)	0.17 (0.04)	0.02 (0.04)
FF	0.14 (0.10)	0.15 (0.10)	0.20 (0.10)	0.62 (0.13)		0.32 (0.04)	0.21 (0.04)	0.46 (0.03)	0.45 (0.03)	0.15 (0.04)	−0.09 (0.04)
VW	0.80 (0.04)	0.80 (0.04)	0.72 (0.05)	0.30 (0.18)	0.23 (0.10)		0.70 (0.02)	0.76 (0.02)	0.46 (0.04)	0.65 (0.02)	−0.03 (0.04)
VSI	0.06 (0.11)	0.06 (0.11)	−0.08 (0.11)	−0.43 (0.15)	0.25 (0.10)	0.61 (0.07)		0.43 (0.04)	0.85 (0.01)	0.16 (0.04)	0.01 (0.04)
LW	0.68 (0.06)	0.69 (0.06)	0.64 (0.07)	0.29 (0.17)	0.45 (0.09)	0.81 (0.04)	0.45 (0.09)		0.85 (0.01)	0.53 (0.03)	−0.07 (0.04)
HSI	0.15 (0.10)	0.16 (0.10)	0.12 (0.11)	0.22 (0.17)	0.54 (0.08)	0.45 (0.09)	0.54 (0.08)	0.81 (0.04)		0.19 (0.04)	−0.05 (0.04)
HeW	0.92 (0.03)	0.92 (0.03)	0.95 (0.03)	0.54 (0.16)	−0.06 (0.12)	0.70 (0.06)	−0.01 (0.12)	0.55 (0.09)	0.06 (0.12)		0.58 (0.03)
CSI	−0.02 (0.15)	−0.01 (0.15)	0.08 (0.16)	0.49 (0.22)	−0.26 (0.14)	−0.08 (0.16)	−0.16 (0.16)	−0.15 (0.16)	−0.19 (0.15)	0.39 (0.13)	

Cudomar, which also resulted in higher heritability estimates. One of the possible consequences of genotype by environment interaction is heterogenous genetic variances across environments (Calus, 2006). The heterogenous genetic variances between the two environments (Table 4) leads to scaling effects. It appears that the environmental conditions (both measured and unmeasured) in Cudomar were more favorable than in Galaxidi, which led to higher genetic variances. This may imply that when breeding for these two environments, keeping the selection candidates at Cudomar may increase the selection response due to the higher genetic variances observed in Cudomar. Higher heritabilities would also lead to higher accuracies of EBVs.

Harvest weight was moderately heritable in Galaxidi and highly heritable in Cudomar. The heritability of harvest weight in Galaxidi (0.37 ± 0.05) is very similar to the value reported for gilthead seabream (0.34 ± 0.06) by Navarro et al. (2009b), although their estimation comes from a population that consisted of a combination of tank-farmed and cage-farmed fish. The value reported by Fernandes et al. (2017) (0.41 ± 0.03) for harvest weight of tank-farmed gilthead seabream is in between the values estimated for Galaxidi (0.37 ± 0.05) and Cudomar (0.55 ± 0.05). The genetic correlation between harvest weight and TGC was almost one, which indicates that these traits are controlled by the same set of genes. The heritability estimates of harvest weight and TGC were almost equal. These may be related to how the TGC was calculated. TGC depends on harvest weight, stocking weight, water temperature, and duration of the grow-out period (Section 2.2). In this study, individual stocking weights were not available, and an average was used for all fish in the same location. The stocking weights, however, did not affect TGC to a high degree because they were very small, less than 1% of the harvest weights. Therefore, the variation in TGC was dominated by the variation in harvest weight.

Fillet percentage was lowly heritable in both production environments (0.07 ± 0.04 in Galaxidi and 0.13 ± 0.04 in Cudomar), similar to the value reported by Navarro et al. (2009a) (0.12 ± 0.03) for a population that consisted of a combination of tank-farmed and cage-farmed fish and slightly lower than the estimate reported by Vandeputte et al. (2020) (0.22 ± 0.05) for cage-farmed gilthead seabream. The heritability estimates of fillet percentage are typically found to be lower than the heritability of fillet weight (Navarro et al., 2009a; Thodesen et al., 2012; Vandeputte et al., 2017), which is also the case in this study. The differences in heritability estimates for fillet percentage may partly be caused by different filleting methods (skin-off, trimmed in Galaxidi and skin-on, not trimmed in Cudomar) used in the two production environments (Kocour et al., 2007; Thodesen et al., 2012). The genetic coefficient of variations for fillet percentage were very small, which indicates that the prospect of genetic improvement of this trait by direct selection is not good. Fillet percentage may be improved to some extent by selecting on harvest weight based on the positive genetic correlation between harvest weight and fillet percentage in Cudomar.

