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Fishmeal Replacement by Full-Fat and Defatted *Hermetia illucens* Prepupae Meal in the Diet of Gilthead Seabream (*Sparus aurata*)

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Abstract: Insect proteins are considered as suitable low environmental impact alternatives to fishmeal for sustainable aquafeeds. Among the different insect species, *Hermetia illucens* has attracted research and industrial interest due to its ability to grow well on organic side streams, its high protein content and favorable amino acid profiles. Its lipid content although high is characterized by a lack of EPA and DHA that are essential to fish nutrition and thus a defatted form of *Hermetia* meal might be of better use in fish diets. Hence, two feeding trials were conducted to investigate the effects of the partial fishmeal replacement by increasing levels of a full-fat (up to 276 g/kg) and a defatted (up to 174 g/kg) *H. illucens* meal on feed intake, growth, feed utilization and nutrient compositions of gilthead seabream (*Sparus aurata*). Results showed that both the fat content and the inclusion level of *H. illucens* meal are critical for the success of fishmeal replacement in the diets of *S. aurata* as they strongly affect feed consumption. A lower palatability of *H. illucens* meal was observed when included at high dietary levels with the defatted form being more readily accepted by fish. The defatted *H. illucens* meal is more suitable than the full-fat type to replace fishmeal, with a dietary level of about 81–104 g/kg supporting the highest feed consumption, the highest growth, an unaffected proximate composition and a better feed utilization by *S. aurata*.

Keywords: insects; sustainable aquaculture; aquafeeds; growth performance; feed utilization; proximate composition

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1. Introduction

Nowadays, it has become evident that the further development of modern aquaculture depends on the successful inclusion of sustainable feed ingredients that could further substitute the dietary wild-sourced fishmeal in aquafeeds. Over the last decade, the sector has been focusing on the use of insect-based meals [1–3] as they possess several relevant characteristics, with the research in this field growing exponentially [4,5]. From an environmental point of view, insect culture and the production of insect meal has been considered as beneficial in terms of waste and by-product recycling, feed conversion efficiency, sustainable use of land and water and lower carbon emissions compared to livestock farming [2,6,7], but the high energy consumption for rearing and drying insects is of major concern [7–9].

From a nutritional point of view, the nutrient composition of insect meal is highly variable between taxonomic groups, rearing substrates, and technological process with most insect species being rich in protein (40–80%, as noted in reviews by Makkar et al. [10],

Henry et al. [11], Nogales-Merida [12]). This protein quantity is comparable to that of several conventional plant meals, and in some species to that of fishmeal; thus, insect meals can be included as major protein sources in aquafeeds. In addition, their protein quality is high with certain insect species such as the silkworm, *Bombyx mori* (L.) (Lepidoptera: Bombycidae) and the house fly, *Musca domestica* L. (Diptera: Muscidae), being usually higher in methionine than fishmeal [13], while others such as the black soldier fly, *Hermetia illucens* (L.) (Diptera: Stratiomyidae), are rich in lysine [10,14]. Insect meals can also provide valuable minerals and vitamins to fish nutrition [15,16]. The lipid contents of insects can also be high (can reach 40%, [10–13]), but this is disadvantageous for fish nutrition as they are characterized by only traces of the valuable EPA and DHA [12,15]. In addition, their high lipid contents carry an increased risk of lipid oxidation [11] and may alter the fish lipid quality that in turn could affect their sensory properties, though not in a negative manner [17]. Although the poor n-3 fatty acid quality of insects can be improved by feeding them on fisheries by-products, microalgae and seaweeds [18–20] the defattening process is a more practical attempt to overcome this handicap of full-fat insect meals and simultaneously to increase the protein content in the defatted end-product. Beside the nutrient quality, it is worth mentioning that insect meals could also yield immunostimulating and antimicrobial effects to the fish diet due to their high contents of chitin, antimicrobial peptides and short chain fatty acids [21–23].

Among the different insect species, *H. illucens* has attracted industrial interest for mass rearing as it can be raised on a wide variety of organic side streams fitting well with circular economy strategies, can serve as a feed for livestock, pets and fish and unlike other fly species is not a disease vector [4,24]. The species is also considered one of the most studied by fish nutritionists due to its high protein content that can reach up to 61% (on dry matter basis, [10,12,25]), its high protein digestibility [26,27], its richness in essential amino acids and in particular its lysine content [10,14] and its success in dietary fishmeal protein replacement (reviewed by Mohan et al. [25]). Feeding trials have showed that even a total replacement of fishmeal protein by a full-fat *H. illucens* meal, regardless of their inclusion levels, was achievable without impairing the feed efficiency and the growth performance of several fish species such as Atlantic salmon (*Salmo salar*) [28,29]), Nile tilapia (*Oreochromis niloticus*) [30,31], Jian carp (*Cyprinus carpio* var. *Jian*) [32] and mirror carp (*Cyprinus carpio* var. *specularis*) [33], while similar results were obtained using defatted *H. illucens* meals in zebrafish (*Danio rerio*) [34] and Jian carp [35]. On the other hand, several other feeding trials testing the partial or total fishmeal replacement have showed that the increased inclusion levels of either full-fat or defatted *H. illucens* meal in the diet can exert a negative effect on the feed efficiency and growth of rainbow trout (*Oncorhynchus mykiss*) [36–39], *S. salar* [40], African catfish (*Clarias gariepinus*) [41], yellow catfish (*Pelteobagrus fulvidraco*) [42,43], barramundi (*Lates calcarifer*) [44], Siberian sturgeon (*Acipenser baerii*) [45], turbot (*Psetta maxima*) [46], Pacific white shrimp (*Litopenaeus vannamei*) [47,48], juvenile striped catfish (*Pangasianodon hypophthalmus*) [49], red sea bream (*Pagrus major*) [50] and Tongue sole (*Cynoglossus semilaevis*) [51].

Gilthead seabream (*Sparus aurata*) is among the most important farmed fish species reared in Europe, mainly in the Mediterranean countries, with an annual world production of around 280,000 mt [52]. Although recent nutritional strategies have reduced the dietary inclusion levels of fishmeal in seabream's diets, the need for further fishmeal reductions remains in order to enhance the sustainability of aquaculture. Despite the increasing interest in *H. illucens* meal for fishmeal replacement in aquafeeds and the importance of *S. aurata* in aquaculture, the studies that have investigated its effects on the species feed intake, growth performance and feed utilization are very limited. So far, studies with the species have assessed, apart from growth, the effects of full-fat meal *H. illucens* meal on the enzyme activities and gut microbiome [53], the fillet fatty acid profiles [54], the amino acid catabolism [55] and proximate composition [56], and the effects of defatted meal *H. illucens* on the body proximate composition [27,57], blood chemistry and hepatic metabolic enzymes [58], the nutrient digestibility [27,57], fillet fatty acid profiles [59], the

gut and histopathology [60] and the appetite regulation and fish fillet quality [61] of the species. Therefore, the aim of the present study was to investigate the effects of fishmeal protein replacement by a full-fat and a defatted *H. illucens* meal on the feed intake, growth performance, feed utilization and body and muscle proximate compositions of *S. aurata*. The current study also reassessed the preliminary findings of our previous investigation [56].

