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Dietary hydroxyproline improves the growth and muscle quality of large yellow croaker *Larimichthys crocea*

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ABSTRACT

The present study was conducted to estimate the effect of dietary hydroxyproline (Hyp) on growth, muscle texture and collagen content of large yellow croaker. Six isonitrogenous and isolipidic practical diets were formulated to contain graded levels of Hyp (0.17%, 0.26%, 0.33%, 0.50%, 0.69% and 0.86% of dry matter). Fish with similar size (initial body weight, 189.87 ± 0.89 g) were distributed into 18 floating net-cages (1.5 m × 1.5 m × 2.0 m). Each diet was hand-fed to triplicate groups of large yellow croaker for 82 days. The results showed that the specific growth rate (SGR) of fish fed diet with 0.33% of Hyp was significantly higher than those fed with the basal diet (0.17% Hyp) ($P < 0.05$). No significant differences were found in survival rate, viscerosomatic index, hepatosomatic index, condition factor and feed intake among all treatments ($P > 0.05$). Protein efficiency ratio and feed efficiency significantly increased with increasing levels of dietary Hyp up to 0.33% ($P < 0.05$). Moisture and crude lipid contents in muscle showed no significant difference among all treatments ($P > 0.05$), while crude protein was significantly improved by dietary Hyp ($P < 0.05$). Significant decreases were observed in muscle liquid loss and water loss with increasing levels of dietary Hyp ($P < 0.05$), while little variation was detected in lipid loss ($P > 0.05$). A statistically significant difference was observed in muscle pH with dietary Hyp ($P < 0.05$). Except for the cohesiveness and adhesiveness, all other analyzed texture properties including hardness, springiness, chewiness in muscle were significantly affected by dietary Hyp. Alkaline-soluble Hyp reached to the highest value in muscle when fish were fed diet with 0.69% of Hyp. The highest value of the total Hyp content in muscle was found in the treatment with 0.86% of dietary Hyp ($P < 0.05$). No significant difference was detected in muscle alkaline-insoluble Hyp, salt-soluble protein and water-soluble protein ($P > 0.05$) among all treatments. Pyridinium crosslink (PYD) in muscle increased with increasing dietary Hyp content up to 0.69% ($P < 0.05$). Hardness, springiness and chewiness showed a high and positive correlation with alkaline-soluble Hyp, total Hyp and PYD, and negative correlation with liquid loss and water loss. It was concluded that dietary Hyp could benefit fish growth, promote the formation of collagen, and thereafter influence muscle quality of large yellow croaker. Using the broken-line models based on SGR and the total Hyp content in muscle, the optimal dietary Hyp content for large yellow croaker were estimated to be 0.33% and 0.61%, respectively.

Statement of relevance: This study is not a test of commercial aquaculture.

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1. Introduction

Large yellow croaker (*Larimichthys crocea*) is a very popular and commercial farmed fish species, which has been cultured widely especially in south of China because of its delicious meat and high market value. It is now the first major mariculture fish species with 127,917 metric tons produced in 2014 in China (China Fishery Statistical Yearbook, 2015). Previous studies have been reported to estimate the nutrition value of large yellow croaker in farmed (Duan et al., 2001) and wild (Lin et al., 2006). Farmed large yellow croaker tends to have a softer texture, less robust flavor and colour than wild one (Yi et al., 2014b). Compared with farmed fish, consumers in China prefer wild caught fish due to their firmer texture and superior organoleptic qualities (Yi et al., 2014a). It is urgent to find an efficient way to improve the quality of the farmed large yellow croaker.

Flesh quality is a complex concept and has been defined as 'a combination of such characteristics as wholesomeness, integrity and freshness' (Martin, 1988). It is affected by endogenous factors such as genetic background (Larsson et al., 2012), colour, strains (Johnston,

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1999), texture and fat content (Periago et al., 2005). Meanwhile, it is also influenced by exogenous factors such as environmental factors (Johnston, 2008), feed and feeding (Johansson et al., 2000). The main edible portion and quality value of fish flesh is the skeletal muscle tissue, which consists of muscle fiber and intramuscular connective tissue (IMCT). The IMCT is correlated with muscle firmness (Johnston et al., 2000). It principally consists of fibres of the proteins collagen and elastin, surrounded by a proteoglycan matrix (Purslow, 2005). The collagen is a major structural element (Shearer et al., 1994) contributing to the tissues stability and maintaining their integrity of structure (Liu et al., 1996). Collagen content, type and structure are important factors influencing the muscle texture of fish (Cheng et al., 2014; Periago et al. 2005).

Approximately 99.8% of the Hyp in body's stores are found in collagen (Barbul, 2008). Hyp is essential for the formation of triple helical molecules in vivo and is indispensable for intramolecular hydrogen bonds, which maintains the integrity of the collagen fibrils and contributes to the thermal stability of the triple helical structure (Gelse et al., 2003; Myllyharju and Kivirikko, 2004). It is also recognized as a substrate for the synthesis of glycine, pyruvate, glucose and glutamate (Wang et al., 2013; Wu et al., 2010) and now considered as a conditionally essential amino acid in aquatic animals (Li et al., 2009). Aksnes et al. (2008) reported that the growth and Hyp in vertebra of salmon (*Salmo salar* L.) were significantly improved by dietary Hyp addition. In contrast, Zhang et al. (2013) showed that Hyp did not affect growth but improved collagen content in muscle of juvenile turbot (*Scophthalmus maximus* L.).

In the biosynthesis of collagens, the pyridinium crosslink (PYD) is able to connect collagen molecules to make tissue stable (Li et al., 2005). Significant positive correlation was observed between PYD concentration and fillet firmness in Atlantic salmon (*Salmo salar* L.) (Johnston et al., 2006; Li, et al., 2005). Moreover, Johnsen et al. (2011) showed that PYD was the only factor that significantly influenced fillet firmness. Lysyl hydroxylase (LOX) is traditionally known to catalyze the oxidative deamination of the ε-amino group of lysines and hydroxylysines to promote crosslinking, which is the only enzymatic step involved in the formation of the collagen crosslinking (Gelse et al., 2003; Wang et al., 1996). Few studies have evaluated the effects of dietary Hyp on PYD content and LOX activity, and their contribution to muscle texture in fish. It therefore requires further investigation.