Fillet fat percentage was highly heritable in both production environments (0.46 ± 0.05 in Galaxidi and 0.55 ± 0.05 in Cudomar). The heritability of fillet fat estimated in this study is larger than the value reported by Elalfy et al. (2021) (0.27 ± 0.08), who also measured fillet fat of gilthead seabream with Distell equipment. The heritability of fillet fat estimated in this study is also larger than the values reported for striped catfish (0.04 ± 0.03) (Van Sang et al., 2012), for European whitefish (0.26 ± 0.09) (Kause et al., 2011) and for Atlantic salmon (0.28 ± 0.05) (Powell et al., 2008); however, lower than the value reported for common carp (0.68 ± 0.10) (Prchal et al., 2018). High genetic coefficients of variation were found for fillet fat, which indicate that this trait would respond well to genetic selection. Fillet fat content may be regarded as a quality trait of the farmed fish from the perspective of consumers (Van Sang et al., 2009). Consumers in certain markets may prefer to purchase fish with a higher fillet fat content. Even though gilthead seabream farmers are not paid on the basis of quality characteristics of the meat, farmers may wish to advertise their product as having higher quality due to increased fillet fat to allure a certain market and distinguish themselves in the market. On the other hand, fillet fat is positively (unfavorably) correlated to viscera weight. Viscera is a storage for fat in the body. Fat content of the body is expected to be unfavorably correlated to feed conversion ratio and therefore, selecting for increased fillet fat may create fish that are less efficient converters of feed (Kause et al., 2016; Quinton et al., 2007). Therefore, rather than extreme values, an optimum is required for fillet fat percentage.

Heart and liver weights, and indices were moderately heritable in both production environments, although the estimations were higher in Cudomar. In both environments, the genetic correlation between heart and harvest weights was high but not unity. Therefore, selection for growth could result in fish with slightly lower cardiosomatic indices. A lower cardiosomatic index may be associated with reduced cardiac capacity and consequently, reduced robustness of the fish (Vassgård, 2017). Growth rate of the fish has been reported to affect the prevalence of cardiac diseases (Farrell, 2002), which may be caused by the increased pressure on the heart to supply more blood to the fast-growing body. In broiler chickens, cardiac diseases, specifically ascites, was observed to have higher prevalence in faster-growing animals (Closter et al., 2009). The increase of ascites in broilers is related to genetic selection for higher performance (Julian, 1993). Therefore, heart weight is an important trait to monitor for unwanted correlated responses that could affect health and robustness. Heart weight is a difficult to measure trait because measuring of it requires sacrificing the fish. However, genomic selection makes it easier to implement such traits in a breeding program because after phenotyping and genotyping a reference population, the selection candidates do not have to be phenotyped and can still receive accurate breeding values. Hepatosomatic index has been reported to increase in response to differences in lighting regime (Døskeland et al., 2016) and use of additives in feed in Atlantic salmon (*Salmo salar*) (Larsson et al., 2014), exposure to insecticides in Nile tilapia (*Oreochromis niloticus*) (Thomaz et al., 2009), and exposure to toxins in redbreast sunfish (*Lepomis auritus*) (Everaarts et al., 1993). Enlargement of the liver may be positively correlated by its capacity to transform xenobiotics and cleanse the body (Porter and Janz, 2003). Therefore, hepatosomatic index can be regarded as a general health indicator of fish (Thomaz et al., 2009). Suboptimal environmental conditions during grow-out may cause the hepatosomatic indices to increase because the growth of the body is more susceptible to environmental conditions than the growth of the organs (Døskeland et al., 2016). However, the effect of individual environmental factors, such as water temperature and salinity, on hepatosomatic index is unknown.

