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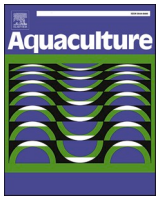

Genomic selection for individual feed efficiency in the European seabass: Response to selection on efficiency, commercial traits and sex

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ABSTRACT

Feed efficiency is a key factor in the sustainability of fish farming. Improving feed efficiency not only results in cost savings, but also helps to reduce the environmental footprint associated with feed production and to mitigate competition for feed resources. However, improving feed efficiency through genetic selection poses challenges, mainly due to the difficulty of accurately estimating it in a large population, especially under conventional rearing conditions. In a previous study, a methodology was developed to estimate the individual feed efficiency of sea bass in separate tanks under controlled feeding regimes during the juvenile phase. This approach allowed precise measurement of growth, feed intake and individual feed conversion ratio (iFCR) of each fish. Daily growth rate (iDGC) was found to be highly heritable ($h^2 = 0.75$), and a reliable predictor of iFCR under restricted feeding conditions. In the present study, we aim to demonstrate the response to selection on feed efficiency, commercial traits and sex.

From a cohort of 399 sea bass with known iDGC and genotyped for 1110 SNP markers, we selected 27 future efficient parents (Eff+), 35 intermediate parents (Eff0) and 29 inefficient parents (Eff-) by genomic selection (GBLUP). Three years later, 3 groups of offspring were produced from 9 Eff + parents, 13 Eff0 parents and 19 Eff- parents. Performances in individual aquaria (iDGC, iFCR) were assessed for 259 of them, as well as group feed efficiency (gFCR) from 142 g. At 240 g, the fish were slaughtered to assess processing traits.

The results showed that the Eff + group had superior efficiency (iFCR and iDGC) and better adaptability to tank conditions compared to the other groups. In the group evaluation phase, significant differences in feed efficiency were observed between Eff- (gFCR = 1.83) and Eff + (gFCR = 1.61) ($p < 0.001$), with Eff0 being intermediate. In addition, Eff + fish were larger (266 g, 27.4 cm) and leaner with lower Fulton K values compared to Eff0 (234 g, 26.1 cm) and Eff- (223 g, 25.5 cm). Although there were no differences in fillet yield, Eff + had a slightly higher viscerosomatic index. There was also a higher proportion of females in the Eff- (57.1 %) and Eff0 (51.6 %) groups compared to Eff + (43.9 %).

In conclusion, selection for feed efficiency in individual tanks is an effective strategy for improving the performance of sea bass, resulting in significant improvements with a marked effect on growth rates. Despite a slight increase in the viscerosomatic index, fillet yield was not significantly affected.

1. Introduction

The last decades, aquaculture has shown an impressive growth for meeting the global demand for seafood. As this sector continues to grow, it is now crucial to develop sustainable approaches for in the meantime improving production efficiency and mitigating environmental consequences. One key route to achieve this sustainability goal is the implementation of selective breeding programs that focus on improving the feed efficiency of commercial populations. Feed efficiency is a critical trait in the aquaculture business, as feed represents the main production cost in fed aquaculture (Iversen et al., 2020). In addition of being key for economic sustainability, feed efficiency is also a major

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driver to reduce the environmental impacts of aquaculture (Besson et al., 2016) either at a local scale (eutrophication) and at a global scale (greenhouse gas emissions, primary energy use, acidification potential). The most frequently used trait to measure feed efficiency is the feed conversion ratio (FCR), which quantifies the ability of fish to convert feed into biomass (FCR = feed intake / body weight gain). Fish that have low FCR eat less feed for a given biomass gained than fish with high FCR. However, despite its obvious interest, feed efficiency *per se* is not part of the selection index in most aquaculture breeding programs, because it is not possible to measure individual feed intake (and hence individual FCR) on selection candidates when they are reared in large groups in tanks or cages, which are the typical conditions of fish farming (de Verdal et al., 2018). Several workarounds have been suggested and tested, such as (1) the use of labelled feed to quantify ingested feed in a single meal with X-rays (Kause et al., 2006; Scholtens et al., 2023), (2) measuring individual weight loss at fasting as an indicator of basal metabolism (Grima et al., 2010), (3) video monitoring of feed intake in small groups of individually tagged fish (de Verdal et al., 2017), (4) recording individual feed intake in isolated fish (Besson et al., 2022, 2019; Silverstein, 2006), (5) using stable isotopes profiles to evaluate components of feed efficiency (Dvergedal et al., 2022) or selecting for correlated traits such as lipid content (Kause et al., 2016). However, although all these methods proved the existence of heritable variation for feed efficiency in various fish species, selection response in the next generation(s) for experimental selection specifically targeted to FCR has been demonstrated in only two studies so far (Besson et al., 2019 for weight loss at fasting de Verdal et al., 2022 for video monitoring of feed intake), while other studies have shown presence (Thodesen et al., 1999; Yamamoto et al., 2015; Vandeputte et al., 2022; Montero et al., 2023) or absence (Ogata et al., 2002; Sanchez et al., 2001) of correlated response in FCR to selection for growth rate.

