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## Potential for genomic selection on feed efficiency in gilthead sea bream (*Sparus aurata*), based on individual feed conversion ratio, carcass and lipid traits

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1                   **Potential for genomic selection on feed efficiency in gilthead sea**  
2                   **bream (*Sparus aurata*) based on individual feed conversion ratio,**  
3                   **carcass and lipid traits**  
4

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8  
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## 14 **Abstract**

15 Genetic improvement of feed efficiency is key to improve the economic and environmental  
16 sustainability of fish farming. However, it requires individual phenotypes of feed efficiency which are  
17 difficult to obtain when fish are reared in groups, in tanks or cages. Here, we applied and validated on  
18 sea bream a method to evaluate individual feed efficiency based on individual rearing of fish in  
19 aquariums under restricted feeding. We also investigated the correlation between carcass and lipid  
20 traits with individual feed efficiency. We collected individual phenotypes of feed efficiency in  
21 aquariums on 538 sea breams (average weight = 54.50 g). Based on these individual phenotypes, fish  
22 (average weight = 174.6 g) were reared in groups of divergent phenotypes (high or low feed  
23 efficiency) during a period of 63 days in which the feed efficiency of each group was estimated. At the  
24 end of this group experiment, fish were harvested and yield traits were measured. All 538 fish, their  
25 parents as well as 794 sibs reared in cages in a production environment, were genotyped on a 57k SNP  
26 array to estimate genomic heritability and correlations between traits. We showed that feed efficiency  
27 was heritable and a GWAS analysis highlighted the polygenic architecture of feed efficiency. We also  
28 showed that feed efficiency was genetically correlated to viscera yield indicating that the most  
29 efficient fish had less viscera than the least efficient ones. Finally, over the 63 days period in groups,  
30 we confirmed that the groups composed of the efficient fish in aquariums were more efficient in group  
31 rearing than the groups composed of the least efficient fish in aquariums. Altogether, these results  
32 support that measuring individual feed efficiency in aquariums under restricted feeding may be used as  
33 a reliable phenotyping method to genetically improve feed efficiency, despite the bias intrinsically  
34 linked to individual rearing.

35

36 **Keywords:** fine phenotyping, selective breeding, aquaculture, genomic, restricted feeding, individual  
37 feed efficiency

## 38 Introduction

39

40 Improvement of the feed conversion ratio (FCR = Feed intake/bodyweight gain), which  
41 quantifies the ability of an animal to convert feed intake into biomass, is an important step in  
42 achieving sustainability in the aquaculture industry (Besson et al., 2016). In fish farming, the cost of  
43 feed ranges from 30 to 70% of the total production cost (Doupé and Lymbery, 2004; Kolstad et al.,  
44 2004). A decrease in the amount of feed needed per ton of fish produced would, therefore, be essential  
45 in enhancing economic sustainability. An example for Atlantic salmon is given by Kolstad et al.  
46 (2004), who state that an improvement in feed efficiency (FE) of 2-5% would save 8-20 million euros  
47 on feed costs in the production of salmon in Norway (considering 600 000 tons of feed consumed per  
48 year). From an environmental perspective, the improvement of FCR increases the proportion of  
49 nutrients converted into fish tissues, which reduces the load of nutrients to the environment at similar  
50 amount of whole fish produced. The production of feed is also a main contributor to the environmental  
51 impacts caused by fish production when analysed within a Life Cycle Analysis framework (Aubin et  
52 al., 2009). Therefore, improving feed efficiency would reduce the amount of feed needed per ton of  
53 fish produced, thus reducing the total environmental impacts per ton of fish produced, either on site  
54 with reduced eutrophication, or at a global scale with less resources consumed (Besson et al., 2017,  
55 2016).

56

57 Genetic improvement and breeding programs have shown their capacity to improve feed  
58 efficiency in livestock production (Knap and Kause, 2018; Willems et al., 2013). However, to be fully  
59 efficient, this option requires collecting individual data to estimate genetic parameters of the trait and,  
60 later on, to estimate breeding values to select the most efficient fish among selection candidates. The  
61 problem is that individual data of feed intake are difficult to obtain for fish living in large groups and  
62 in water. To solve this issue, we recently developed a method based on the rearing of several hundred  
63 fish in individual aquariums under restricted feeding (Besson et al., 2019). Indeed, studies on rabbits  
64 (Drouilhet et al., 2016, 2013) and pigs (Nguyen and McPhee, 2005) showed that selecting for faster  
65 growing animals under restricted feeding was an efficient method to improve feed efficiency in the  
66 next generations. With this method, applied on European sea bass (*Dicentrarchus labrax*), we reported  
67 that individual FCR and growth (measured as Daily Growth Coefficient - DGC) obtained in aquariums  
68 had a genetic basis ( $h^2 = 0.47$  and  $0.76$  respectively, Besson et al., 2019). Furthermore, we showed that  
69 groups of fish consisting of the best fish based on their individual FCR in aquarium (low FCR) were  
70 more efficient than groups of fish composed of the worst fish (high FCR) phenotyped in aquarium.  
71 These results suggest that selecting for fish based on their individual FCR measured under restricted  
72 feeding as proposed as in rabbit or pig would be possible, and would generate an improvement of FCR  
73 in fish reared in groups, which is the standard in the production environment.

74           This method of phenotyping fish in individual aquariums is promising but it is extremely  
75 tedious. In Besson et al. (2019) the phenotyping of 588 sea bass involved a full-time position  
76 dedicated to the daily routine of counting and cleaning uneaten pellets for 200 individually housed fish  
77 over 6 months. Therefore, finding correlated traits to individual feed efficiency that are easier to  
78 measure could enhance or even replace (if the genetic correlation with FCR is high enough) the  
79 selection of feed efficiency via individual phenotyping in aquarium. Gilbert et al. (2017) showed that  
80 nine generations of divergent selection on Residual Feed Intake (RFI, another measure of feed  
81 efficiency) in pigs yielded a favourable correlated response on dressing percentage and higher lean  
82 meat content, while showing a reduction in backfat and viscera weight. Therefore, this means that  
83 selecting on RFI would in fact select for animals that allocate more resources towards lean tissue (i.e.  
84 muscle and/or bones) rather than to fat tissue. This is because deposition of lipids is less efficient in  
85 terms of energy used per unit of wet weight gain than the deposition of protein (Knap and Kause,  
86 2018). Similarly, in broilers, genetic selection over half a century considerably increased carcass yield  
87 while at the same time reducing lipid content and improving feed efficiency (Havenstein et al., 2003a,  
88 2003b). Hence, in many breeding programs, selection for feed efficiency is achieved by indirect  
89 selection of leanest animals, which can be done using non-invasive technology easier to implement  
90 than direct measurement of feed intake (Knap and Wang, 2012). This principle has also been  
91 demonstrated for rainbow trout by Kause et al. (2016) who showed that the most efficient fish had a  
92 lower lipid percentage in the muscle than less efficient fish. Therefore, Knap and Kause (2018)  
93 suggested to select fish against lipid deposition to improve feed efficiency such as in Janhunen et al.  
94 (2017). However, Besson et al. (2019) could not establish any correlation between individual feed  
95 efficiency and intramuscular fat percentage measured indirectly by microwaves (Distell Fish  
96 FatMeter) in sea bass. Still, we know that lipid deposition in different parts of the body are genetically  
97 different traits (Kause et al., 2006; Tobin et al., 2006). In the sea bass, visceral fat has a low  
98 phenotypic correlation ( $r_p=0.31$ ), and no genetic correlation ( $r_g=-0.02 \pm 0.27$ ) with muscle fat (Saillant  
99 et al., 2009). In this species, visceral fat represents 66% of the total visceral weight and the percentage  
100 of viscera is highly phenotypically and genetically correlated to the percentage of visceral fat ( $r_p =$   
101  $0.92$  and  $r_g = 1.00$ , Saillant et al., 2009). A hypothesis therefore would be that selecting for lower  
102 visceral percentage could effectively improve feed efficiency because more resources would be  
103 directed towards muscle growth and because less lipids would be stored by the fish.

104

105           The gilthead sea bream (*Sparus aurata*) is the most important species of Mediterranean  
106 aquaculture, with 228.000 tonnes produced in 2018 (FAO, 2020). Feed efficiency is a key driver of  
107 profitability in this production, and several breeding programs are being operated in Europe, but none  
108 of them directly targets feed efficiency (Chavanne et al., 2016). Given the promising results recently  
109 obtained about selective breeding for individual feed efficiency in sea bass in aquariums (Besson et al.,  
110 2019), we also explore the feasibility of such selection in gilthead sea bream. Testing and validating

111 this method on sea bream would allow to confirm its interest to be more broadly applied in the  
112 aquaculture sector, as it would increase the genericity of this approach. Therefore, the aim of the  
113 present study was to evaluate the genetic basis of individual feed efficiency in gilthead sea bream, and  
114 to investigate the relationships between individual feed efficiency and carcass and adipose traits in this  
115 species.