4.3. Genotype by environment interaction and implications for breeding programs

Genotype by environment interaction may manifest itself as scaling or reranking of genotypes. In case of reranking of genotypes, good performing genotypes in one location may not perform as expected in another location. It was suggested that the reranking of genotypes due to genotype by environment interaction is practically important only if the genetic correlation of the same trait in different environments is below 0.8 (Robertson, 1959). In this experiment, environmental effects that can be controlled, such as feeding and stocking density, were kept as consistent as possible between the two production sites and fish were subject to natural water conditions that cannot be controlled, such as water temperature and salinity. Therefore, any genotype by environment interaction present is most likely due to different water conditions rather than different husbandry practices.

The genetic correlation of harvest weight was 0.45 ± 0.11 and the genetic correlation of TGC was 0.43 ± 0.11 between Galaxidi and Cudomar, which indicates a moderate genotype by environment interaction for these traits. Navarro et al. (2009a) estimated a weaker genotype by environment interaction for harvest weight (0.70 ± 0.10) in gilthead seabream although the experimental fish in that study were reared in different production systems (tanks and sea cages). In tanks, environmental conditions can be controlled, which may then lead to low genotype by environment interaction. Lee-Montero et al. (2015) estimated weak to strong genotype by environment interaction for specific growth rate (0.05 ± 0.18–0.99 ± 0.12) in gilthead seabream among different regions of Spain and varying grow-out conditions including intensive rearing in tanks and sea cages, and semi extensive rearing in ponds. In their study, grow-out conditions as well as geographical distance strongly affected the magnitude of genotype by environment interaction. Growth is the primary trait of interest in aquaculture and highly relevant for breeding programs (Chavanne et al., 2016). Growth and harvest weight had very similar genotype by environment interaction in this study. Moderate genotype by environment interaction detected for growth indicates that an optimization procedure may be applied if the interest is in reaching a balanced performance in the two environments. An obvious optimization procedure is to standardize the environmental conditions between the two environments (Sae-Lim et al., 2013); however, husbandry practices in this experiment were largely standardized and sea cages were subject to naturally fluctuating water conditions that cannot be controlled. Other optimization options are combining the performance of fish in both environments in an index and selecting on this index in a single breeding program or running two separate breeding programs for the two environments (James, 1961). If genotype by environment interaction is present, using performance data from the second production environment in an index increases the genetic gain in that environment significantly (Chu et al., 2018). To decide whether to select on an index or to run separate breeding programs, the "break-even correlation" should be considered. The break-even correlation is the genetic correlation between the same trait in different environments at which the genetic gain of the two approaches is equal when the costs of two smaller breeding programs are the same as the cost

of one large breeding program (Mulder et al., 2006). Mulder et al. (2006) suggests applying separate breeding programs if the genetic correlation is below 0.5–0.7.

The interest of breeding companies that distributes genetic material widely would be to produce fish that performs well in many conditions and environments. Therefore, depending on the genotype by environment interaction, data of more than two locations may need to be used in a breeding program to reach a balanced performance across those locations. Several methods are available to group different types of environments in a breeding program (Chenu, 2015). The number and type of locations depend on the specific interests of the breeding companies.

Genotype by environment interaction for fillet weight was moderate. The GxE interaction for fillet weight was slightly weaker than for harvest weight, although not significantly different. This small difference is in line with the result of Navarro et al. (2009a) who also estimated weaker genotype by environment interaction for fillet weight (0.94 ± 0.19) than harvest weight (0.70 ± 0.10) in two production sites of gilthead seabream. However, their estimate of 0.94 ± 0.19 was much higher than our estimate (0.49 ± 0.12). The magnitude of genotype by environment interaction can depend highly on the specific differences between the environments.

The genetic correlation of fillet fat percentage in Galaxidi and Cudomar was 0.87 ± 0.06, which indicates a very weak genotype by environment interaction. This may mean that accumulation of fat in the muscle is not strongly affected by environmental changes. The weak genotype by environment interaction is in accordance with the result of Elalfy et al. (2021), who estimated no genotype by environment interaction for fillet fat (1.00 ± 0.00) between intensive and semi-extensive grow-out conditions. Navarro et al. (2009b) estimated a much stronger genotype by environment interaction for fillet fat (0.15 ± 0.94) measured with chemical methods in gilthead seabream; however, their estimation was with a very high standard error and probably not significantly different from our estimate. A genetic correlation of 0.86 ± 0.06 for fillet fat percentage indicates that reranking of genotypes is minimal to absent for this trait.

