



The Effects of Different Cycles of Starvation and Refeeding on Growth and Body Composition on European Sea Bass (*Dicentrarchus labrax*)

Aysun Adaklı¹, Oğuz Taşbozan^{1,*}

¹ Çukurova University, Faculty of Fisheries, Department of Aquaculture, 01330, Adana, Turkey.

* Corresponding Author: Tel.: +90.322 3386084; Fax: +90.322 3386439;
E-mail: tasbozan@cu.edu.tr; tasbozan@yahoo.com

Received 14 January 2015
Accepted 21 May 2015

Abstract

This study was designed to investigate the effects of starvation and refeeding cycles on growth performance and body chemical composition of juvenile sea bass. For this purpose, a total of 720 juveniles with an initial mean weight (IW) of 5.85 ± 0.54 g were divided into 12 tanks (400 L) in triplicate groups. During the period of the experiment, the control group (C) was fed to satiation three times a day. The feeding regimes of the other three groups were designed as follows: 2 days starvation / 8 days satiation (G1) (5 cycles), 5 days starvation / 20 days satiation (G2) (2 cycles) and 10 days starvation / 40 days satiation (G3) (1 cycle). After 50 days, only group G1 demonstrated partial compensatory growth. The difference between the final weights (FW) of groups was found statistically significant ($P < 0.05$). Specific growth rates (SGR) of fasting groups were lower than those of the control group ($P < 0.05$). G1 group was determined to have the best values of feed conversion ratio (FCR) and economic conversion ratio (ECR). Hepatosomatic index (HSI) did not differ significantly between groups ($P > 0.05$). Total fat (TF) was lowest in G3 ($P < 0.05$). The partial compensation by group G1 presents possibilities for economic optimization.

Keywords: European sea bass, starvation-refeeding, compensatory growth, body chemical composition, economic evaluation.

Farklı Açlık ve Yeniden Besleme Döngülerinin Avrupa Deniz Levreği (*Dicentrarchus labrax*) Vücut Kompozisyonu ve Büyümesi Üzerine Etkileri

Özet

Bu çalışma farklı açlık ve yeniden besleme döngülerinin, Avrupa deniz levreği juvenilleri büyüme performansı ve vücut kimyasal kompozisyonları üzerine etkilerini araştırmak amacıyla tasarlanmıştır. Bu amaçla, başlangıç ortalama ağırlığı (BOA) $5,85 \pm 0,54$ g olan toplam 720 adet juvenil birey üç tekerrürlü gruplarda 12 adet tanka (400 L) ayrılmıştır. Deneme süresince, kontrol grubu (K) günde üç kez doyana kadar beslenmiştir. Diğer üç grubun besleme rejimi şu şekilde dizayn edilmiştir: 2 gün aç/8 gün tok (G1) (5 döngü), 5 gün aç/20 gün tok (G2) (2 döngü) ve 10 gün aç/40 gün tok (G3) (1 döngü). Elli gün sonrasında, sadece G1 grubu kısmi telafi büyümesi göstermiştir. Grupların son ağırlıkları (SA) arasındaki farklılık istatistiksel olarak önemli bulunmuştur ($P < 0,05$). Aç grupların spesifik büyüme oranları (SBO) kontrol grubundan daha düşük bulunmuştur ($P < 0,05$). G1 grubunun en iyi yem çevirim oranı (YÇO) ve ekonomik çevirim oranı (EÇO) değerlerine sahip olduğu belirlenmiştir. Hepato somatik indeks (HSI) gruplar arasında önemli bir farklılık göstermemiştir ($P > 0,05$). Toplam yağ (TY) en düşük G3 grubunda bulunmuştur ($P < 0,05$). Bu çalışmanın sonuçlarına göre, kısmi telafi gösteren G1 grubu ekonomik optimizasyon olanaklarını sunmaktadır.

Anahtar Kelimeler: Avrupa deniz levreği, telafi büyümesi, yem kullanımı, ekonomik değerlendirme.

Introduction

The purpose of studying different fish feeding regimes is to develop feeding protocols that are economically sustainable and cause less environmental damage by minimizing fish feed and total operational costs. Work on fish feeding attempts to determine the optimal feeding models by taking fish

biology, feed intake, and fish growth into account. Using these strategies, scientists have performed compensatory growth studies based on partial or complete starvation periods in different fish species in recent years. The effects of different feeding protocols on fish feed utilization, growth performance and body composition have been demonstrated previously (Gaylord and Gatlin, 2000; Nikki *et al.*, 2004; Heide

et al., 2006; Cho and Cho, 2009; Kankanen and Pirhonen, 2009; Wang et al., 2009). In turbot, *Scophthalmus maximus* (L.), different restricted feeding regimens were carried out during 41 days and weight loss was observed. Afterwards, all groups were fed without any restricted feeding through 34 days and complete compensation was determined in restricted feeding groups (Saether and Jobling, 1999). Wang et al. (2000), in their 8 week study on hybrid tilapia (*Oreochromis mossambicus* × *O. niloticus*), found the feed intake and specific growth rate values during refeeding period in fish starved for 1, 2 or 4 weeks significantly higher compared to the control group and reported that these fish showed some compensative reactions. During 8 weeks with a single phase of starvation, it was found that growth and chemical composition was related with duration of food deprivation in barramundi, *Lates calcarifer* (Tian and Qin, 2003). In another study, following 2 weeks of restricted feeding, fishes were fed until they were satiated for 5 weeks and it was reported that compensation had not occurred in the highest restricted feeding group (Tian and Qin, 2004). In rainbow trouts starved in 0, 2, 4, 8 or 14 days, it was determined that all groups except the 8 day starvation group showed growth performance at control group levels. The results regarding full compensatory growth in starved fish during their refeeding periods depending on high feed consumption were supported by the strong relationship between body weight gain and feed consumption (Nikki et al., 2004). There is no compensation in a restricted feeding regimen (Eroldoğan et al., 2008) but partial compensation following different starving periods in gilthead sea breams, *Sparus aurata*, has been reported (Eroldoğan et al., 2006a). Hybrid sea basses which were exposed to starvation for 2 weeks showed better growth when compared with a control group. Red sea breams which were exposed to one, two or three weeks of starvation showed full compensatory growth at the end of a 9 week study (Oh et al., 2007). Two weeks starvation and 6 weeks refeeding with olive flounders showed better improvement as compared with a continuous feeding group (Cho and Cho, 2009). No compensatory growth was observed in gilthead sea breams on 60 day restricted feeding regimens (Bavcevic et al., 2010). In another study with sea breams, different starvation periods did not lead to compensatory growth during a 10 week cycle (Peres et al., 2011).