The European sea bass (*Dicentrarchus labrax*) is a major fish species for Mediterranean aquaculture. Improving feed efficiency in this species has become a key priority to increase profitability and sustainability of its mariculture (Vandeputte et al., 2019). However, the challenge to the practical implementation of selection for FCR remains. Recently, we developed a novel approach to estimate FCR by measuring individual feed intake in aquaria in this species (Besson et al., 2019). Genetic parameters of this FCR measured in individual housing under restricted feeding rate (iFCR, $h^2 = 0.47 \pm 0.07$) and of the daily growth coefficient in the same conditions (iDGC, $h^2 = 0.75 \pm 0.05$) were assessed and a strongly negative genetic correlation was observed between both traits (-0.98 ± 0.04). This highlighted the potential for genetic selection on those traits, and particularly iDGC which has the advantage of being estimable without the daily collection and weighing of uneaten pellets (Besson et al., 2019). Furthermore, we demonstrated the existence phenotypic link between iFCR and feed efficiency in group rearing (gFCR), whereby efficient fish in individual tanks under restricted feeding were also efficient in group rearing under *ad libitum* feeding (Besson et al., 2019). We therefore estimated the genetic merit of 399 animals for iDGC using genomic-based best linear unbiased prediction (GBLUP), and 27 efficient fish (Eff+, 15 males and 15 females), 35 inefficient fish (Eff-), and 29 intermediate fish (Eff0) were selected and kept as future broodstock for studying of response to selection.

In the present study, the objective was to evaluate selection response for feed efficiency (1) on individual aquarium performance (the trait under direct selection) and (2) on group feed efficiency (the target trait) comparing the three groups Eff+, Eff0 and Eff-.

2. Material and methods

2.1. Origins of the broodstock

This study was conducted on the European sea bass (*Dicentrarchus labrax*), following a previous experiment (see Besson et al., 2019 for more details). From 399 individuals phenotyped for individual FCR and genotyped for 1110 SNPs, their genomic estimated breeding values (GEBVs) for iFCR and iDGC were calculated as reported by Besson et al. (2019). The genetic merit estimated for iDGC, the best predictor of FCR according to Besson et al. (2019), was used to rank the animals. Three broodstock groups were then created: fish with the 6.8 % highest (Eff+, 27 fish retained), fish around the mean (Eff0, 29 fish retained), and fish with the 8.8 % lowest (Eff-, 35 fish retained) and monitored until maturation. At maturation, 8 Eff+, 10 Eff0 and 15 Eff- males could be cryopreserved for later mating. On the day of mating, 1 Eff+, 3 Eff0 and 4 Eff- dams responded to hormonal stimulation, liberating oocytes for artificial mating in three full factorial designs (see Table 1) following the procedure described by Doan et al. (2017). The mean GEBVs of the genetic lines created by the mating are presented in Table 1 and the individual genomic merits for iDGC and iFCR of the parents used, in comparison of the total population, are displayed in the Fig. 1.

2.2. Initial rearing of the progenies

The fertilized eggs from the three lines were incubated separately, and dispatched each in three replicate tanks of 0.5 m3 each at 50 eggs/l. The fish were reared at 16.5 °C until 70 days post hatching (dph) where the temperature was increased to 21 °C. They were reared with a standard protocol, with *Artemia* nauplii until day 47 dph and then weaning on dry feed (Le Gouessant). Two hundred fish per tank (600 per line, 1800 fish in total) were transferred to larger tanks of 1.5 m3 at 137 dph, with three replicate tanks per line.

2.3. Fish phenotyping for feed efficiency in individual aquaria

The individual feed efficiency phenotyping facility consists of 224 aquariums of 10 l, each supplied with 5 l/h of 21 °C seawater by a recirculating aquaculture system. The phenotyping protocol implemented followed the same steps described by Besson et al. (2019). 259 fish (85 from Eff+, 87 from Eff 0; and 87 from Eff -) were randomly sampled from the nine rearing tanks (28 or 29 fish per tank) and individually marked at 10 g mean weight (180 dph) and phenotyped in two batches (129 in batch 1, 130 in batch 2) interleaved in time but separated by 14 days at the start of each. Each batch included an initial acclimation period of 14 days in small groups, with five fish per aquarium, starting on 30 August 2021 for batch 1 and 13 September 2021 for batch 2. Then, fish were weighed and randomly re-allocated to individual aquaria and reared for an acclimation period in individual aquariums, followed by the trial consisting in two periods of 14 days, with biometric measurements (body weight, body length) between each period. Fish that showed a decrease in weight during the acclimation or during the trial periods were excluded from the later analyses as we considered this an indication that they were not adapting well to the new environment.

Individual BW at each measurement was used to estimate the feeding ration for each individual fish in the following period. This ration (1.3 % BW/day) was half the standard ration (2.6 % BW/day for this size of fish) given by the feed manufacturer, and was distributed in a single

Table 1
Mean genomic estimated breeding values for iDGC and iFCR of the broodstock used to generate the genetic lines.

