

## Protein sparing effect of dietary lipids in common dentex (*Dentex dentex*): a comparative study with sea bream (*Sparus aurata*) and sea bass (*Dicentrarchus labrax*)

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**Abstract** – The common dentex (*Dentex dentex*) is a sparid fish which is considered a suitable candidate for Mediterranean aquaculture. A seven-weeks feeding trial was conducted over the summer period with common dentex, sea bream (*Sparus aurata*) and sea bass (*Dicentrarchus labrax*). All three species were fed to visual satiety with two practical diets with varying crude protein and crude fat levels (55 % protein, 9 % lipids; 46 % protein, 17 % lipids). The initial body weights were 8.2, 11.6 and 17.3 g for common dentex, sea bass and sea bream, respectively. In all cases, specific growth rates were not significantly affected by dietary treatment, but they varied among species (sea bass 1.7–1.8 %; sea bream 2.1–2.3 %; common dentex 3.1–3.2 %). When comparisons between fish species were made, we observed that the increase in growth rates was linked to a decrease of the whole body fat content, as a consequence of a greater utilisation of dietary lipids as energy substrates. Furthermore, in common dentex, the 17 % lipid diet was able to improve protein retention, but this diet effect was less significant in sea bream and sea bass. In contrast to sea bream, the 17 % lipid diet did not up-regulate plasma GH levels in common dentex, which provides additional evidence for a more efficient utilisation of dietary lipids. © Ifremer/Elsevier, Paris

**Growth performance / protein retention / energy availability / growth hormone / *Dentex dentex* / *Dicentrarchus labrax* / *Sparus aurata***

**Résumé** – Rétention de protéines suite à un régime riche en lipides chez le dentex (*Dentex dentex*) : étude comparée avec la daurade (*Sparus aurata*) et le bar (*Dicentrarchus labrax*). Le dentex est un sparidé reconnu comme ayant un potentiel aquacole en Méditerranée. Une étude comparative de croissance entre le dentex, la daurade et le bar a été réalisée. Les trois espèces (poids moyen initial : 8,2 ; 11,6 et 17,3 g respectivement pour le dentex, le bar et la daurade) ont été nourries à satiété avec deux régimes expérimentaux (55 % de protéines brutes avec 9 % de lipides ou 46 % de protéines brutes avec 17 % de lipides). Chez chacune des espèces, le taux de croissance spécifique (TCS) n'a pas varié en fonction du régime alimentaire. En revanche, une différence significative interspécifique a été observée (bar 1,7–1,8 % ; daurade 2,1–2,3 % ; dentex 3,1–3,2 %) avec également une différence significative dans le dépôt lipidique corporel, reflétant des différences dans l'utilisation des apports énergétiques d'origine lipidique. L'effet de rétention de protéines par des lipides a été plus important chez le dentex que chez les deux autres espèces. Par ailleurs, contrairement à ce qui est observé chez la daurade, le régime riche en lipides n'induit pas une régulation de la sécrétion de l'hormone de croissance chez le dentex, indiquant aussi une meilleure utilisation des lipides alimentaires. © Ifremer/Elsevier, Paris

**Croissance / rétention protéinique / énergie digestible / hormone de croissance / *Dentex dentex* / *Dicentrarchus labrax* / *Sparus aurata***

### 1. INTRODUCTION

The common dentex (*Dentex dentex*) is naturally present in the Mediterranean area, and spawns between

March and July at temperatures of 15 °C or higher [25]. This sparid fish inhabits rocky bottoms 200 m deep and preys on fish, mollusks and worms. In nature, the maximum recorded length is 100 cm, but the mean

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size at capture ranges between 35 and 40 cm [35]. Nowadays, common dentex is produced on a pilot scale in Greece, Italy and Spain, but this species is known to be extremely sensitive to handling and opportunistic pathogens [10, 32]. Despite this, fast growth has been reported during larval [1, 41] and fry stages [13] when natural food and moist pellets are used. According to Riera et al. [31], fingerling fish reared in sea cages with natural food can reach 830 g in 16–17 months, with growth rates twice that of sea bass (*Dicentrarchus labrax*) and sea bream (*Sparus aurata*). Under experimental conditions however, with practical diets, feed efficiency has been found to be relatively poor, and within the values reported for sea bass and sea bream [8, 38]. This apparent contradictory finding remains unclear, and could reflect the lack of standard protocols for a correct assessment and comparison of fish growth. Thus, to further address the suitability of common dentex as a candidate for Mediterranean aquaculture, a comparative feeding trial (common dentex vs. sea bass and sea bream) was carried out in the present work.