116

117         To do so, we applied to gilthead sea bream the same method developed by Besson et al. (2019)  
118 on European sea bass to phenotype fish for their individual feed efficiency in individual aquaria. The  
119 animals were genotyped on a 60k SNP array. Then, we could estimate genetic parameters, identify  
120 potential quantitative trait loci (QTL) and assess the efficiency of genomic selection compared to  
121 pedigree-based selection for feed efficiency, when only few animals can be phenotyped. After  
122 collecting individual phenotypes of feed efficiency, we verified that these individual estimations were  
123 well linked to group feed efficiency. At the end of the experiment, the animals were finally harvested  
124 to estimate carcass yield and to estimate genetic correlations with feed efficiency. Finally, to estimate  
125 genetic correlations with the growth and yield performance of fish reared in commercial conditions in  
126 sea cages, a sib group was reared in a sea cage in Greece and harvested at commercial weight.

## 127 **Material and methods**

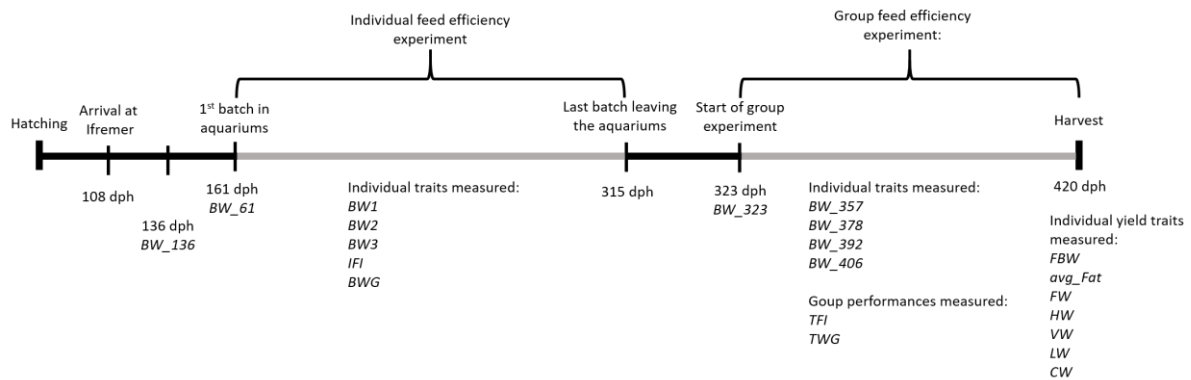
### 128 **Ethics statement**

129 The experiment was evaluated by the Ethical Committee n° 036 and authorized by the French Ministry  
130 of Higher Education, Research and Innovation (Authorization number APAFIS#12550-  
131 2015071718471859v9). All experimental procedures were conducted following the guidelines for  
132 animal experimentation established by Directive 2010-63-EU of the European Union and the  
133 corresponding French legislation.

134

### 135 **Animals, maintenance and summary of trials**

136 The sea bream originated from a partial full factorial mating design performed on the selected line of  
137 Les Fermes Marine du Soleil breeding company (La Brée-les-Bains, France). The general protocol to  
138 produce the families was similar that reported by Aslam et al. (2018). Artificial mating was performed  
139 within a day in September 2018, using 61 sires and 28 dams. Eggs from each dam were fertilized by  
140 10 to 11 different sires and each the semen of each sire fertilized oocytes from 4 to 5 dam. Maternal  
141 half-sib families were incubated separately between dams. After hatching, an equivalent number of  
142 larvae per dam were transferred in a single tank and reared in common environmental conditions. At  
143 91 days post-hatching, about 800 randomly selected sea bream (average body weight= 2.7 g) were  
144 tagged with Passive Integrated Transponders (PIT-tag) and individual fin sampling was performed for  
145 further DNA extraction, genotyping and parentage assignment. The fish were transferred at 108 dph to  
146 Ifremer in Palavas-les-Flots (France) and randomly split in 2 tanks of 1.5 m<sup>3</sup> in a recirculation system  
147 with natural salinity water kept at 20 °C. They were first individually weighed at 136 dph (BW\_136,  
148 mean weight = 17.21 g) and then at 161 dph (BW\_161, mean weight = 27.65 g). At 161 dph, we  
149 started the individual feed efficiency experiment in aquariums (details in “Evaluation of individual  
150 feed efficiency”). Then, at 323 dph, we started the group feed efficiency experiment (details in  
151 “Evaluation of group feed efficiency”). Finally, at 420 dph, fish were euthanized to measure  
152 production and yield traits (details in “Harvest traits”). The timeline of the experiment and a summary  
153 of traits measured are given in figure 1. For the entire experiment, we used a sea bream feed made by  
154 Sparos LDA (Olhão, Portugal). The composition of the feed is given in Appendix 1. The experimental  
155 feed was formulated to fulfil the sea bream nutritional requirements while minimizing the use of fish  
156 meal and fish oil in the diet.



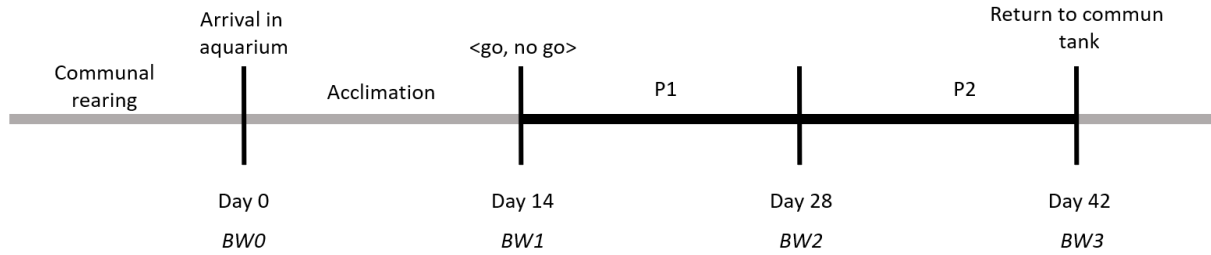
157  
 158 *Figure 1. Timeline of the experiment. Time is expressed in days post hatching (dph). BW refers to body weights, IFI is the*  
 159 *individual feed intake, BWG is the individual body weight gain, TFI is the feed intake of tanks, TWG is the weight gain of*  
 160 *tanks. FBW = final body weight, avg\_Fat = average muscle fat content using Distell Fatmeter, FW = fillet weight, HW = head*  
 161 *weight, VW = viscera weight (except liver), LW = liver weight, CW = carcass weight.*

162 In addition, a group of 1530 sibs was transferred to a 150 m<sup>3</sup> cage in Greece at 128 dph. These fish  
 163 were fed a standard feed (SMART from Irida S.A.). They were reared until 432 dph, when they were  
 164 harvested, and individual fin sampling was performed for further molecular-based parentage  
 165 assignment.

### 166 **Phenotyping individual feed efficiency**

167 For the measurement of individual feed efficiency two hundred 10 L aquariums were used in a  
 168 recirculation system where natural salinity sea water was kept at a temperature of 20 °C. Before the  
 169 start of individual rearing, at 161 dph, the length and weight of all sea bream were measured. At 161  
 170 dph, a first batch of 150 fish was randomly split in the aquariums. After 14 days of acclimation in  
 171 isolation, the fish were weighed again in a “go, no go” step. Fish that lost weight during this  
 172 acclimation period were removed from the aquariums and returned to the 1.5 m<sup>3</sup> communal tanks,  
 173 considering they were not adapted to the individual evaluation system. The fish that gained weight  
 174 during the acclimation period were kept in aquariums for two more periods of 14 days each. In total, a  
 175 “successful” fish stayed 42 days in aquarium and was weighed four times (Figure 2). To reach the  
 176 maximum capacity of the facility (200 fish), new batches of fish were introduced in the aquariums  
 177 every two weeks to replace the fish that did not pass the “go, no go” biometry or the ones that  
 178 completed the 42 days trial. The phenotyping of the first batch of fish started at the age of 161 dph  
 179 (mean weight = 38.41 g for this 129 first fish) while the last batch started at 273 dph (mean weight =  
 180 61.99 g). Before and after the trial in aquariums, the fish were kept in the 1.5 m<sup>3</sup> communal tanks.





