



## Effect of Dietary Composition with Different Feeding Regime on Compensatory Growth of Juvenile Olive Flounder *Paralichthys olivaceus*

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**ABSTRACT** : Compensatory growth of juvenile olive flounder *Paralichthys olivaceus* fed different diets with different feeding regime was compared. Four hundred fifty fish (twenty five fish per tank) were randomly distributed into 18 of 180 L flow-through tanks. Six treatments were prepared: fish were hand-fed with the control (C) diet to satiation twice a day, six days a week, for 8 weeks (C-8W treatment); and other groups of fish were starved for 2 weeks and then fed with the C, high protein (HP), high carbohydrate (HC), high lipid (HL), and combined protein, carbohydrate and lipid (CPCL) diets to satiation twice a day, six days a week, for 6 weeks, referred to as C-6W, HP-6W, HC-6W, HL-6W, and CPCL-6W treatments, respectively. Final body weight of fish in HP-6W treatment was higher than that of fish in C-6W, but not different from that of fish in C-8W, HC-6W, HL-6W and CPCL-6W treatments. Specific growth rate of fish in HP-6W treatment was higher than that of fish in all other treatments except for fish in CPCL-6W treatment. Feeding rate of fish in C-8W treatment was higher than that of fish in HP-6W, HC-6W, HL-6W and CPCL-6W treatments, but not different from that of fish in C-6W treatment. In addition, feeding rate of fish in C-6W treatment was higher than that of fish in HP-6W, HL-6W and CPCL-6W treatments. Feed and protein efficiency ratios of fish in HP-6W, HC-6W, HL-6W and CPCL-6W treatments were higher than those of fish in C-6W treatment. None of moisture, crude protein and ash content of the whole body of fish excluding the liver was different among treatments. Dietary supplementation of protein, carbohydrate, lipid and their combination could improve compensatory growth of fish when fish were fed for 6 weeks after 2-week feed deprivation; especially, supplementation of dietary protein was the most effective to improve compensatory growth of fish. (**Key Words** : Olive Flounder (*Paralichthys olivaceus*), Compensatory Growth, Different Diets, Feeding Regimes)

### INTRODUCTION

When unfavorable environmental conditions such as red tide or coldwater mass occurs during the summer season, which is the season for best growth conditions for most aquaculture fish in Eastern Asia including Korea, Japan and China, fish are usually starved until conditions improve. At the occurrence of unfavorable conditions, economical loss is due to not only mortality, but also a reduction in fish growth during the period of starvation. A feeding strategy leading to compensatory growth can be one of the most effective fish culture methods to overcome this unfavorable environmental condition, by improving feeding activity of fish, accelerating growth rate of fish, and reducing feed and

labor costs (Cho, 2005; Cho et al., 2006; Reigh et al., 2006).

Compensatory growth of fish is the rapid or faster than normal growth rate of fish resulting from refeeding after undernutrition, and varies depending on fish species (Jobling and Koskela, 1996; Gaylord and Gatlin, 2000; Wang et al., 2000; Zhu et al., 2001), fish age (Bilton and Robins, 1973), water temperature (Kim and Lovell, 1995; Cho, 2005; Cho et al., 2006; Huang et al., 2008), feed allowance (Jobling et al., 1994; Jobling and Koskela, 1996; Tian and Qin, 2004), feeding regime (Miglav and Jobling, 1989; Rueda et al., 1998; Gaylord and Gatlin, 2001; Li et al., 2005), duration of feeding trial (Heide et al., 2006), nutritional/physiological status of fish (Miglav and Jobling, 1989; Rueda et al., 1998) and holding status (Hayward et al., 1997, 2000).

Hyperphagia, abnormally increased appetite for and consumption of food, is the common phenomenon used to explain compensatory growth of fish (Rueda et al., 1998;

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Received October 3, 2010; Accepted March 22, 2011

Gaylord and Gatlin, 2000; Wang et al., 2000; Tian and Qin, 2004; Cho, 2005; Cho et al., 2006; Cho, 2011). Moreover, channel catfish *Ictalurus punctatus* subjected to 3-day feed deprivation achieved overcompensation when they were fed to satiation as long as the fish exhibited hyperphagia after 1-, 2- or 3-day feed deprivation (Chatakondi and Yant, 2001). Although determining the critical point of hyperphagia is not easy in commercial fish farms, overcompensation of fish still attracts the attention of both researchers and fish farmers.