The present study selected Hyp as a nutrient added to diet and fed the large yellow croakers for 82 days to analyze muscle collagen content, related enzyme activities, and PYD content in the process of collagen biosynthesis. Muscle quality indexes were also detected. The main purpose of this study is to investigate whether dietary Hyp can influence the growth and muscle quality of large yellow croaker.

2. Materials and methods

2.1. Experimental diets

The ingredients and compositions of the experimental diets are presented in Table 1. L-Hyp (>99% pure) was obtained from Huayang Chemical Co., Ltd. (China). Six isonitrogenous and isolipidic diets were formulated to supplement graded levels of Hyp: 0% (the basal diet), 0.1%, 0.2%, 0.4%, 0.6% and 0.8%, respectively. The analyzed dietary Hyp contents were 0.17%, 0.26%, 0.33%, 0.50%, 0.69% and 0.86%, respectively. The basal diet was formulated to contain fish meal, soybean meal and wheat meal as the intact protein sources. It contained about 43% of crude protein and 12% of crude lipid. The diet was supplemented with lysine-H_2SO_4, DL-methionine, L-threonine, L-arginine, L-isoleucine, L-leucine, L-valine, and L-phenylalanine (crystalline amino acids) as premix to simulate the whole body amino acid pattern of large yellow croaker. The amino acid compositions of the experimental diets are shown in Table 2.

Table 1
Formulation and proximate composition of the experimental diets (% dry matter).

	Dietary Hyp levels					
Ingredients	0%	0.1%	0.2%	0.4%	0.6%	0.8%
Fish meal[a]	25	25	25	25	25	25
Soybean meal[a]	25	25	25	25	25	25
Wheat meal[a]	26	26	26	26	26	26
Fish oil	6	6	6	6	6	6
Soybean lecithin	2.5	2.5	2.5	2.5	2.5	2.5
Mineral premix[b]	2	2	2	2	2	2
Vitamin premix[c]	2	2	2	2	2	2
Choline Chloride	0.2	0.2	0.2	0.2	0.2	0.2
Attractant[d]	1.5	1.5	1.5	1.5	1.5	1.5
Mold inhibitor[e]	0.1	0.1	0.1	0.1	0.1	0.1
Ethoxyquine	0.05	0.05	0.05	0.05	0.05	0.05
Amino acid premix[f]	5.70	5.70	5.70	5.70	5.70	5.70
Microcrystalline cellulose	3.15	3.15	3.15	3.15	3.15	3.15
Alanine	0.8	0.7	0.6	0.4	0.2	0
Hydroxyproline	0	0.1	0.2	0.4	0.6	0.8
Total	100	100	100	100	100	100
Proximate analysis						
Crude protein	43.56	44.20	43.90	43.89	43.42	43.85
Crude lipid	12.82	13.43	12.71	13.35	12.34	12.95
Moisture (% wet weight)	5.32	5.09	5.04	6.41	5.36	5.04
Hydroxyproline	0.17	0.26	0.33	0.50	0.69	0.86

[a] All of these ingredients were supplied by Qingdao Great Seven Biotechnology Co., Ltd., China. Fish meal, crude protein: 74.31%, crude lipid: 8.98%; Soybean meal, crude protein: 57.40%, crude lipid, 1.70%; Wheat meal, crude protein: 17.39%, crude lipid: 1.47%.
[b] Mineral premix (mg/kg diet): Na_2SeO_3 (1%), 20, $Ca(IO_3)_2 \cdot 6H_2O$ (1%), 60; $CoCl_2 \cdot 6H_2O$ (1%), 50; $CuSO_4 \cdot 5H_2O$, 10; $FeSO_4 \cdot H_2O$, 80; $ZnSO_4 \cdot H_2O$, 50; $MnSO_4 \cdot H_2O$, 45; $MgSO_4 \cdot 7H_2O$, 1200; $Ca(H_2PO_4)_2 \cdot H_2O$, 10,000; microcrystalline cellulose, 8485.
[c] Vitamin premix (mg/kg diet): thiamin, 25; riboflavin, 45; pyridoxine HCl, 20; vitamin B_{12}, 10; vitamin K3, 10; inositol, 800; pantothenic acid, 60; niacin acid, 200; folic acid, 20; biotin, $Ca(IO_3)_2$, 60; retinol acetate, 32; cholecalciferol, 5; α-tocopherol, 240; ascorbic acid, 2000; wheat middling, 16,473.
[d] Attractant: glycine: betaine = 1:2.
[e] Mold inhibitor: 50% calcium propionic acid and 50% fumaric acid.
[f] Lysine-H_2SO_4, DL-methionine, L-threonine, L-arginine, L-isoleucine, L-leucine, and L-valine, and L-phenylalanine.

2.2. Experimental procedure

The present study was carried out strictly according to the recommendations in the Guide for the Use of Experimental Animals of Ocean University of China.

The feeding trial was conducted at Xiangshan Harbor of Ningbo, Zhejiang Province, China. Large yellow croaker juveniles were obtained from a commercial hatchery. Prior to the feeding trial, the fish were

Table 2
Amino acid composition of the experimental diets (% dry matter).

	Dietary Hyp levels (%)					
	0.17	0.26	0.33	0.50	0.69	0.86
Aspartic acid	3.57	3.37	3.51	3.41	3.39	3.59
Threonine	1.99	1.87	1.96	1.85	1.88	2.08
Serine	1.80	1.70	1.76	1.70	1.70	1.81
Glutamic acid	7.11	6.67	7.02	6.92	6.85	7.19
Glycine	2.27	2.13	2.21	2.22	2.23	2.19
Alanine	2.85	2.81	2.69	2.29	2.23	2.11
Cysteine	0.43	0.46	0.45	0.45	0.48	0.47
Valine	2.23	2.17	2.18	2.18	2.18	2.28
Methionine	1.23	1.27	1.25	1.32	1.36	1.21
Isoleucine	2.07	1.95	2.03	2.04	1.99	2.07
Leucine	3.87	3.70	3.81	3.80	3.78	3.90
Tyrosine	1.39	1.30	1.35	1.36	1.32	1.34
Phenylalanine	2.17	2.06	2.09	2.14	2.04	2.15
Lysine	3.68	3.52	3.66	3.62	3.60	3.73
Histidine	1.09	1.04	1.09	1.09	1.06	1.12
Arginine	3.80	3.63	3.71	3.71	3.73	3.84
Proline	1.90	1.93	1.97	1.94	1.98	1.96