Line	Parents	N	mean iDGC GEBV (SD)	mean iFCR GEBV (SD)
Eff+	sires	8	0.27 (0.09)	−0.13 (0.04)
	dams	1	0.40 (n.a.)	−0.14 (n.a.)
	mid-parent		0.34	−0.14
Eff0	sires	10	−0.06 (0.02)	0.02 (0.02)
	dams	3	−0.08 (0.01)	0.04 (0.02)
	mid-parent		−0.07	0.03
Eff-	sires	15	−0.49 (0.08)	0.19 (0.04)
	dams	4	−0.49 (0.17)	0.19 (0.08)
	mid-parent		−0.49	0.19

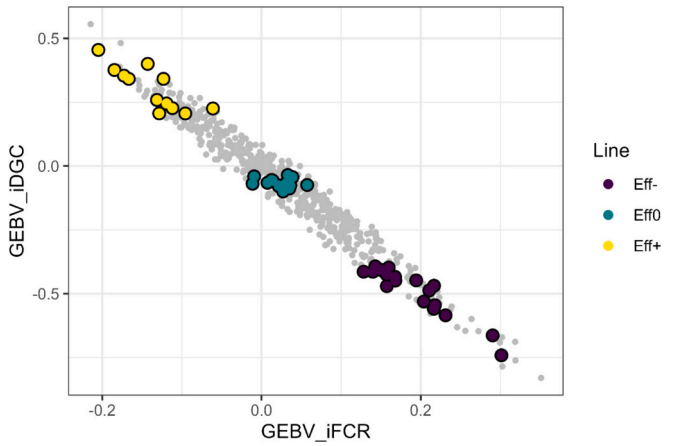

Fig. 1. Broodstock selection among the population based on genomic estimated breeding values (GEBVs) for daily growth coefficient (iDGC) and individual feed conversion ratio (iFCR) in individual aquaria Besson et al. (2019). Yellow dots represent the GEBVs of the breeders used to produce "Eff+" line; turquoise dots the GEBVs of the breeders of the "Eff0" line; and purple dots the GEBVs of the breeders of the "Eff-" line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

distribution in the morning. Every afternoon, the number of uneaten pellets was counted in each aquarium and converted to grams (1 pellet ≈ 0.013154 g). Thus, for each period of individual phenotyping in aquariums, data were available for individual weight gain and individual feed intake. From weight gain and feed intake, iFCR over the full trial (4 weeks) was calculated as:

$$\mathrm{iFCR_i} = \frac{\mathrm{iBWG_i}}{\mathrm{iFI_i}}$$

Where $iFCR_i$ is the feed conversion ratio of fish $\boldsymbol{i}$ over the two periods, $iBWG_i$ is the individual body weight gain of the $\boldsymbol{i}$th fish over the two trial periods, and iFI_i is the individual feed intake of the $\boldsymbol{i}$th fish over the two periods. Individuals displaying either a negative iBWG or an iFCR higher than 4.5 were removed from later analysis. We also calculated iDGC over the 4 weeks of the trial as:

$$\mathrm{iDGC_i} = \frac{\left(\mathrm{BWf_i^{\frac{1}{3}}} - \mathrm{BWi_i^{\frac{1}{3}}}\right)}{\mathrm{D_j}}$$

Where $iDGC_i$ is the daily growth coefficient of the $\boldsymbol{i}$th fish during the trial, BWf_i is the body weight of fish $\boldsymbol{i}$ at the end, BWi_i is the body weight of fish $\boldsymbol{i}$ at the beginning of the trial, D_j is the duration of the trial (28 days).

2.4. Group feed conversion ratio

To evaluate the response to selection on group feed efficiency, 1196 fish from the offspring (not evaluated for individual feed efficiency) were tagged at 269 dph, at a mean body weight of 37 g: 400 fish from Eff+; 399 from Eff 0; and 397 from Eff -. The fish were sampled equally in the three replicate tanks of each group, and then reared in common garden until the feed efficiency trial started at a mean body weight of ~142 g.

For each of the three genetic lines, 5 replicate batches of 78 to 80 fish per line were constituted, and randomly distributed in 15 tanks of 2 m3 connected to the same recirculating aquaculture system providing 1 m3/h water per tank with a 100 % renewal of the system per 24 h, constant temperature (21 °C) and 100 % oxygen saturation maintained. Fish were fed once a day *ad libitum* using an automatic feeder delivering 20 portions over 6 h, starting at the onset of light in the morning. The feeders were filled with a known weight of pellets. Every day, at the end of the automated feeding period, the faecal trap of each individual tank was checked. If pellets were found, it meant that fish had reached *ad libitum*. If a faecal trap was empty or only few pellets (less than 5) were present, an additional portion was given to the tank by activating the feeder manually. Additional portions were then given every 30 min until >5 pellets were collected in the faecal trap, meaning that *ad libitum* was reached. Uneaten pellets from all tanks were then collected, photographed and counted using ImageJ. After two weeks of acclimation, group feed intake was recorded for two successive periods of two weeks. All fish were weighed at the beginning and at the end of each period. The weight gain of the fish and the feed intake of the tanks were used to calculate two metrics of feed efficiency: the group residual feed intake (gRFI) and the group feed conversion ratio (gFCR) of each tank.