It was seen that during starvation, the reserves (especially lipid composition) in the fish decreased. In many studies, the growth of fish during compensation growth was found to be faster. In compensatory growth, it has been observed that somatic growth parameters and lipid levels return to their prior levels compared to those during starvation periods (Ali et al., 2003). Oh et al. (2008), in their study on juvenile black rockfish (*Sebastes schlegeli*) applied 3 different starvation periods (fasted for 5 days, 10 days and 14

days) followed by a 5 day refeeding period. On the 14 day of the study, lipid ratios in lean body mass in 10 day starvation and 14 day starvation groups were lower than those in control and 5 day starvation groups. However, on the 49 day, the 14 day starvation group showed lower lipid ratios compared to the other three groups while no differences were determined among the other three groups. Mattila et al. (2009), in their study on pikeperch (*Sander lucioperca*) measured visceral fat (%), total body fat (%) and energy content in 1+3 (one-day feeding followed by a three-day feed deprivation) and 1+6 (fed once a week) groups. At the end of the study, the researchers reported that the compensation ability improved. Also, the fish showed only a partial compensation tendency in lower feeding frequencies and during decreasing feeding duration periods.

In this study, different feeding protocols were performed by applying 10 total days of starvation in different cycles (1 cycle of 10 days, 2 cycles of 5 days, or 5 cycles of 2 days). For this purpose, optimal feeding protocols were determined in terms of growth performance, feed utilization and chemical composition of juvenile sea bass. Additionally, study groups were evaluated in regard to maintenance of compensation degree and economics.

Materials and Methods

Experimental Design and Management

The experiment was carried out at Marine Research Station of Fisheries Faculty, University of Çukurova, Yumurtalık, Turkey. European sea bass (*Dicentrarchus labrax*) juveniles were supplied by Akuvatur Hatchery (Adana, Turkey). For acclimatization, fish were stocked into a fiberglass tank (water volume 2000 L). During the acclimation period (4-5 weeks), fish were hand-fed with a commercial diet (Çamlı Feed Ltd., Turkey, 2 mm; 49% crude protein, 19% crude fat, 12% moisture and 13% ash according to the manufacturer) twice daily at 09:00 and 16:00 h.

After the acclimation period, 720 fish weighing 5.85 ± 0.54 g (mean \pm SD) were starved for one day to evacuate the gut of feed. Fish were then anaesthetized with 0.5 mg L^{-1} 2-phenoxyethanol to reduce stress before weight measurement. Triplicate groups of fish stocked into 12 fiberglass tanks (water volume 400 L) with 60 fish per tank. The weighing procedure was done individually at the beginning, every 10 days and at the end of the experiment by taking total stock for each tank. Also, in every 10 days interval fish weight measurements, 5 fish were taken from the each tank.

Each tank was continuously supplied with flow-through seawater (40 g L^{-1}) filtered by an $80 \mu\text{m}$ sand filter at a flow rate of approximately 2 L min^{-1} . Dissolved oxygen and temperature were monitored daily and natural photoperiod was used over the course of experiment. The average temperature and

dissolved oxygen of the water were 22.8°C and 6.6 mg L⁻¹, respectively. In order to prevent the fish from jumping, all trial tanks covered with mesh. The experiment lasted for 50 days.

Fish were subjected to four different feeding protocols (Figure 1):

- (I) Control (C) group: continuously fed to satiation
- (II) G1 group: 2 days starvation / 8 days satiation (5 cycles)
- (III) G2 group: 5 days starvation / 20 days satiation (2 cycles)
- (IV) G3 group: 10 days starvation / 40 days satiation (1 cycle)

Feeding was done by hand-feeding three times a day at 09:00, 13:00 and 17:00 h during the experimental period.

Analytical Methods

Twenty fish taken at the beginning of the experiment and five fish from each tank at the end were stored at -20°C until chemical analysis. These samples were also used for determination of hepatosomatic index (HSI) and total fat (TF). Analysis of proximate composition (protein, lipid, moisture and ash) of the whole body was conducted with AOAC (1990) methods. The crude protein (N x 6.25) content was determined by Kjeldahl method, total lipid content was determined by using the ether-extraction method, moisture content was determined by drying the sample in a dry oven at 105°C and ash content was determined by considering gray ash color formed after burning at 550°C for 4 h.