2. Materials and Methods

Two feeding trials were conducted in order to study the effects of fishmeal replacement by either full-fat (feeding trial I) or defatted (feeding trial II) *H. illucens* meal in the diet of *S. aurata*. The feeding trials were conducted by FELASA accredited scientists at the licensed aquaculture facilities (EL-43BIO/exp-01) of the Aquaculture Laboratory (University of Thessaly, Greece) according to the EU Directive 2010/63/EU and after approval by the Institutional Ethics Committee of the University of Thessaly.

2.1. H. illucens Meal

H. illucens larvae, originally sourced from the wild, were reared at the greenhouse facilities of the Laboratory of Entomology and Agricultural Zoology (University of Thessaly, Greece) and fed on vegetable wastes. Prepupae of around 2–3 cm size were collected and dried firstly at 40 °C for 5 h and for another 24 h under vacuum, milled and sieved to less than 1 mm particle size. For defattening of the *H. illucens* meal, petroleum ether was used at a ratio 5:1 (*v*/*w*) and the meal was heated at 40 °C for 1 h under stirring. The mixture was then left in a fume cupboard for 24 h in order to evaporate the solvent and this fat extraction procedure was performed twice. The proximate compositions of the full-fat and defatted *H. illucens* meals, as well as that of the *H. illucens* prepupae are shown in Table 1.

Table 1. Proximate composition (% of wet weight) of *H. illucens* prepupae, full-fat and defatted meals of *H. illucens*, and of fishmeals used in the experimental diets.

	***H. illucens* Prepupae**	***H. illucens* Full-Fat Meal**	***H. illucens* Defatted Meal**	**Fishmeal (65%)**	**Fishmeal (70%)**
Moisture (%)	59.6	12.2	1.7	7.3	6.0
Crude protein (%)	15.8 (Kp 6.25) 11.8 (Kp 4.67)	31.6 (Kp 6.25) 23.6 (Kp 4.67)	50.6 (Kp 6.25) 37.8 (Kp 4.67)	65.8 (Kp 6.25) 59.7 (Kp 5.67)	70.6 (Kp 6.25) 64.0 (Kp 5.67)
Crude lipid (%)	9.9	27.2	3.0	8.2	7.2
Ash (%)	11.3	15.4	19.7	16.1	16.4
Gross energy (kJ/g)	10.0	20.9	16.2	19.8	19.1

Values represent means (n = 3); Kp, nitrogen-to-protein conversion factor 4.67 for *H. illucens* [62] and 5.67 for fishmeal [63].

2.2. Experimental Diets

For feeding trial I, a fishmeal of 65.8% of crude protein (Table 1) was used in the experimental diets. Four isonitrogenous (total nitrogen 7.55%) and isoenergetic (21.6 MJ/kg) diets were formulated (Table 2) containing increasing dietary levels of full-fat *H. illucens* meal at 0 g/kg (FF-0, control diet), 95 g/kg (FF-95), 194 g/kg (FF-194) and 276 g/kg (FF-276), corresponding to 0%, 9%, 17% and 25%, respectively, of fishmeal replacement. The dietary amino acid profiles were estimated based on the values given by the supplier of each ingredient (fishmeal, wheat, corn gluten) and by feedipedia.org (for *H. illucens*). As such, the diets of trial I were supplemented by lysine and methionine to satisfy the known essential amino acid requirements of the species [64] and by choline to assist the lipid metabolism of insect fat into fish body. For feeding trial II, a fishmeal of 70.6% of crude protein (Table 1) was used in the experimental diets. Four isonitrogenous (total nitrogen 7.55%) and isoenergetic (21.7 MJ/kg) diets were formulated (Table 2) containing increasing dietary levels of defatted *H. illucens* meal at 0 g/kg (DF-0, control diet), 58 g/kg (DF-58), 116 g/kg (DF-116) and 174 g/kg (DF-174), corresponding to 0%, 10%, 20% and 30%,

respectively, of fishmeal replacement. It was estimated that all the diets of trial II satisfied the amino acid requirements of the species and thus no supplementation was practiced.

Table 2. Formulation (g/kg of diet) and proximate composition (% as fed) of the experimental diets containing full fat (FF, feeding trial I) and defatted (DF, feeding trial II) *Hermetia illucens* meal fed to *Sparus aurata* juveniles.

Diets	Feeding Trial I				Feeding Trial II			
	FF-0	**FF-95**	**FF-194**	**FF-276**	**DF-0**	**DF-58**	**DF-116**	**DF-174**
Ingredients (g/kg diet)								
Fishmeal (65%) [1]	450	410	372	340	-	-	-	-
Fishmeal (70%) [2]	-	-	-	-	415	374	332	290
H. illuscens meal, full fat	0	95	194	276	-	-	-	-
H. illuscens meal, defatted	-	-	-	-	0	58	116	174
Corn gluten	260	260	260	260	260	266	271	276
Wheat meal	150	100	45	0	178	147	118	89
Fish oil [3]	120	115	109	104	133	141	149	157
Vitamins & minerals, premix [4]	6	6	6	6	6	6	6	6
MCP	3	3	3	3	3	3	3	3
Choline	3	3	3	3	-	-	-	-
Methionine	2	2	2	2	-	-	-	-
Lysine	1	1	1	1	-	-	-	-
Vitamin E	1	1	1	1	1	1	1	1
Vitamin C	1	1	1	1	1	1	1	1
Anti-moulting agent	3	3	3	3	3	3	3	3
Proximate composition (% as fed)								
Dry matter	88.8	88.7	88.6	88.5	91.4	91.2	91.1	91.3
Total dietary nitrogen (N) [5]	7.52	7.52	7.57	7.60	7.43	7.55	7.61	7.62
Crude protein (N × 6.25)	47.0	47.0	47.3	47.5	46.4	47.2	47.6	47.6
Crude protein (estimated) [6]	42.1	41.4	40.9	40.5	41.8	42.0	41.8	41.4
Crude lipid	15.2	17.2	19.2	21.5	20.7	19.4	18.9	18.5
Crude carbohydrate [7]	19.6	16.2	12.5	8.9	16.3	14.1	14.0	13.9
Ash	7.0	8.3	9.6	10.7	7.9	10.5	10.6	11.3
Gross energy (MJ/kg)	21.3	21.5	21.6	21.8	21.9	21.6	21.6	21.8