reared in floating net cages (3.0 × 3.0 × 3.0 m) in the sea for 2 weeks to acclimate to the experimental diet and conditions. There were 4 cages, and 250 fish per cage. At the start of the feeding trial, fish were fasted for 24 h and weighed. Fish of similar sizes (initial body weight: 189.87 ± 0.89 g) were randomly distributed to 18 floating sea cages (1.5 × 1.5 × 2.0 m), and 38 fish per cage. Each diet was assigned to triplicate cages. Fish were hand-fed to apparent satiation twice (05:00 and 17:30) daily. The feeding trial lasted for 82 days. During this period, feed consumption was recorded daily. The water temperature ranged from 26.5 to 32.5 °C, the salinity from 32 to 36‰, and the dissolved oxygen content exceeded 6 mg L^{-1}.

2.3. Sample collection

At the termination of the feeding trial, the fish were fasted for 24 h and anaesthetized with MS-222 (1:10,000) (purity 99%, Shanghai Reagent, China) before sampling. Fish in each cage were weighed and counted to determine the specific growth rate (SGR), and survival rate (SR). Before sampling, fish were sacrificed by a sharp blow to the head. Six fish for each treatment were sampled respectively to detect the individual body weight, body length, liver weight and viscerosomatic weight. Another twelve fish from each treatment were manually filleted. One side of the dorsal fillet in the epaxial myotomes below the dorsal fin of each fish for texture, pH and liquid holding capacity analysis were packed in covered polystyrene boxes to deliver to the laboratory. Specimens were kept on ice during the whole study and analyzed in 24 h. A sample of the corresponding fillet of the other side for collagen content, PYD content, amino acid and enzyme activity analysis were put in centrifuge tube and frozen in liquid nitrogen and stored at −80 °C until analysis.

2.4. The diet and muscle composition analysis

The diets and muscle samples were analyzed for dry matter, and crude protein using standard methods (AOAC, 1995). Samples of diets and muscle were dried to constant weight at 105 °C to determine moisture. Crude protein was determined using the Kjeldahl (2300-Kjeldahl apparatus, FOSS, Denmark) method by measuring nitrogen (N × 6.25). Muscle lipid was measured by chloroform-methanol method (Folch et al., 1957).

For amino acids (except for methionine and cystine), the samples were hydrolyzed with 15 mL of 6 N HCl at 110 °C for 24 h and the analysis was performed using an automatic amino acid analyzer (L-8900, Hitachi, Japan) with the method described by Xie et al. (2012). Methionine and cysteine were determined by the method of Spindler et al. (1984) with some modifications. The samples were oxidized with performic acid at −10 °C for 3 h to obtain methionine sulfone and cysteic acid, and then were freeze-dried twice with deionized water. The freeze-dried ingredients were hydrolyzed and analyzed as the process of other amino acids above.

2.5. Muscle pH, liquid holding capacity (LHC) and texture analysis

Muscle pH value was analyzed using a pH meter (PB-10, Sartorius, Germany) with the method of Fuentes et al. (2010). One gram of minced muscle was homogenized in 10 mL distilled water before measuring.

The LHC was measured by gravimetric method (GÓmez-guillén et al., 2000), Each sample was measured in duplicated. One gram of skinned muscle of large yellow croaker was weighed (S) and wrapped in the filter paper (V1), put in centrifuge tube, then centrifuged at 500 ×*g* for 10 min at 10 °C. The wet paper (V2) was then weighed and dried in the oven (75 °C) to constant weight (V3). The liquid loss was calculated as 100 × (V2 − V1) × S^{-1}, water loss as 100 × (V2 - V3) × S^{-1}, and lipid loss as 100 × (V3 − V1) × S^{-1}.

Three sampling points were selected in each fillet (between dorsal and tail, above lateral line). Texture analysis was performed instrumentally using a texture analyzer (TMS-PRO, FTC, America) equipped with an 8 mm cylinder probe. Double compression was applied to construct the texture profile analyses (TPA) parameters. The test condition involved two consecutive cycles of compression with a constant speed of 30 mm/min with the deformation 60% of the original length, and the initial force is 0.1 N. Hardness, cohesiveness, springiness, adhesiveness and chewiness were determined (Ginés et al., 2004).

2.6. Collagen determination

Alkaline-soluble and alkaline-insoluble Hyp were prepared according to an established method (Li et al., 2005). Duplicate samples of 1 g muscle were minced by hand before homogenization in 9 mL cold water for 1 min at 30,000 rpm. About 10 mL ice cold 0.2 M NaOH was added immediately. The sample was mixed on a wheel roller at 4 °C for 4 h. The homogenate was centrifuged at 10,000 ×*g* for 30 min at 4 °C using ultracentrifuge (CR21GII, Hitachi, Japan). The suspending liquid was used in alkaline-soluble Hyp analysis. The pellet containing the alkaline-insoluble Hyp was re-suspended in 3 mL 6 M HCl and transferred to a 5 mL ampoule bottle. The sample was hydrolysed at 110 °C for 20 h and diluted in distilled water to 10 mL.

The determination of Hyp was carried out using the procedure reported by Zhang et al. (2013). *A*1 mL standard Hyp (prepared from stock solution of Hyp (Sigma-Aldrich Corp., St. Louis, MO, USA): 1 mg/mL in 1 mM HCl) or the hydrolysed tissue sample and 2 mL buffered chloramines T reagent (1.4 g chloramines T dissolved in 20 mL water, and then diluted with 30 mL n-propanol and 50 mL acetate-citrate buffer (pH 6.5) were mixed and incubated for 20 min at room temperature. Then, 2 mL perchloric acid (18.9%) was added. The mixture was incubated for 5 min at room temperature, and then 2 mL P-DMAB solution (10% *w*/*v* P-DMAB in n-propanol) was added. The mixture was heated for 20 min at 60 °C, and then cooled. The absorbance was determined at 560 nm. The Hyp concentration was determined from a standard curve. The collagen content was estimated by multiplying the hyp content by 8 (AOAC, 2000).