Calculations and Statistical Analysis

Growth performance, feed utilization, economic index and body index parameters were calculated as follows:

Specific growth rate (SGR, % day⁻¹) = 100 x (Ln final body weight - Ln initial body weight) / days

Feed intake (FI, %/fish/day) = 100 x total amount of the feed consumed (g) / [(W_o + W_t)/2] / t

(W_t and W_o were the final and initial fish weights, respectively and t was the duration of experimental days)

Feed conversion ratio (FCR) = total amount of consumed feed (g) / weight gain (g)

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

Economic conversion ratio (ECR) = feed conversion ratio (FCR) x price of diet (\$)

Compensation coefficient (CC) = $\Delta T \times \Delta C^{-1}$

(ΔT was the average weight gain (g) in the treatment group tanks divided by the number of feeding days and ΔC was the average weight gain (g) in the control group tanks divided by the number of feeding days; thus, CC > 1.0 would indicate compensation)

Hepatosomatic index (HSI, %) = 100 x wet liver weight (g) / fish weight (g)

Total fat (TF, %) = perivisceral fat (%) + peritoneal fat (%)

In calculations in which the number of fish were a factor, the diminishing number of fish was taken into account (see also materials and methods for fish number)

Statistical analyses were carried out using Sigma Stat® 3.1 (Systat Software, Inc. 2004). Statistical Software and the presence of statistical differences among groups were determined with one-way variance analysis (ANOVA). Duncan's multiple range test (Duncan, 1955) was used to test the differences of each variable between treatments. Differences were considered significant at a probability level of 0.05. Results are expressed as mean ± SD.

Results

Growth, Feed Utilization and Economic Index Parameters

Variation of fish body weights observed at measurement periods (every 10 days) during the study is given in Figure 2. At 20 days, control group and group G1 showed similar body weight gains. The control group showed increased body weight gain during the last 30 days. Groups G2 and G3, which

	Day 10	Day 20	Day 30	Day 40	Day 50
Control	White	White	White	White	White
G1	Shaded	White	Shaded	White	Shaded
G2	Shaded	White	Shaded	White	White
G3	Shaded	White	White	White	White

Figure 1. Schematic overview of the experimental set-up¹ (Shaded fields indicate starvation and white fields feeding to satiation).

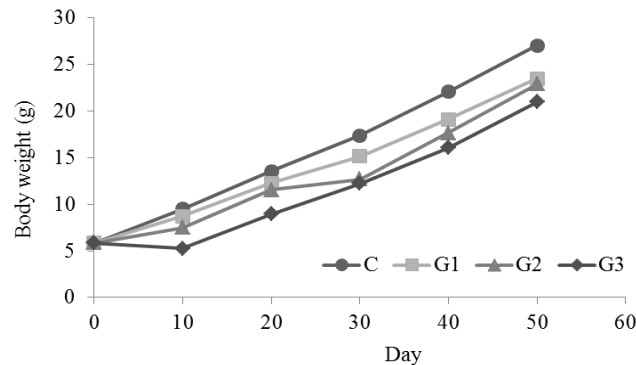


Figure 2. Changes in body weight (g) of sea bass juveniles subjected to the follow feeding regimes during the experiment from day 10 to day 50: continuously fed to satiation (C group); 2 days starvation/8 days satiation (G1 group); 5 days starvation/20 days satiation (G2 group); 10 days starvation/40 days satiation (G3 group).

were exposed to same amount of starvation (10 days) and the same amount of satiation (20 days) over a 30 day period, showed similar weight gain. However, G2 gained more weight compared to G3 at the end of the study. Growth performance, feed utilization and economic index parameters are shown in Table 1. The highest final body weight was found in the control group at the end of experiment; G1, G2 and G3 follow this group respectively ($P < 0.05$). Accordingly, SGR parameters showed the same trend at the end of the experiment. However, SGR values of the fish starved in 10 day intervals until the end of the study except the first 10 days during the refeeding periods were found to be higher compared to the control group (Figure 3).

The differences between FI values among the groups were found to be significant on the 10th day ($P < 0.05$). FI values of G1 and G2 starvation groups were found to be lower than those of the control group (Figure 4). FI values of the G1 group were parallel to those of the control group by the 20th day until the end of the trial. With the refeeding of G3 group starting from the 10th day, FI values were higher than those of the control group until the 50th day ($P < 0.05$). However, evaluating the data obtained during the study (0-50 days), this group had the lowest feed consumption (Table 2).

At the end of the trial, FCR values of the G1 and G3 groups were parallel to those of the control group. G2 was found to have the highest FCR value. Similar protein efficiency ratios were obtained in all groups except group G2 ($P < 0.05$). According to the ECR values, the most efficient group in an economic sense was G3, while C and G1 groups had the same tendencies as G3. The result obtained in G2 group was economically negative (Table 1).

In order to express the compensatory growth in numerical sense, compensation coefficient (CC) was calculated (Figure 5). G3 group showed no compensation tendency during the trial ($CC < 1$). G1 group showed compensation tendencies on all measurement days except the 10th and the 30th ($CC > 1$). G2 group showed compensated growth for their starvation days only on the 40th and the 50th

days ($CC > 1$). At the end of the trial, CC values of groups G1, G2 and G3 were 1.04, 1.00 and 0.89, respectively; thus G1 and G2 groups were found to provide growth compensation.

Proximate Composition, Hepatosomatic Index and Total Fat

While the values of protein, moisture and ash were not found statistically different in terms of nutritional composition ($P > 0.05$), lipid value shows distinction ($P < 0.05$) (Table 2). The highest lipid value, 8.53, was found in group G2 and the lowest in group G3 with 7.77. Group G1 showed similarity with the control group. There was no statistical distinction in HSI values among groups ($P > 0.05$). The total lipid ratios of the groups were 8.78, 8.15, 8.44 and 7.19 respectively ($P < 0.05$).