[1] Sardine fishmeal (65% crude protein). [2] super prime fishmeal made by anchovy, sprat, pilchard and sand eels (70% crude protein). [3] Salmon and sardine oil (50:50) containing 21% of n-3 HUFA. [4] Vitamin and mineral supplement (per kg of mixture): Vitamins: E, 58.3 g; K3, 3.3 g; A, 1500 IU/g; D3, 200 IU/g; B1, 3.3 g; B2, 6.6 g; B6, 3.3 mg; B12, 10 mg; folic acid, 3.3 g; biotin, 100 mg; inositol, 40 g; C, 33.3 g; nicotinic acid, 16.6 g; pantothenic acid, 13.3 g. Minerals: Co, 170 mg; I, 248 mg ($Ca(IO_3)_2$); Mn, 10 g (MnO); Zn, 33 g (ZnO); Ca, 235 g; Se, 2.5 mg (Na_2SeO_3); Na, 247.5 mg (Na_2SeO_3); Fe, 2 g; Mg, 121.3; Cu, 0.8 g. [5] based on Kjeldahl analysis. [6] Values were obtained by the following calculations: (i) contribution of each ingredient to total dietary N = (100 × inclusion level of ingredient/total inclusion level of all proteinaceous ingredients) × (total dietary N/100), where proteinaceous ingredients include fishmeal, *H. illucens* meal, corn gluten, wheat meal, methionine and lysine; (ii) contribution of each ingredient to Crude Protein = contribution of ingredient to total dietary N × nitrogen to protein factor specific for the ingredient (4.67 for *H. illucens* [62]; 5.67 for fishmeal [63]; 5.52 for wheat flour [65], 5.62 for corn gluten [65] and 6.25 for amino acids); (iii) Crude protein (estimated) = summation of the contributions of all proteinaceous ingredients to dietary crude protein. [7] Calculated as 100 minus the sum of the percentages of crude protein, crude fat, moisture and ash.

In both sets of diets, corn gluten meal was used as the major plant protein source, while wheat meal was used as an energy source and filler ingredient for the protein replacements. All the diets had constant inclusion levels of a premix of vitamins and minerals, monocalcium phosphate, vitamin E, vitamin C, and antimoulting agent. Fish oil was used as the major lipid source to satisfy the known n-3 essential fatty acid requirements of seabream. All dietary ingredients were ground in a grain feed mill (KoMo Fidibus, PGS, Germany) and were mixed in a mixer (Bosch MaxxiMUM MUMXL20G). Fish oil and boiling water were then added to produce a homogenous stiff dough. Diets were pelletized by a California Pellet Mill (CL-2, IRMECO GmbH, The Netherlands) to produce pellets of 1.5 mm diameter. The pellets were then dried with forced air at room temperature for 24 h and stored in air-sealed bags at 4 °C until used.

2.3. Feeding Trials I and II

In both trials, *S. aurata* juveniles were obtained from a commercial fish hatchery and transferred to the Departmental aquaculture facilities (University of Thessaly, Greece). Fish were stocked in 12 glass tanks (125 L) within a closed recirculation seawater system and left to acclimatize for 10 days fed on their corresponding control diet. In trial I, 240 juveniles of 1.47 ± 0.22 g initial mean weight were distributed in triplicate groups (20 fish/tank, 3 tanks/dietary group), while in trial II, 300 juveniles of 2.40 ± 0.27 g initial mean weight were distributed in triplicates (25 fish/tank, 3 tanks/dietary group).

In both trials, water quality parameters were monitored routinely with water temperature being maintained at 21.0 ± 1.0 °C, pH at 8.0 ± 0.4, salinity at 33 ± 0.5 g/L, dissolved oxygen at >6.5/L, total ammonia–nitrogen at <0.1 mg/L, and photoperiod at 12:12 h (light:darkness). Fish were hand-fed to apparent satiation twice a day (10:00 and 17:00) for 10 weeks in total for both trials. Special care was given to ensure that all feed supplied was consumed.

2.4. Sampling

Pooled samples of 20 fish of the initial population of each trial were taken for whole-body proximate composition analysis. At the end of each trial, fish were fasted for 24 h before sampling. All remaining live fish were individually weighed after being euthanized with an overdose (1.0 mg/L) of 2-phenoxyethanol. Three fish were randomly selected from each tank (9 fish/dietary group), minced into a meat grinder and homogenate subsamples of each fish were obtained for whole-body proximate composition. The dorsal muscle tissue of another three fish per tank (9 fish/dietary group) was taken, devoid of bones, skin and blood stains, for muscle proximate composition. Liver and viscera of three fish per tank (9 fish/dietary group) were removed quickly and weighed for the determination of hepatosomatic (HSI) and viscerosomatic (VSI) indices, respectively. All samples were immediately frozen and stored at −40 °C until analyzed.

2.5. Proximate Composition

Proximate composition was conducted to determine the nutrient composition of feed ingredients, diets, whole body and muscle tissue of fish samples. Thermal drying to constant weight in an oven at 105 °C for 24 h was applied to determine moisture content. Total nitrogen (N) content was determined by Kjeldahl analyses (behr Labor-Technik, Germany). For crude protein determination, a specific nitrogen to protein factor (Kp) was applied to each dietary ingredient: 4.67 for both full-fat and defatted *H. illucens* larvae meal [62], 5.67 for fishmeal [63], 5.52 for wheat flour [65], 5.62 for corn gluten [65], 6.25 as conventional value for lysine and methionine. Then, the crude protein of the diets was determined as (i) dietary N × 6.25 and (ii) summation of the contributions of all proteinaceous ingredients to dietary crude protein (crude protein estimated). Crude fat was determined by exhaustive Soxhlet extraction using petroleum ether (40–60 °C, BP) using a Soxtherm Multistat/SX PC (Sox-416 Macro, Gerhard, Germany). Ash content was determined by dry ashing in porcelain crucibles in a muffle furnace (Nabertherm L9/12/C6, Lilienthal, Germany) at 600 °C for 5 h and gross energy content was determined adiabatically using an IKA oxygen bomb calorimeter (C5000, IKA Werke, Staufen, Germany).

2.6. Calculation of Growth and Nutritional Indices

$$\text{Survival (\%)} = 100 \times \text{final fish number/initial fish number}$$

$$\text{Weight gain (WG, g/fish)} = \text{FBW} - \text{IBW}$$

$$\text{Specific Growth Rate (SGR, \%/day)} = 100 \times [(\text{LnFBW} - \text{LnIBW})]/\text{days}$$

$$\text{Feed Consumed (FC, g/fish)} = \text{total amount of feed consumed (g) per fish}$$

$$\text{Voluntary Feed Intake (VFI, \% BW/day)} = 100 \times \text{feed consumed (g/fish)}/[(\text{IBW} + \text{FBW})/2 \times \text{days}]$$

$$\text{Feed Conversion Ratio (FCR)} = \text{feed consumed (g)}/\text{wet weight gain (g)}$$

$$\text{Protein efficiency ratio (PER)} = \text{weight gain (g)}/\text{protein intake (g)}$$

$$\text{Nutrient retention} = 100 \times \text{nutrient gain (g)}/\text{nutrient intake (g)}$$

$$\text{Hepatosomatic index (HSI, \%)} = 100 \times \text{liver weight (g)}/\text{FBW (g)}$$

$$\text{Viscerosomatic index (VSI, \%)} = 100 \times \text{visceral weight (g)}/\text{FBW (g)}$$

$$\text{Condition factor (CF)} = 100 \times \text{FBW (g)}/\text{TL (cm)}^3$$

where IBW and FBW are the initial and final body weight, respectively, TL is the total length.

