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Effect of selection for fasting tolerance on feed intake, growth and feed efficiency in the European sea bass *Dicentrarchus labrax*☆

Sophie Daulé [a,b], Marc Vandeputte [a,b,]*, Alain Vergnet [a], Bruno Guinand [c,d], Laure Grima [a,b], Béatrice Chatain [a]

[a] Ifremer, UMR110 INTREPID, Chemin de Maguelone, F-34250 Palavas-les-Flots, France
[b] INRA, UMR1313 GABI, F-78350 Jouy-en-Josas, France
[c] UMR CNRS 5554 ISE-M, F-34000, Montpellier, France
[d] Université Montpellier 2, F-34000, Montpellier, France

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ABSTRACT

Feed efficiency is a major goal for aquaculture sustainability, and selecting fish to genetically enhance this trait would be highly valuable. However, no selective breeding program specifically targeted to feed efficiency exists for farmed fish, mostly because of the difficulty of measuring individual feed intake. However, a negative phenotypic correlation between feed efficiency and weight loss at fasting has been previously demonstrated in sea bass submitted to feed deprivation (FD). We mated sea bass parents selected for their high (FD^{+}) or low (FD^{-}) weight loss at fasting to produce FD^{+} and FD^{-} progeny, which were reared in a single tank to avoid common environmental effects. At 8 months of age, 1200 of those fish were submitted to three alternating periods of fasting (3 weeks) and re-feeding (3 weeks). Individuals were weighed at the end of each feeding and fasting period. Their line of origin was identified by genotyping of 12 microsatellite markers, resulting in 1130 unambiguously assigned fish (484 FD^{-}, 686 FD^{+}). FD^{-} offspring lost significantly less weight than FD^{+} offspring in this feed deprivation trial. After that, the feed efficiency of eight groups of 50 FD^{+} fish and eight groups of 50 FD^{-} fish was evaluated in four successive 20-day periods. At the end of the fourth period, 10 fish per tank were sacrificed to evaluate their carcass yield. The FD^{-} fish had a better overall growth and were fatter, and FD^{+} fish had a better carcass yield. A better feed efficiency was expected for the FD^{-} fish, but differences between the two groups for this trait, measured either with feed efficiency ratio or with residual feed intake, were not consistently significant. Although the two lines were clearly divergent for several traits, demonstration of feed efficiency differences between the FD^{+} and the FD^{-} lines was not consistently observed in sea bass. A second generation of selection may allow further divergence in the lines and reveal differences in feed efficiency.

1. Introduction

Feed efficiency is a very important issue in aquaculture, particularly for carnivorous species, which are partially fed with fish meal and fish oil. This dependency upon marine capture fisheries is a problem because of the lack of availability and the increasing price of fish meal and oil (Tacon and Metian, 2008). Pressure on natural resources and production costs of fish farming could be diminished by enhancing feed efficiency. A better feed efficiency would also reduce waste production and the associated environmental impact (Talbot and Hole, 1994).

Feed efficiency, the capacity to generate biomass from food consumed, is expressed through two indices. The feed efficiency ratio (FER) is the number of growth units per unit of quantity eaten. The residual feed intake (RFI) is the difference between the observed feed intake and a theoretical feed intake accounting for production level. FER have the advantage to be a simple index with direct economic impact, but it varies with growth and age, whereas RFI is not influenced by growth.

Feed efficiency of fish productions has already been increased by enhancing rearing and feeding processes. Indeed, in fish, feed efficiency depends on physical factors, like temperature (Buentello et al., 2000; Handeland et al., 2008; Imsland et al., 2006; Wang et al., 2009), photoperiod (Biswas et al., 2005), oxygen concentration (Buentello et al., 2000), and nutritional factors, like food digestibility (Aksnes et al., 1997). Since the 1980s, progress in feed formulation and in feed processing technologies has enabled a significant increase in feed efficiency (Bureau and Hua, 2010), and selective breeding could lead to further improvements.