181  
182 *Figure 2. Timeline of the individual feed efficiency experiment. BW refers to body weights.*

183 Individually reared sea breams were fed once in the morning with an automatic feeder. Each day, 3  
184 mm feed pellets were delivered at a rate of 1.54% (corresponding to 70% of a standard feeding rate) of  
185 an individual's body weight (fish body weight range: 9.4 - 114.9g), re-evaluated at the beginning of  
186 each 14 days period. Fish were fed once in the morning with an automatic feeder. One and a half hours  
187 after feed delivering, uneaten pellets were counted and removed from the aquariums. Each day, for  
188 each fish, the total number of uneaten pellets eaten was converted into grams (1 pellet  $\approx$  0.01814 g)  
189 and subtracted to the fixed ration to estimate daily individual feed intake.

190 Among the 669 fish tested in the aquariums, 103 fish lost weight during the acclimation period. The  
191 remaining 566 sea bream completed the 42 days of individual evaluation. For these fish, the cumulated  
192 FCR (FCR), and the cumulated DGC (daily growth coefficient) were calculated:

193

194 
$$FCR = \frac{IFI}{BWG}$$

195

196 
$$DGC = \frac{BW3^{\frac{1}{3}} - BW1^{\frac{1}{3}}}{N\_DAYS} \cdot 100$$

197

198 Where BWG is the body weight gain measured over periods 1 and 2 (BW3-BW1) and IFI the  
199 cumulated individual feed intake in periods 1 and 2. N\_DAYS is the number of feeding days of  
200 periods 1 and 2 (23 or 24 days). Due to the skewed distribution of the data, DGC and FCR were log  
201 transformed to obtain log(DGC) and log(FCR). Additionally, we calculated the residual body weight  
202 gain (rBWG) as:

203

204 
$$rBWG = BWG - (\beta_0 + \beta_1 \times MBW_i + \beta_2 \times IFI)$$

205

206 MBW<sub>i</sub> is the initial metabolic body weight (BW1<sup>0.8</sup>).  $\beta_0$  is the regression intercept,  $\beta_1$  is the partial  
207 regression coefficient of animal's BWG on metabolic weight and  $\beta_2$  is the partial regression  
208 coefficient of animal's BWG on total feed intake.

209

## 210 **Evaluation of group feed efficiency**

### 211 *Group constitution*

212 Among the 538 fish well phenotyped in aquarium, we excluded fish with strong spinal malformations  
213 (N=80), with a negative cumulated FCR or FCR higher than 2.8. The 458 remaining fish were grouped  
214 following the procedure of Besson et al., (2019) in two steps:

215 - First, we made 7 groups of each 64 or 66 fish based on their relative daily feed intake  
216 (relative\_DFI) calculated as:

$$217 \text{ relative\_DFI} = \frac{\text{IFI}}{\text{BW1} \times \text{N}_{\text{DAYS}}} \cdot 100$$

218  
219 - Second, within each group of 64-66 fish with similar DFI we divided the fish into two  
220 subgroups of 32 or 33 individuals, depending on the fact that their relative BWG ((BW3-  
221 BW1)/BW1) was higher (subgroup A) or lower (subgroup B) than the median of that group.  
222 Thus, the fish in subgroups A had a better (lower) FCR than their counterparts from subgroup  
223 B.

224  
225 The aim of this grouping strategy was to compare groups of efficient fish to groups of less efficient  
226 fish at the same relative feed intake in aquarium. In total, 14 groups of 32 or 33 fish were distributed in  
227 14 tanks of 2 m<sup>2</sup> covered by black plastic to reduce the amount of stress.

### 229 *Experimental protocol*

230 The group feed efficiency experiment started at the age of 323 dph (average weight = 176.4 g) and  
231 lasted a total of 77 days in a recirculation system where water temperature was set between 22 and  
232 23°C, with a 12L:12D photoperiod. First, 14 days were used for acclimation to the new environment,  
233 followed by one recording period of 21 days and 3 periods of 14 days. In each period, fish were not  
234 fed on the day of the biometry and two days before, and thus received 18 or 11 meals. On feeding  
235 days, fish were fed *ad libitum* with an automatic feeder delivering the daily ration in 20 portions  
236 between 5.30 a.m. and 8.35 a.m. The frequency of delivery was every 4 min for the first 10 portions,  
237 every 10 min for the following 5 portions, and then every 20 min for the last 5 portions. We used 4  
238 mm pellet size for this experiment. All uneaten pellets were collected in a faecal trap. At the end of the  
239 automatic delivery, if no pellets were found, additional feed was given via a manual trigger until first  
240 pellets were collected in the faecal trap, meaning *ad libitum* was reached. Then, 60 minutes after  
241 feeding, all uneaten pellets were recovered, washed, photographed and analysed with the program  
242 ImageJ and the function “analyze particles” (Abràmoff et al., 2004). The picture was taken using  
243 backlighting with a 60x60 cm LED panel. This procedure allowed us to estimate the total surface  
244 covered by pellets on each photo measured in number of pixels. We chose to work with surface of  
245 pixels covered rather than the number of pellets because, after few hours in water, some pellets were

246 too soft and tented to break. Counting pellets would have resulted in an overestimation of the number  
247 of uneaten pellets, and then an underestimation of feed intake and feed conversion ratio.

248 The downside of working with surface of pixels is that the estimation depends on the focus of the  
249 camera which, in our case, was adapted every day. Hence, to avoid bias in the counting of pixels, we  
250 included a 5 cents euro coin on every photo (21.25 mm of diameter). Then, the surface of pixels  
251 occupied by pellets was divided by the number of pixels occupied by the coin to measure the surface  
252 of pellets in unit of coin surface. To convert a unit of coin surface into number of pellets, we took  
253 photos of eight batches of 200 pellets which gave us the average number of pellets per unit of coin  
254 surface. Finally, given the average weight of a single pellet, we could estimate the amount of uneaten  
255 feed per day and per period. Feed intake per tank (TFI) was calculated as the difference between the  
256 quantity of feed distributed and the quantity of uneaten feed over a certain period of time. All feeders  
257 were filled with a known quantity of feed at the start of a period, and were emptied to weigh the  
258 remainder feed at the end of each period, thus the amount of feed distributed per tank over the period  
259 could be precisely recorded.

260

#### 261 *Individual and group data available in the group experiment*

262 All fish were weighed at the start of the experiment and at the end of each period. Thus, five body  
263 weight measurements were available for each fish. The measurements of all fish in a tank were added  
264 to calculate total weight gain for each tank and for each period of test (TWG). Then, from TWG we  
265 could calculate the TFCR per tank per period of test as:

266

$$267 \quad \text{TFCR} = \frac{\text{TFI}}{\text{TWG}}$$

268 Where TFI is the feed intake of a given tank.

269

#### 270 *Statistical analysis*

271 To test potential difference in TFCR between subgroups A and B we used a two-sided paired t-test.  
272 This was done within each of the four periods and for the combined period. Then, as the mean weight  
273 of fish in a tank could affect TFCR, we also analysed body weight gain in each tank, corrected for feed  
274 intake and metabolic body weight in an ANCOVA analysis:

275

$$276 \quad \text{avg\_TWG}_{ij} = \beta_0 + \text{subg}_i + \beta_1 \times \text{avg\_MBW}_{ij} + \beta_2 \times \text{avg\_FI}_{ij} + \varepsilon_{ij}$$

277

278 Where  $\text{avg\_TWG}_{ij}$  is the average body weight gain of a fish (TWG divided by the number of fish in  
279 the tank) from subgroup  $i$  in tank  $j$  during a predefined period.  $\text{subg}_i$  is the effect of subgroup A or B  
280 ( $i=1, 2$ ).  $\text{avg\_MBW}_{ij}$  is the mean metabolic body weight of the fish in the same tank at the start of the  
281 period,  $\text{avg\_FI}_{ij}$  is the average feed intake of one fish in the same tank (TFI divided by the number of

282 fish in the tank) and  $\epsilon_{ij}$  is the random residual.  $\beta_0$  is the regression intercept,  $\beta_1$  is the partial regression  
283 coefficient of  $\text{avg\_TWG}_{ij}$  on  $\text{avg\_MBW}_{ij}$  and  $\beta_2$  is the partial regression coefficient of  $\text{avg\_TWG}_{ij}$  on  
284  $\text{avg\_FI}_{ij}$ .