2.7. Statistical Analysis

Results are presented as means ± standard deviation. Percentages were arcsine-transformed prior to statistical analysis. Data were tested for normality by Shapiro–Wilk's and for homogeneity by Levene's test and were transformed whenever required before being subjected to one-way analysis of variance (ANOVA) followed by Tukey's post-hoc test to rank the groups using SPSS 26.0 (IBM SPSS Statistics 26). Differences were regarded as significant at $p < 0.05$. A cubic polynomial regression analysis ($Y = a + b + cx^2 + dx^3$) was performed as best fit for FC, FCR, SGR and PER for determining the optimum dietary inclusion level of defatted *H. illucens* meal (g/kg). The effect of feed consumption on SGR was analyzed using linear regression analysis. Regressions were considered significant at $p < 0.05$ and $R^2 \geq 0.70$.

3. Results

3.1. Fish Growth and Feed Efficiency

All groups of fish promptly accepted the experimental diets. In the feeding trial I, survival ranged at 84.4–95.6% and was similar ($p > 0.05$) among the fish groups (Table 3). The voluntary feed intake (% BW/day) was also similar among the groups, but when the consumption was calculated on a basis of g feed/fish then all three *H. illucens*-based diets had a lower ($p < 0.05$) feed consumption compared to the control FF-0 group (Table 3). FCR gradually increased as the dietary level of full-fat *H. illucens* meal increased, but this trend was not significant. The three insect-fed groups of fish (FF-95, FF-194 and FF-276) had also significantly lower growth performance in terms of FBW, TL, WG and SGR compared to the control FF-0 fish (Table 3). PER values were lower in FF-194 and FF-276 fish but this trend was not significant. Protein retention was getting reduced with the elevated levels of full-fat *H. illucens* meal in the diet, being significantly lower in the FF-276 fish, while lipid retention was gradually ($p < 0.05$) reduced. The CF was similar in all groups of fish, but the hepatosomatic and viscerosomatic indices were elevated in fish fed the full-fat insect meal.

In the feeding trial II, a decreased survival (70.0%) was observed in the DF-174 group of fish, but this was not significantly lower than those found in the other fish groups (Table 4). The DF-276 fish had also a significantly lower feed intake (VFI and FC), growth performance (FBW, TL, CF, WG, SGR), feed utilization (FCR, PER, protein retention, lipid retention) and morphometric indices (HSI and CF) (Table 4) compared to the rest of the groups.

Table 3. Growth performance and feed utilization of *Sparus aurata* feeding on the fishmeal (FF-0) and the full-fat *Hermetia illucens* meal (FF) based diets (feeding trial I).

	FF-0	FF-95	FF-194	FF-276
Survival (%)	95.6 ± 7.7	90.0 ± 14.1	84.4 ± 13.9	86.7 ± 7.1
VFI (% BW/day)	2.69 ± 0.08	2.55 ± 0.01	2.66 ± 0.04	2.65 ± 0.02
FC (g/fish)	17.92 ± 1.51 ^{a}	12.40 ± 0.75 ^{b}	12.36 ± 1.30 ^{b}	11.59 ± 1.25 ^{b}
IBW (g)	1.47 ± 0.00	1.47 ± 0.02	1.47 ± 0.00	1.48 ± 0.01
FBW (g)	17.59 ± 1.96 ^{a}	12.41 ± 0.15 ^{b}	11.91 ± 1.20 ^{b}	11.01 ± 1.38 ^{b}
TL (cm)	11.12 ± 0.34 ^{a}	9.58 ± 0.16 ^{b}	9.40 ± 0.23 ^{b}	9.24 ± 0.42 ^{b}
WG (g/fish)	16.12 ± 1.96 ^{a}	10.94 ± 0.15 ^{b}	10.44 ± 1.19 ^{b}	9.53 ± 1.39 ^{b}
SGR (%/day)	3.54 ± 0.16 ^{a}	3.05 ± 0.20 ^{b}	2.99 ± 0.14 ^{b}	2.86 ± 0.18 ^{b}
FCR	1.12 ± 0.05	1.13 ± 0.01	1.18 ± 0.01	1.22 ± 0.04
PER ^{1}	2.13 ± 0.10	2.13 ± 0.02	2.06 ± 0.02	2.03 ± 0.07
Protein retention (%) ^{1}	34.43 ± 1.48 ^{a}	33.70 ± 0.26 ^{ab}	32.59 ± 0.20 ^{ab}	30.80 ± 1.01 ^{b}
Lipid retention (%)	45.46 ± 1.83 ^{a}	38.81 ± 0.87 ^{b}	33.83 ± 0.85 ^{c}	26.79 ± 0.72 ^{d}
HSI (%)	1.67 ± 0.07 ^{a}	2.46 ± 0.14 ^{b}	2.17 ± 0.15 ^{b}	2.22 ± 0.14 ^{b}
VSI (%)	6.00 ± 0.29 ^{a}	8.77 ± 0.75 ^{ab}	8.39 ± 1.24 ^{ab}	9.72 ± 0.90 ^{b}
CF	1.27 ± 0.02	1.29 ± 0.01	1.28 ± 0.00	1.30 ± 0.01

Values represent means ± st. deviation (n = 3). ^{1} based on estimated CP. Means within a row not sharing a common superscript letter are significantly different ($p < 0.05$). Where no letters exist, no significant differences were noted. FC, feed consumed VFI, voluntary feed intake; IBW, initial body weight; FBW, final body weight; TL, final total length; WG, weight gain; SGR, specific growth rate; FCR, feed conversion ratio; PER, protein efficiency ratio; HSI, hepatosomatic index; VSI, viscerosomatic index; CF, condition factor.

Table 4. Growth performance and feed utilization of *Sparus aurata* feeding on the fishmeal (DF-0) and the defatted *Hermetia illucens* meal (DF) based diets (feeding trial II).