Indeed, selection based on feed efficiency is a usual practice in poultry breeding (Emmerson, 1997). In cattle, feed efficiency has been studied in research, and future selection programs based on this criterion are possible (Crews, 2005). In fish, feed efficiency has a significant genetic variation. In Atlantic salmon, the full-sib family effect has been shown to

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* Corresponding author at: Ifremer, UMR110 INTREPID, Chemin de Maguelone, F-34250 Palavas-les-Flots, France. Tel.: +33 4 67 13 04 07.

E-mail address: marc.vandeputte@jouy.inra.fr (M. Vandeputte).

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explain 31% to 77% of feed efficiency variation (Kolstad et al., 2004; Thodesen et al., 2001), and Grima et al. (2008) showed a strong genetic effect on residual feed intake in rainbow trout. Conversely, a heritability of 0.03 ± 0.10 has been found for feed efficiency in rainbow trout (Kinghorn, 1983). Nevertheless, selection programs directly based on this criterion are not implemented, primarily due to difficulties accurately measuring feed efficiency on individual fish. Estimating individual feed efficiency requires the measurement of individual growth and individual feed intake, which implies rearing fish individually (Martins et al., 2006; Nikki et al., 2004) or estimating feed intake on X-ray images of fish fed with labelled food (Talbot and Higgins, 1983). The disadvantage of individual rearing is that it does not consider social interactions. According to Silverstein (2006), feed efficiency measured on individually housed fish is informative concerning the efficiency of the group, but gives better performances than measurement in groups, probably because of the energetic cost of social interactions. For Martins et al. (2008), behaviour variability explains part of the variability of feed efficiency. Consequently, it is necessary to measure feed efficiency on group-reared fishes in order to reveal the maximum of feed efficiency variability. Selection to diminish feed intake using the X-ray method was shown to be promising in rainbow trout (Kause et al., 2006), so we can suppose that a breeding program based on the X-ray method could also enhance feed efficiency. However, this technique has a low repeatability (Kause et al., 2006), could be difficult to use for recently domesticated species as it implies frequent handling of the fish (Grima, 2010) and would be difficult to apply in a routine breeding program. Consequently, our goal is to set up a selection trial based on an easily measurable indirect criterion, highly correlated with feed efficiency.

The major trait selected for in fish breeding is rapid growth, but it gives divergent results on feed efficiency. In Atlantic salmon (Thodesen et al., 1999) and in Coho salmon (Neely et al., 2008), feed efficiency was better in the selected line; whereas in brown trout (Mambrini et al., 2004; Sanchez et al., 2001), the selected line did not differ from the control line for feed efficiency. In red sea bream, Ogata et al. (2002) reported that feed efficiency had decreased after selection for rapid growth. Hence, selection for growth cannot be considered a generally reliable means to improve feed efficiency.

Recently, a significant negative correlation of feed efficiency with weight loss during feed deprivation (FD) and with weight gain during re-feeding (RF) was demonstrated in rainbow trout (Grima et al., 2008) and in sea bass (Grima et al., 2010a). It was predicted by Grima et al. (2010b), that an individual selection based on FD performances with a selection intensity of one would lead to 0.55% feed saving per generation in sea bass.

Fat metabolism and retention needs to be considered in developing breeding programs for feed efficiency, as fat retention differences could explain some of the differences in feed efficiency. Indeed, a negative correlation has been found between feed efficiency and whole body lipid content in European whitefish (Quinton et al., 2007) and in Coho salmon (Neely et al., 2008). It is supposed that a preferential use of lipid for energetic requirements, keeping protein for growth, is responsible of the better feed efficiency (Neely et al., 2008). However, Grima et al. (2010b) found a positive correlation between feed efficiency and muscle fat content in sea bass.

In the present experiment, we performed a selection trial based on weight loss during feed deprivation in sea bass, expecting that offspring of FD^- parents (losing less at feed deprivation) would have a better feed efficiency than offspring of FD^+ parents (losing more weight at feed deprivation). We first tested the selection response on the trait selected (weight loss at feed deprivation), then we measured feed efficiency in FD^- and FD^+ offspring. We also examined whether fat content differed between the two lines.

