Lack of compensatory growth response in gilthead seabream (*Sparus aurata*) juveniles following starvation and subsequent refeeding

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ABSTRACT

This study assessed the effect of short (one or two weeks) feed deprivation periods on compensatory growth response of gilthead seabream juveniles. A 10 weeks growth trial was performed and three different feeding protocols were tested: control group (C) fed to apparent satiation twice a day, 6 days a week, during the whole experimental period; one week or two weeks unfed groups (groups U1 and U2, respectively) and re-fed for the rest 8 weeks of the trial as the control group. Each feeding protocol was tested in triplicate groups of fish with an initial body weight of 58 g.

Starvation for one or two weeks induced significant losses of body weight that, comparatively to the control group, totaled 18.5 and 30.5% for U1 and U2 group, respectively. An intense mobilization of liver lipid and glycogen was observed after 1 or 2 weeks of starvation while perivisceral lipids, eviscerated-body lipids and energy contents were only decreased in fish unfed for 2 weeks. During the subsequent re-feeding period no recovery of body weight lost was noticed in the previously unfed groups, and feed intake and feed efficiency were identical in all groups. No differences between slopes of growth trajectory between the control and unfed groups were noticed, indicating no convergence of growth of unfed groups towards that of control group.

A total recovery of the whole-body composition, organ indices, liver and viscera composition was observed at the end of the trial.

Overall, gilthead seabream juveniles were not able to compensate growth after the feed starvation imposed. Therefore, it can be concluded, that under the experimental conditions applied short – one or two weeks – feed restriction periods are not advisable as management strategy to be used in gilthead seabream production.

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1. Introduction

Compensatory growth (CG) is a physiological process characterized by a phase of accelerated growth following a period of restricted feeding, aiming to reach the expected weight that would be attained in the absence of such feed restriction (Nicieza and Álvarez, 2009). During CG the growth trajectory of previously feed restricted animals converges to that of animals which experienced favorable feeding conditions throughout the whole period. The magnitude of growth compensation varies largely from over, full, partial or no compensation, according to the biomass attained by the restricted animals comparatively to their unrestricted counterparts (Ali et al., 2003). Growth compensation response is species-specific and depends mostly on type, length and severity of restriction, being more effective when duration and severity of restriction are short (Bull and Metcalfe, 1997; Boujard et al., 2000; Eroldogan et al., 2006; Tian and Qin, 2004). For gilthead seabream submitted to different starvation and refeeding

protocols only slight compensatory growth was observed by Eroldogan et al. (2006). However, Bavcevic et al. (2010) showed that following restriction feeding gilthead seabream were able to full compensate for weight but not for length.

The perception that fish can modulate its growth rate to compensate the low weight gain during periods of feed restriction has stimulated research in this area, due to its potential application in fish farm management. Indeed, CG may be used as a tool to enhance growth (Eroldogan et al., 2008; Huang et al., 2008; Johansen et al., 2001; Maclean and Metcalfe, 2001; Qian et al., 2000; Zhu et al., 2005) or feed utilization (Eroldogan et al., 2008; Huang et al., 2008; Jobling et al., 1994; Wang et al., 2000); to reduce fish size variations (Ali et al., 2003) or to improve water quality and reduce work labor and feeding costs (Blanquet and Oliva-Teles, 2010; Reigh et al., 2006). Compensatory growth might also be used to manipulate body composition, for instance by preventing excessive lipid deposition during finishing period, therefore making it a functional tool to optimize meat quality for human consumption (Hayward et al., 1997; Jobling et al., 1994; Eroldogan et al., 2006; Grigorakis and Alexis, 2005; Heide et al., 2006; Turchini et al., 2007).

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The adaptive physiological basis of CG is still not fully understood, but it probably involves different mechanisms such as increased feed intake and/or improved efficiency of feed utilization (Ali et al., 2003). Besides, growth is also influenced by several nutritionally related factors, such as whole-body fatness and maintenance of overall energy balance (Boujard et al., 2000). Based on this presumption, Jobling and Johansen (1999) proposed the lipostatic model as an indicator to predict CG. According to it, a reduction of lipid to lean body mass ratio leads to feed intake increase and consequently to CG response, to restore equilibrium. However, some limitations of this model have been described by several authors (Johansen et al., 2001; Xie et al., 2001; Tian and Qin, 2004; Zhu et al., 2005) while others confirmed a lipostatic regulation of feed intake (Johansen, et al., 2001, 2003; Tian and Qin, 2004). Therefore, both morphological and biochemical parameters seem to be essential to evaluate the utilization sequence, depletion severity and degree of endogenous energy reserves from different tissues during starvation and following subsequent resumption of feeding (Collins and Anderson, 1995).

Despite the high number of published papers, evidence for CG is still hampered by poor experimental design and inappropriate statistical analysis that can lead to false detection of CG (Ali et al., 2003). The size dependence of growth rate, which causes nonlinearity of growth trajectories, and the temporal overlapping of structural growth and of energy reserves replenishment after a period of starvation have been pointed out as the two main particularities of the phenomena that difficult detecting CG (Nicieza and Álvarez, 2009). Due to the potential application of CG in aquaculture (Hayward et al., 1997; Jobling et al., 1994; Eroldogan et al., 2006), there is a need to further study this phenomenon, using appropriated methodologies and statistical analysis, to clearly establish if over or full growth compensation occurs as these are the only responses with commercial interest in fish farming. Partial growth compensation means that fish failed to catch up the weight of unrestricted fish leading to a reduction of the aquaculture production and increasing production cycle. Therefore, the purpose of this study was to investigate the effects of starvation and subsequent re-feeding on growth performance, feed utilization and endogenous energy mobilization in gilthead seabream (*Sparus aurata*) juveniles.