Increased dietary protein levels from 32 to 37% seemed to effectively improve cumulative weight gain of channel catfish subjected to 3-day feed deprivation followed by 11-day satiation feeding in three cycles for 6 weeks (Gaylord and Gatlin, 2001). Furthermore, the specific nutrient (lipid) in fish was primarily utilized for the energy source for maintenance of basal metabolism and survival while fasted (Miglav and Jobling, 1989; Rueda et al., 1998; Ali et al., 2003). Since body lipid of fish is generally affected by nutrient quantity and/or quality of the consumed feed, manipulation of dietary nutrient composition can also affect compensatory growth of fish.

Olive flounder *Paralichthys olivaceus*, whose optimum temperature condition for growth was known to be 20-25°C (Iwata et al., 1994) is one of the most commercially important marine fish species for aquaculture in Eastern Asia. In earlier studies (Cho, 2005; Cho et al., 2006) juvenile olive flounder subjected to 2-week feed deprivation were able to achieve full compensatory growth during 8-

week feeding trials. In the present study, therefore, the effect of manipulation of dietary nutrient composition on compensatory growth of juvenile olive flounder under different feeding regime was determined.

## MATERIALS AND METHODS

### Fish and the experimental conditions

Juvenile olive flounder were purchased from a private hatchery (Tongyoung City, Korea) and transferred into the laboratory. Before the initiation of the feeding trial, fish were acclimated to the experimental conditions for 2 weeks. During the acclimation period, fish were fed with extruded pellets (Ewha Oil and Fat Industry Co. Ltd., Korea) containing 50% crude protein and 7% crude lipid twice a day. Four hundred fifty fish (an initial body weight of fish: 16.0±0.01 g, twenty five fish per tank) were randomly chosen and distributed into 18, 180 L flow-through tanks (water volume: 150 L). The flow rate of water into each tank was 6.5 L/min. The water source was the sand-filtered natural seawater with aeration supplied to each tank. Water temperature ranged from 16.0 to 25.5°C (Mean±SD: 23.6±0.26°C) and photoperiod followed natural condition. Fish in each tank were collectively weighed bi-weekly after they were starved for a day.

### Preparation of the experimental diets

Five experimental diets were established: control (C), high protein (HP), high carbohydrate (HC), high lipid (HL),

**Table 1.** Ingredients and nutrient composition (% , DM basis) of the experimental diets

	Diets				
	C	HP	HC	HL	CPCL
<b>Ingredients</b>					
Fishmeal	60	74	60	60	68
Cellulose	10		2	6.3	
α-starch	5	5	13	5	9
Wheat flour	19.3	16.6	19.3	19.3	15.3
Squid liver oil	2	0.7	2	2	2
Soybean oil				3.7	2
Vitamin premix <sup>1</sup>	1.5	1.5	1.5	1.5	1.5
Mineral premix <sup>2</sup>	2	2	2	2	2
Choline	0.2	0.2	0.2	0.2	0.2
<b>Nutrient</b>					
Dry matter	90.4	88.3	90.0	89.7	90.0
Crude protein	48.6	56.3	48.1	48.1	53.1
Crude lipid	7.3	7.3	7.4	12.4	9.2
Ash	10.0	12.1	9.8	9.9	11.0
Fiber	11.6	0.9	3.0	7.6	0.9
NFE <sup>3</sup>	22.5	23.4	31.6	22.0	25.8
Estimated energy (kJ/g) <sup>4</sup>	14.6	16.1	16.1	16.4	16.6

<sup>1</sup> Vitamin premix. <sup>2</sup> Mineral premix were same as Cho (2011)'s study. <sup>3</sup> NFE (Nitrogen-free extract) calculated by differences.

<sup>4</sup> Estimated energy was calculated based on Garling and Wilson (1976)'s study.

and combined protein, carbohydrate and lipid (CPCL) diets (Table 1). Crude protein (48.6%) and lipid (7.3%) contents in the C diet satisfied requirements of juvenile olive flounder, known as to be 45-50% and 6-7%, respectively (Lee et al., 2000a, 2002; Lee and Kim, 2005). Crude protein, carbohydrate (nitrogen-free extract, NFE) and lipid contents were increased to be 56.3, 31.6 and 12.4% in the HP, HC and HL diets, respectively, by an increase in fishmeal,  $\alpha$ -starch and soybean oil at the expense of cellulose. Finally, combined crude protein, carbohydrate and lipid contents increased to 53.1, 25.8 and 9.2%, respectively in the CPCL diet by a combined increase in fishmeal,  $\alpha$ -starch and soybean oil at the expense of cellulose. Fishmeal,  $\alpha$ -starch and wheat flour, and squid liver and soybean oils were used as the protein, carbohydrate, and lipid sources of the experimental diets, respectively. Ingredients of the experimental diets were well mixed with water at the ratio of 7:3 and pelletized by a pellet-extruder. The experimental diets dried overnight at room temperature and stored at -20°C until use.