gRFI was calculated as the difference between the measured feed intake (gFI) and the expected feed intake (eFI), resulting from of a linear model based on energy balance, as proposed by Crews (2005):

$$\mathrm{eFI_k} = \beta_0 + \beta_1 \times \mathrm{gBWG_k} + \beta_2 \times \mathrm{gMW_k}$$

where eFI_k is the expected feed intake of tank $\boldsymbol{k}$, β_0 is the regression intercept, β_1 is the partial regression coefficient of gFI on the body weight gain of tank $\boldsymbol{k}$ ($gBWG_k$), β_2 is the partial regression coefficient of gFI on the total metabolic body weight of tank $\boldsymbol{k}$ (gMW_k). The metabolic weight (iMW) of each fish was calculated as the weight estimated at the midpoint of the cycle, raised to the power 0.8 (Lupatsch et al., 2003), and gMW_k was the sum of the metabolic weights of the fish of the tank $\boldsymbol{k}$. The model coefficients β_0, β_1 and β_2 were estimated using a multiple regression model implemented in 'lme4' R package (Bates et al., 2015). The tank group FCR was calculated as:

$$\mathrm{gFCR_k} = \frac{\mathrm{gBWG_k}}{\mathrm{gFI_k}}$$

Where $gFCR_k$ is the feed conversion ratio of the tank $\boldsymbol{k}$ over the two periods of 14 days, $gBWG_k$ is the sum of the individual body weight gains of the fish in the tank $\boldsymbol{k}$ over the two periods, and gFI_k is the group feed intake of the $\boldsymbol{k}$th tank over the two periods.

2.5. Processing traits recording

To assess the correlated response to selection on processing traits, fish were slaughtered at the end of the feed efficiency trial at a mean weight of ~240 g. At that point, each fish was recorded for body weight and body length at slaughter (BWS and BLS), fillet fat content (fat%) was measured with a Distell Fish Fatmeter, and the fish were manually processed in order to evaluate headless carcass weight (HCW), head weight (HW), fillet weight (FW), viscera weight (VW), liver weight (LW) and gonad weight (GW). They were all sexed by visual observation of the gonads. These data were used to compute carcass weight (CW=HCW + HW), and to calculate processing yields, including fillet percentage (fillet%), head percentage (head%) and viscerosomatic index (viscera %). The Fulton's K condition factor was computed as follows:

$$K = 100 \times \frac{BWS\ (\mathrm{g})}{BLS^3\ (\mathrm{cm})}$$

2.6. Statistical analyses

To test for significant differences between fish lines (Eff+, Eff0 and Eff-) for the different traits recorded, we used one-way analysis of variance with the Satterthwaite's approximation for degrees of freedom, using the relevant combination of random effects (tank and/or individuals) as a residual. Multiple comparisons of Least Square means were performed with Tukey's HSD. In addition, we conducted Chi-squared tests to assess differences in successful phenotyping and sex ratios between lines.

3. Results

3.1. Fish phenotyping for feed efficiency in individual aquaria

Among the 259 fish evaluated in the individual aquaria, 79 were removed after the acclimation period because they had lost weight (10 from Eff+, 32 from Eff0 and 37 from Eff-). In addition, 35 fish showing a weight loss during the evaluation period (7 from Eff+, 18 from Eff0 and 11 from Eff-), and 7 fish with an iFCR >4.5 (2 from Eff+, 2 from Eff0 and 3 from Eff-) were removed. Finally, 137 fish were kept for further statistical analysis (see Fig. 2 and Table 2).

Across the two phenotyping batches, 78 % of the Eff + fish were correctly phenotyped (*i.e.* not removed due to weight loss during acclimation or evaluation period, or outlier) while this was the case for only 40 % of the Eff0 and 41 % of the Eff-. This ability to be phenotyped in individual aquaria was significantly different between lines (Chi-squared test, $p < 0.001$).

From the phenotypes recorded on the 137 fish retained, both criteria of feed efficiency, iFCR (log transformed to improve normality) and iDGC were examined. Log(iFCR) was significantly different between lines ($F_{2,134} = 3.97$, $p \approx 0.022$, Fig. 3A), with Eff0 being significantly less efficient than Eff + ($p < 0.01$), and Eff- ($p < 0.05$). Regarding iDGC, which is the trait for which the parents were selected (Fig. 3B), the effect of fish lines was highly significant ($F_{2,134} = 8.54$, $p < 0.001$), with the Eff + line showing a higher iDGC than Eff0 (+32 %, $p < 0.0001$) and Eff- (+30 %, $p < 0.05$).