285

## 286 **Phenotyping harvest traits**

### 287 *Harvest traits on experimental fish*

288 After the group experiment, at the age of 420 dph, fish were euthanized with an overdose of  
289 benzocaine (150 mg/l). Then, we measured several harvest traits:

- 290 - Harvest weight (Harvest\_W)
- 291 - Average muscle fat content from one measure on both sides of the fish using a Distell fatmeter  
292 (avg\_Fat) according to Haffray et al. (2005)
- 293 - Left fillet weight (ribs and skin on)
- 294 - Half headless carcass weight (weight of the headless carcass after the left fillet was removed)
- 295 - Head weight (Head\_W)
- 296 - Viscera weight (Viscera\_W without liver)
- 297 - Liver weight (Liver\_W)

298 From those base data, we calculated:

- 299 - Fillet weight (Fillet\_W), calculated by multiplying the weight of left fillet by two
- 300 - Headless carcass weight (HC\_W) representing the sum of the weight the left fillet and of the  
301 half carcass.

302

### 303 *Harvest traits on sea-caged reared sibs*

304 Additionally, 1112 fish from the same families reared in cages in Greece were harvested at 432 dph  
305 using ice. We measured:

- 306 - Harvest weight (Harvest\_W\_cage)
- 307 - Fat content (avg\_FAT\_cage) as reported above
- 308 - Viscera weight (Viscera\_W\_cage)
- 309 - Headless carcass weight (HC\_W\_cage)

## 310 **Genetic analysis**

### 311 *Genotyping and parentage assignment*

312 We genotyped the 89 parents and 750 offspring of sea bream of the “individual feed efficiency”  
313 groups using the ThermoFisher SaurChip sea bream array of 60k SNP markers (Griot et al., 2021).  
314 SNP calling was done using ThermoFisher software AxiomAnalysisSuite™. Preliminary quality  
315 controls were applied with threshold values of 95% for SNP call rate and 90% for sample call  
316 rate. We could keep 50,417 effective SNP on 740 sea bream and their 89 parents. Then, we used a  
317 subset of 1,000 highly polymorphic SNP to retrieve the pedigree of the individuals using the R  
318 package APIS (Griot et al., 2020). 719 fish out of 740 could successfully be linked to a single parental  
319 pair (97.2%). For the group of fish sent to cages, among the 1112 fish harvested, 794 were genotyped  
320 on the same SNP array and all (100%) were successfully assigned to their parents.

321

### 322 *Genetic parameters*

323 Variance components for all traits were computed based on multivariate linear mixed animal models.  
324 In these multivariate models, three traits were included and we always included BW<sub>136</sub> as a  
325 “reference trait” as it has been measured on all animals of the individual feed efficiency group at the  
326 same time.

327 For traits measured in aquariums (log(FCR), log(DGC) and rBWG), fixed effects were the initial  
328 rearing tank (A or B), the batch (referring to the group of fish which started the phenotyping in  
329 aquarium together, 9 batches) and the deformities (presence or absence).

330 For all yield traits measured at harvest on experimental fish (Fillet<sub>W</sub>, Head<sub>W</sub>, Viscera<sub>W</sub> and  
331 HG<sub>W</sub>) and on cage-reared sibs (Viscera<sub>W\_cage</sub> and HC<sub>W\_cage</sub>), final body weight was always  
332 included (Harvest<sub>W</sub> or Harvest<sub>W\_cage</sub>) as covariable in the model following practice from  
333 Kennedy et al. (1993) and Vandeputte et al. (2020). To highlight the fact that these regressed traits  
334 were representative of yields (weight of the body part adjusted to body weight), they were noted as  
335 rFillet<sub>W</sub>, rViscera<sub>W</sub>, rHC<sub>W</sub>, with r standing for “residual”.

336 The models were fitted by restricted maximum likelihood in AIREMLF90 (Miszta et al., 2002) to  
337 compute the classical heritabilities using pedigree and the genomic heritabilities using SNP data. We  
338 considered significant all correlations with an associated standard error lower than half the absolute  
339 value of the correlation. We applied the same rule for heritabilities.

340

### 341 *Breeding values*

342 The breeding values were also computed with classical pedigree-based BLUP (PBLUP) and genomic  
343 BLUP (GBLUP) using the genomic relationship matrix. The conventional pedigree-based EBVs were  
344 estimated using the following model:

$$345 \quad y = Xb + Zu + e$$

346 Where  $\mathbf{y}$  is the vector of phenotypes,  $\mathbf{b}$  is the vector of fixed effects (batch, rack, line and column for  
347 the phenotypes measured in aquariums) and  $\mathbf{X}$  an appropriate incidence matrix,  $\mathbf{u}$  is the vector of  
348 random additive genetic animal effects,  $\mathbf{Z}$  the appropriate incidence matrix and  $\mathbf{e}$  is vector of random  
349 error variance. The additive (animal) genetic effects were assumed to follow  $N(\mathbf{0}, V \otimes A)$ , with  $\mathbf{V}$  the  
350 genetic (co) variance matrix between traits and  $\mathbf{A}$  the numerator relationship matrix relating all  
351 animals in the pedigree, while the residual effects were assumed to follow  $N(\mathbf{0}, R \otimes I)$ ,  $\mathbf{R}$  the residual  
352 (co) variance matrix between traits and  $\mathbf{I}$  an appropriate identity matrix. To estimate the SNP based  
353 EBV (GEBV) we used GBLUP method where the relationships between fish are based on the genomic  
354 relationship matrix described by VanRaden (2008) ( $\mathbf{G}$  matrix) instead of the classical pedigree-based  
355 relationship matrix ( $\mathbf{A}$  matrix).

356

### 357 *GWAS*

358 We used the BLUPF90 suite of programs to perform GWAS under multi-marker linear regression  
359 models using GBLUP for individual feed efficiency traits (rBWG, log(FCR) and log(DGC)). The  
360 breeding values were estimated with BLUPF90 using the linear model described in the previous  
361 section. The p-values were obtained from POSTGSF90 (Aguilar et al., 2019). The  $-\log_{10}$  of the p-  
362 values were compared to the chromosome-wide significance threshold and to the genome-wide  
363 significance threshold at 5% after Bonferroni correction for the average number of markers per  
364 chromosome and the total number of markers, respectively.

365

### 366 *Estimation of accuracy via cross validation*

367 To assess the potential interest of using genomic information for the genetic selection of feed  
368 efficiency traits, we performed cross-validation tests and estimated the accuracies of PBLUP and  
369 GBLUP models. These accuracies were assessed using a cross validation scheme which followed four  
370 steps:

371

- 372 1) First, we estimated the corrected phenotypes ( $Y$ ). In this step, all performances recorded for  
373 rBWG were corrected for fixed effects using the PREDICTF90 software.
- 374 2) Second, we estimated the EBV for rBWG of all 516 fish while masking the phenotypes of a  
375 validation group composed of 20% of the fish (103 fish with phenotypes set missing). The  
376 EBVs were estimated with a bivariate model including rBWG and BW\_136 (weight at 136  
377 dph) using the BLUPF90 program. Here, on the same validation group set, we estimated  
378 GEBVs with genomic information in a GBLUP model and the EBVs (only with pedigree  
379 information) in a PBLUP model.
- 380 3) Then, we calculated the correlation between corrected phenotypes ( $Y$ ) and predicted EBV  
381 ( $r_{EBV,Y}$ ) for the 103 fish of the validation group.

382 4) The accuracies ( $R_{EBV,BV}$ ) of PBLUP and GBLUP models was estimated using the following  
383 formula:

384 
$$R_{EBV,BV} = \frac{r_{EBV,Y}}{\sqrt{h_{ped}^2}}$$

385 Where  $h_{ped}^2$  is the heritability of rBWG estimated using pedigree including all fish with phenotypes.

386 5) Finally, all steps from 2) were repeated 50 times to get 50 estimates of accuracy for GBLUP  
387 and PBLUP models. Each time, another 103 fish were randomly picked with phenotypes set to  
388 missing. We reported the average accuracy and its standard error.

389 **Results**

390 **Individual feed efficiency in aquarium**

391 *Phenotypic and genetic parameters*

392 We could obtain 538 reliable phenotypes from fish in the experiment in individual aquariums. The fish  
 393 with reliable phenotypes were all fish with an FCR\_tot below 2.8. This number includes fish with  
 394 deformities (N = 74). Among those 538 fish, 520 were successfully assigned to their parents and used  
 395 to estimate phenotypic and genetic parameters. Basic phenotypic statistics are given in table 1.