## 2. MATERIALS AND METHODS

### 2.1. Animals

Experimental fish were obtained as fry from two Spanish fish farms (Cupimar, Cadiz; Gesa, Mallorca). Rearing was conducted in 150-L aquaria with running seawater free of organic matter. Photoperiod and water temperature followed the natural cycle.

### 2.2. Diets

Two experimental diets which differed in crude protein (CP) and crude fat (CF) levels were formulated (55CP:9CF and 46CP:17CF, *table I*). The gross energy (GE) content was 20.8 and 22.4 kJ·g<sup>-1</sup> dry matter. Dry pellets were manufactured using a laboratory pellet mill without steam conditioning, and stored at 4 °C until use.

### 2.3. Feeding trial

Fingerling fish averaging 8.2 (common dentex), 11.6 (sea bass) and 17.3 g (sea bream) were randomly allocated to duplicate groups of 60 fish for each dietary treatment. Fish were fed to satiety by hand three times a day. Water temperature ranged from 23 to 26 °C over the course of the trial (7 weeks, July–September). At the end of the experiment and following an overnight fasting, 20 fish per dietary treatment were withdrawn and anaesthetised with MS-222 (Sigma, St Louis, MO). Blood was obtained from caudal vessels, centrifuged 30 min, at 2 500 × g and the resulting plasma samples were stored at -30 °C until analysed. Additionally, 10 fish at the beginning and 15 fish from each tank at the end of the experiment were withdrawn and

**Table I.** Ingredient content and proximate composition of experimental diets. CP: Crude protein; CF: crude fat.

	Diet	
	55CP:9CF	46CP:17CF
g:100 g wet matter <sup>-1</sup>		
Fish soluble protein concentrate (CPSP)	5	5
Fish meal (Norway)	55	40
Corn gluten meal	10	10
Fish oil	2	11
Extruded peas (Aquatex, France)	24	30
Mineral premix <sup>1</sup>	2	2
Vitamin premix <sup>2</sup>	2	2
Proximate composition		
Dry matter (DM, %)	84.3	88.0
Crude protein (% DM)	55.3	46.4
Crude fat (% DM)	9.3	17.4
Total phosphorus (% DM)	1.7	1.4
Ash (% DM)	11.8	9.4
Gross energy (kJ·g <sup>-1</sup> DM)	20.9	22.4
Protein:energy ratio (mg·kJ <sup>-1</sup> )	26.5	20.7

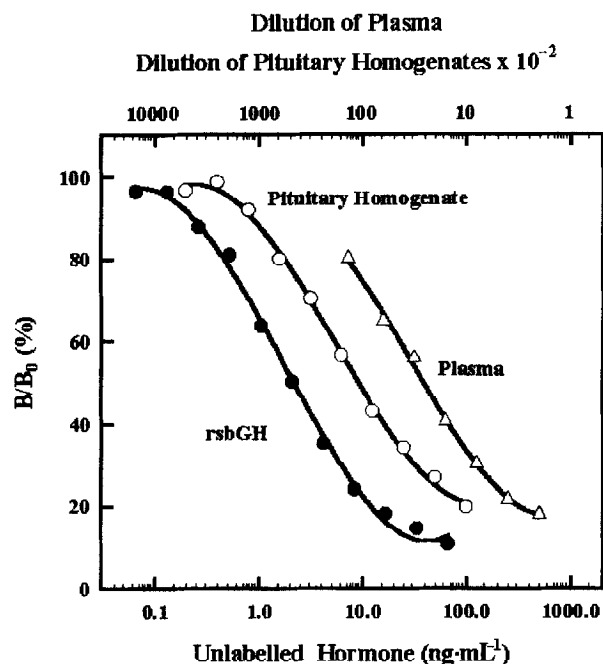
<sup>1</sup> Supplied the following (per kg<sup>-1</sup> diet): calcium carbonate (40 % Ca), 2.15 g; magnesium hydroxide (60 % Mg), 1.24 g; potassium chloride, 0.9 g; ferric citrate, 0.2 g; potassium iodine, 4 mg; sodium chloride, 0.4 g; calcium hydrogen phosphate, 50 g; copper sulfate, 0.3 mg; zinc sulfate, 40 mg; cobalt sulfate, 2 mg; manganese sulfate, 30 mg; sodium selenite, 0.3 mg.