3.2. Feed conversion ratio of groups

During the group feed efficiency experiment, one of the five replicates of Eff + showed a significant deviation due to a technical dysfunction of the automatic feeder. Therefore, the performance of this tank was discarded for later analysis.

Mean group residual feed intake (gRFI) was −18 g for Eff+, 24 g for Eff0 and − 9.5 g for Eff-. Although this suggests better efficiency for Eff+, the differences were not significant. However, we point a potential issue with the interpretation of these results due to the way the gRFI is estimated. As shown in Fig. 4, the expected feed intake (eFI) values for the different selected lines do not overlap (from 2396 to 2507 for Eff-; from 2538 to 2597 for Eff0; and from 2600 to 2711 for Eff+). This lack of overlap in expected feed intake between groups raises concerns about the validity and usefulness of the regression used to estimate gRFI. Here, the regression line tends to simply connect the average values of each line, rather than representing a true relationship across the entire range of expected feed intakes. As a result, the residuals derived from this regression become less meaningful for comparing line differences. Without shared ranges of expected feed intake across lines, it becomes challenging to determine whether any observed differences in residuals are due to selection effects or because we are comparing residuals at different levels of expected feed intake.

Regarding the second index of efficiency evaluated, the log-transformed group feed conversion ratio (Fig. 5), significant differences were observed between fish lines ($F_{2,11} = 7.244$, $p < 0.001$). Pairwise post-hoc Tukey's Honest Significant Difference showed that Eff + were significantly more efficient than Eff- ($p < 0.001$), and the difference between Eff0 and Eff- was close to significance threshold ($p \approx 0.056$).

3.3. Processing traits among the genetic groups

In total 1182 fish used for the group feed efficiency trial were slaughtered, and processing traits were recorded, see Table 3. From the analyses of variance between genetic groups with the tank of feed efficiency trial as a nested random effect, significant differences were observed between Eff + and the others for BWS, BLS, GHCW and viscera %, in favour of Eff+. Although generally not significantly different from Eff-, the Eff0 lines performance was most of the time intermediate between Eff + and Eff-. Although FW was significantly higher in Eff+, this difference is due to the difference in BW, and fillet% was not significantly affected by the selection process. Similarly, no significant difference between groups was observed for head% or Fat. Fulton's K was significantly different between lines, Eff + and Eff0 fish being significantly more elongated than Eff- fish. Finally, we could observe significant differences on sex-ratio, with Eff + having significantly less females than the other lines.

4. Discussion

4.1. Response to selection in individual aquaria

As the parent fish were selected for their iDGC in individual aquaria, it was important to first evaluate direct selection response for the selected trait. Selection response was indeed high for iDGC with a daily growth rate improved in Eff + by 24 % relative to Eff0 and by 42 % relative to Eff-. This is consistent with the fact that iDGC was the trait chosen for selecting the parents of the present population (G4), as its heritability (h2 = 0.75 ± 0.05) was higher than the heritability of the log(iFCR) (h2 = 0.47 ± 0.07), with a very strong genetic correlation

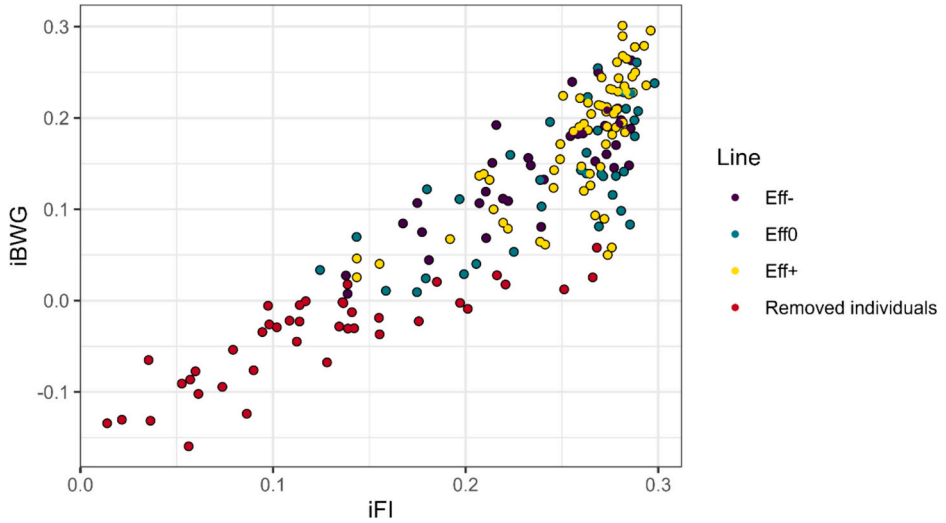

Fig. 2. Scatter plot of individual body weight gain (iBWG) and individual feed intake (iFI) of the 180 fish evaluated in individual aquaria.

Table 2
Number and percentage of fish evaluated per batch and selection group. Fish removed after weight loss during acclimation period (R_acclim) or after the evaluation period (R_eval), outlier fish (Out) with feed conversion ratio > 4.5 and remaining phenotyped fish (Pheno).

