

Aquaculture

February 2010, Volume 300, Issues 1-4, Pages 50-58

<http://dx.doi.org/10.1016/j.aquaculture.2010.01.003>

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Archimer
<http://archimer.ifremer.fr>**In search for indirect criteria to improve residual feed intake in sea bass (*Dicentrarchus labrax*): Part I: Phenotypic relationship between residual feed intake and body weight variations during feed deprivation and re-feeding periods**Laure Grima^{a, b}, Marc Vandeputte^{a, b, *}, François Ruelle^a, Alain Vergnet^a, Muriel Mambrini^b and Béatrice Chatain^a^a Ifremer, Station expérimentale d'aquaculture, chemin de Maguelone, 34250 Palavas-les-Flots, France^b INRA, UMR 1313 Génétique Animale et Biologie Intégrative, Domaine de Vilvert, 78350 Jouy-en-Josas, France

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Marc.Vandeputte@jouy.inra.fr**Abstract:**

No commercial breeding programs have yet started to improve feed utilization efficiency in fish, mainly because of the difficulty in accurately measuring individual feed intake in fish reared in groups. Our general goal is to propose indirect criteria to be used for breeding of commercial lines. In a previous study undertaken with rainbow trout clones, a genetic correlation was detected between residual feed intake (RFI), and body weight variation during successive periods of feed deprivation (FD) and re-feeding (RF). To assess the pertinence of such indirect criteria for future breeding programs, we set up a large experiment using sea bass (*Dicentrarchus labrax*), a recently domesticated species with broad genetic diversity. The objectives of the present study were to analyze the relationship of FD and RF with RFI, and to assess the consistency of such indirect criteria over time and their correlation with carcass quality. Fish originating from a full factorial design combining eight dams and 41 sires, were raised in the same tank. At 306 days post fertilization 2000 fish were individually tagged and their body weight recorded over a growth period of three weeks, followed by two successive periods of three weeks of feed deprivation and three weeks of ad libitum re-feeding. Fish performances were then classified, FD-, FD+, RF- and RF+ for fish exhibiting loss (FD) or gain (RF) of weight relatively lower (-) and higher (+) than the population mean. Fish were sorted into four groups (FD-/RF-, FD+/RF+, FD-/RF+, FD+/RF-). Each of the 4 groups was split between three replicated tanks of 50 fish. Body weight gain and feed intake were measured for each replicate every three weeks over a six months period to estimate residual feed intake. The fish then underwent a period of three weeks of feed deprivation followed by a period of three weeks of ad libitum re-feeding. At the end of each period, individual weight gain variations were recorded, as well as muscle fat using ultrasonic measurement.

The relationship with RFI variations was high for FD ($P = 0.04$, $n = 12$), and close to significance for a criterion merging FD and RF performances ($P = 0.06$, $n = 12$). FD but not RF was negatively correlated with muscle fat ($P < 0.05$, $n = 600$). In conclusion, selecting fish losing less weight during a three week feed deprivation period should lead to improve RFI, but also to increase muscle fatness. Using a combination of FD and RF as indirect criteria would result in slower progress in RFI, but would not impact carcass quality traits. The next step for inferring the potential genetic gain that can be expected is to assess the heritability of such criteria.

Keywords: European sea bass; *Dicentrarchus labrax*; Feed efficiency; Residual feed intake; Feed deprivation; Compensatory growth; Selective breeding

1. Introduction

In farmed fish, feed represents at least 50 % of production costs and is responsible for a substantial part of their environmental loading. Improving feed utilization efficiency thereby provides real hope to significantly reduce the cost and ecological impact of aquaculture production. These stakes are particularly important in European sea bass (*Dicentrarchus labrax*) which is one of the major aquaculture fish in the Mediterranean. Sea bass feed efficiency is low (g weight gain/g feed intake between 0.4 and 0.8) compared to other cultured fish species.

Large improvements in productivity can be expected with selective breeding in fish. The genetic variability of most production traits is large, probably due to the recent domestication of most species (Gjedrem, 2000). This is especially true for sea bass production, which has begun only about 20 years ago and, in many cases, still relies on wild broodstock. Heritability of growth traits is high for this species (Dupont-Nivet et al., 2008). A first attempt of experimental selection has led, with 5 % selection pressure, to a gain of 23 % body weight at commercial size in the first generation (Vandeputte et al., 2009).

In fish, feed utilization efficiency presents sufficient genetic variability to be detected in rearing conditions (Thodesen et al., 2001; Henryon et al., 2002; Kolstad et al., 2004). However, to the best of our knowledge, no selective breeding program for improving feed utilization efficiency has started yet with any species of fish. This is explained by the lack of knowledge regarding its genetic basis. In endothermic land vertebrates, RFI is the trait that is now widely used to study the genetic variability of feed utilization efficiency. It is calculated as the difference between actual and expected intake of an individual over a given weight gain interval. What is required is an accurate measurement of individual intake, and models describing the relationship between intake and growth. RFI presents the advantage of not being a ratio. Moreover, expected intake being generally predicted from maintenance and production requirements, RFI is assumed to be stable through life stages (Crews, 2005). In land vertebrates, RFI heritability is moderate and breeding programs aimed at improving this trait have been successful (Pitchford, 2004). In fish, improvements can be expected with selective breeding since recent experiments on rainbow trout pointed out significant genetic variability for RFI (Silverstein et al., 2005; Grima et al., 2008). However, because fish are reared in groups, individual feed intake can not be recorded directly. Also, because most of the fish species reared have been domesticated only recently, reference models are still lacking – although studies are underway (Bureau and Hua 2008). Indirect criteria for RFI are, therefore strongly needed for developing future breeding programs. Such criteria should be non invasive and easily recordable at the individual level.

Selection for growth is often seen as a way to indirectly improve feed utilization efficiency by reducing the importance of maintenance costs relative to body weight gain (Pym, 1990). However, body weight gain, *per se*, may not be an accurate indirect criterion in fish. In some experiments, a positive genetic correlation between growth and feed efficiency can be seen (Thodesen et al., 1999; Kause et al., 2006; Quinton et al., 2007), while in other experiments selection for growth does not lead to improved feed efficiency (Sanchez et al., 2001; Ogata et al., 2002; Mambrini et al., 2004). Variability in the selection schemes and in the experimental conditions -in particular the feeding regime and the fish line chosen- may explain these discrepant conclusions. In land vertebrates, maintenance requirements have been identified as one of the major process explaining variation in feed utilization efficiency (Herd et al., 2004). In fish, maintenance requirements are usually estimated by energy loss at zero intake (Cho and Bureau, 1998; Bureau et al., 2002; Lupatsch et al., 2003). This trait can be measured either by recording oxygen consumption of fish being feed deprived since three to seven days, either by measuring carcass energy loss after a long feed deprivation period (Lupatsch et al., 2003). None of those traits can be easily used to evaluate the performances of breeding candidates, as measurement of oxygen consumption needs very specific equipment, and carcass energy loss measurement is lethal. Fish, because of their relatively low maintenance requirements for energy as compared to mammals, can sustain