	DF-0	DF-58	DF-116	DF-174
Survival (%)	96.7 ± 5.8	90.0 ± 17.3	93.3 ± 7.6	70.0 ± 13.2
VFI (% BW/day)	2.11 ± 0.09 ^{ab}	2.09 ± 0.03 ^{ab}	2.22 ± 0.11 ^{a}	1.77 ± 0.19 ^{b}
FC (g/fish)	9.25 ± 0.53 ^{a}	9.70 ± 0.13 ^{ab}	10.19 ± 0.16 ^{a}	5.03 ± 0.36 ^{b}
IBW (g)	2.40 ± 0.02	2.40 ±0.01	2.41 ±0.01	2.40 ±0.01
FBW (g)	10.12 ± 0.20 ^{a}	10.83 ± 0.26 ^{a}	10.72 ± 0.44 ^{a}	5.76 ± 0.23 ^{b}
TL (cm)	8.85 ± 0.09 ^{a}	9.03 ± 0.34 ^{a}	9.08 ± 0.29 ^{a}	7.51 ± 0.12 ^{b}
WG (g/fish)	7.73 ± 0.18 ^{a}	8.42 ± 0.26 ^{a}	8.31 ± 0.44 ^{a}	3.35 ± 0.24 ^{b}
SGR (%/day)	2.06 ± 0.02 ^{a}	2.15 ± 0.04 ^{a}	2.14 ± 0.06 ^{a}	1.23 ± 0.07 ^{b}
FCR	1.20 ± 0.04 ^{a}	1.15 ± 0.03 ^{a}	1.23 ± 0.09 ^{a}	1.60 ± 0.30 ^{b}
PER ^{1}	2.00 ± 0.07 ^{a}	2.07 ± 0.05 ^{a}	2.00 ± 0.05 ^{a}	1.59 ± 0.22 ^{b}
Protein retention (%) ^{1}	33.83 ± 1.28 ^{a}	37.28 ± 0.82 ^{a}	35.27 ± 2.30 ^{a}	31.01 ± 2.94 ^{b}
Lipid retention (%)	43.62 ± 1.74 ^{a}	48.30 ± 0.88 ^{a}	48.18 ± 2.82 ^{a}	14.01 ± 1.87 ^{b}
HSI (%)	2.05 ± 0.17 ^{a}	2.17 ± 0.22 ^{a}	2.15 ± 0.21 ^{a}	1.28 ± 0.32 ^{b}
CF	1.46 ± 0.05 ^{a}	1.47 ± 0.05 ^{a}	1.48 ± 0.05 ^{a}	1.35 ± 0.01 ^{b}

Values represent means ± st. deviation (n = 3). ^{1} based on estimated CP. Means within a row not sharing a common superscript letter are significantly different ($p < 0.05$). Where no letters exist, no significant differences were noted. FC, feed consumed VFI, voluntary feed intake; IBW, initial body weight; FBW, final body weight; TL, final total length; WG, weight gain; SGR, specific growth rate; FCR, feed conversion ratio; PER, protein efficiency ratio; HSI, hepatosomatic index; VSI, viscerosomatic index; CF, condition factor.

3.2. Proximate Composition

The whole body and muscle tissue proximate compositions of the fish are given in Table 5 (feeding trial I) and Table 6 (feeding trial II). In feeding trial I, the whole body proximate composition of the fish was unaffected ($p > 0.05$) by the diet, but significant differences were observed in their muscle tissues. Specifically, there was a graded muscle lipid deposition in fish with the increase of the full-fat *H. illucens* meal in the diet, with the FF-276 fish having significantly a higher value compared to the FF-0 control group. Also, the gross energy contents of the muscle of all three FF-fed groups of fish were significantly higher than that of the FF-0 fish.

Table 5. Proximate composition (as % of dry weight) of *Sparus aurata* feeding on the fishmeal (FF-0) and the full-fat *Hermetia illucens* meal (FF) based diets (feeding trial I).

	FF-0	FF-95	FF-194	FF-276
Whole body				
Moisture (% of wet weight)	72.57 ± 2.69	73.60 ± 2.68	73.36 ± 0.97	74.07 ± 1.85
Crude protein (%)	58.04 ± 3.84	58.58 ± 3.95	57.63 ± 3.39	57.13 ± 2.84
Crude lipid (%)	25.90 ± 2.88	26.55 ± 3.77	26.86 ± 1.87	25.11 ± 2.74
Ash (%)	14.06 ± 1.08	14.22 ± 1.16	14.02 ± 1.67	14.61 ± 1.34
Gross energy (kJ/g)	23.52 ± 0.98	24.15 ± 1.14	24.05 ± 0.76	23.25 ± 0.98
Muscle tissue				
Moisture (% of wet weight)	76.59 ± 0.36	76.90 ± 0.74	76.89 ± 0.61	76.26 ± 0.78
Crude protein (%)	79.47 ± 2.67	79.49 ± 1.14	79.73 ± 1.63	77.64 ± 0.76
Crude lipid (%)	8.88 ± 1.31 ^{a}	10.93 ± 1.2 ^{ab}	10.26 ± 1.59 ^{ab}	11.67 ± 0.54 ^{b}
Ash (%)	8.95 ± 0.34	8.08 ± 0.43	8.21 ± 0.31	8.69 ± 0.28
Gross energy (kJ/g)	22.66 ± 0.12 ^{a}	23.26 ± 0.10 ^{b}	23.11 ± 0.11 ^{b}	23.20 ± 0.11 ^{b}

Values represent means ± st. deviation (n = 9). Means within a row not sharing a common superscript letter are significantly different ($p < 0.05$). Where no letters exist, no significant differences were noted.

Table 6. Proximate composition (as % of DW) of *Sparus aurata* feeding on the fishmeal (DF-0) and the defatted *Hermetia illucens* meal (DF) based diets (feeding trial II).

	DF-0	DF-58	DF-116	DF-174
Whole body				
Moisture (% of wet weight)	67.95 ± 0.27 ^{a}	67.42 ± 0.35 ^{a}	68.43 ± 0.20 ^{a}	72.01 ± 1.61 ^{b}
Crude protein (%)	51.42 ± 0.71 ^{a}	53.36 ± 0.96 ^{a}	53.88 ± 2.04 ^{a}	63.08 ± 2.95 ^{b}
Crude lipid (%)	27.90 ± 0.90 ^{a}	27.79 ± 0.28 ^{a}	29.52 ± 1.09 ^{a}	12.62 ± 0.98 ^{b}
Ash (%)	15.23 ± 0.23 ^{a}	15.28 ± 0.37 ^{a}	14.39 ± 0.45 ^{a}	22.57 ± 0.13 ^{b}
Gross energy (kJ/g)	24.06 ± 0.42 ^{a}	23.24 ± 0.28 ^{a}	24.04 ± 0.44 ^{a}	18.47 ± 0.35 ^{b}
Muscle tissue				
Moisture (% of wet weight)	74.72 ± 0.27	74.95 ± 0.75	74.57 ± 0.76	75.69 ± 0.28
Crude protein (%)	71.70 ± 1.00 ^{a}	74.14 ± 2.61 ^{ab}	74.57 ± 1.48 ^{ab}	76.96 ± 0.88 ^{b}
Crude lipid (%)	21.62 ± 0.58 ^{a}	18.95 ± 1.97 ^{b}	18.88 ± 0.64 ^{b}	15.67 ± 0.23 ^{b}
Ash (%)	6.55 ± 0.13 ^{a}	6.61 ± 0.14 ^{a}	6.46 ± 0.05 ^{a}	7.28 ± 0.06 ^{c}
Gross energy (kJ/g)	25.13 ± 0.06 ^{a}	24.98 ± 0.05 ^{b}	24.88 ± 0.04 ^{b}	23.90 ± 0.04 ^{c}

Values represent means ± st. deviation (n = 9). Means within a row not sharing a common superscript letter are significantly different ($p < 0.05$). Where no letters exist, no significant differences were noted.