2.7. Analysis of the water soluble and salt soluble protein in muscle

Water-soluble and salt-soluble proteins were extracted with phosphate buffer alone or with KCl (Sigholt et al., 1997). The sample (1 g) was homogenized for 10 s at 4 °C in 20 mL phosphate buffer (0.05 M), pH 7 and then centrifuged (8000 g, 20 min). The supernatant was added into 25 mL volumetric flasks with phosphate buffer to provide the water-soluble fraction. The precipitate was homogenized for 10 s (4 °C) in KCl (0.6 M) in 20 mL phosphate buffer (0.05 M) at pH 7, and then centrifuged. The supernatant was decanted to the volume and adjusted to 25 mL with KCl-phosphate buffer, which provide the salt-soluble fraction. The protein contents of the water-soluble and salt-soluble fractions were determined using the Coomassie brilliant blue of commercial assay kit (Nanjing Jiancheng Bioengineering Institute, Nanjing, China).

2.8. The pyridinium crosslink (PYD), lysyl hydroxylase (LOX), prolyl 4-hydroxylase (P4H) assay

The PYD content, LOX and P4H activity in tissue samples were assayed using the PYD, LOX and P4H ELISA kit (Nanjing Jiancheng Bioengineering Institute, Nanjing, China), respectively.

2.9. Calculations and statistical analyses

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

$$\text{Specific growth rate (SGR)} = 100 \times (\text{LnW}_t - \text{LnW}_0)/t$$

Feed intake (FI) = 100 × dry feed intake (g)
/[(final body weight + initial body weight)/2]/t

Protein efficiency ratio (PER) = weight gain (g)/protein fed (g)

Feed efficiency (FE) = weight gain (g)/dry feed intake (g)

Protein retention (PR) = 100 × retained protein (g)/protein fed (g)

Viscerosomatic index (VSI) = 100 × viscera wet weight/final body weight

Hepatosomatic index (HSI) = 100 × liver wet weight/final body weight

Condition factor (CF) = 100 × final body weight/body length^3

where W_t is final body weight; W_0 is initial body weight; t is feeding trial duration in day.

Data were subjected to the one-way analysis of variance (ANOVA) using SPSS 17.0 for Windows. When overall differences were significant ($P < 0.05$), Tukey's test was used to compare the means among individual treatments. All data were expressed as means ± standard error. The effects of dietary treatments on flesh characteristics were analyzed by principal component analysis (PCA) (SPSS 17.0).

The PCA correlation loading plot of corresponding variables visualises the correlations between the different variables, and variables located close to each other have a positive correlation, while variables with loadings of opposite signs are negatively correlated (Veiseth-Kent et al., 2010). The relationship between dietary Hyp levels and SGR or the total Hyp content in muscle was analyzed by the broken-line model (Robbins et al., 1979). The optimal dietary Hyp levels for growth and the total Hyp content in muscle of large yellow croaker was estimated by the broken-line model.

3. Results

3.1. Survival and growth

Survival rate and growth performance are shown in Table 3. After the 82-day feeding trial, no significant difference was observed in survival rate (SR), which varied from 84.21% to 92.11% among all the treatments ($P > 0.05$). The specific growth rate (SGR) was significantly affected by dietary Hyp levels. It increased with the increasing dietary Hyp contents up to 0.50% ($P < 0.05$), and then no further increase was found. The optimal dietary Hyp content for the growth of large yellow croaker was estimated to be 0.33% on the basis of SGR using broken-line model (Fig. 1). There were no significant differences in feed intake (FI) among all the treatments ($P > 0.05$). Feed efficiency (FE) of fish fed diet with 0.33% of Hyp was significantly higher than those in the control and in the 0.26% Hyp groups ($P < 0.05$). The protein efficiency ratio (PER) was significantly affected by dietary Hyp levels ($P < 0.05$). It increased with higher levels of dietary Hyp up to 0.33%. No significant difference was observed in protein retention (PR) among all the treatments ($P > 0.05$).

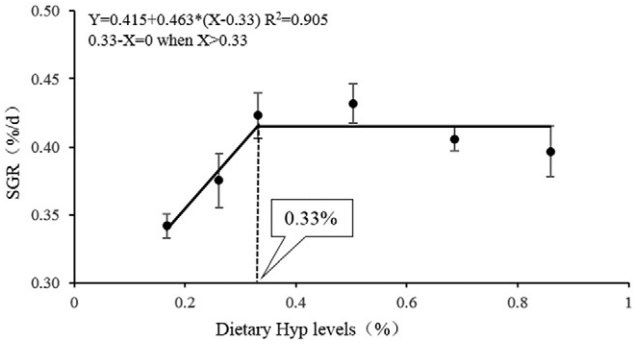

Fig. 1. Relationship between dietary Hyp levels and SGR of large yellow croaker fed the experimental diets for 82-day by the broken-line model. The breakpoint of the broken-line is 0.33% of dry diet. Each point represents the mean of three replicates.

3.2. Body physical indicators

Body physical indicators are shown in Table 4. There were no significant differences in hepatosomatic index (HSI), viscerosomatic index (VSI) and condition factor (CF) among all the treatments ($P > 0.05$).

3.3. Muscle pH and liquid holding capacity (LHC)

Muscle pH and LHC are shown in Table 5. The values of pH in muscle of fish fed diet with 0.69% or 0.86% of Hyp were significantly higher than that in the treatment with 0.17% of dietary Hyp ($P < 0.05$). Water loss and liquid loss were significantly decreased with the increasing dietary Hyp up to 0.69% ($P < 0.05$), and the lowest values were 17.18% and 19.14%, respectively. Lipid loss ranging from 1.62% to 2.16% was not significantly influenced by dietary Hyp levels ($P > 0.05$).