<sup>2</sup> Supplied the following (mg·kg<sup>-1</sup> diet): retinyl acetate, 2.58; DL-cholecalciferol, 0.037; DL-cholecalciferol tocopheryl acetate, 30; menadione sodium bisulfite, 2.5; thiamine, 7.5; riboflavin, 15; pyridoxine, 7.5; nicotinic acid, 87.5; folic acid, 2.5; calcium pantothenate, 2.5; vitamin B12, 0.025; ascorbic acid, 250; inositol, 500; biotin, 1.2; choline chloride, 500.

killed to perform body composition analysis. Whole body samples were ground before analyses. A small aliquot was dried in an oven at 110 °C for 24 h in order to estimate water content. The remaining samples were freeze-dried, and chemical analyses were performed according to AOAC methods: crude protein by Kjeldahl (N × 6.25) after acid-digestion, fat according to the method of Folch et al. [14], ash after 2 h of combustion at 600 °C, and gross energy using an adiabatic bomb calorimeter.

### 2.4. Biochemical analyses

Plasma glucose levels were determined spectrophotometrically using a commercial kit (Sigma). Plasma growth hormone (GH) levels were determined using a sensitive and specific radioimmunoassay (RIA) for recombinant sea bream GH (rsbGH) [20]. The sensitivity and midrange (ED<sub>50</sub>) of the assay were 15 and 210 pg, respectively. To validate this GH assay for common dentex, the parallelism of standard curve with serial dilutions of plasma and pituitary homogenates was established (*figure 1*). The recovery of rsbGH



**Figure 1.** Competitive displacement of  $^{125}\text{I}$ -rsbGH by unlabelled rsbGH and serial dilutions of plasma and pituitary homogenates of common dentex. Initial dilution of pituitary homogenate: 1 mL RIA buffer-100  $\text{g}^{-1}$  body weight. Each value is the mean of 3–4 replicates.

added to plasma samples of common dentex was  $97.3 \pm 1.5$  ( $n = 4$ ).

### 2.5. Statistics

Data were analysed by one-way analysis of variance, followed by Duncan's multiple range test. Curve parallelism was tested by covariance analysis.  $P < 0.05$  was considered statistically significant.

## 3. RESULTS

### 3.1. Growth performance

Data on growth performance of the three marine teleosts are summarised in *table II*. Under our experimental conditions of unrestricted feeding, the total voluntary feed intake was not significantly affected ( $P < 0.05$ ) by diet composition in any of the fish species examined. However, expressed as a percentage of mean body weight, the daily feed intake of sea bass and sea bream was slightly higher in fish fed the 17% lipid diet. Differences in specific growth rates (SGR) were found among fish species (common dentex > sea bream > sea bass) but, for each fish species, it was not significantly affected ( $P < 0.05$ ) by dietary treatment. The slope of plot regression of weight vs. culture time (*figure 2*) was also higher in common dentex, indicating that differences in SGR between species were not only due to differences in initial body weight.

In common dentex, feed gain ratio (FGR) was near to 1 with both experimental diets. In sea bass and sea bream, FGR was 1.25 and 1.5 with the 9 and 17% lipid diet, respectively. Protein efficiency ratios (PER) were also found to differ between species. In common dentex, PER in fish fed the 9% lipid diet was 1.7, and increased up to 1.9 with the 17% lipid diet. In both sea bass and sea bream, PER remained around 1.4 with both dietary treatments.

### 3.2. Body composition

Data on whole body composition are reported in *table III*. In all cases, fish fed the 17% lipid diet exhibited a higher whole body lipid content (% dry matter) in combination with a decreased protein content. Common dentex showed the lowest daily fat gain ( $\text{g}\cdot\text{kg}^{-1}$  body weight) followed by sea bream and sea bass. An opposite trend was found in terms of daily N gain