396

397 *Table 1. Summary of individual phenotypes measured in aquariums on the 537 fish with reliable phenotypes. ADG refers to*  
 398 *average daily gain during P2 and P3 periods of individual phenotyped. FCR\_tot is the feed conversion ratio over P2 and P3.*  
 399 *DGC is the daily growth coefficient over P2 and P3.*

Trait	Mean	Median	s.d.	CV
ADG_P2 (in % of body weight per day)	0.94	0.97	0.27	29.2 %
ADG_P3 (in % of body weight per day)	0.94	0.98	0.28	30.5 %
FCR_tot	1.3	1.19	0.35	26.8 %
DGC	1.17	1.22	0.28	24.0 %

400

401 The genomic heritabilities estimated for individual feed efficiency traits were moderate, ranging from  
 402 0.17 to 0.25 (table 2). It was also clear that, in these conditions of restricted feeding in individual  
 403 aquarium log(FCR) and log(DGC) were strongly negatively correlated ( $r = -0.93$ ). A similar strong  
 404 negative phenotypic correlation was also observed between log(FCR) and rBWG ( $r = -0.86$ ). These  
 405 results at phenotypic level were confirmed by the strong genomic correlations between all three traits  
 406 (table 2).

407 *Table 2. Heritabilites and genomic correlations between individual feed efficiency traits. Heritabilites are on the diagonal,*  
 408 *genomic correlations above the diagonal and phenotypic correlations below the diagonal. Standard error of estimates*  
 409 *between brackets.*

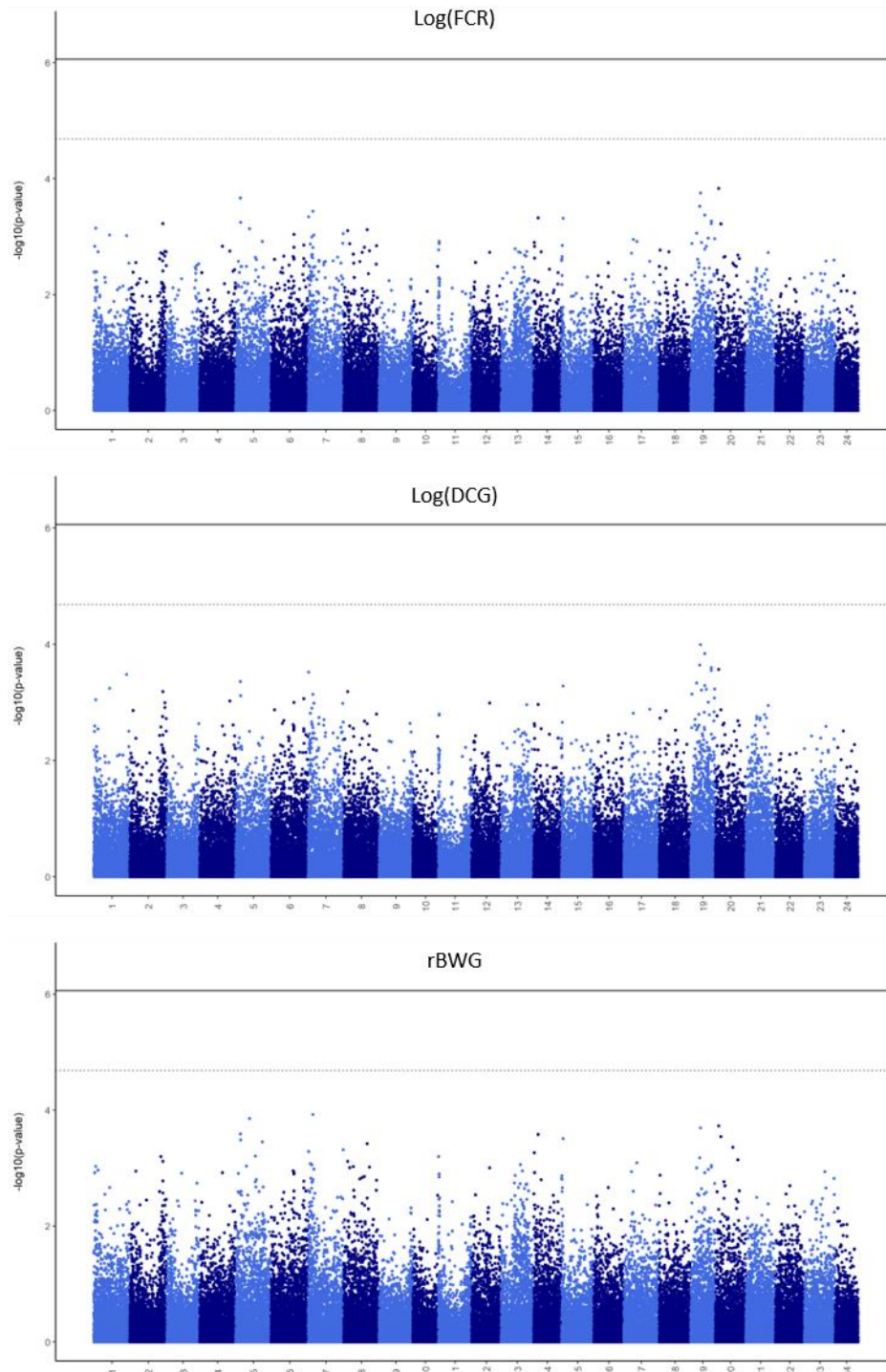
	log(FCR)	log(DGC)	rBWG
log(FCR)	0.20 (0.07)	-0.93 (0.56)	-0.95 (0.16)
log(DGC)	-0.93	0.17 (0.06)	0.90 (0.17)
rBWG	-0.86	0.70	0.25 (0.07)

410



411 *GWAS*

412 In the GWAS performed by GBLUP analysis, there were no markers with a p-values above the  
413 genome-wide significance threshold nor above the chromosome-wide threshold for log(FCR),  
414 log(DGC) or (rBWG) (Figure 3).

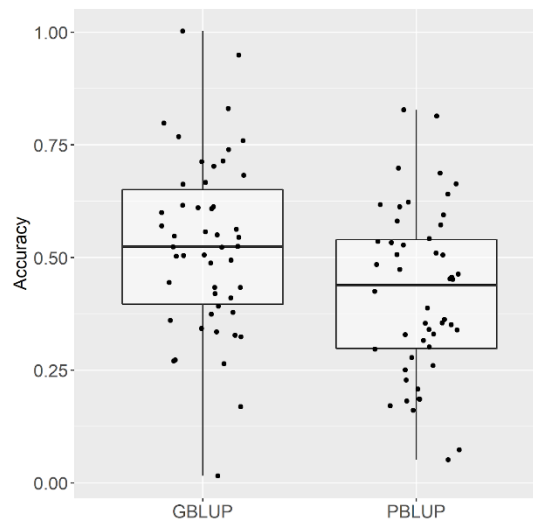


415

416 *Figure 3. Manhattan plot of  $-\log_{10}(\text{p-value})$  obtained by GWAS for log(FCR), log(DGC) and rBWG (from top to bottom). The*  
417 *horizontal full black line represents the genome-wide significance threshold while the dashed black line represents the*  
418 *chromosome-wide significance threshold calculated with the Bonferroni correction.*

419 *Accuracy of GBLUP VS PBLUP*

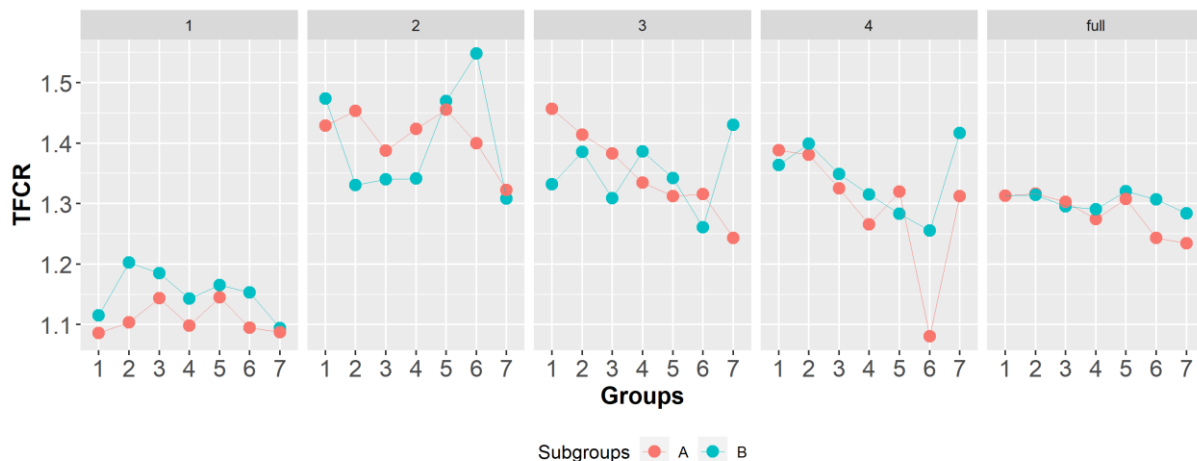
420 The correlations between corrected phenotypes and predicted EBV ( $r_{EBV,Y}$ ) for rBWG were 0.25 for  
 421 the GBLUP model and 0.20 for the PBLUP model. Consequently, as the pedigree heritability for  
 422 rBWG was 0.22, the corresponding accuracies were 0.53 for the GBLUP model and 0.42 for the  
 423 PBLUP model (Figure 4). A pairwise t-test showed that the difference in accuracy between GBLUP  
 424 and PBLUP models was significant ( $t_{49} = 6.1896, p < 0.001$ ).