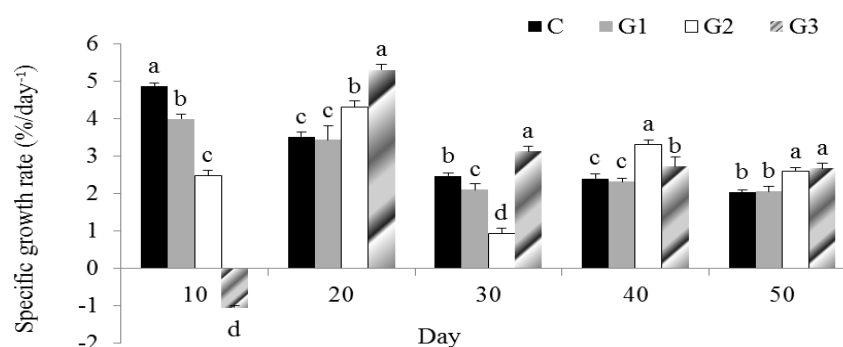
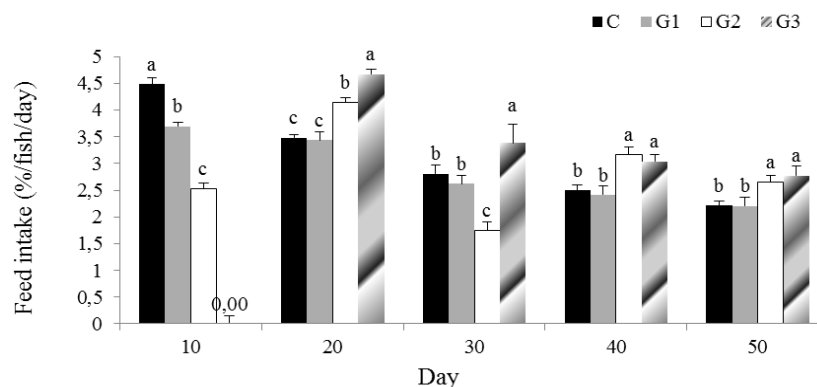
Discussion

In terms of final body weight, among the starved groups, only the 2 days starvation / 8 days satiation group (G1) showed a partial compensatory growth compared to the control group. Some similar partial compensation results have been obtained in previous studies carried out on different fish species and feeding models (Jobling *et al.*, 1993; Hayward *et al.*, 2000; Ali and Jauncey, 2004; Wang *et al.*, 2005, 2009; Eroldoğan *et al.*, 2006a, 2008; Mattila *et al.*, 2009; Liu *et al.*, 2011). Additionally, full compensation (Kim and Lovell, 1995; Gaylord and Gatlin, 2001; Zhu *et al.*, 2001, 2005; Tian and Qin, 2003, 2004; Nikki *et al.*, 2004; Oh *et al.*, 2007) and over compensation levels have also been obtained (Hayward *et al.*, 1997; Turano *et al.*, 2007). Also there have been many studies in which the starvation periods were short vs. long (Rueda *et al.*, 1998; Şahin *et al.*, 2000; Ali and Wootton, 2001; Tian and Qin, 2003, Eroldoğan *et al.*, 2006b; Cho and Cho, 2009; Ribeiro and Tsuzuki, 2010; Chatzifotis *et al.*, 2011) or the starvation and refeeding cycles were single vs. multiple (Aranyakananda *et al.*, 1996; Wang *et al.*, 2000, 2005, 2009; Cho *et al.*, 2006; Heide *et al.*,

Table 1. Growth, feed utilization and economic evaluation performance of juvenile sea bass subjected to different cycles of starvation and refeeding for 50 days¹

	C	G1	G2	G3
Initial weight (g/fish)	5.85±0.53	5.85±0.59	5.85±0.53	5.85±0.52
Final weight (g/fish)	27.08±0.43 ^a	23.49±1.51 ^b	22.90±1.16 ^{bc}	20.97±0.93 ^c
SGR (g day ⁻¹)	3.06±0.10 ^a	2.78±0.18 ^b	2.73±0.13 ^b	2.55±0.15 ^c
FI (%/fish/day)	3.10±0.10 ^a	2.88±0.14 ^b	2.85±0.12 ^b	2.77±0.14 ^b
FCR	1.04±0.02 ^b	1.07±0.04 ^b	1.17±0.04 ^a	1.03±0.04 ^b
PER	1.96±0.04 ^a	1.91±0.07 ^a	1.74±0.06 ^b	1.98±0.07 ^a
ECR	1.80±0.04 ^b	1.84±0.06 ^b	2.03±0.07 ^a	1.79±0.08 ^b

¹ Continuously fed to satiation (C group); 2 days starvation / 8 days satiation (G1 group) (5 cycles); 5 days starvation / 20 days satiation (G2 group) (2 cycles); 10 days starvation / 40 days satiation (G3 group) (1 cycle). Means in the same row with different superscript letters are significantly different ($P < 0.05$). Data are mean±SD.

**Figure 3.** Changes in specific growth rate of sea bass juveniles subjected to the follow feeding regimes during the experiment from day 10 to day 50: continuously fed to satiation (C group); 2 days starvation/8 days satiation (G1 group); 5 days starvation/20 days satiation (G2 group); 10 days starvation/40 days satiation (G3 group).**Figure 4.** Changes in feed intake (%/fish/day) of sea bass juveniles subjected to the follow feeding regimes during the experiment from day 10 to day 50: continuously fed to satiation (C group); 2 days starvation/8 days satiation (G1 group); 5 days starvation/20 days satiation (G2 group); 10 days starvation/40 days satiation (G3 group).

*The first 10-day FI values of group G3 were not calculated because the group was in 10-day starvation group and not fed.