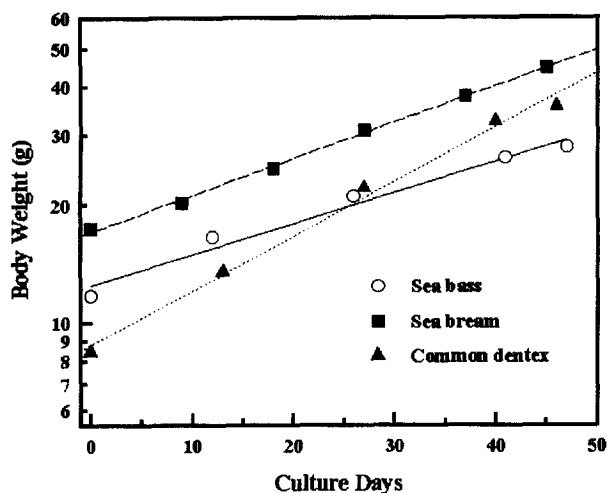
**Table II.** Growth performance of sea bass, sea bream and common dentex fed the experimental diets for seven weeks. Values are means  $\pm$  SEM of duplicate tanks. Values that share a common letter are not significantly different ( $P < 0.05$ ). CP: Crude protein; CF: crude fat.

Diet	Sea bass		Sea bream		Common dentex	
	55CP:9CF	46CP:17CF	55CP:9CF	46CP:17CF	55CP:9CF	46CP:17CF
Feed intake						
Dry matter (g)	20.3 $\pm$ 0.88 <sup>a</sup>	21.9 $\pm$ 0.01 <sup>a</sup>	40.3 $\pm$ 0.70 <sup>b</sup>	43.8 $\pm$ 2.13	30.3 $\pm$ 1.30 <sup>c</sup>	30.5 $\pm$ 1.52 <sup>c</sup>
Dry matter (% BW/day)	2.19 $\pm$ 0.04 <sup>a</sup>	2.44 $\pm$ 0.04 <sup>ab</sup>	2.63 $\pm$ 0.01 <sup>b</sup>	3.07 $\pm$ 0.11 <sup>c</sup>	2.91 $\pm$ 0.08 <sup>c</sup>	3.09 $\pm$ 0.04 <sup>c</sup>
Growth performance						
Initial body weight (BW <sub>0</sub> ) (g)	11.6 $\pm$ 0.07 <sup>b</sup>	11.6 $\pm$ 0.19 <sup>b</sup>	17.5 $\pm$ 0.95 <sup>c</sup>	17.1 $\pm$ 0.17 <sup>c</sup>	8.4 $\pm$ 0.04 <sup>a</sup>	8.0 $\pm$ 0.12 <sup>a</sup>
Final body weight (BW <sub>f</sub> ) (g)	27.8 $\pm$ 1.02 <sup>a</sup>	26.5 $\pm$ 0.36 <sup>a</sup>	49.9 $\pm$ 1.20 <sup>c</sup>	45.5 $\pm$ 0.39 <sup>c</sup>	36.9 $\pm$ 1.64 <sup>b</sup>	34.7 $\pm$ 1.56 <sup>b</sup>
SGR <sup>1</sup>	1.86 $\pm$ 0.09 <sup>a</sup>	1.76 $\pm$ 0.01 <sup>a</sup>	2.31 $\pm$ 0.04 <sup>b</sup>	2.15 $\pm$ 0.02 <sup>ab</sup>	3.23 $\pm$ 0.06 <sup>c</sup>	3.19 $\pm$ 0.14 <sup>c</sup>
FGR <sup>2</sup>	1.25 $\pm$ 0.03 <sup>a</sup>	1.47 $\pm$ 0.02 <sup>b</sup>	1.24 $\pm$ 0.01 <sup>a</sup>	1.54 $\pm$ 0.04 <sup>b</sup>	1.06 $\pm$ 0.01 <sup>c</sup>	1.14 $\pm$ 0.03 <sup>c</sup>
PER <sup>3</sup>	1.44 $\pm$ 0.03 <sup>a</sup>	1.42 $\pm$ 0.02 <sup>a</sup>	1.46 $\pm$ 0.02 <sup>a</sup>	1.40 $\pm$ 0.04 <sup>a</sup>	1.70 $\pm$ 0.02 <sup>b</sup>	1.90 $\pm$ 0.03 <sup>c</sup>
Mortality (%)	–	–	–	–	4–7	4–6

<sup>1</sup> SGR: Specific growth rate =  $100 \times (\ln \text{BW}_f - \ln \text{BW}_0) / \text{days}$ .

<sup>2</sup> FGR: Feed gain ratio = dry feed intake/wet weight gain.