#### Design of the feeding trial

Six treatments were established in triplicate. In the C-8W treatment, which was used as the control group, fish were hand-fed with the C diet to apparent satiation, as much as fish voluntarily consume twice a day (09:30 and 17:00), six days a week, for 8 weeks. Other groups of fish were starved for 2 weeks and then fed with the C, HP, HC, HL and CPCL diets to satiation twice a day, six days a week, for 6 weeks referred to as C-6W, HP-6W, HC-6W, HL-6W, and CPCL-6W treatments, respectively.

#### Analysis of chemical of the experimental diets and fish

The experimental diets were analyzed for proximate analysis. Fifteen fish at the beginning and five fish from each tank at the end of the feeding trial were randomly sampled for proximate analysis. Fish were dissected and the whole body excluding the liver and liver of fish were separated. The whole body of fish excluding liver and the liver were separately homogenized before proximate analysis. Crude protein content determined using Kjeldahl method (Kjeltec 2100 Distillation Unit, Foss Tecator, Hoganas, Sweden), lipid content determined using ether-extraction method, moisture content determined by drying sample in a dry oven at 105°C for 24 h, fiber content determined using automatic analyzer (Fibertec, Tecator, Sweden) and ash content determined using muffle furnace at 550°C for 4 h, all methods were according to standard AOAC (1990).

#### Calculation and statistical analysis

Calculation was made as follows: specific growth rate (SGR) =  $100 \times [(\ln W_f - \ln W_i) / t]$ , feeding rate (FR, % body

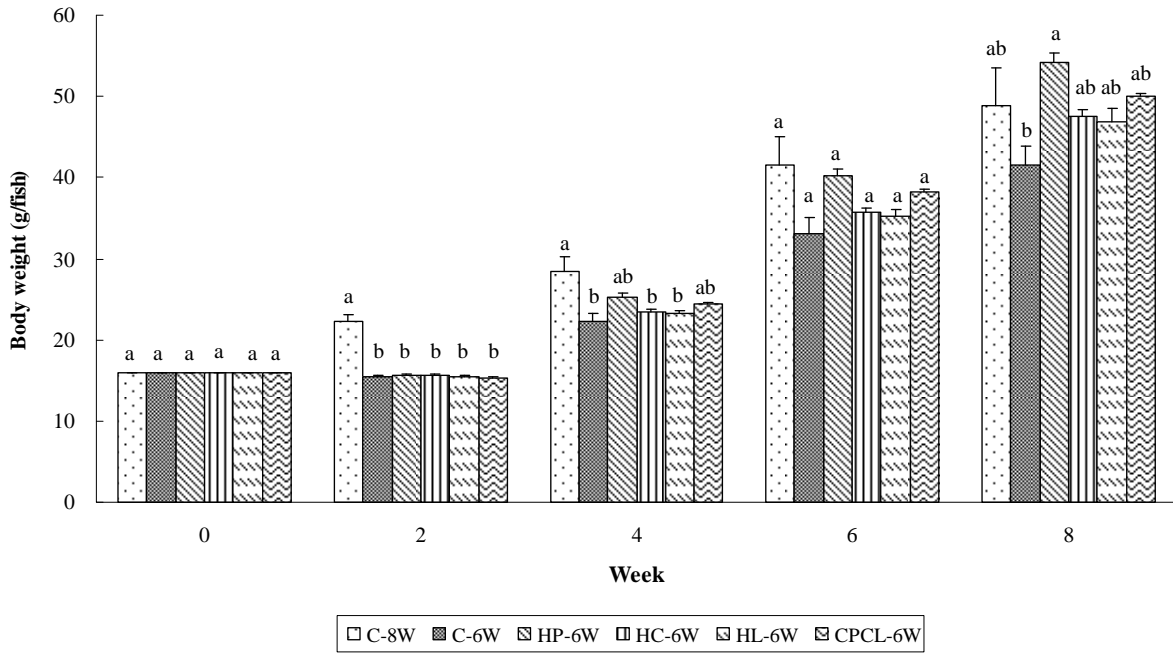
weight/day) =  $100 \times C / \{[(W_i + W_f) / 2] / t\}$ ; feed efficiency ratio (FER) =  $(W_f - W_i) / C$ ; protein efficiency ratio (PER) =  $(W_f - W_i) / C_p$ , where,  $W_i$  and  $W_f$  are initial and final weights,  $t$  is feeding duration (days),  $C$  is feed consumption (g) and  $C_p$  is protein consumption (g).