In the feeding trial II, the inclusion of the defatted insect meal significantly affected the whole body and muscle proximate compositions of the fish. Specifically, the body moisture was similar among the groups, but the muscle moisture was significantly higher in the DF-174 fish compared to the rest of the groups. The DF-174 fish had significantly lower body lipid and energy contents, significantly higher body ash and the highest body protein compared to the other fish groups. This group also exhibited the highest ash and protein contents and the lowest lipid and energy contents in their muscle. All DF-fed fish had significantly lower lipid and energy contents in their muscle tissue compared to the DF-0 fish.

4. Discussion

In the present study the effects of dietary fishmeal replacement by either full-fat (trial I) or defatted (trial II) *H. illucens* prepupae meal were investigated with regard to feed consumption and utilization, growth performance and proximate composition of gilthead seabream. In trial I, the inclusion of the full-fat *H. illucens* meal even at 95 g/kg significantly reduced the feed consumption (g/fish), although the voluntary feed intake (VFI, % of BW/day) was unaffected. In trial II, when the defatted *H. illucens* meal was included up to 116 g/kg both the feed consumption (g/fish) and the VFI were unaffected, but significantly reduced in the higher inclusion level (174 g/kg). These findings denote a

lower acceptability and palatability of *H. illucens* meal compared to fishmeal when it is included at relatively high dietary levels and show that the defatted form is more readily accepted than the full-fat type.

The palatability of insect meals for fish is still questionable. A reduced feed intake associated with the inclusion of *H. illucens* meal replacing dietary fishmeal protein has also been observed in other studies on *S. aurata* [53,60,61] and on other fish species such as *O. niloticus* [30], *P. maxima* [46], *S. salar* [28] and *O. mykiss* [38]. Fabrikov et al. [53] reported that a dietary inclusion of full-fat *H. illucens* meal at 109 g/kg and higher, replacing fishmeal at more than 30%, led to a reduced VFI in *S. aurata* and the authors assumed that this could be due to a reduced activity of certain amino acid metabolism enzymes. Randazzo et al. [60] reported a decreased feed intake using a partially defatted *H. illucens* meal at 162 g/kg and higher, along with vegetable proteins totally replacing fishmeal protein, while similar findings were reported by Pulido-Rodriguez et al. [61] using diets with defatted *H. illucens* meal as low as 81 g/kg. An observed lower palatability of insect meals has been linked with factors such as their fat susceptibility to oxidation [66], their high chitin content [46], their bad odor owing to the presence of essential oils, flavonoids and terpenoids in their diet [66,67] or even to their pupal hormone—ecdysone [67], amongst others.

On the other hand, Mastoraki et al. [58] and Moutinho et al. [57] reported an unaffected feed intake in *S. aurata* fed on diets containing defatted *H. illucens* meals up to 195 g/kg and up to 450 g/kg (totally replacing dietary fishmeal), respectively. Li et al. [51] even observed an enhanced VFI in *C. semilaevis* with a high inclusion of a defatted *H. illucens* meal at 432 g/kg and higher, totally replacing fishmeal. It has been argued that *H. illucens* meal as fishmeal replacer could affect the acceptability of nutritionally balanced diets due to its differential contents of nutrients that act as feed stimulants [68]. Thus, Oteri et al. [68] showed that the dietary fishmeal replacement by 110 g/kg and higher of a defatted *H. illucens* meal led to increased amounts of glycine and alanine that are known potent odorants stimulating feed intake. The authors reported also that the high inclusion of defatted *H. illucens* meal differentiate the taste of the diets compared to a conventional fishmeal-based diet. It has been argued that the defattening of insect meals can enhance their palatability [1,11,69] and this was confirmed in the present study. It is worth mentioning, also, that a large number of studies with several fish species have shown that the inclusion of *H. illucens* meal did not affect the feed intake of fish [36,50,70–74] even when dietary fishmeal was totally replaced [29,32]. Interestingly, Pulido-Rodriguez et al. [61] analyzing appetite-related genes in the central nervous system and in the intestine, found that none of the *H. illucens* based diets depressed the central neuro-endocrine mechanisms involved in appetite stimulus.

In the present study, the inclusion of full-fat *H. illucens* meal even at low levels (95 g/kg replacing 9% of fishmeal inclusion level) significantly depressed the growth performance of *S. aurata* and although the values of FCR and PER remained significantly unaffected, the values of nutrient retentions were reduced with the higher inclusion of this insect meal in the diet. When the defatted form was used in trial II, a dietary inclusion level at 116 g/kg, replacing 20% of fishmeal, was suitable for not impairing fish growth and feed utilization. However, the inclusion of the defatted *H. illucens* meal at levels as high as 174 g/kg (DF-174 diet) significantly reduced fish growth performance and feed utilization. These findings suggest that both the fat content and the inclusion level of *H. illucens* meal are critical for the success of fishmeal replacement in the diets of *S. aurata*. The depression in growth of fish fed the three full-fat *H. illucens* meal diets and the defatted *H. illucens* meal diet with the higher inclusion level (DF-174) can be mainly explained by their lower feed consumption. In both trials, there was a strong linear regression of SGR with the feed consumption (g/fish) (Figure 1). Thus, the lower nutrient and energy intake in these groups of fish was a key parameter for their growth determination and this fact has been stressed in other studies (reviewed by Finke [66]). The current findings redefine our preliminary results [56] where we had suggested that the full-fat *H. illucens* meal can replace up to 30% of dietary fishmeal without exerting significantly negative effects on fish growth and feed utilization. As mentioned before, the dietary inclusion of the full-fat *H. illucens* meal,

regardless the level of fishmeal replacement, significantly reduced the nutrient and energy intake of fish, but the inclusion of low levels of defatted *H. illucens* meal did not exert such an effect. The cubic regression analysis revealed that a dietary level at about 104 g/kg of the defatted *H. illucens* meal (Figure 2a) would support the highest feed consumption. In addition, the cubic regression analyses revealed that a dietary level at about 81–96 g/kg of the defatted *H. illucens* meal (Figure 2b–d) would support the highest growth and feed utilization performance of the fish.