large periods of feed deprivation, and are able, when they are re-fed, to boost their performance in terms of intake and feed utilization efficiency to recover their weight gain (Ali et al., 2003). Because the objective is to rank individuals or lines according to their relative variations in feed utilization efficiency, our assumption is that individual discrepancies of weight loss during feed deprivation (FD) and weight gain during a following re-feeding period (RF) can reflect variations in feed utilization efficiency. Because they are easily recordable in usual farm conditions, they could be pertinent indirect criteria to be used in selective breeding programs aiming to improve feed utilization efficiency. The first step to examine this assumption is to look at the genetic correlations between these indirect criteria and RFI itself. We therefore used rainbow trout clones and found that a criterion integrating body weight loss during feed deprivation and body weight gain during subsequent re-feeding periods could explain 59 % of the genetic variation in RFI (Grima et al. 2008). Clones are highly appropriate models for separating genetic and environmental variation components, but they do not offer high genetic diversity in an experimental population. The next step would be to verify the pertinence of such indirect criteria in population of larger diversity. Sea bass populations are extremely diverse, mainly because their production still partly relies upon wild-caught broodstock.

The objective of the present study was to test if FD and RF could be pertinent for selecting RFI variations with sea bass. We set up a protocol to assess the relationship between RFI variations and FD plus RF performance. In addition, we analyzed the consistency over time of FD and RF performance. As selection for body weight variations can also lead to variations in carcass quality traits, such as increased fatness when selecting for body weight gain in fish (Gjedrem, 1997; Kause et al., 2007). The present study then also aimed to infer the impact of using such traits on muscle quality.

2. Materials and methods

We aimed to produce 328 families based a full factorial mating design using wild broodstock. We took care to raise fish in the same common environment as early as possible. The study comprised two main experimental phases and 4 steps (Fig. 1); 1) phase 1 step 1: individual growth, FD and RF performance were recorded on the largest number of fish representative of the families and reared in a common tank, 2) step 2: fish performance were classed as FD⁻, FD⁺, RF⁻ and RF⁺ for fish exhibiting loss (FD) and gain (RF) of weight relatively lower (-) and higher (+) than the population mean and were separated into four triplicate groups FD⁻/RF⁻, FD⁺/RF⁺, FD⁻/RF⁺ and FD⁺/RF⁻ 3) phase 2 step 3: group RFI was estimated based on body weight gain and feed intake recorded over a period of 6 months and 4) step 4: at the end of the experiment individual FD and RF performance were checked; muscle fat and perivisceral fat content of the fish from each group were evaluated.

2.1. Fish production

Fish were produced according to a full factorial mating design combining eight dams and 41 sires (see also Grima et al., 200X). Immediately after fertilization, eggs were pooled for 48 h incubation (14°C), then 50 ml of viable eggs (~ 40,000) were collected and placed in a single 0.5 m³ incubator. Standard rearing conditions were used, water temperature was gradually increased from 14°C to 20°C in the first 68 days. Fish were transferred into a common 5 m³ fiberglass tank until the start of the experiment. During this pre-growing phase, salinity varied between 24 and 39 g.l⁻¹.

2.2. Experimental phase 1: Individual weight loss and weight gain performance, and subsequent group composition

2.2.1. Recording performance: At day 306 post fertilization (pf), 2,000 fish were randomly chosen, individually tagged with a Passive Integrated Transponder (AEG-Id, Germany) and individually weighed. We checked the pedigree of 1,300 fish using six microsatellite markers and can assess that at least 261 families were represented (see also Grima et al., 200X). They were placed into a single 5 m³ tank equipped with recirculated water system; water temperature was maintained around 20°C and salinity was on average 37 g.l⁻¹. Fish were fed *ad libitum* a standard commercial diet (Neogrower, Le Gouessant, France), containing 45 % protein and 17 % lipid, using a self feeder to which the fish had day-long access. Individual weight was recorded at day 341 and day 370 pf for assessing the basic growth (BG). Fish were then submitted to two successive periods, each consisting of three weeks of feed deprivation (FD1 day 371 to day 392 pf, and FD2 day 415 to day 436 pf) followed by three weeks of *ad libitum* re-feeding (RF1 day 393 to day 414 pf, and RF2 day 437 to day 458 pf). To record individual weight, free access to food was stopped 24 h before the measurement for BG and RF periods, fish were anaesthetized (2-phenoxy-ethanol 0.4 ml. l⁻¹), individually identified using a PIT-Tag reader and weighed to the nearest 0.1 g. They were re-fed the day after the measurements, except when the following period was FD. Growth rate in each period was expressed as the Thermal Growth Coefficient, which offers a standardized measure of growth that is unaffected by body weight, time interval and water temperature (Iwama and Tautz, 1981).

$$\text{Thermal growth coefficient (TGC)} = \frac{(W_f^{1/3} - W_i^{1/3})}{\sum T} \times 100$$

Where W_f and W_i are the final and initial body weights of the considered period, and $\sum T$ is the sum of day temperatures during the period. Growth rates for the different periods are referred to as TGC_{BG} , TGC_{FD1} , TGC_{RF1} , TGC_{FD2} , and TGC_{RF2} .

2.2.2. Separation into groups: The objective was to sort the fish according to the TGC values measured during the feed deprivation and re-feeding periods: low or high weight loss during feed deprivation (FD⁻ and FD⁺, respectively), low or high TGC during re-feeding (RF⁻ and RF⁺, respectively), low or high TGC during re-feeding (RF⁻ and RF⁺, respectively) and constitute four groups: FD⁻/RF⁻, FD⁺/RF⁺, FD⁻/RF⁺ and FD⁺/RF⁻. The sorting was realized at the end the second re-feeding period (day 458 post fertilization), so groups were constituted based on the performance of the two TGC_{FD} (1 and 2), which were averaged (TGC_{FD}), and only one RF (TGC_{RF1}) periods. Among the 2,000 fish, 1,907 had valid data for all TGCs and could be used.

Body weight gain and loss during feed deprivation and re-feeding periods are closely linked to individual growth performances. Because we want to characterize the direct relationship between RFI and FD or RF performance, we corrected TGC_{FD} and TGC_{RF1} values by growth performance. Moreover, as fish lose proportionally less weight during deprivation periods than they gain during re-feeding periods, the corrected TGC values were standardized (mean = 0; SD = 1) to give as much importance to weight loss as to weight gain. In practice, TGC_{FD} and TGC_{RF1} were each regressed on TGC_{BG} and BW_{341} in a multiple linear regression. The residuals of the regressions were standardized and their values (FD_{corr} and RF_{corr}, Table 1) were used to constitute the groups (Fig. 2). We wish to rise to the reader that fish identified as FD⁻ are those fish that lose little weight during feed deprivation, and then are fish with a positive value of FD_{corr}, while FD⁺ fish lose much weight and have a negative value of FD_{corr}. We selected 208 fish from each group, representing 10.9% of the initial experimental population. Among those fish, 150 were randomly chosen to be used in the present study.