One-way ANOVA and Duncan's multiple range test (Duncan, 1955) were used to analyze the significance of the difference among the means of treatments for survival and proximate analysis by using SAS Program Version 9.1 (SAS Institute, Cary, NC, USA). Repeated measures ANCOVA (Analysis of covariance) were used to assess the effect of treatment on fish weight from week 2 to week 8 in the bi-week interval, and SGR, FR, FER and PER from week 4 to week 8 in the bi-week interval during the refeeding period. The initial weight of fish was used as a covariate to test the effect of treatment on fish weight. The initial fish weight at bi-week was used as a covariate to assess the treatment effect on SGR, FR, FER and PER. All percentage data were arcsine-transformed prior to analysis.

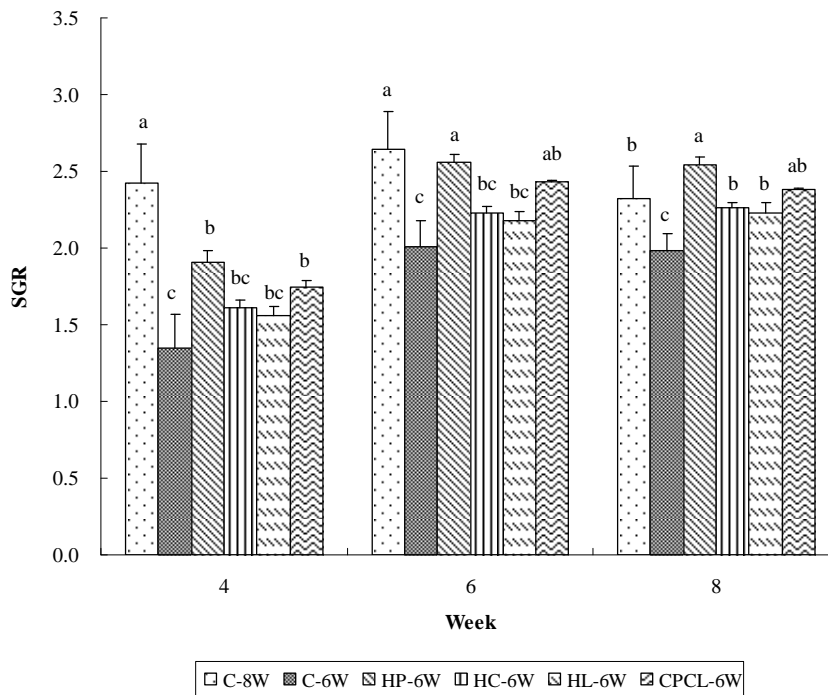
## RESULTS

Relatively high survival ( $\geq 96\%$ ) was observed in all fish groups, but no significant (One-way ANOVA;  $p > 0.07$ ) difference was found among treatments. No significant difference in an initial body weight of fish was observed among all treatments. However, a significant (Repeated measures ANCOVA;  $p < 0.0001$ ) difference in body weight of fish was observed between C-8W and all other treatments with 2-week feed deprivation at week 2 (Figure 1). Body weight of fish in C-8W treatment was significantly (Repeated measures ANCOVA;  $p < 0.02$ ) higher than that of fish in C-6W, HC-6W and HL-6W treatments, but not significantly ( $p > 0.05$ ) different from that of fish in HP-6W and CPCL-6W treatments at week 4. Body weight of fish in HP-6W treatment was significantly (Repeated measures ANCOVA;  $p < 0.05$ ) higher than that of fish in C-6W, but not significantly ( $p > 0.05$ ) different from that of fish in C-8W, HC-6W, HL-6W and CPCL-6W treatments at week 8.