Table 2. Whole body composition of juvenile sea bass subjected to cycles of food deprivation and refeeding during the experiment¹

Variables	Initial	C	G1	G2	G3
Protein	17.28±0.87	17.78±0.49	17.63±0.74	17.82±0.30	17.42±0.29
Lipid	3.03±0.14	8.08±0.49 ^{ab}	8.28±0.33 ^{ab}	8.53±0.33 ^a	7.77±0.21 ^b
Moisture	70.46±0.96	67.19±0.85	68.56±0.66	67.55±0.99	68.82±0.99
Ash	5.53±0.82	2.33±0.40	2.41±0.51	2.20±0.44	2.46±0.41
HSI	3.05±0.10	3.05±0.10	3.00±0.45	3.20±0.24	2.94±0.30
TF		8.78±0.19 ^a	8.15±0.55 ^a	8.44±0.15 ^a	7.19±0.51 ^b

¹ Continuously fed to satiation (C group); 2 days starvation / 8 days satiation (G1 group) (5 cycles); 5 days starvation / 20 days satiation (G2 group) (2 cycles); 10 days starvation / 40 days satiation (G3 group) (1 cycle). Means in the same row with different superscript letters are significantly different ($P < 0.05$). Data are mean±SD.

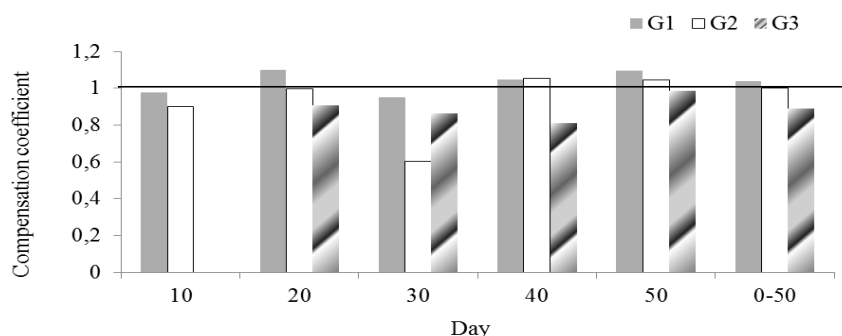


Figure 5. Changes in compensation coefficient of sea bass juveniles in three feeding groups subjected to the follow feeding regimes during the experiment from day 10 to day 50: 2 days starvation/8 days satiation (G1 group); 5 days starvation/20 days satiation (G2 group); 10 days starvation/40 days satiation (G3 group). CC>1 indicates compensation.

2006; Kankanen and Pirhonen, 2009; Yarmohammadi *et al.*, 2012; Sevgili *et al.*, 2013). In this comprehensive study, both single and multiple starvation and refeeding cycles were applied and short and long term starvation periods were tested alongside each other. According to the results, short term starvation and multiple cycles showed partial compensation.

Starved fishes have been reported to have higher SGR and feed intake compared to a control group during the refeeding period (Nikki *et al.*, 2004; Turano *et al.*, 2007; Wang *et al.*, 2009). Similarly, 10-day sampling periods of our study, both SGR and FI values increased during the refeeding period in 2 cycled 5 day starvation / 20 days satiation (G2) and single cycle 10 days starvation / 40 days satiation (G3) groups compared to the control group. The tendencies of SGR values depending on the length of the starvation period were reported for three cyprinid species (*Leuciscus cephalus*, *Chalcalburnus chalcoides mento*, and *Scardinius erythrophthalmus*) (Wieser *et al.*, 1992), hybrid tilapia (Wang *et al.*, 2000, 2005), barramundi (Tian and Qin, 2003), red sea bream (Oh *et al.*, 2007) and olive flounder (Cho and Cho, 2009) species. The higher feed intake in starved fishes compared to the control group during the refeeding period was interpreted as an effort for compensate for body weight lost during the starvation period.

Increased feed intake and low feed conversion ratio are the most important indicators during compensation growth (Wang *et al.*, 2000; Eroldoğan *et al.*, 2006a). Group G2 had the highest feed consumption and did not utilize the feed effectively. However, G3 group had higher FI values in the interval sampling days compared to all other groups, therefore it seemed to have higher feed consumption value, the effective feed conversion and conversely it showed lower growth rates. This result may be associated with the continuous feeding of this group throughout the study following the single starvation period during the first 10 days. Moreover, in FI was calculated and evaluated by considering all interval sampling days for this group. Consequently, neither G2 nor G3 are recommended for aquaculture

activities. However, the 2 days starvation / 8 days satiation feeding strategy, which yielded the most effective feed utilization and effective conversion to meat in the body and also had a better FCR value, was determined as an efficient feeding model.

Hyperphagia (extreme appetite for feed or consumption observed especially after the starvation period) is regarded as an important mechanism for fishes in compensation growth studies. In other studies, hyperphagic responses have been obtained in many fish species during compensation growth (Hayward *et al.*, 1997; Gaylord and Gatlin 2000; Tian and Qin, 2003; Zhu *et al.*, 2005; Oh *et al.*, 2007; Bavcevic *et al.*, 2010). Ali *et al.* (2003) explained that in short food deprivation periods where sufficient food is available between the starvation periods, a hyperphagic reaction during refeeding can prevent measurable growth depression, thus the growth patterns of continuously fed and temporarily deprived fish become almost identical. In our study, fishes which were exposed to long starvation periods (G2 and G3) consumed more feed and gave stronger hyperphagic responses during refeeding phases compared to G1. This is thought to be caused by long starvation period and lower number of cycles. In our study, protein efficiency ratios were affected by feeding regimes. PER values did not significantly change in single and multiple cycle fed Atlantic halibut (Heide *et al.*, 2006), varied cycle fed olive flounder (Cho and Cho, 2009) and single cycle fed rainbow trout (Sevgili *et al.*, 2013). However, some studies have reported that PER values were affected by feeding model during compensation growth, as is the case in our study (Ali and Jauncey, 2004; Cho *et al.*, 2006, Eroldoğan *et al.*, 2008). At the end of our study, single (G3) and multiple cycled (G1) groups effectively utilized the protein, which is the most important source of energy in the feed, while G2 starvation group is thought to have utilized the feed mostly for other metabolic activities (e.g., foraging food).