3.4. Muscle texture

Muscle texture is shown in Table 6. The hardness was significantly increased by dietary Hyp levels ($P < 0.05$). The highest value of hardness was found as 513.19 g in the treatment with 0.86% of dietary Hyp. The springiness was also significantly increased with increasing dietary Hyp up to 0.69% ($P < 0.05$). Fish fed diets with 0.69% of Hyp or more gave a significant higher chewiness than those fed diets with 0.26% of dietary Hyp or less ($P < 0.05$). No significant difference was observed in adhesiveness and cohesiveness among all the treatments ($P > 0.05$).

3.5. Muscle compositions, water-soluble and salt-soluble protein

Contents of moisture, crude lipid, water-soluble protein and salt-soluble protein in muscle were not significantly influenced by dietary

Table 3
Survival rate and growth performance of large yellow croaker after the 82-day feeding trial.

	Dietary Hyp levels, % dry matter					
	0.17	0.26	0.33	0.50	0.69	0.86
Initial weigh(g)	190.00 ± 0.31	189.65 ± 0.35	190.00 ± 0.00	189.47 ± 0.53	190.35 ± 0.93	189.65 ± 0.76
Final weigh (g)	251.46 ± 3.92^a	258.03 ± 4.71^{ab}	268.88 ± 4.14^b	270.24 ± 3.60^b	265.51 ± 1.46^{ab}	262.60 ± 4.12^{ab}
SGR (%/d)	0.34 ± 0.01^a	0.37 ± 0.02^{ab}	0.42 ± 0.02^b	0.43 ± 0.01^b	0.40 ± 0.01^{ab}	0.40 ± 0.02^{ab}
FI (%)	0.71 ± 0.04	0.76 ± 0.04	0.72 ± 0.03	0.77 ± 0.03	0.76 ± 0.01	0.75 ± 0.02
FE	0.48 ± 0.02^a	0.49 ± 0.02^{ab}	0.58 ± 0.02^c	0.56 ± 0.00^{bc}	0.53 ± 0.01^{abc}	0.53 ± 0.02^{abc}
PER	1.10 ± 0.04^a	1.11 ± 0.06^a	1.33 ± 0.05^b	1.27 ± 0.01^{ab}	1.22 ± 0.03^{ab}	1.19 ± 0.04^{ab}
PR (%)	16.33 ± 1.25	16.08 ± 0.84	19.58 ± 0.29	17.88 ± 0.77	20.35 ± 0.87	18.10 ± 1.40
SR(%)	84.21 ± 4.02	89.48 ± 6.62	86.84 ± 1.52	92.11 ± 3.04	85.10 ± 3.82	89.47 ± 1.52

All data were expressed as mean ± SE. Mean values within the same row with different superscripts are significantly different ($P < 0.05$; Tukey's test).
SGR: Specific growth rate; FI: Feed intake; FE: Feed efficiency; PER: Protein efficiency ratio; PR: Protein retention; SR: Survival rate.

Table 4
Hepatosomatic index (HSI), visceralsomatic index (VSI), and condition factor (CF) of large yellow croaker after the 82-day feeding trial.

	Dietary Hyp levels, % dry matter					
	0.17	0.26	0.33	0.50	0.69	0.86
HSI (%)	1.31 ± 0.20	1.23 ± 0.16	1.43 ± 0.17	1.24 ± 0.13	1.34 ± 0.26	1.24 ± 0.22
VSI (%)	9.93 ± 0.43	10.15 ± 0.96	8.46 ± 0.94	9.70 ± 0.61	10.35 ± 0.35	9.94 ± 0.51
CF (%)	2.00 ± 0.05	1.99 ± 0.11	2.18 ± 0.07	1.98 ± 0.10	1.89 ± 0.08	1.83 ± 0.06

All data were expressed as mean ± SE.

Table 5
Liquid holding capacity (LHC) and pH in the muscle of large yellow croaker after the 82-day feeding trial.

	Dietary Hyp levels, % dry matter					
	0.17	0.26	0.33	0.50	0.69	0.86
Liquid loss (%)	23.80 ± 0.34^{c}	22.8 ± 0.87^{bc}	22.28 ± 0.98^{bc}	21.41 ± 0.93^{abc}	19.14 ± 0.37^{a}	20.39 ± 0.62^{ab}
Water loss (%)	21.87 ± 0.66^{c}	21.41 ± 1.11^{bc}	20.65 ± 1.17^{bc}	18.89 ± 1.31^{abc}	17.18 ± 0.43^{a}	17.96 ± 0.37^{ab}
Lipid loss (%)	1.93 ± 0.17	1.94 ± 0.09	1.62 ± 0.19	2.16 ± 0.15	1.96 ± 0.18	2.14 ± 0.26
pH	6.63 ± 0.01^{a}	6.70 ± 0.02^{ab}	6.67 ± 0.03^{ab}	6.69 ± 0.01^{ab}	6.76 ± 0.02^{b}	6.74 ± 0.03^{b}

All data were expressed as mean ± SE. Mean values within the same row with different superscripts are significantly different ($P < 0.05$; Tukey's test).

Hyp levels ($P > 0.05$) (Table 7). The crude protein in muscle significantly increased with dietary Hyp levels from 0.17% to 0.69% ($P < 0.05$).

3.6. Hydroxyproline and collagen contents in muscle

Hydroxyproline (Hyp) contents are shown in Table 7. Alkaline-soluble Hyp contents in muscle were significantly increased with dietary Hyp levels up to 0.69%, and then no further increase was found ($P < 0.05$). Alkaline-insoluble Hyp contents in muscle ranging from 0.23 to 0.28 mg/g did not show significant differences among all the treatments ($P > 0.05$). Total Hyp contents in muscle increased with increasing dietary Hyp levels, the highest value was 0.62 mg/g in fish fed diet with 0.86% of Hyp ($P < 0.05$). Based on the broken-line analysis, the optimal dietary Hyp level for the total Hyp content in muscle of large yellow croaker was estimated to be 0.61% (Fig. 2). The variation tendency of total collagen content with dietary Hyp were similar to those of the total Hyp content in muscle.

3.7. Pyridinium crosslink (PYD) contents and enzyme activities in muscle

The PYD contents (2.03–3.04 ng/mg protein) in muscle were significantly increased by dietary Hyp levels ranging from 0.17% to 0.69% ($P < 0.05$) (Table 8). There was no significant difference in P4H activities in liver ($P > 0.05$). However, significant difference was observed in muscle ($P < 0.05$). Activities of LOX in muscle were significantly increased by dietary Hyp levels ranging from 0.17% to 0.69% ($P < 0.05$). Liver LOX activities significantly increased with increasing levels of dietary Hyp up to 0.50% ($P < 0.05$).