<sup>3</sup> PER: Protein efficiency ratio =  $100 \times (\text{wet weight gain} / \text{crude protein intake})$ .

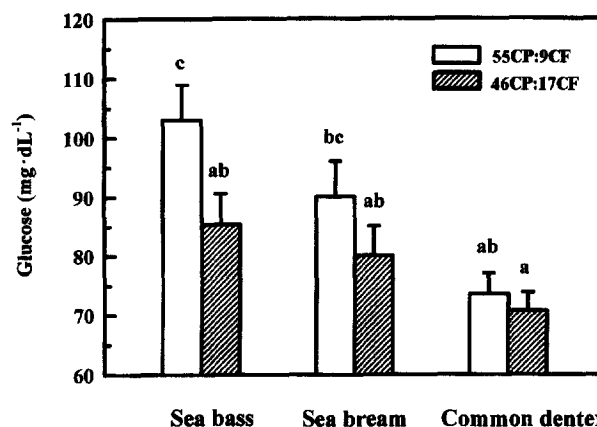


**Figure 2.** Plot regression of body weight (BW) versus days (d) of culture in common dentex ( $\log BW = 0.942 + 0.014 d$ ;  $r^2 = 0.99$ ), sea bream ( $\log BW = 1.230 + 0.0092 d$ ;  $r^2 = 0.99$ ) and sea bass ( $\log BW = 1.097 + 0.0077 d$ ;  $r^2 = 0.97$ ). No significant differences were found between dietary treatments, and each value is the mean of the two experimental groups.

( $\text{mg}\cdot\text{kg}^{-1}$  body weight) (common dentex > sea bream > sea bass). For all three species, fat retention was always lower in fish fed the 17% lipid diet than in those fed the 9% lipid diet. In common dentex, protein retention increased significantly with the increase of dietary lipids, while a slight but not significant decrease was found in sea bream and sea bass.

### 3.3. Plasma glucose and growth hormone

Significant differences in mean plasma glucose levels were observed between species (figure 3). Following overnight fasting, a significant effect of diet composition on plasma glucose levels was found only in sea bass. However, as a general pattern, plasma glucose levels were lower in fish fed the 17% lipid diet.



**Figure 3.** Plasma glucose levels following overnight fasting in sea bass, sea bream and common dentex fed the experimental diets for seven weeks. Each value is the mean  $\pm$  SEM of 15–20 fish. Values that share common letters were not significantly different ( $P < 0.05$ ).

Plasma GH levels were not measured in sea bass due to the lack of a validated assay. Comparisons among fish species were therefore limited to sea bream and common dentex (figure 4). The mean plasma GH concentration was higher in sea bream than in common dentex. In sea bream, plasma GH levels increased significantly in fish fed the 17% lipid diet. An opposite, although non-significant effect, was found in common dentex.

## 4. DISCUSSION

Literature data on the growth of Mediterranean marine finfish species appear to be rather highly variable (table IV), probably due to differences in fish strains, water quality and temperature, oxygen availability, biomass density and biological value of dietary protein and non-protein energy substrates. Most of the experimental data are also clearly in contrast with the

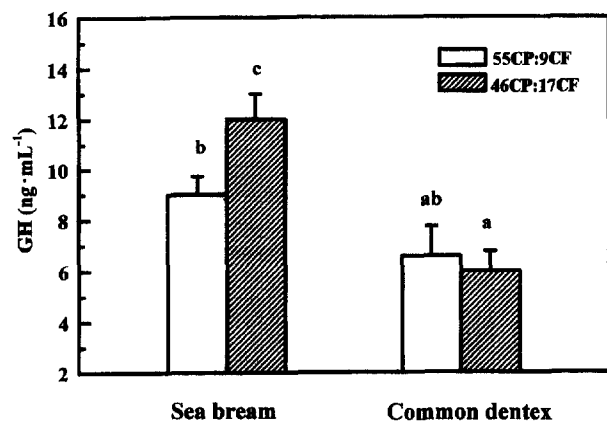
**Table III.** Whole body composition and nutrient utilisation in sea bass, sea bream and common dentex fed the experimental diets for seven weeks. Values are means  $\pm$  SEM of duplicate tanks. Values that share a common letter are not significantly different ( $P < 0.05$ ). CP: Crude protein; CF: crude fat.