ECR values calculated by setting the feed price as 1.73 US\$/kg were found to be undesirably higher in G2 group at the end of our study. The first thing that comes to mind here is the FCR which is used in

the calculation of the economic conversion. FCR is known to be directly proportional to economic conversion. Therefore, the higher economic value of G2 group at the end of the trial shows that this group did not utilize the feed effectively following the starvation period. Eroldoğan *et al.* (2008) reported that in sea breams, the ECR values (1.47 US\$/kg) of the fishes fed in 2 days starvation / 2 days satiation (12 cycles) periods were lower than those of control group (1.53 US\$/kg). Hernandez *et al.* (2007) fed sharpsnout seabreams, *Diplodus puntazzo*, alternatively with feed containing 20%, 40%, or 60% soybean flour instead of fish meal and found that the ECR values were lower than those of the control groups. Both the application of limited feeding regime and using the alternative sources in the feed showed that more profitable aquaculture can be conducted by adopting different feeding models (e.g. cycled starvation-satiation), as was the case in our study.

G1 and G2 starvation groups showed compensation tendencies during the interim periods of the study with compensation coefficients higher than 1 (CC>1). G3 group, which was exposed to a long starvation period, did not show any compensatory growth tendency until the end of the trial (CC<1). Similarly, it has been reported that whitefish, *Coregonus lavaretus* (L.), showed increased CC values following starvation regimes (Kankanen and Pirhonen, 2009). Mattila *et al.* (2009), in their compensation growth study on pikeperch fishes, determined that 1+3 and 1+6 groups improved their compensation abilities and partially compensated the growth (CC>1). In parallel to these previous studies, starvation periods in this study (short) and cycle frequency had an effect on the compensation coefficient. Compensation was detected in short term and multi-cycled feedings.

Crude protein, moisture, ash and HSI levels showed no significant differences among the groups during our study ($P>0.05$). Similarly, there have been some studies in which the body chemical composition was not affected by the feeding strategies (Gaylord and Gatlin, 2000; Xie *et al.*, 2001; Zhu *et al.*, 2004; Turano *et al.*, 2007). Nevertheless, the lower body lipid composition of G3 compared to the other groups in our study was caused by the reduction of lipids, which is the primary resource in fish, for the protection of basal metabolism and survival during starvation. Similarly, many researchers have reported that the body lipid content decreased as a result of starvation regime applications (Rueda *et al.*, 1998; Wang *et al.*, 2000, 2005, 2009; Zhu *et al.*, 2001; Tian and Qin, 2003; Oh *et al.*, 2007; Peres *et al.*, 2011). TF values, which indicate the fattening of body cavities and internal organs, were similar in all groups except G3 group. This result proves that the long term and single cycled starvation period causes less fattening and higher energy consumption.

Conclusively, the best group in terms of partial compensation growth, feed utilization and economic

data was the short term and multiple cycle feeding protocol group, G1. The feeding model applied in this group is thought to be useful for the aquaculture industry. Although our experiment was a short term (50 days) study, it will provide a basis for subsequent long term starvation-refeeding studies which is intended to be carried out.

Acknowledgement

This work was supported by the Scientific Research Project Unit of Çukurova University, Turkey under Grant (SÜF2010YL23).

References

- Ali, M. and Wootton, R.J. 2001. Capacity for growth compensation in juvenile three-spined sticklebacks experiencing cycles of food deprivation. *J. Fish Biol.*, 58: 1531-1544. doi:10.1111/j.1095-8649.2001.tb02310.x
- Ali, M., Nicieza, A. and Wootton, R.J. 2003. Compensatory growth in fishes: a response to growth depression. *Fish and Fisheries*, 4: 147-190. doi: 10.1046/j.1467-2979.2003.00120.x
- Ali, M.Z. and Jauncey, K. 2004. Evaluation of mixed feeding schedules with respect to compensatory growth and body composition in African catfish *Clarias gariepinus*. *Aquaculture Nutrition*, 10: 39-45. doi:10.1046/j.1365-2095.2003.00278.x
- AOAC (Association of Official Analytical Chemists) 1990. Official methods of analysis, 15th edition. Association of Official Analytical Chemists, Arlington, Virginia, USA.
- Aranyakananda, P., Moore, N. and Singhagrain, T. 1996. Effects of feeding frequency on compensatory growth of Asian sea bass, *Lates calcarifer*. *ARRI Newsl.*, 3: 11-13.
- Bavcevic, L., Klanjscek, T., Karamarko, V., Anicic, I. and Legovic, T. 2010. Compensatory growth in gilthead sea bream (*Sparus aurata*) compensates weight, but not length. *Aquaculture*, 301: 57-63. doi:10.1016/j.aquaculture.2010.01.009
- Chatzifotis, S., Papadaki, M., Despoti, S., Roufidou, C. and Antonopoulou, E. 2011. Effect of starvation and re-feeding on reproductive indices, body weight, plasma metabolites and oxidative enzymes of sea bass (*Dicentrarchus labrax*). *Aquaculture*, 316: 53-59. doi: 10.1016/j.aquaculture.2011.02.044
- Cho, S.H., Lee, S., Park, B.H., Ji, S., Lee, J., Bae, J. and Oh, S. 2006. Compensatory growth of juvenile olive flounder *Paralichthys olivaceus* L. and changes in proximate composition and body condition indexes during fasting and after refeeding in summer season. *Journal of the World Aquaculture Society*, 37: 168-174. doi: 10.1111/j.1749-7345.2006.00023.x
- Cho, Y.J. and Cho, S.H. 2009. Compensatory growth of olive flounder, *Paralichthys olivaceus*, fed the extruded pellet with different feeding regimes. *Journal of the World Aquaculture Society*, 40(4): 505-512. doi: 10.1111/j.1749-7345.2009.00270.x
- Duncan, D.B. 1955. Multiple range and multiple F tests. *Biometrics*, 11: 1-42.
- Eroldoğan, O.T., Kumlu, M., Kırıs, G.A. and Sezer, B. 2006a. Compensatory growth response of *Sparus*