2.3. Experimental phase 2: Growth and feed intake of the groups, stability of the indirect criteria

2.3.1. *Fish Management*: The 150 fish from each group were randomly dispatched into three replicated tanks (1 m³; 50 fish per tank). Tanks were supplied with flow-through seawater, temperature varied between 16 and 22°C, and salinity between 30 and 39 g.l⁻¹. Fish were hand-fed once daily (seven days a week) to apparent satiation with the same commercial diet as the one used in the first experimental phase, each meal lasting approximately one hour.

After a six weeks adaptation period (day 505 post fertilization), group body weight and intake were recorded once or two times a month until day 679 post fertilization. Individual body weight were measured as previously described. To measure feed intake, feed distributed and feed waste were weighed for each replicate as described in Helland et al. (1996).

2.3.2. *Consistency of weight loss and weight gain performance and relationship with carcass traits*: From day 679 pf on, fish were subjected to a feed deprivation (day 679 to day 700 pf) followed by a re-feeding (day 701 to day 722 pf) and then a final feed deprivation period (day 723 to day 744 pf). At the end of each period, fish were individually weighed as previously described and the dorsal muscle lipid content was assessed using indirect ultrasonic measurement (Distell Fish Fatmeter, FM 692) according to the method described by Douirin et al. (1998). In short, after a fish had been anaesthetized and weighed, the Fatmeter was applied at four different locations on each side of the spine (anterior, posterior, left and right). At day 744 pf, half of the fish per replicate were slaughtered (lethal dose of 2-phenoxy-ethanol, 1.5 ml.l⁻¹) and eviscerated. The weight of the dressed carcass was recorded. Perivisceral fat was delicately dissected from the digestive tract and weighed to the nearest 0.1g.

2.4. Traits measured

Body weight gain (BWG) and feed intake recorded for each replicated tank between day 505 and day 679 pf, were used to estimate RFI. During this period nine fish obviously did not eat, as they continuously lost weight, and were thus removed from the analysis. Body weight per replicate was calculated as the sum of the individual body weights of the fish present in the tank. BWG calculated as the difference between the final body weight (BW₆₇₉) and initial body weight (BW₅₀₅). For each replicate, feed intake was calculated as the difference between feed distributed and feed waste over the period lasting from day 505 to day 679 pf. For each replicate, the mean metabolic body weight (MMWT) was calculated as the weight at the midpoint of the test period (day 596 pf) raised to the power 0.8, used to account for the decrease in metabolic rate with increasing body weight (Lupatsch et al., 2003).

The expected FI was estimated using the following model (Crews, 2005):

$$Y_i = \beta_0 + \beta_1 BWG_i + \beta_2 MMWT_i$$

where Y_i is the expected FI over the test period of the replicate i , β_0 is the regression intercept, β_1 is the partial regression coefficient of FI on BWG, β_2 is the partial regression coefficient of FI on MMWT. RFI was calculated as the difference between Y_i and the observed FI of each replicate.

The TGC during the subsequent feed deprivation (between day 679 and day 700 pf, FD3) and re-feeding (between day 701 and day 722 pf, RF3) periods were calculated as previously described, and will be referred to as TGC_{FD3} , TGC_{RF3} .

Muscle fat content (% of wet weight) was calculated as the mean of the four ultrasonic measurements recorded at day 679 pf (Fat content₆₇₉) and at the end of the subsequent feed deprivation (Fat content_{FD3}) and re-feeding (Fat content_{RF3}) periods.

The other variables were the peri-visceral fat weight (g) and the carcass yield measured at day 744 pf, the latter being calculated as follows:

Carcass yield (%) = dressed carcass weight (g) ÷ body weight (g) × 100

2.5. Statistical analyses

The effect of group (FD⁻/RF⁺, FD⁻/RF⁻, FD⁺/RF⁻, FD⁺/RF⁺) was assessed using ANOVA and ANCOVA (GLM procedure, SAS Inst., Inc., Cary, NC), after having verified residual homoscedasticity and the independence of the variance from the mean.

The initial performance of the fish before their separation into groups was re-examined. TGC_{BG} , TGC_{FD1} , TGC_{RF1} , TGC_{FD2} , and TGC_{RF2} for each fish were re-assigned according to group. The analysis was performed using individual fish as the experimental unit ($n = 600$) with the following model:

$$Y_{ij} = \mu + group_i + e_{ij}$$

where Y_{ij} is the performance of an individual fish, μ is the population mean, $group_i$ is the fixed effect of the group i ($i=1,..4$), and e_{ij} is the random residual.

The effect of the groups was assessed on each variable recorded during the second phase. In addition, to test the effect of feed deprivation performance alone, we merged the data obtained for the FD⁻/RF⁻ group with that from FD⁻/RF⁺, and did the same for FD⁺/RF⁻ and FD⁺/RF⁺. In the same way, we merged the data obtained for FD⁻/RF⁻ with that for FD⁺/RF⁻, and data for FD⁻/RF⁺ with that for FD⁺/RF⁺, to test the contrast between fish with low (RF⁻) and high (RF⁺) weight gain during re-feeding.

Group effects on FI and RFI were analyzed using tank replicate as the experimental unit (as FI and RFI cannot be estimated on individuals) with the following model:

$$Y_{ij} = \mu + group_i + e_{ij}$$

where Y_{ij} is the performance of the replicate, μ is the population mean, $group_i$ is the fixed group effect, and e_{ij} is the random residual.

BWG, TGC_{FD3} and TGC_{RF3} analyses were performed using individual fish as the experimental unit ($n = 600$) and the following mixed model:

$$Y_{ijk} = \mu + group_i + replicate(group)_{ij} + e_{ijk}$$

Where Y_{ijk} is the performance of an individual fish, μ is the population mean, $replicate(group)_{ij}$ is the random tank replicate effect nested within group, and e_{ijk} is the random residual.

Analyses on muscle fat content_(679, FD3, RF3), and fish carcass quality (carcass yield, peri-visceral fat) were performed with individual fish as the experimental unit (600 fish for fat content in the dorsal muscle, 300 for carcass quality), using the following model:

$$Y_{ijk} = \mu + group_i + replicate(group)_{ij} + aBW + e_{ijk}$$

Where Y_{ijk} is the performance of an individual fish, μ is the population mean, $replicate(group)_{ij}$ is the random tank replicate effect nested within group, BW is the individual body weight at the date at which the data were recorded (day 679, 701, and 723 for Fat content_(679, FD3, RF3), and day 744 for the carcass yield and peri-visceral fat) used as a covariate, and e_{ijk} is the random residual.

The correlations between RFI and the other variables were examined with the CORR procedure of SAS, using tank as the experimental unit ($n = 12$).

The consistency of fish response to feed deprivation and re-feeding periods was assessed by the correlations between $TGC_{FD1\&2}$ and TGC_{FD3} and between $TGC_{RF1\&2}$ and TGC_{RF3} ($n = 600$), using the CORR procedure of SAS.