2. Materials and methods

2.1. Broodstock selection

The parental broodstock was selected from the offspring of a full factorial mating involving 41 sires and eight dams collected from the wild in the West Mediterranean (Grima et al., 2010b). Parents were chosen for their growth performance during two consecutive feed deprivation (FD) periods (Grima et al., 2010b). The trait selected was the average thermal growth coefficient (TGC) from the two periods, corrected by the initial weight and the initial TGC (FDcorr in Grima et al., 2010a). FDcorr data from 1920 individual sea bass were available, and we selected 5 dams and 20 sires at both ends of the distribution. The average selection differential was +1.49 phenotypic standard deviations (σ_P) for FDcorr in the five FD^- selected dams, +2.25 σ_P in the 20 FD^- selected sires, −1.81 σ_P in the five FD^+ selected dams and −1.74 σ_P in the 20 FD^+ selected sires. Sperm from the selected males was collected and cyopreserved in 250-ml straws according to the method described by Fauvel et al. (1998). Offspring were produced mating five FD^+ dams with twenty FD^+ sires, and five FD^- dams with twenty FD^- sires, in order to obtain around 600 FD^+ fish from 100 full-sib families and 600 FD^- fish from 100 full-sib families. After hormonal induction of ovulation (10 μg/kg luteinizing hormone-releasing hormone; Sigma, D-TRP6LHRH), eggs were obtained by hand stripping of the 5 FD^+ dams and 5 FD^- dams. Twenty aliquots of 10-ml eggs each were collected from each dam. Each aliquot was individually fertilized with thawed sperm from a single sire of the same type so that all FD^- dams were fertilized by all FD^- sires, and all FD^+ dams were fertilized by all FD^+ sires. Five minutes after fertilization, eggs were pooled by dam for incubation. At 48 h post-fertilization, 8 ml of viable (floating) eggs was collected from each incubation tank and mixed in a single 0.5 m^3 tank containing all families. Standard rearing condition were used, except for early temperature which gradually increased from 13.5 °C to 18 °C over the first 12 days, and further increased to 25 °C at 49 days post-fertilization (dpf), coming back to natural temperature (20–22 °C) at 112 dpf.

2.2. Initial growing period and parental assignment

At 126 dpf, fish were transferred to a 1.5-m^3 fiberglass tank. At 227 dpf, 1200 randomly chosen fish were individually tagged with a passive integrated transponder (AEG-id, Germany), measured for initial body weight and length, and transferred to a 5-m^3 fiberglass tank. Fish were anesthetized with 2-phenoxy-ethanol (0.4 ml/l) during tagging and biometry. Feeding was stopped 24 h before the biometry and fish were immediately re-fed after the measurement. A piece of fin from each fish was collected for DNA extraction for parentage assignment. Twelve microsatellite markers were used for the genotyping by LABOGENA (Jouy en Josas, France). The software VITASSIGN (Vandeputte et al., 2006) was used to perform parentage assignment based on the multilocus microsatellite genotype of the fish, with two allelic mismatches tolerated, resulting in 94.2% of the fish being assigned to a single parental pair. Among the 1130 assigned offspring, there were 484 FD^- fish belonging to 77 full-sib families and 646 FD^+ fish belonging to 86 full-sib families.

2.3. Experimental phase 1: alternance of feed deprivation and re-feeding

In the 5-m^3 fiberglass tank, we first measured the initial growth over a 6-week period, from 227 to 276 dpf (BG; see Fig. 1). The initial 6-week feeding was followed by alternating periods of feed deprivation for 3 weeks (FD_1, FD_2, FD_3; see Fig. 1) and four (RF_1) or three (RF_2, RF_3) weeks of re-feeding (see Fig. 1). At the end of each period, all fish were individually identified by their PIT tag and measured for weight (nearest 0.1 g) and total length (nearest mm). During feeding periods, fish were fed *ad libitum* using a self-feeder with a standard commercial diet (Neogrower, Le Gouessant, France) containing 45% protein and 17% lipid.