	Batch 1				Batch 2			
lines	R_acclim	R_eval	Out	Pheno	R_acclim	R_eval	Out	Pheno
Eff + ($N = 85$)	6 (14 %)	4 (10 %)	1 (2 %)	31 (74 %)	4 (9 %)	3 (7 %)	1 (2 %)	35 (81 %)
Eff0 ($N = 87$)	12 (28 %)	8 (19 %)	1 (2 %)	23 (52 %)	20 (45 %)	9 (22 %)	1 (2 %)	13 (30 %)
Eff- (N = 87)	17 (39 %)	2 (5 %)	2 (5 %)	22 (51 %)	20 (47 %)	10 (22 %)	1 (2 %)	13 (30 %)

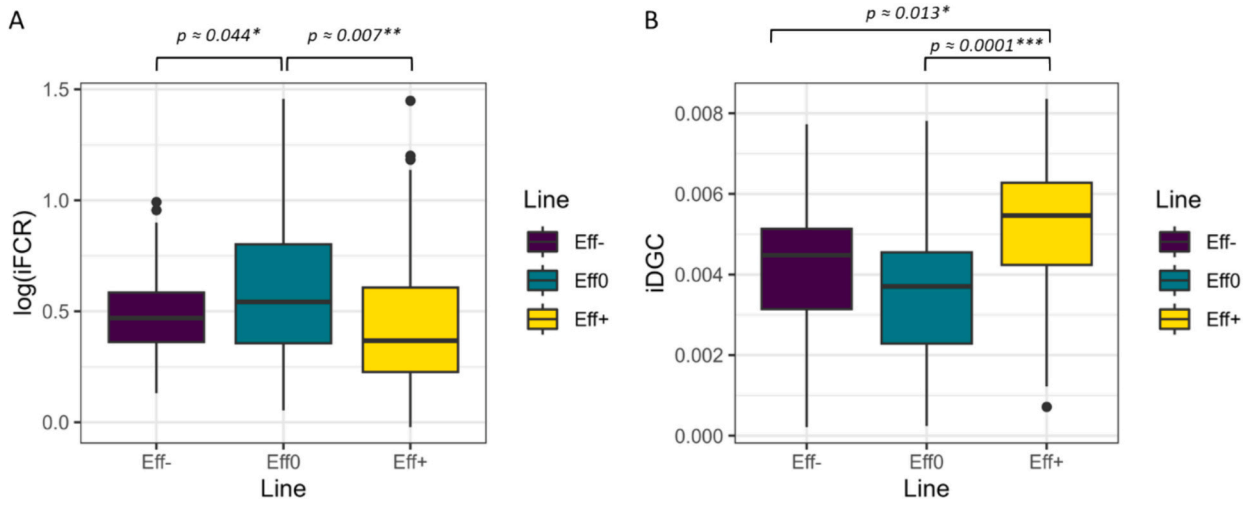

Fig. 3. Boxplots at the level of selected groups for: A. log transformed individual feed conversion ratio (log(iFCR)), B. and daily growth coefficient (iDGC) under restricted feeding in individual tanks

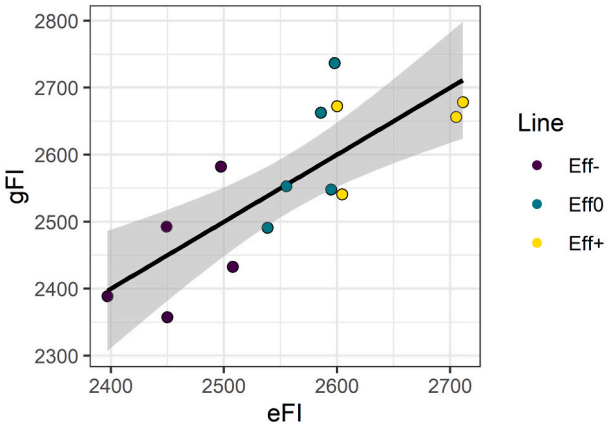

Fig. 4. Linear regression between expected feed intake and measure group feed intake during the group feed efficiency trial.

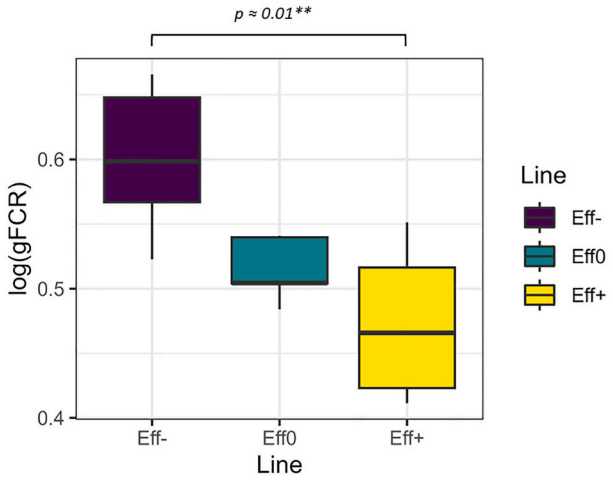

Fig. 5. Boxplots at the level of selected groups for log transformed group feed conversion ratio (log(gFCR))