Diet	Sea bass		Sea bream		Common dentex	
	55CP:9CF	46CP:17CF	55CP:9CF	46CP:17CF	55CP:9CF	46CP:17CF
Water (%)	66.9 $\pm$ 0.4 <sup>a</sup>	64.8 $\pm$ 0.6 <sup>b</sup>	69.5 $\pm$ 0.4 <sup>c</sup>	67.9 $\pm$ 0.4 <sup>a</sup>	72.8 $\pm$ 0.2 <sup>d</sup>	71.9 $\pm$ 0.3 <sup>d</sup>
Protein (% fresh weight)	16.2 $\pm$ 0.2 <sup>a</sup>	15.6 $\pm$ 0.5 <sup>a</sup>	16.9 $\pm$ 0.1 <sup>a</sup>	16.7 $\pm$ 0.1 <sup>a</sup>	16.67 $\pm$ 0.1 <sup>a</sup>	16.1 $\pm$ 0.4 <sup>a</sup>
Fat (% fresh weight)	11.1 $\pm$ 0.3 <sup>d</sup>	13.7 $\pm$ 0.2 <sup>c</sup>	8.6 $\pm$ 0.4 <sup>c</sup>	11.0 $\pm$ 0.1 <sup>d</sup>	4.5 $\pm$ 0.5 <sup>a</sup>	6.1 $\pm$ 0.2 <sup>b</sup>
Ash (% fresh weight)	4.0 $\pm$ 0.2 <sup>a</sup>	3.9 $\pm$ 0.2 <sup>a</sup>	4.6 $\pm$ 0.2 <sup>a</sup>	4.2 $\pm$ 0.2 <sup>a</sup>	4.6 $\pm$ 0.2 <sup>a</sup>	4.6 $\pm$ 0.1 <sup>a</sup>
Gross energy ( $\text{kJ}\cdot\text{g}^{-1}$ DM)	24.1 $\pm$ 0.4 <sup>b</sup>	24.6 $\pm$ 0.1 <sup>b</sup>	23.0 $\pm$ 0.3 <sup>b</sup>	24.2 $\pm$ 0.3 <sup>b</sup>	21.0 $\pm$ 0.6 <sup>a</sup>	21.5 $\pm$ 0.2 <sup>a</sup>
N gain ( $\text{mg}\cdot\text{kg}^{-1}$ BW·day <sup>-1</sup> )	444.7 $\pm$ 30.7 <sup>a</sup>	392.3 $\pm$ 23.3 <sup>a</sup>	580.1 $\pm$ 7.3 <sup>c</sup>	525.4 $\pm$ 2.8 <sup>b</sup>	754.5 $\pm$ 8.7 <sup>d</sup>	733.3 $\pm$ 14.3 <sup>d</sup>
Fat gain ( $\text{mg}\cdot\text{kg}^{-1}$ BW·day <sup>-1</sup> )	2.23 $\pm$ 0.17 <sup>b</sup>	2.89 $\pm$ 0.02 <sup>c</sup>	1.93 $\pm$ 0.02 <sup>b</sup>	2.58 $\pm$ 0.01 <sup>c</sup>	1.31 $\pm$ 0.16 <sup>a</sup>	1.87 $\pm$ 0.04 <sup>b</sup>
Protein retention <sup>1</sup>	22.9 $\pm$ 1.1 <sup>a</sup>	21.7 $\pm$ 1.7 <sup>a</sup>	25.0 $\pm$ 0.3 <sup>a</sup>	23.1 $\pm$ 0.7 <sup>a</sup>	29.0 $\pm$ 0.3 <sup>b</sup>	32.6 $\pm$ 0.2 <sup>c</sup>
Fat retention <sup>2</sup>	109.5 $\pm$ 5.9 <sup>d</sup>	68.1 $\pm$ 2.2 <sup>c</sup>	78.9 $\pm$ 0.7 <sup>c</sup>	48.4 $\pm$ 1.7 <sup>b</sup>	48.7 $\pm$ 6.9 <sup>b</sup>	34.6 $\pm$ 1.0 <sup>a</sup>

Initial body composition for sea bass, sea bream and common dentex: water: 69.4, 71.6, 75.6%; protein: 16.7, 17.1, 15.45%; fat: 8.8, 7.8, 3.4%; ash: 4.2, 4.0, 4.0%.