5. Conclusion

Local water conditions may differ considerably between production sites, which indicates that local niches play an important role in the production of gilthead seabream. In this study, moderate genotype by environment interaction was detected for harvest weight, TGC, fillet weight and liver weight, and weak genotype by environment interaction was detected for fillet fat percentage and heart weight. This shows that the relative genetic merit of gilthead seabream in different farms can vary considerably and that breeding programs need to consider using data from multiple locations if the produced fish must perform in different locations. With the moderate genetic correlations observed, separate breeding programs may be needed.

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Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Wageningen University & Research advises Galaxidi Marine Farm on their gilthead seabream breeding program.

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References

Axelsson, M., Fritsche, R., 1991. Effects of exercise, hypoxia and feeding on the gastrointestinal blood flow in the Atlantic cod Gadus morhua. J. Exp. Biol. 158, 181 LP – 198.

Azaza, M.S., Dhraïef, M.N., Kraïem, M.M., 2008. Effects of water temperature on growth and sex ratio of juvenile Nile tilapia Oreochromis niloticus (Linnaeus) reared in geothermal waters in southern Tunisia. J. Therm. Biol. 33, 98–105. https://doi.org/10.1016/j.jtherbio.2007.05.007.

Besson, M., Vandeputte, M., van Arendonk, J.A.M., Aubin, J., de Boer, I.J.M., Quillet, E., Komen, H., 2016. Influence of water temperature on the economic value of growth rate in fish farming: the case of sea bass (Dicentrarchus labrax) cage farming in the Mediterranean. Aquaculture 462, 47–55. https://doi.org/10.1016/j.aquaculture.2016.04.030.

Calus, M.P.L., 2006. Estimation of Genotype x Environment Interaction for Yield, Health and Fertility in Dairy Cattle. Wageningen University. https://edepot.wur.nl/121773.

Calus, M.P.L., Vandenplas, J., 2019. Calc_grm—a program to compute pedigree, genomic, and combined relationship matrices. In: Anim. Breed. Genomics Centre, Wageningen UR Livest. Res.

Chavanne, H., Janssen, K., Hofherr, J., Contini, F., Haffray, P., Komen, H., Bargelloni, L., 2016. A comprehensive survey on selective breeding programs and seed market in the European aquaculture fish industry. Aquac. Int. 24, 1287–1307. https://doi.org/10.1007/s10499-016-9985-0.

Chenu, K., 2015. In: Sadras, V.O., Calderini, D.F.B.T.-C.P. (Eds.), Chapter 13 - Characterizing the crop environment – nature, significance and applications, Second E. Academic Press, San Diego, pp. 321–348. https://doi.org/10.1016/B978-0-12-417104-6.00013-3.

Chu, T.T., Bastiaansen, J.W.M., Norberg, E., Berg, P., 2018. On farm observations to increase genetic gain in breeding schemes for village poultry production – a simulation study. Acta Agric. Scand. Sect. A — Anim. Sci. 68, 1–10. https://doi.org/10.1080/09064702.2018.1543444.

Closter, A.M., van As, P., Groenen, M.A.M., Vereijken, A.L.J., van Arendonk, J.A.M., Bovenhuis, H., 2009. Genetic and phenotypic relationships between blood gas parameters and ascites-related traits in broilers. Poult. Sci. 88, 483–490. https://doi.org/10.3382/ps.2008-00347.

Domingos, J.A., Goldsbury, J.A., Bastos Gomes, G., Smith, B.G., Tomlinson, C., Bade, T., Jerry, D.R., 2021. Genotype by environment interactions of harvest growth traits for barramundi (Lates calcarifer) commercially farmed in marine vs. freshwater conditions. Aquaculture 532, 735989. https://doi.org/10.1016/j.aquaculture.2020.735989.

Døskeland, I., Imsland, A.K.D., Fjelldal, P.G., Stefansson, S.O., Roth, B., Eriksen, K.E., Handeland, S., 2016. The effect of low temperatures and photoperiods on growth and vertebra morphometry in Atlantic salmon. Aquac. Int. 24, 1421–1434. https://doi.org/10.1007/s10499-016-9999-7.