(−0.98 ± 0.04). Selection response for iFCR was also present but less clear, as both Eff + and Eff- fish were more efficient than Eff0. It was still noteworthy that the largest difference in efficiency was found between Eff + and Eff0. An unexpected effect of selection was the significant differential adaptation of the genetic groups to the experimental individual aquaria facility. About 80 % of the Eff + fish showed continuous growth in isolated conditions *vs.* only 40 % of the Eff0 and Eff- fish. The experimental procedure for individual feed efficiency in isolated condition constitutes a strong challenge for the fish, as shown by the fact that a significant proportion of them do not adapt to the system and lose weight. Indeed, this was already observed in the parental generation, where 23 % of the fish did lose weight in the individual tanks. Thus, it is likely that the growth measured in individual housing does not reflect the true growth capacity of the fish, but its capacity to grow in a stressful environment. European sea bass behaviour is strongly influenced by genetics (Ferrari et al., 2016). Thus, the selection criterion is likely a combination of fast growth and tolerance to individual housing, and it is therefore logical to see a response in both components. While stress induced by isolation and by aquaculture condition differ, tolerance to stress can be seen as a favourable trait for aquaculture (Milla et al., 2021). Although, in a previous experiment in seabass, the phenotypic link between individual feed efficiency in individual housing and the metabolic rate was not clearly pointed (Rodde et al., 2021), variation in oxygen consumption between isolated fish and group of fish was reported in swimming trials and could influence the response (Herskin and Steffensen, 1998; Killen et al., 2011). Thus, the correlated response

Table 3
Trait means, standard errors of the means (under brackets), statistic values, *p* values and grouping after least squares means pairwise comparisons for processing traits at slaughter: body weight (BWS), body length (BLS), gutted headless carcass weight (GHCW), fillet weight (FW), fillet%, head%, viscera%, Fulton's K, Female% and fat%. (n.s. = not significant).

	Statistic value (p value)	Eff + (*N* = 397)	Eff0 (N = 397)	Eff- (*N* = 388)
BWS (g)	F = 19.8 (*p* < 0.001)	266 (±3.3) [a]	234 (±3.3) [b]	223 (±3.2) [b]
BLS (cm)	F = 35.9 (p < 0.001)	27.4 (±0.11) [a]	26.1 (±0.12) [b]	25.5 (±0.12) [c]
GHCW(g)	F = 20.2 (p < 0.001)	179 (±2.3) [a]	158 (±2.3) [b]	151 (±0.2.2) [b]
FW (g)	F = 21.0 (p < 0.001)	74 (±0.95) [a]	65 (±0.95) [b]	62 (±0.92) [b]
fillet% (%)	F = 0.1 (n.s.)	55.7 (±0.1)	55.8 (±0.1)	55.6 (±0.1)
head% (%)	F = 0.4 (n.s.)	18.4 (±0.1)	18.3 (±0.1)	18.2 (±0.1)
viscera% (%)	F = 9.0 (p < 0.01)	12.6 (±0.1) [a]	11.6 (±0.1) [b]	12.1 (±0.1) [b]
Fulton's K	F = 8.0 (p < 0.01)	1.28 (±0.01) [b]	1.29 (±0.01) [b]	1.32(± 0.01) [a]
Fat%	F = 1.0 (n.s.)	2.89 (±0.05)	3.03 (±0.05)	2.85 (±0.06)
Female% (%)	X^2 = 13.7 (*p* = 0.001)	43.9 (±2.5) [b]	51.6 (±2.5) [a]	57.1 (±2.5) [a]

between selection for individual feed efficiency and metabolic rate should be further investigated.

4.2. Response to genetic selection in group efficiency trial

Although, for practical reasons, we selected the parental fish for their feed efficiency as juveniles in individual aquaria with restricted feeding, the real target trait is feed efficiency in normal rearing conditions, allowing social interactions between animals and with *ad libitum* feeding. The size (or age) of the fish is also important, as fish consume more feed in the last phases of the production cycle, the economic and environmental impacts are expected to be maximal if feed efficiency is improved during the (late) on growing phase (de Verdal et al., 2018). This is why we chose to evaluate group feed efficiency from 140 to 250 g. In our study, the group feed conversion ratio of the Eff + line ($gFCR_{Eff+}$ = 1.61) was significantly lower (better) than that of the Eff- line ($gFCR_{Eff-}$ = 1.83). This difference corresponds to a difference of 12 % between the lines. Although the differences were not statistically significant, the middle line Eff0 showed intermediate performances for feed conversion ratio ($gFCR_{Eff0}$ = 1.67) between Eff + (−4 %) and Eff- (+8 %). We therefore demonstrated a significant response to selection, at least between the extreme lines. Considering the observed difference of 12 % between Eff + and Eff-, we can speculate that a 6 % improvement can be obtained by generation while applying a 6.8 % selection pressure in a similar design as proposed in this study.