425  
 426 *Figure 4. Boxplot of accuracy of GBLUP and PBLUP models for rBWG considering 50 runs with a validation group of 103 fish.*

427 **Feed efficiency in groups and growth rates across experiments**

428 First, we compared the TFCR of the tanks from subgroup A and of the tanks from subgroup B for the  
 429 five periods (four single periods and the full period) using a paired sample t-test. We showed a  
 430 significant difference for the first period ( $t_6 = - 3.035, p = 0.023$ ). In that period, subgroup B  
 431 (composed of individuals with bad FCR in aquarium) had a higher FCR than subgroup A (composed  
 432 of individuals with good FCR in aquarium). It meant that tanks of subgroups B were less efficient than  
 433 tanks of subgroup A (Figure 5). We did not find significant differences for the other periods (period 2:



434  $t_6 = - 0.14, p = 0.89$ , period 3:  $t_6 = - 0.011, p = 0.99$ , period 4:  $t_6 = - 1.50, p = 0.18$ ). In those periods,

*Figure 5. Results of TFCR for each tank for the four period of test plus the full period of 9 weeks. On the x-axis is the group of the tanks and the colors refers to the subgroups A (in red, tanks composed of fish with good FCR in aquariums) or B (in green, tanks composed of fish with bad FCR in aquariums).*

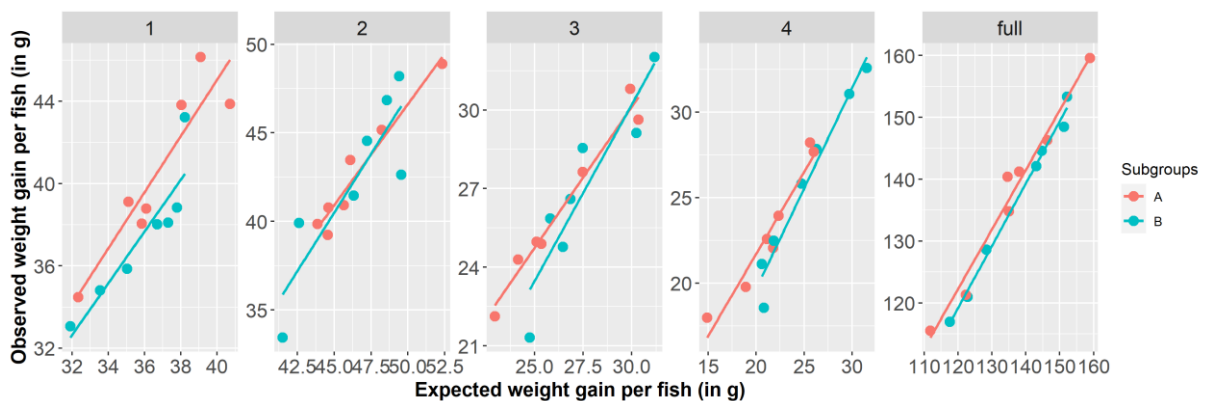
435 there was always at least one tank of subgroup B that had better FCR than the corresponding tank of  
 436 subgroup A (Figure 5). When all periods were combined, we also did not find significant differences  
 437 ( $t_6 = -1.68$ ,  $p = 0.14$ ) in TFCR between subgroup A and subgroup B.

438

439 To account for a possible effect of mean metabolic body weight on TFCR, body weight gain in each  
 440 tank was evaluated for each subgroup, after adjustment for feed intake and metabolic body weight, in  
 441 an analysis of covariance. This showed that there was a significant effect of subgroup on body weight  
 442 gain during the first period ( $F_{1,10} = 6.09$ ,  $p = 0.033$ ) and the full period of 9 weeks ( $F_{1,10} = 6.26$ ,  $p =$   
 443  $0.031$ ). For those periods, the fish in tanks from subgroups A showed a higher body weight gain than  
 444 fish from subgroups B, once corrected for the effect of feed intake and metabolic body weight (Figure  
 445 6). Hence, tanks of subgroups A were more efficient over the period of nine weeks. However, for  
 446 periods 2, 3 and 4, there was no significant effect of subgroups on TFCR.

447

Figure 6. Regression of observed body weight gain on expected body weight gain (estimated from feed intake and metabolic body weight) in tanks with fish from subgroups A (low individual FCR) and B (high individual FCR). The left panel show the regression for the first period of the experiment while the right panel show the regression for the full experimental period of 9 weeks. The solid line is the linear regression and the color refers to the subgroups of each tanks.



448

449

450 Finally, we calculated the phenotypic and genomic correlations between DGC measured between 136  
 451 and 161 dph ( $\log(\text{DGC}_{\text{juv}})$ ), DGC measured in aquariums ( $\log(\text{DGC})$ ) and DGC measured during  
 452 the 9 weeks of the group experiment ( $\log(\text{DGC}_{\text{group}})$ ). First, the heritabilities of the three growth

453 rates where moderate (Table 3). Second, due to high standard error, none of the genomic correlations  
 454 were significant, although they were much higher than the phenotypic correlations, which were all  
 455 close to zero (Table 3). Only the phenotypic correlation between DGC\_juv and DGC\_group was  
 456 found significant, but was surprisingly negative ( $r = -0.17$ ,  $F_{1,427} = 4.521$ ,  $p = 0.0003$ ).

457

458 *Table 3. Heritabilities and genomic correlations between growth rates across experiments. Heritabilities are on the diagonal*  
 459 *and genomic correlation are above the diagonal.*

	log(DGC_juv)	log(DGC)	log(DGC_group)
log(DGC_juv)	0.15 (0.05)	-0.02 (0.38)	-0.44 (0.32)
log(DGC)		0.17 (0.06)	0.76 (0.48)
log(DGC_group)			0.21 (0.07)

465

#### 466 **Harvest traits and individual feed efficiency on experimental fish**

467 Harvest traits could be measured on 451 fish previously phenotyped for their individual feed  
 468 efficiency performances in aquarium. The phenotypic results for each trait are presented in table 4.

469

470 *Table 4. Summary of phenotypes measured at harvest.*

Fish group	Trait	Mean	CV
Fish with individual feed efficiency phenotypes (n = 451)	Harvest_W	363.0 g	20.2 %
	avg_FAT	9.5%	26.3 %
	Fillet_W	207.1 g	22.2 %
	HC_W	251.9 g	21.7%
	Head_W	81.3 g	17.5 %
	Viscera_W	14.9 g	28.9%
Cage-reared sibs	Harvest_W_cage	330.8 g	22.5 %
	avg_FAT_cage	12.8%	27.7%
	Viscera_W_cage	28.5 g	31.1%
	HC_W_cage	232.4 g	24.0 %

471

472 Among harvest traits measured on experimental animals in sea cage, the strongest phenotypic  
 473 correlations were observed between Harvest\_W and avg\_fat ( $r = 0.58$ ,  $F_{1,432} = 224.1$ ,  $p < 0.001$ ),  
 474  $r_{Fillet\_W}$  and  $r_{Head\_W}$  ( $r = -0.70$ ,  $F_{1,432} = 451.1$ ,  $p < 0.001$ ) and between  $r_{Carcass\_W}$  and  
 475  $r_{Viscera\_W}$  ( $r = -0.74$ ,  $F_{1,432} = 528.1$ ,  $p < 0.001$ ). All harvest traits displayed moderate to high  
 476 heritability (table 5).