- aurata* following different starvation and refeeding protocols. *Aquaculture Nutrition*, 12: 203-210. doi: 10.1111/j.1365-2095.2006.00402.x
- Eroldoğan, O.T., Kumlu, M. and Sezer, B. 2006b. Effects of starvation and re-alimentation periods on growth performance and hyperhagic response of *Sparus aurata*. *Aquaculture Research*, 37: 535-537. doi: 10.1111/j.1365-2109.2006.01445.x
- Eroldoğan, O.T., Taşbozan, O. and Tabakoğlu, S. 2008. Effects of restricted feeding regimes on growth and feed utilization of juvenile Gilthead sea bream, *Sparus aurata*. *Journal of The World Aquaculture Society*, 39: 267-274. doi: 10.1111/j.1749-7345.2008.00157.x
- Gaylord, T.G. and Gatlin III, D.M. 2000. Assessment of compensatory growth in Channel catfish, *Ictalurus punctatus*, R. and associated changes in body condition indices. *Journal of The World Aquaculture Society*, 31: 326-336. doi: 10.1111/j.1749-7345.2000.tb00884.x
- Gaylord, T.G. and Gatlin III, D.M. 2001. Dietary protein and energy modifications to maximize compensatory growth of channel catfish (*Ictalurus punctatus*). *Aquaculture*, 194: 337-348. doi:10.1016/S0044-8486(00)00523-8
- Hayward, R.S., Noltie, D.B. and Wang, N. 1997. Use of compensatory growth to double hybrid sunfish growth rates. *Transactions of American Fisheries Society*, 126: 316-322. doi:10.1577/1548-8659(1997)126<0316:NUOCGT>2.3.CO;2
- Hayward, R.S., Wang, N. and Noltie, D.B. 2000. Group holding impedes compensatory growth of hybrid sunfish. *Aquaculture*, 183: 299-305. doi:10.1016/S0044-8486(99)00301-4
- Heide, A., Foss, A., Stefansson, S.O., Mayer, I., Norberg, B., Roth, B., Jessen, M.D., Nortvedt, R. and Imsland, A.K. 2006. Compensatory growth and fillet crude composition in juvenile Atlantic halibut: Effects of short term starvation periods and subsequent feeding. *Aquaculture*, 261: 109-117. doi: 10.1016/j.aquaculture.2006.06.050
- Hernandez, M.D., Martinez, F.J., Jover, M. and Garcia Garcia, B. 2007. Effects of partial replacement of fish meal by soybean meal in sharpsnout sea bream (*Diplodus puntazzo*) diet. *Aquaculture*, 263: 159-167. doi:10.1016/j.aquaculture.2006.07.040
- Jobling, M., Jøergensen, E.H. and Siikavuopio, S.I. 1993. The influence of previous feeding regime on the compensatory growth response of maturing and immature Arctic charr, *Salvelinus alpinus*. *Journal of FishBiology*, 43: 409-419. doi: 10.1111/j.1095-8649.1993.tb00576.x
- Kankanen, M. and Pirhonen, J. 2009. The effect of intermittent feeding on feed intake and compensatory growth of whitefish *Coregonus lavaretus* L. *Aquaculture*, 288: 92-97. doi: 10.1016/j.aquaculture.2008.11.029
- Kim, M.K. and Lovell, R.T. 1995. Effect of restricted feeding regimes on compensatory weight gain and body tissue changes in channel catfish *Ictalurus punctatus* in ponds. *Aquaculture*, 135: 285-293. doi:10.1016/0044-8486(95)01027-0
- Liu, W., Wei, Q.W., Wen, H., Jiang, M., Wu, F. and Shi, Y. 2011. Compensatory growth in juvenile Chinese sturgeon (*Acipenser sinensis*): effects of starvation and subsequent feeding on growth and body compensation. *J. Appl. Ichthyol.*, 27: 749-754. doi: 10.1111/j.1439-0426.2011.01723.x
- Mattila, J., Koskela, J. and Pirhonen, J. 2009. The effect of the length of repeated feed deprivation between single meals on compensatory growth of pikeperch *Sander lucioperca*. *Aquaculture*, 296: 65-70. doi: 10.1016/j.aquaculture.2009.07.024
- Nikki, J., Pirhonen, J., Jobling, M. and Karjilainen, J. 2004. Compensatory growth in juvenile rainbow trout, *Oncorhynchus mykiss* (Walbaum), held individually. *Aquaculture*, 235: 285-296. doi: 10.1016/j.aquaculture.2003.10.017
- Oh, S.Y., Noh, C.H. and Cho, S.H. 2007. Effect of restricted feeding regimes on compensatory growth and body composition of Red sea bream, *Pagrus major*. *Journal of The World Aquaculture Society*, 38: 443-449. doi: 10.1111/j.1749-7345.2007.00116.x
- Oh, S.Y., Noh, C.H., Kang, R.S., Kim, C.K., Cho, S.H. and Jo, J.Y. 2008. Compensatory growth and body composition of juvenile black rockfish *Sebastes schlegeli* following feed deprivation. *Fisheries Science*, 74: 846-852. doi: 10.1111/j.1444-2906.2008.01598.x
- Peres, H., Santos, S. and Oliva-Teres, A. 2011. Lack of compensatory growth response in gilthead seabream (*Sparus aurata*) juveniles following starvation and subsequent refeeding. *Aquaculture*, 318: 384-388. doi:10.1016/j.aquaculture.2011.06.010
- Ribeiro, F.F. and Tsuzuki M.Y. 2010. Compensatory growth responses in juvenile fat snook, *Centropomus parallelus* Poey, following food deprivation. *Aquaculture Research*, 41: 226-233. doi: 10.1111/j.1365-2109.2010.02507.x
- Rueda, F.M., Martinez, F.J., Zamora, S., Kentouri, M. and Divanach, P. 1998. Effects of fasting and refeeding on growth and body composition of red porgy, *Pagrus pagrus* L. *Aquacult. Res.*, 29: 447-452. doi: 10.1046/j.1365-2109.1998.00228.x
- Saether, B.S. and Jobling, M. 1999. The effects of ration level on feed intake and growth, and compensatory growth after restricted feeding, in turbot *Scophthalmus maximus* L. *Aquaculture Research*, 30: 647-653. doi: 10.1046/j.1365-2109.1999.00368.x
- Sevgili, H., Hoşsu, B., Emre, Y. and Kanyılmaz, M. 2013. Effect of various lengths of single phase starvation on compensatory growth in rainbow trout under summer conditions (*Oncorhynchus mykiss*). *Turkish Journal of Fisheries and Aquatic Sciences*, 13: 465-477. doi: 10.4194/1303-2712-v13_3_09
- Şahin, T., Akbulut, B. and Aksungur, M. 2000. Compensatory growth in sea bass (*Dicentrarchus labrax*), sea bream (*Sparus aurata*) and rainbow trout (*Oncorhynchus mykiss*). *Turk. J. Zool. Tubitak*, 24: 81-86.
- Tian, X. and Qin, J.G. 2003. A single phase of food deprivation provoked compensatory growth in barramundi *Lates calcarifer*. *Aquaculture*, 224: 169-179. doi: 10.1016/S0044-8486(03)00224-2
- Tian, X. and Qin, J.G. 2004. Effects of previous ration restriction on compensatory growth in barramundi *Lates calcarifer*. *Aquaculture* 235: 273-283. doi: 10.1016/j.aquaculture.2003.09.055
- Turano, M.J., Borski, R.J. and Daniels, H.V. 2007. Compensatory growth of pond-reared hybrid striped bass, *Morone chrysops* x *Morone saxatilis*, fingerlings. *Journal of The World Aquaculture Society*, 38: 250-261. doi: 10.1111/j.1749-7345.2007.00094.x
- Wang, Y., Cui, Y., Yang, Y.X. and Cai, F.S. 2000. Compensatory growth in hybrid tilapia, *Oreochromis*