<sup>1</sup> Protein retention =  $100 \times (\text{fish protein gain}/\text{protein intake})$ .

<sup>2</sup> Fat retention =  $100 \times (\text{fish lipid gain}/\text{lipid intake})$ .



**Figure 4.** Plasma growth hormone (GH) levels following overnight fasting in sea bream and common dentex fed the experimental diets for seven weeks. Each value is the mean  $\pm$  SEM of 15–20 fish. Values that share common letters were not significantly different ( $P < 0.05$ ).

predicted values of Russell et al. [33] for 15-g fish (SGR  $\leq$  1; FGR  $>$  4).

In the present study, SGR (1.7–1.8 %) and FGR (1.2–1.5) of fingerling sea bass were better or within the range of previous studies (table IV). This observation can also be extended to sea bream, where a SGR of 2.3 % and a FGR of 1.25 was achieved with 17–50-g fish. In the study of Tandler et al. [37], 10-g sea bream reared at 25–26 °C showed growth rates of only 1 % body weight per day. For fish of a lower body weight range (5–30 g), a better growth (2.5–2.9 %) and FGR (1.4–1.6) was reported by Vergara et al. [42] under a fixed feeding level. However, these values were still far from the best feed conversion in fast growing fish, since a SGR near 3 % with a FGR close to 1 can be achieved with 15–50-g fish, when they are fed with high protein and low lipid diets [21].

Fast growth and efficient feed conversion were observed with common dentex. Thus, when growth

rates and protein retention were considered together, the obtained values were better than those previously reported not only for sea bass and sea bream, but also for common dentex (see table IV). With three protein (45, 50 and 55 %) and two lipid levels (12 and 17 %), Tibaldi et al. [38] reported a protein sparing effect of dietary lipids in 20–46-g common dentex. However, SGR was relatively low (1.4 %) and protein retention reached a maximum value of 22 %. With the same range of body size, Cardenete et al. [8] observed a protein sparing effect when dietary lipid levels increased from 17 to 22 % with 54 % crude protein diets, but growth rates remained low. For 10–40-g fish, the same authors [7] indicated that common dentex can exhibit a SGR of 3 % with a FGR of 1.1–1.3, although the protein sparing effect of an increase in dietary lipids was not clear and PER remained around 1.5. In the present study, under similar experimental conditions, with comparable SGR, PER was found to increase with the decrease of dietary protein:energy ratio.

Taking together all the above data, when comparisons are made between the three species, common dentex had the best growth performance and daily protein accretion (N gain). A possible explanation is a more efficient utilisation of dietary lipids as energy substrates, as shown by a lower fat retention and body fat content. Under our experimental conditions of high temperature and unrestricted feeding, dietary lipids appear to spare proteins for growth purposes in dentex. However, in both sea bass and sea bream, present data do not suggest any improvement of protein retention with the increase of dietary lipids. This finding is in apparent contradiction with the recent work of Dias et al. [11], in which sea bass fingerlings were shown to grow efficiently at 18 °C with a 42 % protein and 18 % lipid diet. They also found that the protein sparing effect was less significant with high protein diets. However, as it was pointed out in a previous work [6],

**Table IV.** Data base of published papers for sea bass, sea bream and common dentex.

Fish species	Weight range (g)	Temp (°C)	SGR* (%)	FGR*	PER*	Reference
Sea bass	3–6	19–22	1.6–2	1.6–2.7	–	Tsevis et al. [40]
“	3–17	26–28	1.6–2	1.4–2.2	0.9–1.7	Pérez et al. [26]
“	6–11	19	0.7–0.8	1.3–1.7	1.2–1.7	Dias et al. [11]
“	15	20	1	$>$ 4	–	Russell et al. [33]
“	31–56	20	1	1.5–1.6	1.3	Hidalgo and Alliot [16]
“	75–115	19	0.4–0.5	2.0–2.3	0.7–0.9	Metailler et al. [24]
“	75–230	23–27	0.5–0.6	1.6–1.9	1.2–1.3	Ballestrazzi et al. [3]
“	80–329	23	0.6–0.7	1.4–1.6	1.2–1.5	Ballestrazzi et al. [2]
Sea bream	10–15	24–27	0.5–1.0	–	–	Tandler et al. [37]
“	5–29	21–22	2.5–2.9	1.4–1.6	–	Vergara et al. [42]
“	13–35	23–26	1.7	1.1	1.9	Calduch-Giner et al. [6]
“	15–51	21–23	2.6–3	1–1.6	1.3–1.4	Martí-Palanca et al. [21]
Common dentex	2–16	24–26	3.8–5.2	0.9–1.1	–	Efthimiou et al. [13]
“	10–40	20	3–3.4	1.1–1.3	1.5	Cardenete et al. [7]
“	21–46	20	1.2–1.3	1.8–2.1	1–1.3	Tibaldi et al. [38]
“	31–61	20	0.7–0.8	1.4–1.6	1.2–1.4	Cardenete et al. [8]