2. Material and methods

2.1. Fish rearing

This experiment was directed by trained scientists (following FELASA category C recommendations) and was conducted according to the European Economic Community animal experimentation guidelines Directive of 24 November 1986 (86/609/EEC). The study was performed at the Marine Zoology Station, Porto University, with gilthead seabream (*Sparus aurata*) juveniles obtained in a commercial fish farm (Timar, Algarve, Portugal).

The growth trial lasted 10 weeks and was performed in a thermo-regulated recirculating water system, equipped with 9 fiberglass cylindrical tanks of 300-L capacity, supplied with continuous flow of filtered seawater at 3–3.5 L min^{-1}. During the trial water temperature averaged 25 ± 0.5 °C, salinity averaged 35 ± 1‰ and oxygen averaged 7–7.5 mg L^{-1}. A natural photoperiod was adopted. Temperature, dissolved oxygen, salinity and nitrogenous compounds were monitored during the entire trial and maintained at levels within limits recommended for this species.

Two hundred fish were acclimatized to the experimental facilities and water temperature for two weeks before the beginning of the feeding trial. During this period fish were fed a commercial diet once a day, 5 times per week. Thereafter, 9 homogenous groups of 18 seabream, with a mean initial body weight of 57.5 g, were randomly distributed to each tank. The trial lasted 10 weeks and triplicate groups of fish were submitted to three different feeding protocols: the control group (C group) was fed to apparent satiety, by hand, twice a day, six days a week, during the whole experimental period; one week unfed group (U1 group) was fed as group C during the first week and deprived of feed during the second week; then, and up to the end of the trial fish were re-fed as group C; two week unfed group (U2 group) was unfed for two weeks and then re-fed as group C up to the end of the trial. During the feeding period, fish were fed by hand to apparent satiety which was defined as the time when fish refuse to eat 2–3 pellets. Feed intake was record daily. To account for any uneaten feed, pellets that were flushed out were counted and multiplied by the average pellet weight.

During the trial fish were fed a fish meal based diet that was formulated to contain 48% crude protein and 15% crude lipids. All dietary ingredients were finely ground, thoroughly mixed and dry pelleted in a laboratory pellet mill (CPM), through a 3 mm die. The pellets were air dried at room temperature and stored in a freezer until used. Ingredients and proximate composition of the experimental diet are presented in Table 1. Fish were bulk weighted and counted once a week, under moderate anesthesia, after one day of fasting. Thus, fish were feed for six days, starved on the 7th day and weighted on the morning of the 1st day next week. The imposed starvation before weight permitted a faster appetite recovery, allowing minimal reduction in feed intake on the weighing day compared to other feeding days. Three fish from the initial stock population and from each experimental tank at the end of week 2, 3 (data not presented) and 10 were randomly sampled for body composition analysis. Whole fish, viscera and liver weights were also recorded for determination of hepatosomatic and visceral indices. Eviscerated fish, viscera and liver samples were individually frozen at −80 °C for subsequent composition analysis.

2.2. Analytical analysis and calculations

Chemical analyses of the experimental diet and whole eviscerated fish were made in triplicate according to the following procedures: dry matter after drying in an oven at 105 °C until constant weight; ash by incineration in a muffle furnace at 450 °C for 16 h; protein (N×6.25) by the Kjeldahl method after acid digestion using a Kjeltec system; lipid by petroleum ether extraction in a Soxtec System HT apparatus, and energy by direct combustion in an adiabatic bomb calorimeter (PARR model 1261). Hepatic glycogen and lipids were measured as

Table 1
Composition and proximate analyses of the experimental diet.

Ingredients (% dry weight)	
Fish meal[a]	66.6
Dextrin	21.1
Cod liver oil	8.8
Vitamin premix[b]	1.0
Choline chloride (50%)	0.5
Mineral premix[c]	1.0
Binder[d]	1.0
Proximate analyses (% dry weight)	
Dry matter (%)	91.1
Crude protein	50.8
Crude fat	15.7
Ash	13.7
Gross energy (kJ g^{-1} DM)	21.8

[a] Steam Dried LT fish meal, Pesquera Diamante, Perú (CP: 72.1% DM; GL: 9.3% DM).
[b] Vitamins (mg kg^{-1} diet): retinol, 18,000 (IU kg^{-1} diet); calciferol, 2000 (IU kg^{-1} diet); alpha tocopherol, 35; menadion sodium bis., 10; thiamin, 15; riboflavin, 25; Ca pantothenate, 50; nicotinic acid, 200; pyridoxine, 5; folic acid, 10; cyanocobalamin, 0.02; biotin, 1.5; ascorbyl monophosphate, 50; inositol, 400.
[c] Minerals (mg kg^{-1} diet): cobalt sulfate, 1.91; copper sulfate, 19.6; iron sulfate, 200; sodium fluoride, 2.21; potassium iodide, 0.78; magnesium oxide, 830; manganese oxide, 26; sodium selenite, 0.66; zinc oxide, 37.5; potassium chloride, 1.15 (g kg^{-1} diet); sodium chloride, 0.40 (g kg^{-1} diet); dibasic calcium phosphate, 5.9 (g kg^{-1} diet).
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