- mossambicus* x *O. niloticus*, reared in seawater. Aquaculture, 189: 101-108. doi: 10.1016/s0044-8486(00)00353-7
- Wang, Y., Cui, Y., Yang, Y. and Cai, F. 2005. Partial compensatory growth in hybrid tilapia *Oreochromis mossambicus* x *O. niloticus* following food deprivation. J. Appl. Ichthyol., 21: 389-393. doi: 10.1111/j.1439-0426.2005.00648.x
- Wang, Y., Li, C., Qin, J.G. and Han, H. 2009. Cyclical feed deprivation and refeeding fails to enhance compensatory growth in Nile tilapia, *Oreochromis niloticus* L. Aquaculture Research, 40: 204-210. doi: 10.1111/j.1365-2109.2008.02083.x
- Wieser, W., Krumschnabel, G. and Ojwang-Okwor, J.P. 1992. The energetic of starvation and growth after refeeding in juveniles of three cyprinid species. Environmental Biology of Fish, 33: 63-71. doi: 10.1007/BF00002554
- Yarmohammadi, M., Shabani, A., Pourkazemi, M., Soltanloo, H. and Imanpour, M.R. 2012. Effect of starvation and re-feeding on growth performance and content of plasma lipids, glucose and insulin in cultured juvenile Persian sturgeon (*Acipenser persicus* Borodin, 1897). J. Appl. Ichthyol., 28: 692-696. doi: 10.1111/j.1439-0426.2012.01969.x
- Zhu, X., Cui, Y., Ali, M. and Wootton, R.J. 2001. Comparison of compensatory growth responses of juvenile three-spined stickleback and minnow following similar food deprivation protocols. Journal of Fish Biology, 58: 1149-1165. doi: 10.1006/jfbi.2000.1521
- Zhu, X., Xie, S., Zou, Z., Lei, W., Cui, Y., Yang, Y. and Wootton, R.J. 2004. Compensatory growth and food consumption in gibel carp, *Carassius auratus gibelio*, and Chinese longsnout catfish, *Leiocassis longirostris*, experiencing cycles of feed deprivation and re-feeding. Aquaculture, 241: 235-247. doi:10.1016/j.aquaculture.2004.07.027
- Zhu, X., Xie, S., Lei, W., Cui, Y., Yang, Y. and Wootton, R.J. 2005. Compensatory growth in the Chinese longsnout catfish, *Leiocassis longirostris* following feed deprivation: Temporal patterns in growth, nutrient deposition, feed intake and body composition. Aquaculture, 248: 307-314. doi: 10.1016/j.aquaculture.2005.03.006
- Xie, S., Zhu, X., Cui, Y., Lei, W., Yang, Y. and Wootton, R.J. 2001. Compensatory growth in the gibel carp following feed deprivation: temporal patterns in growth, nutrient deposition, feed intake and body composition. Journal of Fish Biology, 58: 999-1009. doi: 10.1111/j.1095-8649.2001.tb00550.x