3. Results

As expected, fish overcame feed deprivation and had higher growth rates during the re-feeding periods than during the BG period (Fig. 3; Table 1). Mortality was lower than 2% over the two experimental phases. Fish displayed large inter-individual variability of performance during the successive periods of the first experimental phase (BG, FD1, RF1, FD2 and RF2, Fig. 3, Table 1). This enabled us to sort the four groups with significantly different FD and RF performance (Table 1, Fig. 2).

During the second experimental phase, fish separated into groups exhibited significant variations in body weight gains during the period dedicated to RFI estimation (Fig. 4, Table 2). The model generated for estimating expected FI was the following:

$$\text{- Expected FI} = 5917.1 + 1.245 \times \text{MMBW} + 0.842 \times \text{BWG}$$

RFI varied among groups. It was significantly lower for groups with lower body weight loss during feed deprivation (Table 3). The highest RFI was recorded for the FD⁺/RF⁺ group and the lowest for the FD⁻/RF⁻ group, the differences were close to significance ($P = 0.061$). The observed variations in RFI between groups were not linked to initial body weight, BWG, or FI variations (Table 4). However, the correlation between RFI and FI was close to significance ($P = 0.061$), indicating that there may be a tendency for low RFI to be associated with low FI. In addition, variation in RFI was not correlated with variation in muscle fat content (Table 4). RFI was comparable among RF groups, and RF⁺ fish had a better growth than RF⁻ fish (Table 3). It appears that the higher body weight of RF⁺ fish can be explained by higher intakes. In contrast, FD⁻ fish had a growth comparable to FD⁺ fish, but had a lower RFI.

Concerning FD and RF performance at the end of the experiment, contrary to what was observed during the first experimental phase, there was no significant difference among groups during the feed deprivation period (TGC_{FD3} ; Table 5). But performances of the FD⁺ groups were highly variable. Indeed, when the performances of the FD groups are merged, TGC_{FD3} of fish from FD⁻ groups was significantly less than that of fish from FD⁺ groups. The performances of fish during the last re-feeding period were as expected: fish from the RF⁺ groups grew better than fish from the RF⁻ groups. At the individual level, the phenotypic correlations between performances recorded during the initial and last periods of feed deprivation were low to moderate but highly significant (TGC_{FD1} and TGC_{FD3} , $r = 0.30$; $P < 0.001$; TGC_{FD2} and TGC_{FD3} ; $r = 0.35$; $P < 0.001$), and quite similar to the correlation between TGC_{FD1} and TGC_{FD2} ($r = 0.45$; $P < 0.001$). On the other hand, the phenotypic correlations of the weight gains between the initial and last re-feeding periods, were weak (TGC_{RF1} and TGC_{RF3} ; $r = 0.08$; $P = 0.06$), unlike the correlation between TGC_{RF1} and TGC_{RF2} ($r = 0.51$; $P < 0.001$). It should, however, be noted that the growth rates during RF3 period were low compared to those during the RF1 and RF2 periods.

Dorsal muscle fat content_(679, RF3, FD3) was comparable among groups (Table 5). However, when performance of FD groups were merged, fish from FD⁻ groups did have greater muscle fat content than fish from FD⁺ groups at day 701 and day 723 pf (Table 5). No differences in muscle fat content_(679, FD3, RF3) were observed between the RF groups (Table 5). As a general pattern, fish tended to lose muscle fat during the feed deprivation period and regain muscle fat during re-feeding periods (Table 5). The correlation between muscle fat contents at day 679 pf and after the last feed deprivation was highly significant ($r = 0.812$, $P < 0.001$), as was the correlation between Fat content_{FD3} and Fat content_{RF3} ($r = 0.853$, $P < 0.001$), indicating that rankings for this trait were not severely affected by the feed deprivation and re-feeding periods. Finally, there were no differences in carcass yield or in perivisceral fat weight between groups, but it must be noticed that this last trait was highly variable among individuals (Table 5).

4. Discussion

The aim of the present study was to test the suitability of indirect criteria that could be used in future breeding programs to improve feed utilization efficiency in sea bass. Our assumption was that body weight variations during successive periods of feed deprivation (FD) and re-feeding (RF) should be pertinent. In the present study we have shown that the traits measured meet the quality requirements of indirect criteria, because they i) are easy to record under usual rearing conditions, ii) are representative of variations of RFI - not merely variation evident in one day's intake and growth measurement, iii) are independent from growth rates, so as to reflect feed utilization efficiency *per se*, and iv) if we refer to our previous study with rainbow trout clones (Grima et al., 2008), seem applicable to a range of fish species. In addition, we have shown that they are rather consistent along time, and that they correlate with fish flesh quality.

Here we showed that sea bass inter-individual variation in FD and RF is high, even if fish are reared in the same environment. Moreover, weight loss during feed deprivation is a trait that is stable over a long period (308 days), even though fish went through various rearing conditions. This suggests that the genetic determinism of such traits is strong. In the present study, we noticed that fish losing less weight during feed deprivation are also those that exhibit the highest muscle fat content. Thus FD is likely linked to individual variations in lipid utilization. This has to be further investigated and we may suggest three complementary directions: fish behavior and activity, lipid turnover rate and source of energy supply during feed deprivation (*i.e.* protein or lipid).

In designing the experiment, our hypothesis was clearly that variations in FD and RF were linked to variations in RFI. Indeed the four groups selected according to FD and RF performance exhibited contrasted RFI values. The group of fish that had lost less weight during the feed deprivation periods was also the most efficient groups. Because fish from the FD⁻ group had a comparable growth rate to fish from FD⁺ group, it can be inferred that selecting fish which lose less weight during a three week period of feed deprivation, will lead to improved feed utilization efficiency without affecting growth. However, it must be taken into account that FD⁻ is linked to higher muscle fat. Regarding RF performances they were neither correlated with variations in RFI, nor with variations in muscle fatness, but were linked to variations in weight gain, RF⁺ group exhibiting a higher body weight gain than RF⁻ group. If we consider these performances in addition to FD performances, the most efficient group (*i.e.* lower RFI), tended to be FD⁻/RF⁻ and the least efficient group, FD⁺/RF⁺. We estimated that for a BWG of 100 g, the average population would consume 152.1 g, while the FD⁻ fish would eat 147.3 g, and FD⁻/RF⁻ fish would eat 147.6 g. This improvement corresponds to 3.12 % and to 2.93 % feed saving for FD⁻ fish and FD⁻/RF⁻ fish, respectively.