3.8. Principal component analysis (PCA)

The PCA results are given in Fig. 3. A 75.29% of the variation in the PCA model was explained by PC1 (55.25%) and PC2 (20.03%). The instrumental measured texture characteristics (springiness, hardness and chewiness) were located next to the crude protein, total Hyp and

Table 6
Muscle texture of large yellow croaker after the 82-day feeding trial.

	Dietary Hyp levels, % dry matter					
	0.17	0.26	0.33	0.50	0.69	0.86
Hardness(g)	446.80 ± 11.46^{a}	458.72 ± 10.48^{ab}	474.51 ± 14.27^{abc}	484.28 ± 13.61^{abc}	511.26 ± 14.28^{bc}	513.19 ± 12.84^{c}
Springiness (mm)	2.45 ± 0.06^{a}	2.46 ± 0.08^{a}	2.54 ± 0.08^{ab}	2.53 ± 0.08^{ab}	2.80 ± 0.05^{b}	2.62 ± 0.09^{ab}
Chewiness (mJ)	285.94 ± 10.36^{a}	307.96 ± 9.32^{ab}	330.65 ± 8.48^{bc}	349.11 ± 11.29^{bc}	359.21 ± 11.32^{c}	353.33 ± 10.53^{c}
Cohesiveness	0.25 ± 0.01	0.26 ± 0.01	0.27 ± 0.01	0.26 ± 0.01	0.27 ± 0.01	0.26 ± 0.00
Adhesiveness (g*mm)	21.37 ± 1.17	19.72 ± 1.06	19.5 ± 1.07	18.65 ± 1.03	17.52 ± 0.55	17.68 ± 1.02

All data were expressed as mean ± SE. Mean values within the same row with different superscripts are significantly different ($P < 0.05$; Tukey's test).

Table 7
Proximate composition and contents of the water-soluble protein, salt-soluble protein, Hyp and collagen content in muscle of large yellow croaker after the 82-day feeding trial.

	Dietary Hyp levels, % dry matter					
	0.17	0.26	0.33	0.50	0.69	0.86
Moisture (%)	73.41 ± 0.26	72.54 ± 0.38	72.11 ± 0.24	73.33 ± 0.52	72.59 ± 0.38	73.64 ± 0.48
Crude lipid (% DM)	15.39 ± 2.70	16.47 ± 2.52	21.40 ± 2.26	20.05 ± 1.94	14.28 ± 1.48	16.50 ± 2.97
Crude protein (% DM)	68.63 ± 1.17^{a}	69.18 ± 0.89^{a}	71.54 ± 1.5^{ab}	72.87 ± 1.09^{ab}	74.92 ± 0.98^{b}	72.16 ± 0.88^{ab}
Water-soluble protein (g/100 g wet tissue)	6.66 ± 0.63	6.00 ± 0.49	5.81 ± 0.64	5.77 ± 0.32	5.69 ± 0.55	4.91 ± 0.32
Salt-soluble protein (g/100 g wet tissue)	5.91 ± 0.28	6.49 ± 0.47	5.90 ± 0.32	6.75 ± 0.45	5.61 ± 0.28	5.95 ± 0.55
Alkaline-soluble Hyp (mg/g wet tissue)	0.09 ± 0.02^{a}	0.12 ± 0.04^{a}	0.15 ± 0.02^{ab}	0.27 ± 0.07^{abc}	0.36 ± 0.04^{c}	0.34 ± 0.05^{bc}
Alkaline-insoluble Hyp (mg/g wet tissue)	0.23 ± 0.04	0.27 ± 0.03	0.26 ± 0.04	0.27 ± 0.03	0.23 ± 0.02	0.28 ± 0.04
Total Hyp (mg/g wet tissue)	0.32 ± 0.05^{a}	0.40 ± 0.05^{ab}	0.41 ± 0.02^{ab}	0.54 ± 0.06^{ab}	0.59 ± 0.04^{b}	0.62 ± 0.07^{b}
Total collagen (mg/g wet tissue)	2.57 ± 0.37^{a}	3.18 ± 0.43^{ab}	3.30 ± 0.17^{ab}	4.30 ± 0.48^{ab}	4.70 ± 0.32^{b}	4.98 ± 0.58^{b}

All data were expressed as mean ± SE. Mean values within the same row with different superscripts are significantly different ($P < 0.05$; Tukey's test). DM: dry matter.

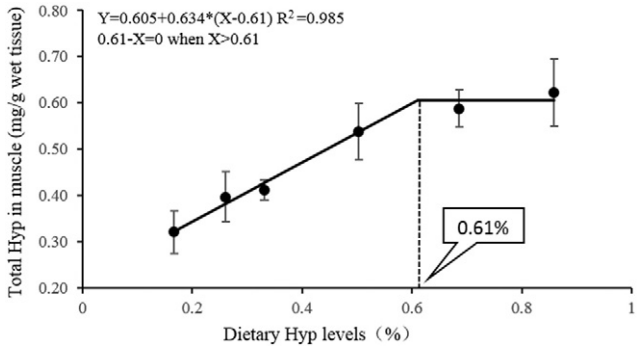

Fig. 2. Relationship between dietary Hyp levels and total Hyp in muscle of large yellow croaker fed the experimental diets for 82-day by the broken-line model. The breakpoint of the broken-line is 0.61% of dry diet. Each point represents the mean of three replicates.

collagen, PYD and pH, and on the opposite side of the plot compared to liquid loss, water loss in muscle. It indicated that the texture characteristics (springiness, hardness and chewiness) show a high and positive correlation with PYD and Hyp contents in muscle, but high and negative correlation with LHC (water loss and liquid loss).