477

478 *Table 5. Heritabilities and genomic correlations between harvest traits measured on the experimental fish. Heritabilities are*  
 479 *underlined on the diagonal and genomic correlation are above the diagonal. In bold only are the genetic correlations close*  
 480 *to significance.*

	rBWG	BW_136	Harvest_W	avg_FAT	rFillet_W	rHC_W	rHead_W	rViscera_W
rBWG	<u>0.25 (0.07)</u>	0.11 (0.22)	0.41 (0.25)	-0.17 (0.34)	-0.04 (0.35)	0.13 (0.26)	0.25 (0.30)	<b>-0.41 (0.22)</b>
BW_136	-0.10	<u>0.43 (0.06)</u>	<b>0.56 (0.13)</b>	0.32 (0.21)	-0.29 (0.23)	-0.18 (0.20)	0.35 (0.21)	0.07 (0.15)
Harvest_W	0.23	0.60	<u>0.26 (0.07)</u>	0.21 (0.32)	-0.49 (0.32)	<b>-0.51 (0.25)</b>	<b>0.81 (0.23)</b>	0.23 (0.21)
avg_FAT	0.007	0.36	0.59	<u>0.24 (0.08)</u>	0.03 (0.46)	0.24 (0.41)	0.14 (0.68)	0.26 (0.24)
rFillet_W	-0.15	-0.08	0	0.32	<u>0.21 (0.07)</u>	<b>0.95 (0.12)</b>	<b>-0.99 (0.12)</b>	-0.29 (0.24)
rHC_W	0.03	0.03	0	0.03	0.40	<u>0.29 (0.08)</u>	-0.92 (0.70)	<b>-0.51 (0.22)</b>
rHead_W	0.17	0.11	0	-0.31	-0.70	0.03	<u>0.25 (0.07)</u>	0.24 (0.35)
rViscera_W	-0.11	-0.06	0	0.01	-0.19	-0.75	-0.1	<u>0.44 (0.07)</u>

481 Furthermore, weak but significant phenotypic correlations were observed between Harvest\_W and  
 482 rBWG ( $r = 0.23$ ,  $F_{1,432} = 23.94$ ,  $p < 0.001$ ), rFillet\_W and rBWG ( $r = -0.15$ ,  $F_{1,432} = 9.808$ ,  $p = 0.001$ ),  
 483 rHead\_W and rBWG ( $r = 0.17$ ,  $F_{1,432} = 11.54$ ,  $p < 0.001$ ) and between rViscera\_W and rBWG ( $r = -$   
 484  $0.11$ ,  $F_{1,432} = 5.686$ ,  $p = 0.017$ ) (table 5). However, only few genomic correlations were not statistically  
 485 different to zero. For the first time in this species, we report a very high genetic correlation between  
 486 rFillet\_W and rHC\_W ( $r_g = 0.95 \pm 0.12$ ). We found a close to significance negative genetic correlation  
 487 between rBWG measured in aquariums and rViscera\_W ( $r_g = -0.41 \pm 0.22$ ). It means that the most  
 488 efficient fish had less viscera (and hence less visceral fat) than less efficient fish at the same weight.  
 489 Although not significant, the genetic correlation between rBWG and muscle fat measured with the  
 490 Distell fatmeter was also negative ( $r_g = -0.17 \pm 0.34$ ). Finally, the genomic correlation between  
 491 Harvest\_W and rBWG ( $r_g = 0.41 \pm 0.25$ ) was positive and close to significance.

#### 492 **Harvest traits and individual feed efficiency on cage-reared sibs**

493 The genetic parameters are shown in Table 6. Although none of the traits was significantly genetically  
 494 correlated with feed efficiency (measured as rBWG), the signs of the correlations of sib traits with  
 495 rBWG were similar to those of the traits recorded on the feed efficiency animals themselves. The  
 496 correlation was positive with Harvest\_W\_cage (0.22) and rHW\_cage (0.55), and negative with  
 497 avg\_FAT\_cage (-0.20) and rVisceral\_W\_cage (0.17).

498

499 *Table 6. Heritabilities and genomic correlations of processing traits on cage-reared sibs with individual residual body weight*  
 500 *gain measured in aquariums. Heritabilities are on the diagonal and genomic correlations are above the diagonal. Genetic*  
 501 *correlations significantly different from zero in bold.*

	rBWG	Harvest_W_cage	avg_fat_cage	rHC_W_cage	rVisceral_W_cage
rBWG	0.23 (0.07)	0.22 (0.56)	-0.20 (0.35)	0.55 (0.44)	-0.17 (0.34)
Harvest_W_cage		0.23 (0.08)	<b>0.59 (0.24)</b>	<b>0.98 (0.12)</b>	<b>0.68 (0.18)</b>
avg_fat_cage			0.25 (0.08)	0.16 (0.48)	0.002 (0.25)
rHC_W_cage				0.16 (0.07)	<b>-0.67 (0.31)</b>
rVisceral_W_cage					0.48 (0.1)

502

## 503 Discussion

504

505 Investigating the genetic background of feed efficiency in fish started in the 90s. However, measuring  
506 individual feed efficiency of fish living in groups in a 3D water column is not an easy task, because  
507 phenotyping for individual feed intake in such conditions is not straightforward. If selective breeding  
508 for growth rate (which is done in virtually all breeding programs) would generate indirect selection  
509 gain in feed efficiency, that would make genetic improvement of feed efficiency feasible without  
510 going into complex methods to evaluate individual feed intake. Although all studies performed so far  
511 on selection for growth agreed that selection for growth rate in fish leads to animals with higher feed  
512 intake, the link between the increase in growth rate and the improvement of feed efficiency remains  
513 uncertain with some studies showing positive association, while others show no association between  
514 growth rate and feed efficiency (Ogata et al., 2002; Sanchez et al., 2001; Silverstein et al., 2005;  
515 Thodesen et al., 1999; Yamamoto et al., 2015). It is therefore likely that feed conversion ratio and  
516 growth rate are either not correlated or weakly negatively correlated (a negative correlation of growth  
517 and FCR implies that selecting for fast growth will reduce FCR and thus improve feed efficiency).  
518 When feed conversion ratio and growth rate have a genetic correlation comprised between 0 and -0.45,  
519 integrating a specific evaluation of FCR in a breeding program would largely improve economic  
520 returns and reduce environmental impacts, while if the correlation is more strongly negative (<0.45),  
521 selecting only for growth also provides the benefits of improved feed efficiency (Besson et al., 2020).  
522 Developing an efficient method of phenotyping individual feed efficiency is thus essential to breed for  
523 more efficient fish without being dependent on the potential correlation that feed efficiency could have  
524 with growth rate.

525

526 In this regard, the method we developed using restricted feeding of fish in individual aquariums is  
527 promising. We were able to phenotype more than 500 sea bream over a period of 5 months. The  
528 phenotyping of 500 juvenile European sea bass was already achieved by Besson et al. (2019) in this  
529 system, and thus we showed that it was reproducible for another fish species. Individual FCR values  
530 measured for sea bream were in the same range as the ones obtained on sea bass, with a mean of 1.30  
531 while it was 1.38 in the sea bass experiment (Besson et al., 2019). The heritability of individual FCR  
532 was moderate (0.16) but lower than other heritability estimates for individual FCR in aquatic animals,  
533 which were 0.32 in Nile tilapia *Oreochromis niloticus* (de Verdal et al., 2019, 2018), 0.47 in sea bass  
534 (Besson et al., 2019) and 0.58 to 0.69 in Pacific white shrimp *Litopenaeus vannamei* (Dai et al.,  
535 2017). A reason that could explain this lower heritability is a potential confusion between genetic and  
536 environmental effects. Indeed, to avoid phenotyping big fish in the 10L aquariums, we picked the  
537 biggest fish from the holding tank at the start of each batch, hence generating some confusion between  
538 batch and body weight effects. Such confusion could have reduced the apparent genetic variance of  
539 FCR and thus reduced the heritability, especially if FCR and growth rate are correlated. From a

540 technical point of view, the experimental procedure could thus be improved by increasing the number  
541 of aquariums allowing to phenotype more fish at the same time, and/or by starting to phenotype earlier  
542 to avoid issues with fish too large for the system.