In the present study the combination of FD and RF is linked to the variations of RFI. This is in line with what has been formerly found with rainbow trout clones (Grima et al., 2008). However, the indirect criterion explaining most of variations of RFI varies among those two studies. It was FD in the present study, while in the study of Grima and collaborators (2008), RF was more closely linked to RFI. Besides the specific effect linked to the differences in protocol and variations in the physiological status, the discrepancy may reflect inter-species differences in nutrient utilization. In salmonids, protein and lipid utilization vary among species (Azevedo et al., 2004a and b), while in marine species such traits appears to be rather constant (Lupatsch et al., 2003). Nutrient turnover rate has been more extensively studied in rainbow trout than in sea bass, and we can not infer from literature data the major features of metabolism for each of those two species. What is known for a long time is that sea bass compared to rainbow trout deposit more fat in the liver and less in the digestive tract and muscle (Sheridan, 1988; Corraze and Kaushik, 1999). Whether particularities of lipid storage influence the relationship between RFI and FD or RF can not be inferred from the present data. What is apparent from our study in trout (Grima et al., 2008) and the present one is that the relationship between RFI and FD or RF may vary in both studies between species or experimental conditions. Nevertheless, the criterion combining FD and

RF appears systematically significantly related to RFI. This strengthens the recommendation to merge these two traits when studying the variations in feed utilization efficiency. Although the correlations between FD, RF, and RFI need to be verified in other fish species, it appears that, at least for species as different as rainbow trout and sea bass, these two traits are sufficient to select fish with variable feed utilization efficiency.

In land vertebrates, the relationship between metabolism and RFI variations has been widely studied. Variations in maintenance requirement (Archer et al., 1999; Herd and Bishop, 2000; Bulle et al., 2007), or in the rate of fractional protein degradation (McDonagh et al., 2001) are closely linked to variations in RFI. In rainbow trout (Silverstein, 2006), as in land vertebrates (Archer et al., 1998; Arthur et al., 2001; Rauw et al., 2006), feed intake is generally positively correlated with RFI. The positive relationship between FI and RFI is assumed to be due to the higher loss of energy with the heat increment of feeding (Herd et al., 2004). The positive relationship between RFI and FI that we underlined in the present study is in line with this assumption.

The correlation between RFI and Fat content estimated in our study differs from previous results in the literature. In whitefish, improved feed utilization may be a correlated response to selection for lower fat (Quinton et al., 2007). The relationship between feed utilization efficiency and fatness is, however, generally weak or null in most other species studied until now (Archer et al., 1999; Quinton et al., 2007; Cai et al., 2008). In contrast, our present results in sea bass suggest that selection based on FD will lead to an improvement of RFI but also to a fattening of the flesh. However, using a criterion merging FD and RF would result in stable carcass quality traits. The link between maintenance requirement and lipid metabolism requires further investigation in this species. However, to draw definitive conclusions on the genetic consequences of selecting on FD and RF for fat content, genetic correlations shall be estimated.

To conclude, in the present study we showed that the weight loss during a three weeks feed deprivation period and the weight gain during a subsequent three weeks period of re-feeding are linked to variations in RFI in sea bass as in rainbow trout. Such traits could be used as indirect criteria for improving RFI in fish through selective breeding, provided they are heritable. The present study highlights that selecting FD fish would significantly improve RFI but would also lead to fatter flesh. Using RF trait in addition to FD should allow to select for RFI improvement without affecting carcass quality traits. These indirect criteria (FD, and combination of FD and RF) are of potential high interest for individual selection for reduced RFI, but their heritability and their genetic correlation with RFI must be estimated, to be able to estimate the genetic gain that a breeding program based on such traits could generate in terms of RFI and then ultimately in terms of reduced feed costs and effluents in sea bass culture.

Acknowledgements

We thank the three referees for constructive comments on the earlier version of the manuscript. This study was financed by INRA and Ifremer in the frame of their common research group (GDR) "Genetic improvement of fish".

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Figures

Figure 1

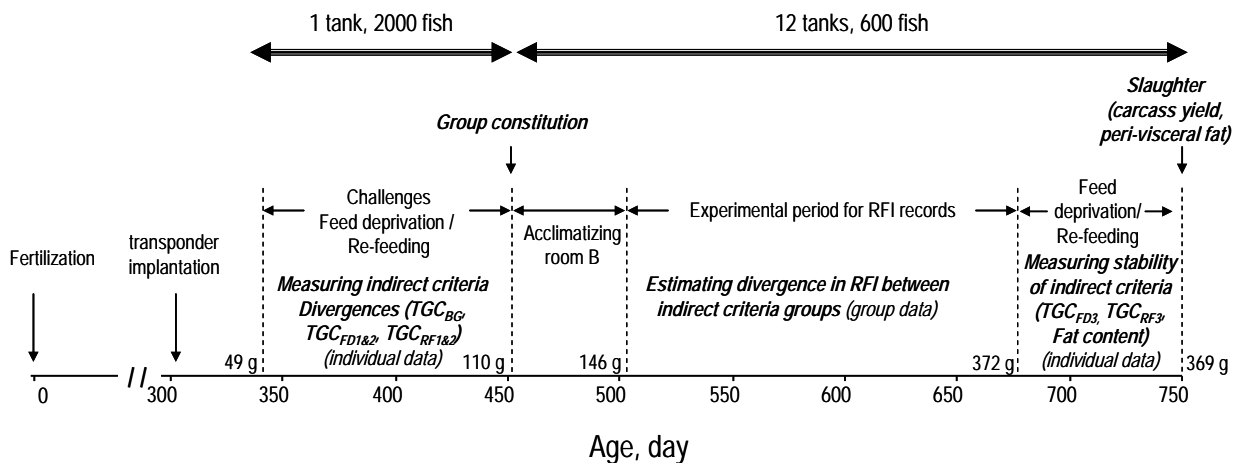


Figure 1. Schematic outline and time frame of the experimentation conducted with sea bass. The recorded traits are listed between brackets.