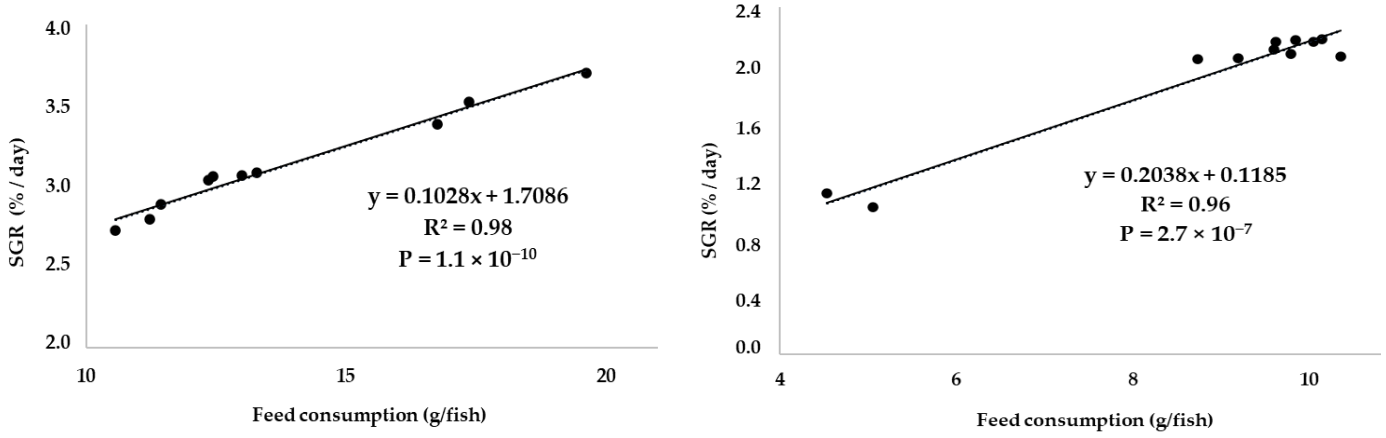

Figure 1. Linear regression of SGR (%/day) and feed consumption (g/fish) for: (**a**) trial I (full-fat *Hermetia illucens* meal); (**b**) trial II (defatted *Hermetia illucens* meal).

Despite the increasing interest on *H. illucens* as fishmeal replacer in aquafeeds and the importance of *S. aurata* in aquaculture, not many studies have investigated its effects on the species growth performance and feed utilization. Fabrikov et al. [53], similarly to our findings, reported a decline in growth performance and feed utilization of *S. aurata* feeding on a full-fat *H. illucens* meal at 109–180 g/kg of diet, regardless the level of fishmeal replacement. The authors found a reduced feed digestibility and changes in the protease activities of fish fed the full-fat *H. illucens* meal compared to the control. On the other hand, high nutrient digestibilities, similar to those of the control ones, have been reported for diets containing defatted [57] or partially defatted [27] meals replacing fishmeal. Contrary to our findings, the use of defatted meals at 195 g/kg [58] and up to 450 g/kg [57] did not compromise the growth performance of the species and its feed efficiency. Randazzo et al. [60] and Pulido-Rodriguez et al. [61] reported even significantly higher SGR and lower FCR values for *S. aurata* fed on defatted *H. illucens* meals with inclusion levels at 162–324 g/kg compared to a fishmeal-based diet. Certainly, discrepancies among studies can be due to several influencing factors such as diet formulation, degree of the defatting process and the nutritional quality of *H. illucens* meals used. The latter is known to be highly variable depending on the feed substrate and even on strain and developmental stage (prepupae vs. larvae) among others [75,76].

The present study revealed that a dietary inclusion level of full-fat *H. illucens* meal at 95 g/kg replacing fishmeal impaired the growth of *S. aurata*, while a dietary level at about 81–96 g/kg of the defatted meal would support the highest growth and feed utilization performance of fish. It seems that other fish species can tolerate higher inclusion levels of *H. illucens* meal in their diet replacing fishmeal protein. For example, in *O. mykiss* the inclusion levels of a full-fat meal at 109 g/kg [77], of a partially defatted meal at 400 g/kg [78] and of a defatted meal at 281 g/kg [79] were succesful without adverse effects on fish growth and feed efficiency. Even higher inclusion levels of a full-fat meal were succesfull in *S. salar* (147–250 g/kg) [29,40], in *O. niloticus* (100–208 g/kg) [30,31], in *C. carpio specularis* (175 g/kg) [33], in *P. hypophthalmus* (174 g/kg) [49], in *C. carpio Jian* (140 g/kg) [32], in *L. calcarifer* (155 g/kg) [44] and in *Dicentrarchus labrax* (148 g/kg) [72].

In *P. fulvidraco*, Xiao et al. [43] reported an unaffected growth and feed efficiency using a full-fat meal as high as 343 g/kg, but Hu et al. [42] found that when the inclusion of full-fat meal was raised from 113 g/kg to 141 g/kg, the weight gain ratio of fish was significantly reduced compared to the fishmeal-fed fish. Similarly, the defatted meal has been used succesfully at higher dietary levels in other fish and crustacean species such as *D. rerio* (500 g/kg) [34], *P. major* (281 g/kg) [50], *A. baerii* (185 g/kg) [45], *Litopenaeus vannamei* (235 g/kg) [48], *D. labrax* (195 g/kg) [71], *C. semilaevis* (144 g/kg) [51] and *C. carpio Jian* (106 g/kg) [35].