Duan, Y., Dong, X., Zhang, X., Miao, Z., 2011. Effects of dissolved oxygen concentration and stocking density on the growth, energy budget and body composition of juvenile Japanese flounder, Paralichthys olivaceus (Temminck et Schlegel). Aquac. Res. 42, 407–416. https://doi.org/10.1111/j.1365-2109.2010.02635.x.

Elalfy, I., Shin, H.S., Negrín-Báez, D., Navarro, A., Zamorano, M.J., Manchado, M., Afonso, J.M., 2021. Genetic parameters for quality traits by non-invasive methods and their G x E interactions in ocean cages and estuaries on gilthead seabream (Sparus aurata). Aquaculture 537, 736462. https://doi.org/10.1016/j.aquaculture.2021.736462.

Everaarts, J.M., Shugart, L.R., Gustin, M.K., Hawkins, W.E., Walker, W.W., 1993. Biological markers in fish: DNA integrity, hematological parameters and liver somatic index. Mar. Environ. Res. 35, 101–107. https://doi.org/10.1016/0141-1136(93)90021-Q.

Falconer, D.S., Mackay, T.F.C., 1996. Introduction to Quantitative Genetics, Fourth, edi. ed. Longman Group, Ltd.

FAO, 2017. Fishery and Aquaculture Country Profiles. Saudi Arabia (2003). Country Profile Fact Sheets. [WWW Document]. FAO Fish. Div. [online]. Rome. Updat. 1 March 2017. URL. http://www.fao.org/fishery/facp/SAU/en#CountrySector-Overview (accessed 1.14.21).

FAO, 2021. Fishery and aquaculture statistics. In: Global Aquaculture Production 1950–2019 (FishstatJ).

Farrell, A.P., 2002. Coronary arteriosclerosis in salmon: growing old or growing fast? Comp. Biochem. Physiol. Part A Mol. Integr. Physiol. 132, 723–735. https://doi.org/10.1016/S1095-6433(02)00126-5.

Fernandes, T., Herlin, M., Belluga, M.D.L., Ballón, G., Martinez, P., Toro, M.A., Fernández, J., 2017. Estimation of genetic parameters for growth traits in a hatchery population of gilthead sea bream (Sparus aurata L.). Aquac. Int. 25, 499–514.

Gilmour, A.R., Gogel, B.J., Cullis, B.R., Welham, S.J., Thompson, R., 2015. ASReml User Guide Release 4.1 Structural Specification. Hemel hempstead VSN Int. ltd.

Green, B.S., Fisher, R., 2004. Temperature influences swimming speed, growth and larval duration in coral reef fish larvae. J. Exp. Mar. Biol. Ecol. 299, 115–132. https://doi.org/10.1016/j.jembe.2003.09.001.

Hernández, J.M., Gasca-Leyva, E., León, C.J., Vergara, J.M., 2003. A growth model for gilthead seabream (Sparus aurata). Ecol. Model. 165, 265–283. https://doi.org/10.1016/S0304-3800(03)00095-4.

Imsland, A.K., Foss, A., Gunnarsson, S., Berntssen, M.H.G., FitzGerald, R., Bonga, S.W., Stefansson, S.O., 2001. The interaction of temperature and salinity on growth and food conversion in juvenile turbot (Scophthalmus maximus). Aquaculture 198, 353–367. https://doi.org/10.1016/S0044-8486(01)00507-5.

James, J.W., 1961. Selection in two environments. Heredity (Edinb). 16, 145–152. https://doi.org/10.1038/hdy.1961.17.

Janssen, K., Chavanne, H., Berentsen, P., Komen, H., 2015. Gilthead Seabream (Sparus aurata)–Current status of selective breeding in Europe. In: Abstract Book of the International Symposium on Genetics in Aquaculture XII. Santiago de Compostela, Spain.

Janssen, K., Berentsen, P., Besson, M., Komen, H., 2017. Derivation of economic values for production traits in aquaculture species. Genet. Sel. Evol. 49, 5. https://doi.org/10.1186/s12711-016-0278-x.

Julian, R.J., 1993. Ascites in poultry. Avian Pathol. 22, 419–454. https://doi.org/10.1080/03079459308418934.

Kause, A., Quinton, C., Airaksinen, S., Ruohonen, K., Koskela, J., 2011. Quality and production trait genetics of farmed European whitefish, Coregonus lavaretus1. J. Anim. Sci. 89, 959–971. https://doi.org/10.2527/jas.2010-2981.