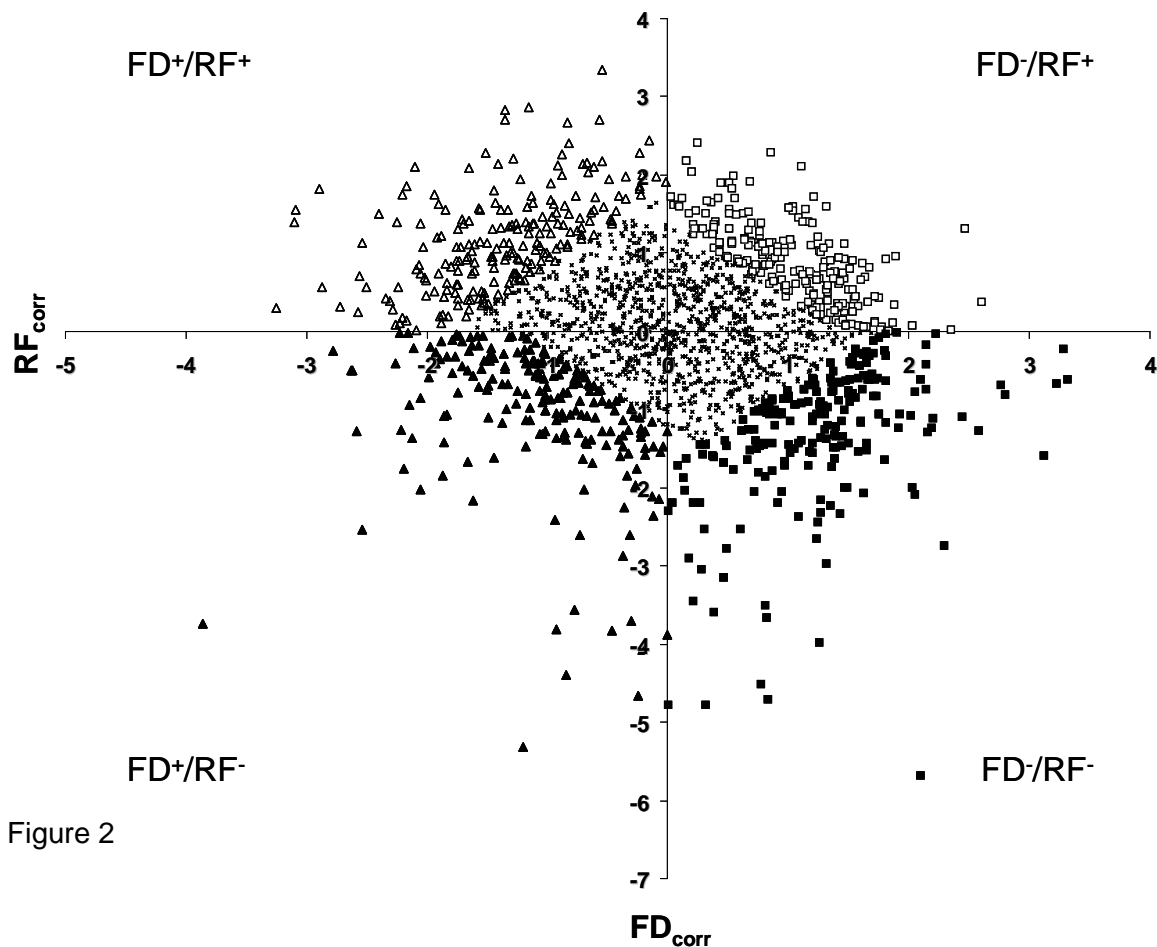


Figure 2

Figure 2. Individual performances of sea bass in terms of body weight loss during two periods of three weeks feed deprivation (FD_{corr}) and weight gain during an intermediate period of three weeks re-feeding (RF_{corr}), based on 1907 sea bass from a factorial cross combining eight dames and 41 sires. Squares (□ ■) correspond to the fish that showed a small weight loss during feed deprivation (FD^-), triangles (△ ▲) correspond to FD^+ fish. White symbols (□ △) correspond to fish selected for high weight gain after re-feeding (RF^+), black symbols (■ ▲) to RF^- fish; × symbols correspond to fish that were not classified in this way. Performances are expressed in units of phenotypic standard deviations.

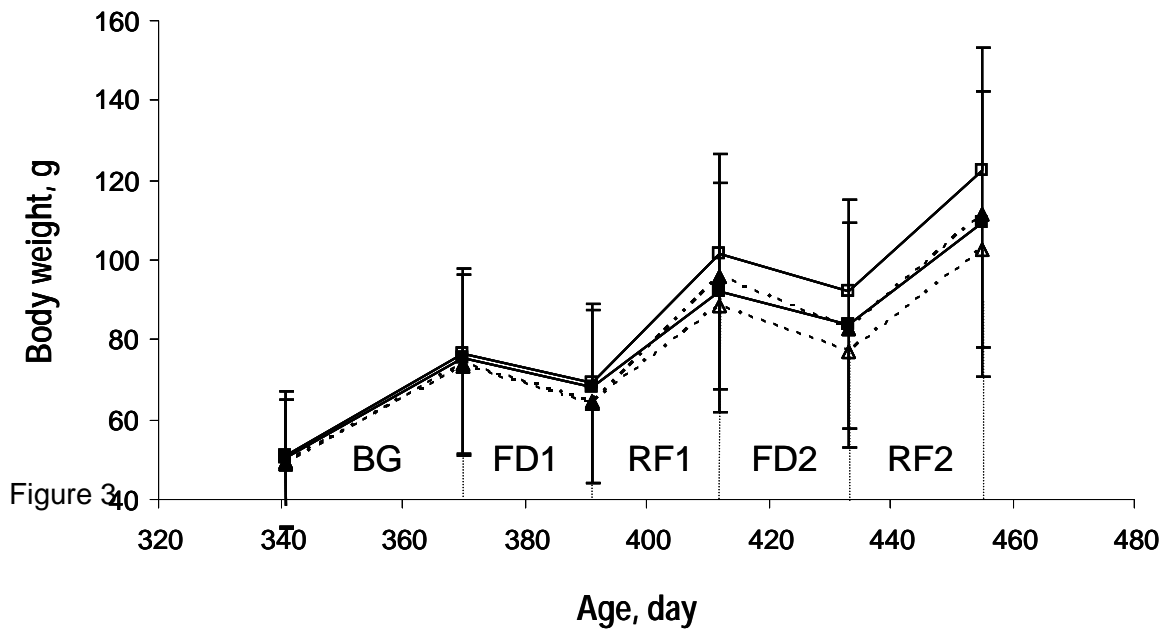


Figure 3. Mean body weight evolution ($g \pm SE$) of the four groups of sea bass before they were separated (first experimental period), during the first period of growth and two successive periods of feed deprivation and re-feeding. BG corresponds to the basic growth period, FD1 and FD2 correspond respectively to the first and the second period of feed deprivation, and RF1 and RF2 correspond respectively to the first and the second period of re-feeding. Squares (■ □) correspond to the groups of fish selected for a small weight loss during feed deprivation (FD⁻), triangles (△ ▲) correspond to the groups with FD⁺ fish. White symbols (□ △) correspond to groups of fish selected for high weight gain after re-feeding (RF⁺), black symbols (■ ▲) to the groups with RF⁻ fish. Continuous lines correspond to FD⁻ groups, dotted lines to FD⁺ groups.