4. Discussion

Contents of Hyp in fish meal (1.86 g/100 g sample) are much higher than that in plant protein sources, such as soybean meal (0.08 g/100 g sample) and peanut meal (0.07 g/100 g sample) (Li et al., 2011). The present basal diet was formulated by the low inclusion level of fish meal and thus expected to be suboptimal level of Hyp to inspect the influence of dietary Hyp supplementation on growth, muscle texture and collagen content in large yellow croaker. This study showed that fish growth was significantly improved by the optimum concentration of dietary Hyp levels. The results were consistent with the findings in previous studies in Atlantic salmon reported by Aksnes, et al. (2008) but were different from the other study also in Atlantic salmon (Albrektsen, et al., 2010). Big difference was presented in fish size with body weight of the 246–264 g (Aksnes et al., 2008) and 2.4 kg (Albrektsen et al., 2010), respectively, in the two previous studies. It suggested that the effect of dietary Hyp on fish growth could be partly attributed to the animal size. In the present study, FE and PER but not FI was also significantly improved by dietary Hyp. The FE can be improved by decreased food intake for growth until a certain optimal level (Jobling, 1995). However, diet with Hyp supplementation did not reduce the FI in the present study, which could provide more feeds to promote fish growth. Fish weigh gain is primarily attributed to the accretion of lipids and proteins in muscle (Bureau et al., 2000). The muscle of fish is the maximal tissue and the main segment used for human food. The present study showed that muscle crude protein was significantly increased with Hyp level of 0.69% diet, while no significant difference in muscle lipid content was found among all the treatments.

Muscle pH of post-mortem fish is an important flesh quality parameter (Johnsen et al., 2011; Periago et al., 2005; Wang et al., 2015). An impaired aerobic glycolysis may lead to increased glycogen depositions (DiMauro and Tsujino, 1994). The level of muscle glycogen is the principal determinant of pH due to its anaerobic breakdown to lactic acid via glycolysis (Love, 1988). The present study showed that the post-mortem muscle pH value was 6.63 in fish fed diet with 0.17% of Hyp and then significantly increased to 6.76 with 0.69% of dietary Hyp, which indicated that dietary Hyp could increase the fish muscle pH. A similar result has been reported in Atlantic salmon (Albrektsen et al., 2010). A lower muscle pH may reduce connective tissue strength and cause softer flesh (Lavety et al., 1988). Studies have been reported that muscle pH in wild sea bass with firmer texture was significantly higher than that in farmed one (Fuentes et al., 2010; Periago et al., 2005). The PCA correlation loading plot showed that the pH value highly and positively correlated with texture index (hardness, chewiness and springiness) in the present study. It was suggested that higher muscle pH could be benefit for muscle firmness.

The liquid holding capacity evaluated by water loss, lipid loss and liquid loss is another important flesh quality parameter in fish (Johnsen et al., 2011; Rørå et al., 2003). The correlation loading plot profiles indicated that liquid loss showed a high and positive correlation with water loss, but not with lipid loss. Fish is rich of water in the body. Water made up about 73% in fish muscle, while crude lipid (in wet weight basis) ranged from 3.92% to 6.00% in this study. Partly based on this aspect, water loss rather than lipid loss largely contributed to liquid loss. Water loss and liquid loss in muscle, in the present study, significantly decreased with dietary Hyp levels. It suggested that a suitable Hyp in diet could improve LHC. The enhancement of muscle LHC by dietary Hyp could be partially ascribed to the increment of muscle collagen content. Approximately 99.8% of the body's stores of Hyp are found in collagen, which renders assays of this amino acid useful as a marker for the total amount of collagen present (Barbul, 2008). In the present study, liquid loss and water loss highly and negatively correlated with total Hyp and collagen content in muscle. A similar result was reported that the LHC can be influenced by collagen (Loje et al., 2007; Ofstad et al., 1995). The denaturation of collagen can alter the physical properties of the pericellular layer to form a physical barrier to the release of fluid (Ofstad et al., 1995). It might be that more collagen content could improve LHC in fish muscle. The LHC could also be influenced by pH (Johnsen et al., 2011). It was observed in the present study that liquid loss and water loss was highly and negatively correlated with pH in muscle.

The textural mechanical properties (hardness, springiness, chewiness, cohesiveness and adhesiveness) were routine indexes and widely used to evaluate flesh quality of fish (Ginés et al., 2004; Moreno et al., 2012; Periago et al., 2005). The result of the present study showed that hardness, springiness and chewiness of muscle significantly improved with increasing dietary Hyp levels. A similar result was reported in Atlantic salmon showed that dietary Hyp improved muscle firmness (Albrektsen et al., 2010). The improvement of muscle texture could be partially due to the increases of muscle collagen content. Collagen fibres start to disintegrate within 24 h post-mortem (Ando et al., 1991). The rapid softening of fish muscle during chilled storage is linked to the changes of connective tissue constituents caused by disintegration of collagen rather than myofibrillar protein (Sato et al., 1991). High collagen content has been associated with firmer texture

Table 8
Pyridinium crosslink (PYD) content in muscle, prolyl 4-hydroxylase (P4H), and lysyl hydroxylase (LOX) activity in muscle and liver of large yellow croaker after the 82-day feeding trial.

	Dietary Hyp levels, % dry matter					
	0.17	0.26	0.33	0.50	0.69	0.86
PYD in muscle (ng/mg protein)	2.03 ± 0.11^{a}	2.12 ± 0.07^{a}	2.43 ± 0.09^{ab}	2.85 ± 0.12^{bc}	3.04 ± 0.14^{c}	2.76 ± 0.21^{bc}
P4H in muscle (pg/mg protein)	15.85 ± 0.64^{a}	18.71 ± 0.80^{abc}	19.80 ± 0.41^{bc}	20.42 ± 0.54^{c}	17.63 ± 0.78^{abc}	17.01 ± 0.98^{ab}
P4H in liver (pg/mg protein)	10.18 ± 1.63	14.96 ± 1.06	13.48 ± 0.69	14.13 ± 0.86	11.70 ± 1.64	12.11 ± 0.87
LOX in muscle (ng/mg protein)	9.48 ± 0.49^{a}	9.84 ± 0.59^{ab}	10.07 ± 0.52^{ab}	11.44 ± 0.25^{ab}	11.80 ± 0.69^{b}	10.69 ± 0.46^{ab}
LOX in liver (ng/mg protein)	0.59 ± 0.16^{a}	1.59 ± 0.40^{ab}	2.83 ± 0.34^{bc}	3.12 ± 0.07^{c}	2.86 ± 0.30^{bc}	1.49 ± 0.51^{ab}

All data were expressed as mean ± SE. Mean values within the same row with different superscripts are significantly different ($P < 0.05$; Tukey's test).