543

544 The phenotypic and genetic correlations between  $\log(\text{DGC})$  and  $\log(\text{FCR})$  were as strong as in the sea  
545 bass experiment with the same system (-0.93 in sea bream vs -0.78 in sea bass for the phenotypic  
546 correlation and -0.93 vs -0.98 for the genetic correlation). It confirms that growth in individual tanks  
547 under restricted feeding is a good proxy of FCR measured in these conditions. However, feed  
548 efficiency in aquarium (measured as  $\log(\text{DGC})$  or rBWG) was not correlated to the *ad libitum* growth  
549 rate measured during the group experiment. Our results may have been different if we have estimated  
550 this correlation under restricted feeding regime. However, from harvest data, there was a trend for a  
551 positive genetic correlation between harvest weight and rBWG ( $0.41 \pm 0.25$ ). Nevertheless, it should  
552 be noted that harvest weight was measured on the same animals after individual feed efficiency  
553 phenotyping. As individual feed efficiency was measured under restricted feeding, the most efficient  
554 fish were also necessarily those that grew the most during this individual housing phase. Thus, the  
555 positive link between harvest weight and rBWG might also be partly an artefact. In order to avoid such  
556 artefacts, we also measured harvest traits on a group of cage-reared sibs and family links enabled the  
557 estimation of genetic parameters. In this population, the link between rBWG and harvest weight was  
558 not significantly different than zero ( $0.22 \pm 0.56$ ) although correlations were of the same sign as those  
559 observed on the fish with individual feed efficiency phenotypes. These results are consistent with the  
560 results presented in Besson et al. (2019) in sea bass, and rather similar to those of Pang et al. (2017) on  
561 crucian carp *Carassius auratus*, which also found a low (0.15) correlation between initial weight and  
562 individual feed efficiency. It suggests that feed efficiency measured under restricted feeding in  
563 aquariums is not necessarily associated with faster growth under classical rearing condition and  
564 individual feed efficiency might be independent of growth rate, which is not the general view (Knap  
565 and Kause, 2018; Thodesen et al., 1999). Hence, the phenotyping procedure involving restricted  
566 feeding may not select for the animals with the best growth. This was hypothesized by Cameron et al.  
567 (1994) who suggested that restricted feeding may select for animals with higher partitioning of energy  
568 toward protein deposition rather than fat deposition but may not select for animals with the highest  
569 overall protein deposition. The results obtained on harvest traits tend to support this hypothesis.  
570 Although the genetic correlations between rBWG and harvest traits (measured on the same animals or  
571 on sibs reared in cage) were very uncertain due to their high standard error, they showed a trend for a  
572 negative correlation between rBWG and viscera yield. The most efficient fish would have lower  
573 viscera yield and it was shown in farmed European sea bass that viscera are mostly composed of  
574 visceral fat (Saillant et al., 2009). This is in line with the general knowledge on selection of animals  
575 for feed efficiency which suggests that selecting for leaner animals would improve feed efficiency  
576 (Knap and Kause, 2018). However, the direct genetic correlation between FCR and percentage of

577 intramuscular fat in our experiment was not significant, although again being positive, as expected  
578 under that hypothesis. We could not highlight other significant genetic correlations between rBWG  
579 and processing traits probably because of the small number of phenotypes collected ( $n = 451$   
580 individuals with both efficiency and harvest phenotypes).

581

582 In this context, where a limited number of animals can be phenotyped, genomic data showed their  
583 advantages compared to pedigree to estimate breeding values. Indeed, the prediction of EBV was more  
584 accurate using GBLUP models (using SNP data) than PBLUP models (using only pedigree) by 26%.  
585 This result is in line with previous results on fish for several other traits such as disease resistance  
586 (Aslam et al., 2020; Aslam et al., 2020; Vallejo et al., 2017; Yoshida et al., 2019), growth and quality  
587 traits (Blay et al., 2021; Palaiokostas et al., 2018; Tsai et al., 2016) or reproduction traits (D'Ambrosio  
588 et al., 2020). With GBLUP, the improvement of the accuracy was however lower than the 48%  
589 increase in accuracy we obtained for feed efficiency in European sea bass (Besson et al., 2019), but  
590 was in the range of the values in the previously cited studies. Our results therefore confirm the major  
591 potential benefits of genomics for improving genetic gain in complex traits for which only few  
592 animals can be phenotyped. These results are all the more important as we could not identify any QTL  
593 associated to individual feed efficiency traits, suggesting a highly polygenic architecture of those  
594 traits. These results differs however from previous results from Pang et al. (2017). In their study, they  
595 were able to highlight several QTL for feed efficiency of individually reared carp. Such QTL were  
596 also found for terrestrial farmed animals such as pig (Delpuech et al., 2021) or cattle (Seabury et al.,  
597 2017). In our case, the lack of QTL detection could be caused by the low number of animals  
598 phenotyped and genotyped and also by the family structure: among the 112 full-sib families present in  
599 our dataset, 31 were represented by only one individual.

600

601 To be applicable in a commercial breeding program this phenotyping method in aquarium should be  
602 able to identify fish that would be the most efficient when reared in group conditions, as group rearing  
603 is the normal way of farming fish. A validation experiment in groups is therefore essential. With such  
604 validation in groups, for instance, Rodde et al. (2020) showed that individual measurements of feed  
605 efficiency in aquarium for Nile Tilapia *Oreochromis niloticus* were not correlated to feed efficiency in  
606 groups. Hence, phenotyping feed efficiency in aquarium is probably not an efficient method to  
607 improve feed efficiency of Nile tilapia. Conversely, in shrimp, Dai et al. (2019) found a good genetic  
608 correlation ( $0.79 \pm 0.11$ ) between feed efficiency measured in isolated shrimp or in small groups of 10  
609 shrimp. Our results for sea bream showed a link between individual and group feed efficiency but the  
610 results were less straightforward than those in sea bass (Besson et al., 2019). A significant difference  
611 in TFCR between subgroups A (most individually efficient fish) and B (least individually efficient  
612 fish) was only found for the first period of 2 weeks (out of 4 periods) and for the full period of 9  
613 weeks. Several reasons that may explain this result. First, when looking at short time periods, TFCR



614 could fluctuate between periods due to social dynamics within the tanks or due to environmental  
615 conditions. This variance at small scale would be smoothed when looking at longer time periods such  
616 as 9 weeks. The lack of difference could also be due to health issues that affected the fish. During  
617 group experiments, fish suffered from an unexplained occurrence of bulging eyes, that could neither  
618 be related to nitrogen supersaturation nor to pathogens by veterinarians. This may have caused welfare  
619 issues, and perturbed their feeding pattern, as shown by the sharp increase in FCR, from 1.13 to 1.4,  
620 between periods 1 and 2 of the group feed efficiency experiment. Although the results are not  
621 straightforward, it still seems reasonable to consider that in sea bream, variation in individual feed  
622 efficiency under restricted feeding can be at least partly reflected in differences in feed efficiency  
623 when fish are reared in groups with *ad libitum* feeding.

## 624 **Conclusion**

625

626 The present study confirms the potential of phenotyping individual feed efficiency of fish in individual  
627 aquariums under restricted feeding. With this method, similar to what was previously shown in sea  
628 bass, several feed efficiency traits were shown to be heritable in sea bream, suggesting that genetic  
629 improvement for individual feed efficiency is feasible. Considering a selection index pressure of 10%  
630 and an accuracy of 0.53, the genetic gain could enable reduction of FCR of 1% per generation, from  
631 1.29 to 1.276 in the first generation. At the Mediterranean scale, where 228,000 tonnes of sea bream  
632 were produced in 2018, such reduction of FCR would decrease the use of feed by 3,192 tonnes per  
633 year, with a direct impact on economic and environmental sustainability of sea bream production. The  
634 accuracy estimated in this research is however only an estimate and, ideally, the true response to  
635 selection should be measured with an experimental approach.

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644 **Appendices**

645

646 *Appendix 1. Composition of the feed*

<b>Ingredients</b>	<b>%</b>
Fishmeal Super Prime	5.00
Soy protein concentrate	25.00
Wheat gluten	7.50
Corn gluten	25.00
Rapeseed meal	11.00
Wheat meal	2.00
Pea starch	1.80
Fish oil	10.90
Rapeseed oil	5.70
Soy lecithin	1.65
PERFORMFISH WP1 Premix 1%	1.00
Guar gum	0.20
Monocalcium phosphate	2.10
L-Lysine	0.90
DL-Methionine	0.01
L-Taurine	0.24
<b>Total</b>	<b>100.00</b>
<b>Analysis results</b>	
<b>Moisture (g/100g)</b>	<b>8.2</b>
<b>Crude protein (g/100g)</b>	<b>42.5</b>
<b>Fat (g/100g)</b>	<b>20.3</b>
<b>Crude ash (g/100g)</b>	<b>6.2</b>
<b>Crude fibre (g/100g)</b>	<b>2.1</b>
<b>Total phosphorus (g/100g)</b>	<b>1.1</b>

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