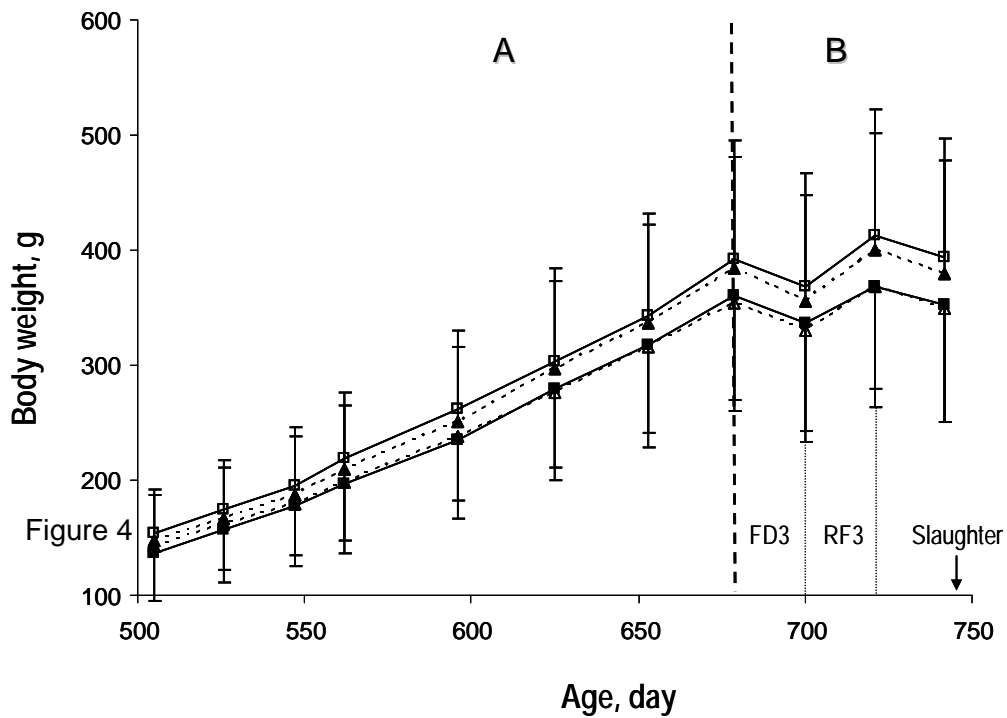


Figure 4. Mean body weight (g \pm SE) evolution of the four groups of sea bass (second experimental period) fed *ad libitum* for 174 days (phase A) then submitted to three weeks feed deprivation followed by three weeks re-feeding (phase B). FD3 corresponds to the third period of feed deprivation and RF3 to the third period of re-feeding. Squares (\blacksquare \square) correspond to the groups of fish selected for a small weight loss during feed deprivation (FD⁻), triangles (\triangle \blacktriangle) correspond to the groups with FD⁺ fish. White symbols (\square \triangle) correspond to groups of fish selected for high weight gain after re-feeding (RF⁺), black symbols (\blacksquare \blacktriangle) to the groups with RF⁻ fish. Continuous lines correspond to FD⁻ groups, dotted lines to FD⁺ groups.

Tables

Table 1. Means \pm SE of the thermal growth coefficient (TGC) in sea bass during a basic growth period (BG), followed by two periods of three weeks feed deprivation (FD1 and FD2) alternated with two periods of three weeks *ad libitum* re-feeding (RF1 and RF2), for the four groups of fish with variable performance in terms of weight loss during feed deprivation (FD⁻/FD⁺) and weight gain during re-feeding (RF⁻/RF⁺). FD_{corr} corresponds to the standardized residuals (mean = 0, SD = 1) of the regression of the mean of TGC_{FD1} and TGC_{FD2} on body weight at day 341 and TGC_{BG}. RF_{corr} corresponds to the standardized residuals of the regression of TGC_{RF1} on body weight at day 341 and TGC_{BG}. n gives the number of fish in each group.

	FD ⁻ /RF ⁺	FD ⁻ /RF ⁻	FD ⁺ /RF ⁺	FD ⁺ /RF ⁻	F ^a
<i>n</i>	147	146	149	149	
TGC _{BG}	0.082 \pm 0.010	0.080 \pm 0.011	0.079 \pm 0.019	0.081 \pm 0.014	1.24
TGC _{FD1}	-0.034 \pm 0.005	-0.033 \pm 0.005	-0.045 \pm 0.006	-0.045 \pm 0.006	245.64***
TGC _{RF1}	0.128 \pm 0.009	0.099 \pm 0.015	0.130 \pm 0.011	0.103 \pm 0.015	240.35***
TGC _{FD2}	-0.035 \pm 0.005	-0.032 \pm 0.005	-0.050 \pm 0.007	-0.047 \pm 0.006	366.85***
TGC _{RF2}	0.103 \pm 0.016	0.091 \pm 0.016	0.104 \pm 0.019	0.096 \pm 0.023	22.45***
FD _{corr}	1.03	1.27	- 1.38	- 1.08	842.47***
RF _{corr}	0.90	-1.35	1.19	-1.05	426.60***

^a F value for the group effect (***) $P < 0.001$)

Table 2. Means \pm SE of initial body weight (BW_{341} , g) *ad libitum* feed intake (FI, g.fish⁻¹.day⁻¹) and body weight gain (BWG, g.fish⁻¹.day⁻¹) for seven periods of two to four weeks in groups of sea bass with variable performance in terms of weight loss during feed deprivation (FD⁻/FD⁺) and weight gain during re-feeding (RF⁻/RF⁺). Based on these performances, residual feed intake was estimated. Exponents indicate the age of the fish (day) when the traits were recorded.

Ind. crit. group	Exp.ini	Period 1 ⁵⁰⁵⁻⁵²⁶		Period 2 ⁵²⁶⁻⁵⁴⁷		Period 3 ⁵⁴⁷⁻⁵⁶²		Period 4 ⁵⁶²⁻⁵⁹⁶		Period 5 ⁵⁹⁶⁻⁶²⁵		Period 6 ⁶²⁵⁻⁵⁴³		Period 7 ⁶⁴³⁻⁶⁷⁹	
		BW ₃₄₁	BWG	FI	BWG	FI	BWG	FI	BWG	FI	BWG	FI	BWG	FI	BWG
FD-	145±39	0.97±0.40	1.34±0.11	1.00±0.37	1.48±0.10	1.38±0.48	1.78±0.14	1.25±0.46	1.92±0.27	1.43±0.51	2.11±0.13	1.60±0.59	2.41±0.21	1.54±0.67	2.34±0.22
FD+	145±40	0.92±0.38	1.45±0.07	0.92±0.37	1.49±0.08	1.34±0.50	1.81±0.19	1.22±0.40	1.97±0.09	1.39±0.50	2.17±0.22	1.67±0.58	2.52±0.11	1.42±0.66	2.32±0.24
<i>F^a</i>	0.00	3.42	3.44	7.78**	0.06	1.60	0.08	0.59	0.20	1.03	0.27	2.22	1.28	4.95*	0.02
RF-	140±39	0.96±0.38	1.39±0.12	0.91±0.35	1.54±0.09	1.22±0.45	1.90±0.13	1.19±0.42	2.03±0.19	1.36±0.50	2.26±0.19	1.63±0.57	2.45±0.21	1.35±0.67	2.47±0.13
RF+	151±40	0.94±0.40	1.40±0.10	1.01±0.38	1.43±0.05	1.50±0.49	1.69±0.11	1.27±0.44	1.86±0.18	1.44±0.51	2.02±0.06	1.65±0.60	2.49±0.14	1.61±0.64	2.18±0.19
<i>F^a</i>	11.84***	0.37	0.05	14.37***	5.47*	55.78***	9.56*	5.80*	2.39	4.09*	8.39*	0.22	0.16	24.07	9.18*
FD- /RF-	153±38	0.94±0.41	1.36±0.15	1.04±0.40	1.54±0.12	1.54±0.48	1.88±0.07	1.30±0.48	2.01±0.29	1.39±0.52	2.18±0.16	1.61±0.62	2.38±0.25	1.65±0.64	2.49±0.18
FD- /RF+	137±38	0.98±0.40	1.33±0.09	0.96±0.34	1.41±0.02	1.23±0.44	1.69±0.12	1.19±0.43	1.82±0.28	1.46±0.50	2.04±0.04	1.59±0.55	2.45±0.21	1.43±0.67	2.19±0.13
FD+/ RF-	148±41	0.90±0.40	1.42±0.10	0.99±0.37	1.53±0.08	1.47±0.50	1.93±0.19	1.24±0.39	2.04±0.06	1.50±0.49	2.33±0.21	1.68±0.56	2.52±0.17	1.57±0.63	2.46±0.09
FD+/ RF+	142±39	0.94±0.37	1.48±0.02	0.85±0.36	1.45±0.08	1.20±0.47	1.70±0.12	1.98±0.42	1.90±0.05	1.27±0.48	2.01±0.08	1.66±0.58	2.53±0.06	1.28±0.66	2.18±0.28
<i>F^a</i>	4.75**	1.33	1.24	7.66***	1.62	19.30***	2.67	2.46	0.74	6.28*	3.16	0.81	0.43	9.82***	2.49