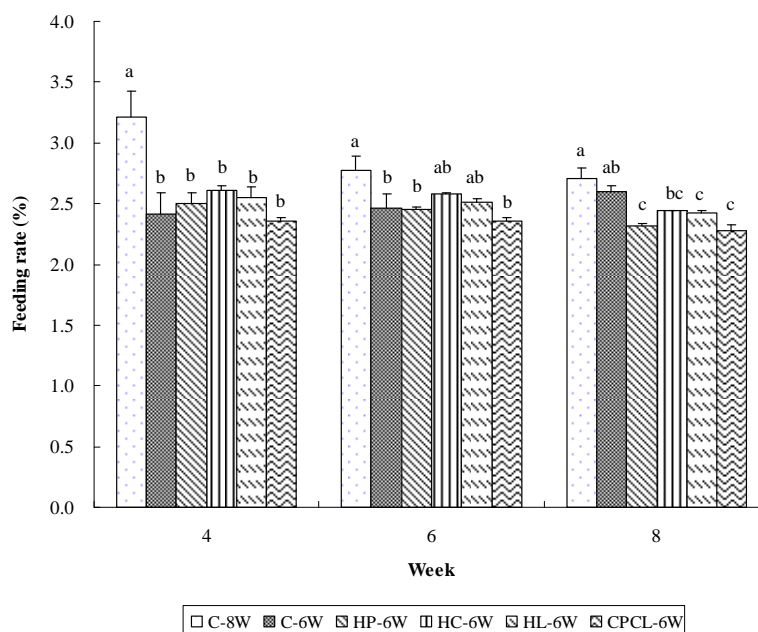
Specific growth rate (SGR) of fish in C-8W treatment was significantly (Repeated measures ANCOVA;  $p < 0.0007$ ) higher than that of fish in all other treatments at week 4 (Figure 2). In addition, SGR of fish in HP-6W and CPCL-6W treatments was significantly higher than that of fish in C-6W treatment, but not significantly ( $p > 0.05$ ) different from that of fish in HC-6W and HL-6W treatments at week 4. SGR of fish in C-8W and HP-6W treatments was significantly (Repeated measures ANCOVA;  $p < 0.0009$ ) higher than that of fish in C-6W, HC-6W and HL-6W treatments, but not significantly ( $p > 0.05$ ) different from that of fish in CPCL-6W treatment at week 6. However, SGR of fish in HP-6W treatment was significantly (Repeated measures ANCOVA;  $p < 0.0005$ ) higher than that of fish in



**Figure 1.** Changes in body weight (g/fish) of olive flounder fed the experimental diets with different feeding strategies (Mean of triplicate±SE); i) fish fed on the control (C) diet for 8 weeks (C-8W); ii) fish fed on the control diet for 6 weeks after 2-week feed deprivation (C-6W); iii) fish fed on the high protein (HP) diet for 6 weeks after 2-week feed deprivation (HP-6W); iv) fish fed on the high carbohydrate (HC) diet for 6 weeks after 2-week feed deprivation (HC-6W); v) fish fed on the high lipid (HL) diet for 6 weeks after 2-week feed deprivation (HL-6W); vi) fish fed on the combined protein, carbohydrate and lipid (CPCL) diet for 6 weeks after 2-week feed deprivation (CPCL-6W). Different letters indicate significant differences among treatments ( $p < 0.05$ ).



**Figure 2.** Specific growth rate (SGR) of olive flounder fed the experimental diets with different feeding strategies from week 4 to week 8 (Mean of triplicate±SE). For treatment abbreviations, refer to Figure 1. Different letters indicate significant differences among treatments ( $p < 0.05$ ).



**Figure 3.** Feeding rate (%) of olive flounder fed the experimental diets with different feeding strategies from week 4 to week 8 (Mean of triplicate $\pm$ SE). For treatment abbreviations, refer to Figure 1. Different letters indicate significant differences among treatments ( $p < 0.05$ ).

all other treatments except for fish in CPCL-6W treatment at week 8. The lowest SGR was obtained in fish in C-6W treatment.

Feeding rate (%) of fish in C-8W treatment was significantly higher than that of fish in all other treatments at week 4 (Repeated measures ANCOVA;  $p < 0.001$ ), that of fish in C-6W, HP-6W and CPCL-6W treatments at week 6 (Repeated measures ANCOVA;  $p < 0.004$ ), and that of fish in HP-6W, HC-6W, HL-6W and CPCL-6W treatments at week 8 (Repeated measures ANCOVA;  $p < 0.0001$ ) (Figure 3). In addition, feeding rate of fish in C-6W treatment was significantly higher than that of fish in HP-6W, HL-6W and CPCL-6W treatments, but not significantly ( $p > 0.05$ ) different from that of fish in HC-6W treatment at week 8.

Feed efficiency ratio (FER) of fish in C-8W, HP-6W and CPCL-6W treatments was significantly (Repeated measures ANCOVA;  $p < 0.0004$ ) higher than that of fish in C-6W, HC-6W and HL-6W treatments at week 4 (Figure 4). However, FER of fish in HP-6W treatment was significantly (Repeated measures ANCOVA;  $p < 0.0001$ ) higher than that of fish in all other treatments except for fish in CPCL-6W treatment at week 6. FER of fish in HP-6W and CPCL-6W treatments was significantly (Repeated measures ANCOVA;  $p < 0.0001$ ) higher than that of fish in all other treatments at week 8.