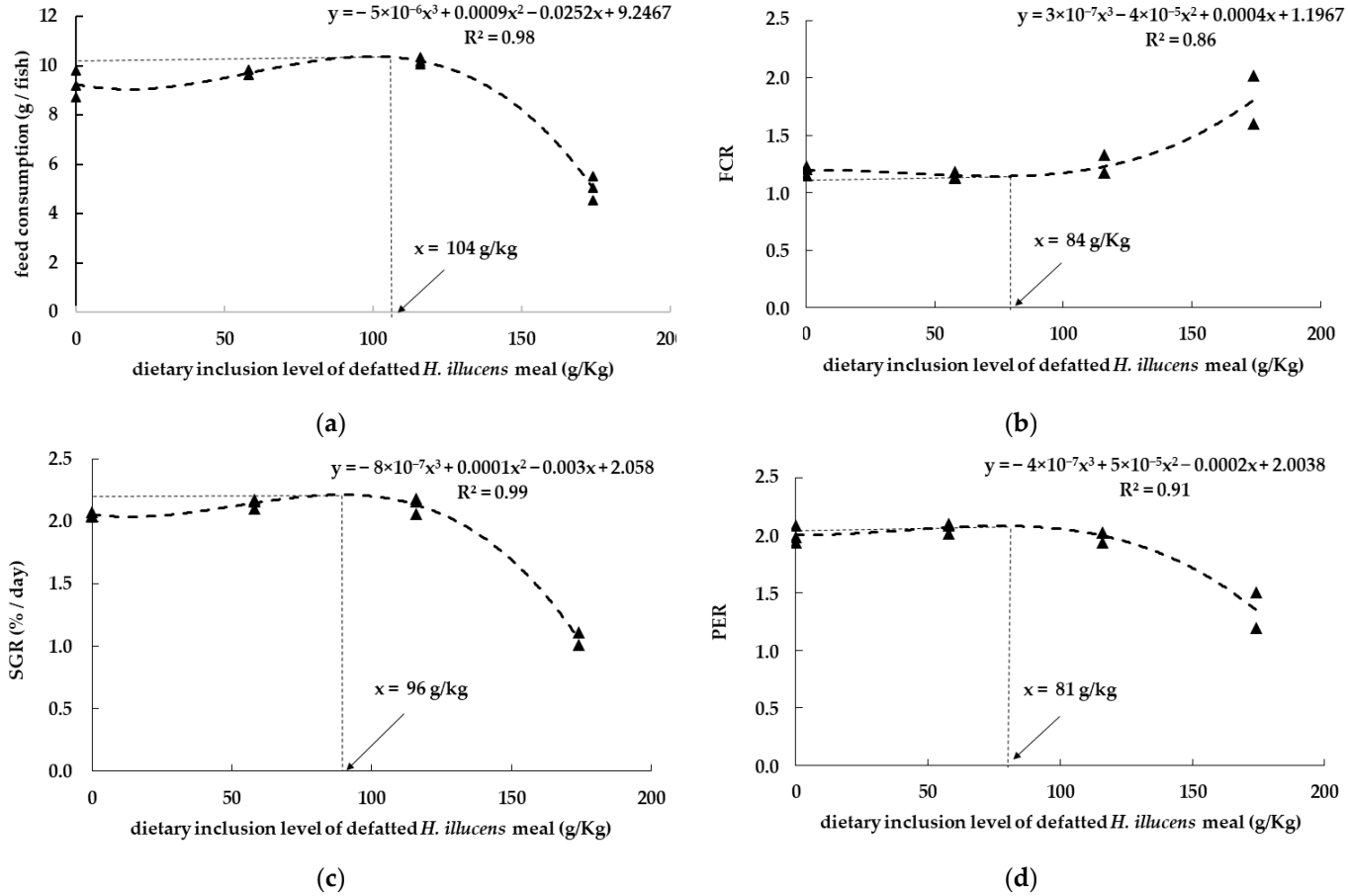

Figure 2. Cubic polynomial regressions of (**a**) feed consumption (g/fish), (**b**) FCR, (**c**) SGR (%/day) and (**d**) PER with dietary inclusion level of defatted *Hermetia illucens* meal (g/kg).

Several studies have investigated the effects of *H. illucens* meal on the proximate composition of fish. It has to be noted here that any alterations in proximate compositions among dietary treatments should be viewed in relation to the specific *H. illucens* meals and diets used in each feeding trial together with the data on feed intake, digestibility, fish species and growth stage that all exert a major influence [80,81], while the percentage of each nutrient is relative to the percentages of the rest with strong positive and inverse relationships among them [82]. In opposition to our findings, some studies have reported that the proximate compositions of fish tissues were not affected by fishmeal replacement with *H. illucens* meal [32,35,72,83,84] and this was also true for *S. aurata* [53,57,58,61]. An unaffected protein content [29,35,42,46,72,78,85,86] sounds reasonable, as this is known to be endogenously controlled and not strongly affected by dietary factors [80], though body alterations in this nutrient have also been reported [38,43,87].

In the present study, the body and muscle protein contents of fish were unaffected by the use of full-fat *H. illucens* meal but were significantly increased in fish fed the high levels of the defatted meal due to their decreased feed consumption. The feed consumption was

the key factor affecting the whole body and muscle proximate compositions of *S. aurata* fish fed with the defatted *H. illucens* meal. Thus, the DF-174 fish had decreased lipid and energy contents, which in turn increased the protein and moisture contents, due to their lower nutrient and energy intakes. At the same time, decreased lipid and energy contents were also found in the muscles of DF-58 and DF-116 fish despite their similar feed intake and growth compared with the control DF-0 group. This is probably due to their lower dietary lipid levels (Table 2), signifying that the low lipid level of the defatted *H. illucens* meal (3%, Table 1) is readily utilized by *S. aurata*. On the other hand, the dietary inclusion of the full-fat *H. illucens* meal did not alter the whole body proximate composition, but led to increased lipids and, in turn, energy deposition in the muscle tissues of *S. aurata*. These groups of fish had a decreased feed consumption and thus their lower energy and nutrient intakes could not justify the increased lipid deposition in their muscles. It could be that the type of fat in the *H. illucens* meal exerted this effect, but it is well known that this is characterized by high amounts of palmitic acid, oleic acid and lauric acid [12,88], which are readily oxidized rather than being stored in fish tissues [88,89]. In addition, the fat of *H. illucens* has been reported to be highly digestible by fish [28,29,78,79,90]. In fact, the three groups of fish fed the full-fat meal exhibited decreased lipid retention values compared to the control, which implies that a significant amount of their dietary lipid had been catabolised. However, the full-fat *H. illucens* meal had a really high lipid content (27.2%, Table 1) that in turn increased the lipid level of the corresponding diets, which probably the fish cannot utilize/catabolize to the same extent as that of the dietary fishmeal leading to muscle lipid accumulation. An increased lipid deposition together with a lower feed intake has been also observed in *O. niloticus* [30] fed on full-fat *H. illucens* diets that totally replaced fishmeal, while Dumas et al. [38] observed the lower lipid digestibility of a partially defatted *H. illucens* meal at high inclusion levels that led to increased body lipid deposition. It has been argued that the high chitin levels of *H. illucens* meal inhibit the nutrient absorption and thus impair the lipid digestibility [38,46,91].

5. Conclusions

This study denoted a lower acceptability and palatability of *H. illucens* meal compared to fishmeal when it was included at relatively high dietary levels and that the defatted form was more readily accepted than the full-fat type. Both the fat content and the inclusion level of *H. illucens* meal are critical for the success of fishmeal replacement in the diets of *S. aurata* as they strongly affect the feed consumption of fish. It was shown that the inclusion of full-fat *H. illucens* meal even at low levels (95 g/kg replacing 9% of fishmeal) and the inclusion of defatted *H. illucens* meal at levels as high as 174 g/kg (replacing 30% of fishmeal) significantly depressed the growth performance of *S. aurata* due to their lower nutrient and energy intakes. Moreover, the high lipid content of the full-fat *H. illucens* meal was not fully catabolized by fish and thus accumulated to their muscle tissues, while the reduced nutrient and energy intakes of fish fed the high levels of the defatted meal led to lower body and muscle lipid contents in fish. These results indicate that the defatted *H. illucens* meal is more suitable than the full-fat type to replace the dietary fishmeal. The cubic regression analyses revealed that a dietary level at about 81–104 g/kg of the defatted *H. illucens* meal would support the highest feed consumption, the highest growth and better feed utilization of *S. aurata*.

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Institutional Review Board Statement: The study was conducted according to the guidelines of EU legal frameworks related to the welfare and protection of animals for scientific purposes (Directive 2010/63/EU) and approved by the Institutional Ethics Committee of the University of Thessaly (protocol code 16048, date 1 August 2019).

Informed Consent Statement: Not applicable.

Data Availability Statement: The data presented in this study are available on request from the corresponding author.

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