^a *F* value for group effect (* : $P < 0.05$; ** : $P < 0.01$; *** : $P < 0.001$)

Table 3. Mean \pm SE of body weight gain (BWG, g.fish⁻¹.day⁻¹), *ad libitum* feed intake (FI, g.fish⁻¹.day⁻¹) and residual feed intake (RFI, per fish) of sea bass between the ages of 505 and 679 day post fertilization, reared in groups with variable performance in terms of weight loss during feed deprivation (FD⁻/FD⁺) and weight gain during re-feeding (RF⁻/RF⁺).

Ind. crit. group	Total Period		RFI
	BWG	FI	
FD ⁻	1.33 \pm 0.10	1.96 \pm 0.11	-6.35 \pm 7.7
FD ⁺	1.28 \pm 0.10	2.01 \pm 0.10	6.40 \pm 7.3
<i>F</i>	1.87	0.59	8.59*
RF ⁻	1.25 \pm 0.08	1.91 \pm 0.07	-2.98 \pm 9.4
RF ⁺	1.36 \pm 0.07	2.05 \pm 0.08	3.03 \pm 10.0
<i>F</i>	12.52***	10.88**	1.14
FD-/RF ⁺	1.37 \pm 0.10	2.03 \pm 0.10	-2.08 \pm 7.4
FD-/RF ⁻	1.28 \pm 0.08	1.89 \pm 0.08	-10.62 \pm 6.3
FD ⁺ /RF ⁺	1.35 \pm 0.04	2.08 \pm 0.06	8.14 \pm 10.8
FD ⁺ /RF ⁻	1.21 \pm 0.09	1.93 \pm 0.07	4.67 \pm 2.7
<i>F</i> ^a	5.00**	3.64	3.73

^a *F* value for group effect (**P* < 0.05, ** *P* < 0.01, *** *P* < 0.001)

Table 4. Correlations and corresponding *P*-values, between residual feed intake (RFI) and body weight at day 505 post fertilization, body weight gain (BWG), feed intake (FI) and the Fat content in the dorsal muscle at day 679 (Fat content₆₇₉), 701 (Fat content_{FD3}) and 723 (Fat content_{RF3}) (*n* = 12) in sea bass.

Trait	RFI	
	<i>r</i>	<i>P</i> -value
BW ₅₀₅	0.18	0.58
BWG	<0.01	0.99
FI	0.55	0.06
Fat content ₆₇₉	-0.22	0.48
Fat content _{FD3}	-0.30	0.33
Fat content _{RF3}	-0.35	0.27

Table 5. Mean \pm SE of thermal growth coefficient (TGC) during the third period of feed deprivation (TGC_{FD3}) followed by a period of *ad libitum* re-feeding (TGC_{RF3}) of groups of sea bass with variable performance in terms of weight loss during feed deprivation (FD⁻/FD⁺) and weight gain during re-feeding (RF⁻/RF⁺). Evolution of the Fat content in the dorsal muscle (% of weight matter) measured using indirect ultrasonic measurements, carcass yield (%) and peri-visceral fat (g) measured at the end of the experimental period after a further three weeks of feed deprivation.

	FD/RF ⁺	FD/RF ⁻	FD ⁺ /RF ⁺	FD ⁺ /RF ⁻	F^a	FD ⁻	FD ⁺	F^a	RF ⁻	RF ⁺	F^a
TGC_{FD3}	-0.036 \pm 0.01	-0.037 \pm 0.01	-0.055 \pm 0.16	-0.060 \pm 0.16	1.46	-0.037 \pm 0.01	-0.058 \pm 0.16	4.08*	-0.049 \pm 0.11	-0.046 \pm 0.11	0.06
TGC_{RF3}	0.066 \pm 0.03	0.052 \pm 0.03	0.067 \pm 0.03	0.060 \pm 0.02	4.88**	0.059 \pm 0.03	0.063 \pm 0.02	1.75	0.056 \pm 0.02	0.067 \pm 0.03	10.88**
Fat content ₆₇₉	8.19 \pm 2.57	7.71 \pm 2.58	7.21 \pm 1.98	7.09 \pm 1.98	1.31	7.95 \pm 2.58	7.15 \pm 1.98	4.42	7.40 \pm 2.31	7.71 \pm 2.35	0.01
Fat content _{FD3}	8.03 \pm 2.17	7.91 \pm 2.47	7.17 \pm 2.65	7.06 \pm 2.22	1.40	7.97 \pm 2.32	7.11 \pm 2.44	4.97*	7.49 \pm 2.38	7.60 \pm 2.45	0.10
Fat content _{RF3}	8.09 \pm 2.07	8.34 \pm 2.67	7.35 \pm 2.10	7.20 \pm 2.09	2.04	8.22 \pm 2.38	7.28 \pm 2.09	5.89*	7.78 \pm 2.46	7.73 \pm 2.11	0.38
Car.Yield	90.7 \pm 1.62	91.0 \pm 1.73	91.0 \pm 1.75	91.7 \pm 1.51	0.96	90.82 \pm 1.67	91.32 \pm 1.67	1.54	91.31 \pm 1.65	90.2 \pm 1.69	1.43
P.-vis.fat	12.80 \pm 6.54	9.56 \pm 4.06	11.34 \pm 6.14	9.52 \pm 5.40	1.47	11.22 \pm 5.69	10.45 \pm 5.84	0.42	9.55 \pm 4.73	12.10 \pm 6.39	2.00

^a F value for group effect (* $P < 0.05$, ** $P < 0.01$)