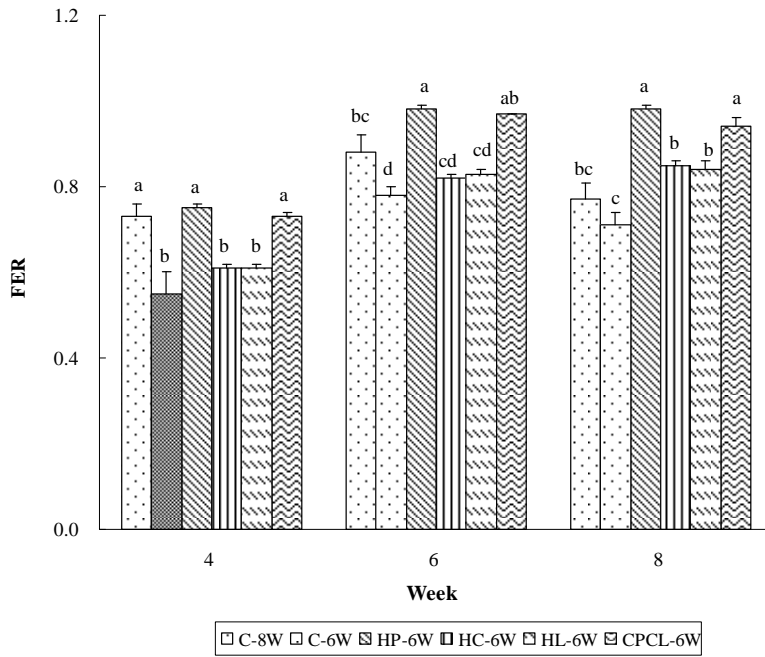
Protein efficiency ratio (PER) of fish in C-8W and CPCL-6W treatments was significantly higher than that of fish in C-6W treatment, but not significantly ( $p > 0.05$ ) different from that of fish in HP-6W, HC-6W and HL-6W treatments at week 4 (Repeated measures ANCOVA;  $p < 0.007$ ) and 6 (Repeated measures ANCOVA;  $p < 0.01$ )

(Figure 5). However, PER of fish in HC-6W and CPCL-6W treatments was significantly higher than that of fish in C-8W and C-6W treatments, but not significantly (Repeated measures ANCOVA;  $p > 0.05$ ) different from that of fish in HP-6W and HL-6W treatments at week 8.

None of moisture (One-way ANOVA;  $p > 0.1$ ), crude protein (One-way ANOVA;  $p > 0.9$ ) and ash (One-way ANOVA;  $p > 0.3$ ) content of the whole body of fish excluding the liver was significantly different among treatments (Table 2). However, crude lipid content of the whole body of fish excluding the liver in HL-6W treatment was significantly (One-way ANOVA;  $p < 0.04$ ) higher than that of fish excluding the liver in C-8W and C-6W treatments, but not significantly ( $p > 0.05$ ) different from that of fish excluding the liver in HP-6W, HC-6W and CPCL-6W treatments. Moisture (One-way ANOVA;  $p < 0.0001$ ) and crude protein (One-way ANOVA;  $p < 0.0001$ ) content of the liver of fish in C-8W and C-6W treatments was significantly higher than those of the liver of fish in HP-6W, HC-6W, HL-6W and CPCL-6W treatments. Moisture and crude protein content of the liver of fish in HP-6W and HC-6W treatments was significantly higher than those of the liver of fish in HL-6W and CPCL-6W treatments. In addition, crude lipid content of the liver of fish in HL-6W and CPCL-6W treatments was significantly higher than that of the liver of fish in C-8W, C-6W and HP-6W treatments.

## DISCUSSION

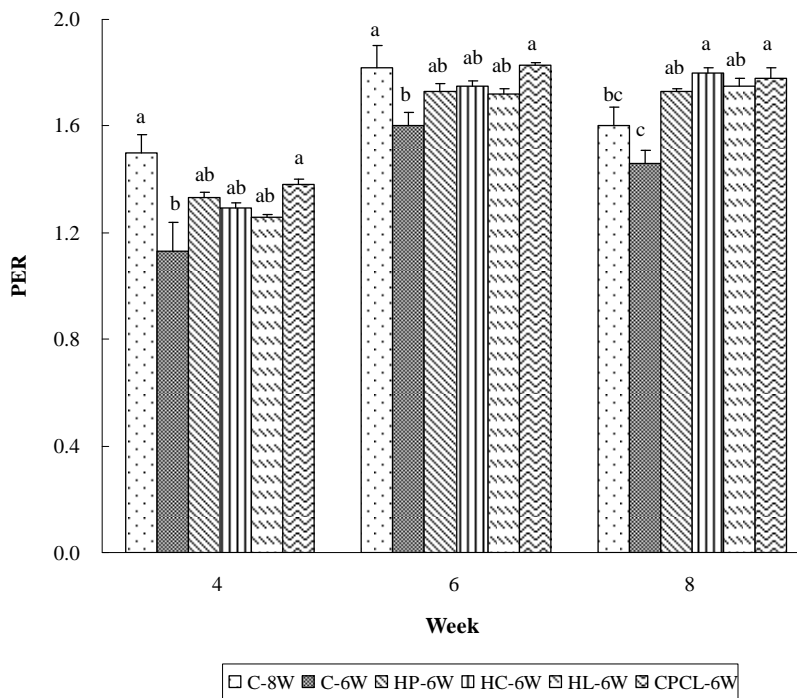
Dietary protein requirement was estimated to be 45%