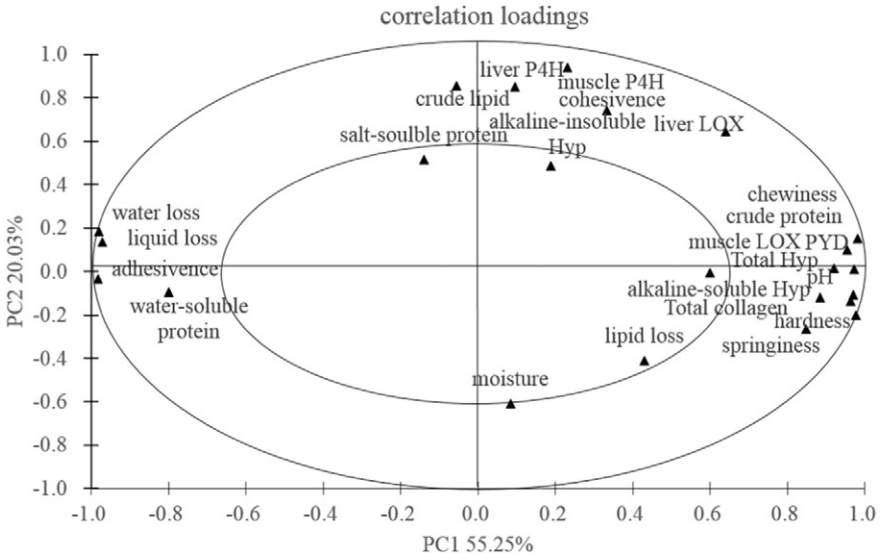

Fig. 3. Correlation loadings plot of PCA of large yellow croaker fed graded levels of dietary Hyp for flesh quality characteristics. The inner circle and the outer circle mark the limits for 50% and 100% explanation of the variation in the data, respectively.

(Periago et al., 2005). The present study found that dietary Hyp significantly improved muscle total Hyp and collagen content, which was in line with previous studies (Aksnes et al., 2008; Zhang et al., 2013). The correlation loading plot showed that texture parameters (hardness, springiness and chewiness) were highly and positively correlated with muscle total collagen content, suggesting that the improvement of texture characteristics could be attributed to the collagen content in muscle. In the process of collagen biosynthesis, P4H plays a vital role to catalyzed proline to Hyp (Gelse, et al., 2003). The rate of collagen biosynthesis can be influenced by the P4H activity (Karpakka et al., 1991; Kivirikko et al., 1989). Results of the present study showed that no significant difference was observed in liver P4H activity. It was similar with a previous study on turbot, suggesting that the liver P4H activity could be independent of dietary Hyp levels (Zhang et al., 2013). Muscle P4H activity was significantly improved by dietary Hyp. This suggested that the increased collagen content could be partially influenced by P4H activity in muscle but not in liver when fish were fed diet with Hyp supplementation.

The alkaline-soluble collagen is rich in degraded collagen, and newly synthesized collagen molecule, while the alkaline-insoluble collagen is composed of reducible and mature cross-linked collagen molecule (Li et al., 2005). Johnsen et al. (2011) reported that alkaline-soluble and alkaline-insoluble Hyp had no significant effect on fillet firmness of Atlantic salmon. However Li et al. (2005) found that there was a significant relationship between the concentration of alkaline-insoluble Hyp or collagen and firmness. The present study showed that alkaline-soluble Hyp was positively correlated with hardness, springiness and chewiness of muscle. Further studies are needed to solve this discrepancy.

Muscle firmness was related to higher collagen stability (Moreno et al., 2012). In Atlantic halibut flesh, cross-linking processes are of great importance for the rigidity and strength of the collagen, and the most important parameter affecting fillet texture was PYD (Hagen et al., 2007). The present study showed that dietary Hyp significantly increased muscle PYD which showed a high and positive correlation with texture index (hardness, springiness and chewiness). It suggested that the improvement of texture could partially due to the formation of PYD in muscle. Similar results were reproted by Li et al. (2005) and Johnsen et al. (2011). The LOX catalyzes the formation of aldehydes from lysine and hydroxylysine residues in the telopeptides (Gelse et al., 2003). It is the only enzymatic step involved in the formation of the collagen crosslinks which gives the connective tissue its mechanical strength (Johnston et al., 2006). In the present study, liver and muscle LOX activity were significanglty improved by dietay Hyp. It was suggeted that the increased PYD content could be partly due to the improvement of LOX activity with dietaty Hyp supplementaiton.

In the present study, the SGR reached to the highest value when fish were fed diet with 0.50% of Hyp, and no significant difference was observed in treatments with 0.33% and 0.50% of dietary Hyp. Broken-line analysis showed that the minimum requirement of dietary Hyp for optimal growth was estimated to be 0.33%. The minimum requirement of dietary Hyp for the highest total Hyp in muscle was 0.61%. According to the present study result, positive correlation was observed between the total Hyp content in muscle and muscle quality. Thus, it inferred that the requirement of dietary Hyp for the optimal quality was higher than that of the optimal growth of large yellow croaker. Under the same condition, the limited nutrient was prior used to meet growth, and then to improve muscle quality. In the study of salmon, the highest SGR was observed in diet with 0.14% of Hyp, while the highest Hyp content in vertebrate was presented in diet with 0.56% of Hyp (Aksnes et al., 2008). Thus, it was suggested that dietary Hyp level for the optimal growth are not always for the optimal quality in fish tissue.

5. Conclusion

The present results confirmed that supplementation of Hyp to plant-protein-based diets was beneficial for the growth of large yellow croaker. Dietary Hyp supplementation was also effective in improving flesh quality including muscle texture, pH and LHC of large yellow croaker. Using the broken-line models based on SGR and the total Hyp content in muscle, the optimal dietary Hyp content for large yellow croaker were estimated to be 0.33% and 0.61%, respectively.

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