Kause, A., Kiessling, A., Martin, S.A.M., Houlihan, D., Ruohonen, K., 2016. Genetic improvement of feed conversion ratio via indirect selection against lipid deposition in farmed rainbow trout (Oncorhynchus mykiss Walbaum). Br. J. Nutr. 116, 1656–1665.

Khaw, H.L., Ponzoni, R.W., Hamzah, A., Abu-Bakar, K.R., Bijma, P., 2012. Genotype by production environment interaction in the GIFT strain of Nile tilapia (Oreochromis niloticus). Aquaculture 326–329, 53–60. https://doi.org/10.1016/j.aquaculture.2011.11.016.

Kocour, M., Mauger, S., Rodina, M., Gela, D., Linhart, O., Vandeputte, M., 2007. Heritability estimates for processing and quality traits in common carp (Cyprinus carpio L.) using a molecular pedigree. Aquaculture 270, 43–50. https://doi.org/10.1016/J.AQUACULTURE.2007.03.001.

Larsson, T., Koppang, E.O., Espe, M., Terjesen, B.F., Krasnov, A., Moreno, H.M., Mørkøre, T., 2014. Fillet quality and health of Atlantic salmon (Salmo salar L.) fed a diet supplemented with glutamate. Aquaculture 426–427, 288–295. https://doi.org/10.1016/j.aquaculture.2014.01.034.

Lee-Montero, I., Navarro, A., Negrín-Báez, D., Zamorano, M.J., Berbel, C., Sánchez, J.A., Afonso, J.M., 2015. Genetic parameters and genotype–environment interactions for skeleton deformities and growth traits at different ages on gilthead seabream (Sparus aurata L.) in four Spanish regions. Anim. Genet. 46, 164–174. https://doi.org/10.1111/age.12258.

Llorente, I., Luna, L., 2013. The competitive advantages arising from different environmental conditions in seabream, Sparus aurata, Production in the Mediterranean Sea. J. World Aquacult. Soc. 44, 611–627. https://doi.org/10.1111/jwas.12069.

Loughnan, S.R., Domingos, J.A., Smith-Keune, C., Forrester, J.P., Jerry, D.R., Beheregaray, L.B., Robinson, N.A., 2013. Broodstock contribution after mass spawning and size grading in barramundi (Lates calcarifer, Bloch). Aquaculture 404–405, 139–149. https://doi.org/10.1016/j.aquaculture.2013.04.014.

Loukovitis, D., Sarropoulou, E., Tsigenopoulos, C.S., Batargias, C., Magoulas, A., Apostolidis, A.P., Kotoulas, G., 2011. Quantitative trait loci involved in sex determination and body growth in the Gilthead Sea Bream (Sparus aurata L.) through targeted genome scan. PLoS One 6, e16599. https://doi.org/10.1371/journal.pone.0016599.

Mayer, P., Estruch, V.D., Jover, M., 2012. A two-stage growth model for gilthead sea bream (Sparus aurata) based on the thermal growth coefficient. Aquaculture 358–359, 6–13. https://doi.org/10.1016/j.aquaculture.2012.06.016.

McKay, L.R., Gjerde, B., 1985. The effect of salinity on growth of rainbow trout. Aquaculture 49, 325–331. https://doi.org/10.1016/0044-8486(85)90089-4.

Mengistu, S.B., Mulder, H.A., Benzie, J.A.H., Khaw, H.L., Megens, H.-J., Trinh, T.Q., Komen, H., 2020a. Genotype by environment interaction between aerated and non-aerated ponds and the impact of aeration on genetic parameters in Nile tilapia (Oreochromis niloticus). Aquaculture 529, 735704. https://doi.org/10.1016/j.aquaculture.2020.735704.

Mengistu, S.B., Mulder, H.A., Benzie, J.A.H., Komen, H., 2020b. A systematic literature review of the major factors causing yield gap by affecting growth, feed conversion ratio and survival in Nile tilapia (Oreochromis niloticus). Rev. Aquac. 12, 524–541. https://doi.org/10.1111/raq.12331.

Morgan, J.D., Iwama, G.K., 1991. Effects of salinity on growth, metabolism, and ion regulation in juvenile rainbow and steelhead trout (Oncorhynchus mykiss) and fall Chinook Salmon (Oncorhynchus tshawytscha). Can. J. Fish. Aquat. Sci. 48, 2083–2094. https://doi.org/10.1139/f91-247.