**Figure 4.** Feed efficiency ratio (FER) of olive flounder fed the experimental diets with different feeding strategies from week 4 to week 8 (Mean of triplicate±SE). For treatment abbreviations, refer to Figure 1. Different letters indicate significant differences among treatments ( $p < 0.05$ ).

for juvenile olive flounder averaging 22.7 g when fish were fed with the diets containing the various protein levels (40-65%) at isocaloric (15.5 kJ/g diet) to satiation twice a day at 19.2°C for 9 weeks (Lee et al., 2002) and their weight gains were between 310 to 384%. Furthermore, dietary optimum

protein and energy levels for juvenile olive flounder averaging 3.1 g were reported to be 50% and 12.6 kJ/g diet, respectively when fish were fed with the diets containing 30, 40 and 50% protein levels at 12.6 and 16.7 kJ/g diet energy levels to satiation twice a day at 21.7°C for 5 weeks (Lee et



**Figure 5.** Protein feed efficiency ratio (PER) of olive flounder fed the experimental diets with different feeding strategies from week 4 to week 8 (Mean of triplicate±SE). For treatment abbreviations, refer to Figure 1. Different letters indicate significant differences among treatments ( $p < 0.05$ ).

**Table 2.** Chemical composition (% , wet weight basis) of the liver and whole body excluding the liver of olive flounder at the end of the 8-week feeding trial

Treatments	Moisture	Crude protein	Crude lipid	Ash
----- Whole body excluding liver -----				
C-8W	75.4±0.1	18.7±0.3	1.3±0.7 <sup>c</sup>	4.1±0.1
C-6W	75.2±0.2	18.6±0.3	1.8±0.3 <sup>bc</sup>	4.0±0.1
HP-6W	75.0±0.0	18.5±0.2	2.4±0.3 <sup>abc</sup>	3.8±0.2
HC-6W	75.1±0.3	18.4±0.3	2.6±0.1 <sup>ab</sup>	3.6±0.2
HL-6W	74.3±0.1	18.3±0.3	3.9±0.2 <sup>a</sup>	3.8±0.2
CPCL-6W	74.3±0.6	18.3±0.4	3.2±0.6 <sup>ab</sup>	3.5±0.1
----- Liver -----				
C-8W	71.0±0.9 <sup>a</sup>	12.7±0.0 <sup>a</sup>	9.9±1.4 <sup>b</sup>	
C-6W	70.9±0.4 <sup>a</sup>	13.0±0.1 <sup>a</sup>	9.2±0.9 <sup>b</sup>	
HP-6W	67.9±0.5 <sup>b</sup>	10.9±0.2 <sup>b</sup>	10.7±0.1 <sup>b</sup>	
HC-6W	67.5±0.8 <sup>b</sup>	10.2±0.2 <sup>b</sup>	12.2±0.9 <sup>ab</sup>	
HL-6W	63.8±0.4 <sup>c</sup>	9.2±0.2 <sup>c</sup>	15.6±0.6 <sup>a</sup>	
CPCL-6W	63.4±0.3 <sup>c</sup>	9.2±0.4 <sup>c</sup>	15.7±0.3 <sup>a</sup>	

Values (Mean of triplicate±SE) in the same column sharing different superscript letters are significantly different (p<0.05).

al., 2000a) and their weight gains were 125 and 223% in the 50% protein diets, respectively. Hence, growth (208% weight gain) of olive flounder in C-8W treatment used as a control group in this study were well within the published growth range. The 10% cellulose content in the C diet did not adversely affect growth of fish in this study, agreeing with other studies showing that 20% incorporated silica, cellulose and a natural zeolite, and 15% cellulose in the diets did not affect performance of European seabass (*Dicentrarchus labrax*), and rainbow trout (*Oncorhynchus mykiss*), respectively (Dias et al., 1998; Hansen and Storebakken, 2007).