See foot notes to table II.

a protein:energy ratio of 20.5–21 mg·kJ<sup>-1</sup> can represent a critical value not only for sea bass but also for sea bream. According to this, in sea bream, a reliable protein sparing effect in fish fed the 17 % lipid diet is achieved under restricted feeding conditions, but such a beneficial effect might disappear in fish fed to visual satiety. In fact, in this latter case, sea bream fingerlings might be considered to have reached a state of metabolic fasting (increased energy expenditure, although not directly measured here), which would protect adipose tissue, and perhaps other organs and tissues, from excessive lipid deposition when non protein energy substrates are available at too high a level.

Comparisons of plasma GH levels between fish species are difficult due to differences in GH batches and GH-antibody affinity. However, it seems that plasma GH concentrations in sea bream are of the same order of magnitude as those found in turbot (*Psetta maxima*) (Le Bail, pers. comm.), and two- to four-fold higher than those of Japanese eel (*Anguilla japonica*) [12], tilapia (*Oreochromis niloticus*) [30], rainbow trout (*Oncorhynchus mykiss*) [29, 36], Atlantic salmon (*Salmo salar*) [4] and chinook salmon (*Oncorhynchus tshawytscha*) [18]. Although the physiological significance of such differences remains to be established, taking into account the key metabolic role of GH, it has been postulated that this fact reflects inter-specific differences in nutrient utilisation and endocrine regulation [27]. It is also worth noting that while a strong positive relationship between growth rates and T<sub>3</sub> has been reported in rainbow trout [15], Atlantic salmon (*Salmo salar*) [5, 22] and red drum (*Sciaenops ocellatus*) [23], sparid fish appear to show some refractoriness to changes in circulating levels of thyroid hormones ([9]; Le Bail, pers. comm.). In the present study, plasma GH levels were found to be lower in common dentex than in sea bream. The use of a sea bream GH assay to measure plasma GH levels in common dentex might be considered to have led to some underestimation of GH values. Nevertheless, given the high GH sequence identity between sea bream [19], *Acanthopagrus butcheri* [17] and *Acanthopagrus latus* [39], a low number of amino acid substitutions is

expected in another sparid fish, such as common dentex.

One important feature is that sea bream fed with the 17 % lipid diet exhibited higher plasma GH levels than fish fed with the 9 % lipid diet. In earlier studies [21, 28], we have observed that sea bream fed high energy diets at high feeding levels show a persistent hypersomatotropism associated with a diminished feed efficiency. However, this tendency is opposite when energy supply for growth purposes is limiting, as under restricted feeding conditions [6]. According to this, low plasma GH levels (increased liver GH-responsiveness) in fast growing fish are indicative of an adequate energy balance (energy input/energy expenditure). Data from the fore-mentioned studies also suggest a close negative relation between circulating GH levels and protein growth expressed as daily N gain. We also find a very similar pattern in the present study. The absence of an up-regulation of plasma GH levels in common dentex fed the diet with the highest energy content (17 % lipid diet) is in agreement with an efficient utilisation of dietary lipids. The low plasma glucose levels in this species provide additional evidence of a true state of low lipogenic potentiality [34]. Whether a further decrease in dietary protein:energy ratio would increase adiposity in growing common dentex warrants investigation.

## 5. CONCLUSION

In comparison with sea bass and sea bream, common dentex not only exhibits high growth rates and protein deposition, but also an increased tolerance to relatively high dietary lipid levels. Plasma growth hormone levels were lower in dentex than in sea bream, indicating the higher growth potential of this species. Given their voracious feeding behaviour, growth potential and protein retention, dentex remains a good candidate for aquaculture. But, although mortality remained low (4–7 %) in the present study, dentex is known to be highly susceptible to handling and opportunistic pathogens [10].

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