Mulder, H.A., Bijma, P., 2005. Effects of genotype x environment interaction on genetic gain in breeding programs. J. Anim. Sci. 83, 49–61.

Mulder, H.A., Veerkamp, R.F., Ducro, B.J., van Arendonk, J.A.M., Bijma, P., 2006. Optimization of dairy cattle breeding programs for different environments with genotype by environment interaction. J. Dairy Sci. 89, 1740–1752. https://doi.org/10.3168/jds.S0022-0302(06)72242-1.

Navarro, A., Zamorano, M.J., Hildebrandt, S., Gines, R., Aguilera, C., Afonso, J.M., 2009a. Estimates of heritabilities and genetic correlations for growth and carcass traits in gilthead seabream (Sparus auratus L.), under industrial conditions. Aquaculture 289, 225–230. https://doi.org/10.1016/j.aquaculture.2008.12.024.

Navarro, A., Zamorano, M.J., Hildebrandt, S., Gines, R., Aguilera, C., Afonso, J.M., 2009b. Estimates of heritabilities and genetic correlations for body composition traits and G x E interactions, in gilthead seabream (Sparus auratus L.). Aquaculture 295, 183–187. https://doi.org/10.1016/j.aquaculture.2009.07.012.

Pastor, F., Valiente, J.A., Palau, J.L., 2018. Sea surface temperature in the mediterranean: trends and spatial patterns (1982–2016). Pure Appl. Geophys. 175, 4017–4029. https://doi.org/10.1007/s00024-017-1739-z.

Peñaloza, C., Manousaki, T., Franch, R., Tsakogiannis, A., Sonesson, A., Aslam, M.L., Tsigenopoulos, C.S., 2020. Development and validation of a combined species SNP array for the European seabass (Dicentrarchus labrax) and gilthead seabream (Sparus aurata). bioRxiv. https://doi.org/10.1101/2020.12.17.423305, 2020.12.17.423305.

Porter, C.M., Janz, D.M., 2003. Treated municipal sewage discharge affects multiple levels of biological organization in fish. Ecotoxicol. Environ. Saf. 54, 199–206. https://doi.org/10.1016/S0147-6513(02)00056-8.

Powell, J., White, I., Guy, D., Brotherstone, S., 2008. Genetic parameters of production traits in Atlantic salmon (Salmo salar). Aquaculture 274, 225–231. https://doi.org/10.1016/J.AQUACULTURE.2007.11.036.

Prchal, M., Bugeon, J., Vandeputte, M., Kause, A., Vergnet, A., Zhao, J., Kocour, M., 2018. Potential for genetic improvement of the main slaughter yields in common carp with in vivo morphological predictors. Front. Genet. 9, 283.

Quinton, C.D., Kause, A., Ruohonen, K., Koskela, J., 2007. Genetic relationships of body composition and feed utilization traits in European whitefish (Coregonus lavaretus L.) and implications for selective breeding in fishmeal- and soybean meal-based diet environments1. J. Anim. Sci. 85, 3198–3208. https://doi.org/10.2527/jas.2006-792.

R Core Team, 2020. R: A Language and Environment for Statistical Computing.

Robertson, A., 1959. The sampling variance of the genetic correlation coefficient. Biometrics 15, 469–485. https://doi.org/10.2307/2527750.

Romana-Eguia, M.R.R., Doyle, R.W., 1992. Genotype-environment interaction in the response of three strains of Nile tilapia to poor nutrition. Aquaculture 108, 1–12. https://doi.org/10.1016/0044-8486(92)90314-B.

Sae-Lim, P., 2013. One Size Fits all?: Optimization of Rainbow Trout Breeding Program under Diverse Preferences and Genotype-by-Environment Interaction. Wageningen University and Research.

Sae-Lim, P., Komen, H., Kause, A., 2010. Bias and precision of estimates of genotype-by-environment interaction: a simulation study. Aquaculture 310, 66–73. https://doi.org/10.1016/j.aquaculture.2010.10.020.

Sae-Lim, P., Kause, A., Mulder, H.A., Martin, K.E., Barfoot, A.J., Parsons, J.E., Komen, H., 2013. Genotype-by-environment interaction of growth traits in rainbow trout (Oncorhynchus mykiss): a continental scale study. J. Anim. Sci. 91, 5572–5581. https://doi.org/10.2527/jas.2012-5949.