4.3. Response to genetic selection on processing traits

We could observe that selection for improved individual feed efficiency (iDGC) had positive impacts on most of the commercially important processing traits. In particular, the Eff + group was significantly heavier and more elongated than the other two. Contrary to the observed effect of selection by the means of fasting tolerance, which leads to an increased fat content in efficient animals (Besson et al., 2019), the present selection scheme by the means of iDGC had no significant impact on the muscle fat content of the animals.

4.4. Are the European sea bass males more efficient than females?

In this study, we observed significant differences in sex-ratio among the different lines. Indeed, the Eff + line had significantly less females than the other lines. Such observation seems counter-intuitive, as females are generally larger than males in sea bass (Saillant et al., 2001). Indeed, this is the case here also, as within the different lines the body weight of the females is always higher than that of the males (21 % heavier in Eff+, 21 % in Eff0, and 28 % in Eff-). Differential feed efficiency between males and females was also pointed out in Nile tilapia (*Oreochromis niloticus*, de Verdal et al., 2017). The better efficiency in Nile tilapia was attributed to a superior growth rate of the males with a limited increase of the feed intake. This was not the case here, as females were larger than males, as usual in sea bass. It is even strange to see less females in the Eff + group, as fish from this line are larger than the other two, and, due to a positive genetic correlation between growth and sex-ratio, it is expected that selection for growth would lead to more females in sea bass (Geffroy et al., 2021; Vandeputte et al., 2007). This warrants further investigation, but unfortunately, in the present study, the sex of the fish evaluated in individual aquaria was not recorded, so we cannot link the individual performance to sex. It would be interesting to collect this information in further experiments.

4.5. Limits and possible bias of the study

This study is an experimental demonstration that does not fully represent a classical breeding programme, and some limitations must be noted. The base population from which the selection process was applied is limited. Only 399 individuals were evaluated by Besson et al. (2019), and the estimated genetic merit of the fish was estimated with a reduced SNP panel (1.1 k SNPs). This may impact the precision of GEBVs, but likely only marginally. Indeed, in European sea bass, as in other aquaculture species, a marker density around 1 K has been shown to be sufficient to achieve a prediction accuracy similar to that of higher density panels (Griot et al., 2021; Kriaridou et al., 2020), even with limited training population (300–500). Although no specific evaluation of the effect of SNP density on prediction accuracy for feed efficiency in seabass has ever been undertaken, the consequence of a reduced accuracy would be a lower observed selection response than the one that could be expected with more markers used. It must be noted that all breeders selected in this study had been individually phenotyped for feed conversion ratio, which may not be the case in a real selective breeding program, where owing to the cost of individual phenotyping, it is likely that only a number of sibs would be phenotyped. Without individual phenotypes for the candidates, it is likely that the realised gain would be affected. Finally, due to maturity issues within the experimental population, only a limited number of parents could be used and the limited number of resulting families examined in each line (1dam x 8 sires, thus 8 families for Eff+, 3dams x 10 sires, thus 30 families for Eff0, and 4dams x 15 sires, thus 60 families for Eff-) may raise concerns about sampling variance, especially between dams, as individual dams could strongly influence the average value of the offspring groups they contribute to, especially for traits with a strong additive genetic component such as sex ratio (Vandeputte et al., 2007).

5. Conclusion

We demonstrated a significant response to genomic selection for individual feed efficiency in European sea bass by the means of daily growth coefficient in individual aquaria under restricted feeding. The response was observed first on the individual performance of the offspring generation in the same evaluation facility, with the Eff + line growing faster than the others in that condition. Interestingly, the response to selection was also significant and strong on the feed conversion ratio of the different lines in conditions more representative of classical aquaculture condition, with 12 % difference in feed conversion ratio between extreme lines, the Eff + line being the most efficient. This suggests a possible improvement of feed conversion ratio of 6 % per generation when selecting European sea bass for daily growth coefficient in individual aquaria under restricted feeding with a selection

pressure of 6.8 % using genomic selection. Furthermore, we demonstrated that this selection process only positively affected the processing traits of the fish at commercial size. Finally, we point an interesting link between sex-ratio and feed efficiency, that deserves further investigation. Although these results are promising for improving feed efficiency in European sea bass, given the experimental limitations discussed above, it would be prudent to confirm the selection response in a population representative of a commercial breeding programme.

CRediT authorship contribution statement

Mathieu Besson: Writing – review & editing, Methodology, Formal analysis, Conceptualization. **Emilie Delpuech:** Writing – review & editing, Investigation, Formal analysis. **Chloé Barrier-Loiseau:** Investigation. **Alain Vergnet:** Resources, Methodology, Investigation, Conceptualization. **Franck Morell:** Investigation. **Marie-Odile Blanc:** Resources, Investigation. **Stéphane Lallement:** Resources, Investigation. **Frédéric Clota:** Writing – review & editing, Investigation. **François Ruelle:** Writing – original draft, Visualization, Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Marc Vandeputte:** Writing – review & editing, Supervision, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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