The accelerated growth of olive flounder with a 2-week feed deprivation at week 6 and 8 resulted in no significant difference in final body weight of fish between the C-8W treatment and all other treatments in this study and indicated that full compensatory growth was achieved in all fish groups. In addition, a higher weight gain of fish in the HP-6W treatment indicated that dietary supplementation of protein was the most effective nutrient to improve compensatory growth of fish. However, a slightly, but not significantly, higher weight gain of fish in HC-6W, HL-6W and CPCL-6W treatments compared to that of fish in C-6W treatment among 2-week feed deprivation groups showed that dietary supplementation of carbohydrate, lipid and their combination might also effectively improve compensatory growth of fish; Furthermore a desirable effect of dietary supplementation of carbohydrate (HC-6W treatment) and lipid (HL-6W treatment) on olive flounder achieving full compensatory growth in this study is well supported by Lee et al. (2000a) study in which juvenile olive flounder responded better on the lower energy (12.6 kJ/g) diet than

higher energy (16.7 kJ/g) diet at both 40 and 50% protein levels. Lee and Kim (2005) also reported that juvenile olive flounder could utilize dietary carbohydrate efficiently as an energy source.

Higher SGR of olive flounder in HP-6W treatment compared to that of fish in C-8W and C-6W treatments at week 8 in this study supported overcompensation of fish in the former. However, since no information on digestibility of dietary nutrient content in olive flounder has been reported yet due to the difficulty of collecting feces from fish, it is difficult to explain exactly how supplementation of dietary nutrients affect compensatory growth of fish. Similarly, juvenile olive flounder fed the high protein and lipid diet (54.8% crude protein and 17.1 kJ/g energy) to satiation twice a day for 7 weeks after 1-week feed deprivation outgrew both the fish fed the control diet to satiation twice a day for 8 weeks (50.2% crude protein and 15.2 kJ/g energy) or 6 weeks after 2-week feed deprivation and the fish fed the high protein and lipid diet with supplementation of 5% amino acids after 2-week feed deprivation (Cho and Heo, 2011). Overcompensation of fish after feed deprivation was also reported in other species of fish: channel catfish, which were fed to satiation after 3-day feed deprivation as long as hyperphagia persisted (Chatakondi and Yant, 2001) and hybrid sunfish, which were held individually and fed *ad libitum* on feeding days after feed deprivation (Hayward et al., 1997, 2000).

No difference in final body weight and feeding rate of fish in between C-8W and C-6W treatments in this study indicated that full compensatory growth was achieved in olive flounder probably resulted from hyperphagia, agreeing with other studies (Rueda et al., 1998; Gaylord and

Gatlin, 2000; Wang et al., 2000; Tian and Qin, 2004; Cho, 2005; Cho et al., 2006; Cho, 2011). However, lower feeding rate, but higher SGR of olive flounder in HP-6W, HL-6W and CPCL-6W treatments compared to those of fish in C-6W treatment in this study indicated that improvement in SGR of fish in the former directly resulted from manipulation of dietary nutrient composition, but not from hyperphagia.

Higher FER and/or PER of olive flounder in HP-6W, HC-6W, HL-6W and CPCL-6W treatments compared to those of fish in C-8W and C-6W in this study indicated that compensatory growth of fish was due to an improvement in feed efficiency, in agreement with other studies (Jobling et al., 1994; Gaylord and Gatlin, 2001; Cho and Heo, 2011) showing that improved feed efficiency occurred in fish achieving full compensatory growth.

High crude lipid content of the liver of olive flounder in HL-6W and CPCL-6W treatments in this study indicated that body lipid content of fish reflected the high lipid content of HL and CPCL diets. Similarly, fish fed the high lipid diets had increased body lipid content (El-Dahhar and Lovell, 1995; Lee et al., 2000a, b; Gaylord and Gatlin, 2001; Cho and Jo, 2002; Cho and Heo, 2011). However, since high body lipid content is an unfavorable condition for fish health as well as shelf life in storage due to easy oxidation, the application of the high lipid diet to achieve effective compensatory growth should be carefully considered.

Results of this study indicated that supplementation of protein, carbohydrate, lipid and their combination into the diets could improve compensatory growth of olive flounder when fish were fed for 6 weeks after 2-week feed deprivation. The supplementation of dietary protein being the most effective of the supplements to improve compensatory growth of fish.

## ACKNOWLEDGMENTS

This work was supported by the Korea Research Foundation Grant funded by the Korean Government (MOEHRD) (KRF-2007-313-F00081).

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