Tandler, A., Anav, F.A., Choshniak, I., 1995. The effect of salinity on growth rate, survival and swimbladder inflation in gilthead seabream, Sparus aurata, larvae. Aquaculture 135, 343–353. https://doi.org/10.1016/0044-8486(95)01029-7.

Thodesen, J., Rye, M., Wang, Y.-X., Bentsen, H.B., Gjedrem, T., 2012. Genetic improvement of tilapias in China: genetic parameters and selection responses in fillet traits of Nile tilapia (Oreochromis niloticus) after six generations of multi-trait selection for growth and fillet yield. Aquaculture 366–367, 67–75. https://doi.org/10.1016/J.AQUACULTURE.2012.08.028.

Thomaz, J.M., Martins, N.D., Monteiro, D.A., Rantin, F.T., Kalinin, A.L., 2009. Cardio-respiratory function and oxidative stress biomarkers in Nile tilapia exposed to the organophosphate insecticide trichlorfon (NEGUVON®). Ecotoxicol. Environ. Saf. 72, 1413–1424. https://doi.org/10.1016/j.ecoenv.2008.11.003.

Urbieta, C., Ginés, R., 2000. Optimisation of slaughtering method in gilthead seabream (Sparus aurata). Industrial application in fish farms. Cah. Opt. Med. 51, 71–77.

Van Sang, N., Thomassen, M., Klemetsdal, G., Gjøen, H.M., 2009. Prediction of fillet weight, fillet yield, and fillet fat for live river catfish (Pangasianodon hypophthalmus). Aquaculture 288, 166–171. https://doi.org/10.1016/J.AQUACULTURE.2008.11.030.

Van Sang, N., Klemetsdal, G., Ødegård, J., Gjøen, H.M., 2012. Genetic parameters of economically important traits recorded at a given age in striped catfish (Pangasianodon hypophthalmus). Aquaculture 344–349, 82–89. https://doi.org/10.1016/j.aquaculture.2012.03.013.

Van Sang, N., Luan, N.T., Van Hao, N., Van Nhien, T., Vu, N.T., Nguyen, N.H., 2020. Genotype by environment interaction for survival and harvest body weight between recirculating tank system and pond culture in Penaeus monodon. Aquaculture 525, 735278. https://doi.org/10.1016/j.aquaculture.2020.735278.

Vandeputte, M., Puledda, A., Tyran, A.S., Bestin, A., Coulombet, C., Bajek, A., Haffray, P., 2017. Investigation of morphological predictors of fillet and carcass yield in European sea bass (Dicentrarchus labrax) for application in selective breeding. Aquaculture 470, 40–49. https://doi.org/10.1016/j.aquaculture.2016.12.014.

Vandeputte, M., Fraslin, C., Haffray, P., Bestin, A., Allal, F., Kocour, M., Dupont-Nivet, M., 2020. How to genetically increase fillet yield in fish: relevant genetic parameters and methods to predict genetic gain. Aquaculture 519, 734877. https://doi.org/10.1016/j.aquaculture.2019.734877.

VanRaden, P.M., 2008. Efficient methods to compute genomic predictions. J. Dairy Sci. 91, 4414–4423. https://doi.org/10.3168/jds.2007-0980.

Vassgård, S., 2017. Quantitative Genetics of Cardiac Traits in Atlantic salmon (Salmo salar L.). Norwegian University of Life Sciences, Ås.

Veerkamp, R.F., Mulder, H.A., Thompson, R., Calus, M.P.L., 2011. Genomic and pedigree-based genetic parameters for scarcely recorded traits when some animals are genotyped. J. Dairy Sci. 94, 4189–4197. https://doi.org/10.3168/jds.2011-4223.

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., François, R., Hester, J., 2019. Welcome to the Tidyverse. J. Open Source Softw. 4, 1686.

Ytrestøyl, T., Takle, H., Kolarevic, J., Calabrese, S., Timmerhaus, G., Rosseland, B.O., Terjesen, B.F., 2020. Performance and welfare of Atlantic salmon, Salmo salar L. post-smolts in recirculating aquaculture systems: Importance of salinity and water velocity. J. World Aquacult. Soc. 51, 373–392. https://doi.org/10.1111/jwas.12682.