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RESEARCH ARTICLE

Determination of the Compensatory Growth Response, Mineral and Antioxidant Enzyme Activities of European Sea Bass Fingerlings (*Dicentrarchus labrax*) in Fasting and Re-feeding

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Abstract: Understanding compensatory growth in European sea bass (*Dicentrarchus labrax*) is also crucial for optimizing aquaculture practices as it can lead to more efficient feeding strategies and improved fish health. To this end, this study evaluated the effects of fasting and re-feeding on growth performance, mineral and antioxidant enzyme activities of European sea bass fingerlings. The experiment involved five treatments, each with three replicates. The control treatment was fed continuously, while treatments A1, A2, A3, and A4 were fasted for one, two, three, and four weeks, respectively. Following the fasting period, all treatments were fed to satiation twice daily for four weeks. At the end of the trial, the control treatment showed the best growth during the fasting period, while the growth of the other treatments decreased with the duration of fasting ($p<0.05$). Consequently, the highest specific growth rate (SGR), feed conversion ratio (FCR) and hepatosomatic index (HSI) were observed in the control treatment ($p<0.05$). During the re-feeding period, potassium (K) and calcium (Ca) levels significantly decreased compared to the fasting period. The ratios of Ca, K, sodium (Na), and iron (Fe) were higher during the fasting period than during the re-feeding period. A4 treatment, which lasted for four weeks, had the highest mineral content during the fasting period compared to the control treatment in both periods. In the re-feeding period, the control treatment had the lowest levels of Ca, Fe, phosphorus (P), manganese (Mn), and zinc (Zn) ($p<0.05$). Antioxidant enzyme activities, including superoxide dismutase (SOD), catalase (CAT), glutathione peroxidase (GPx), and lipid peroxidation (LPO), were highest in treatments A2, C, and A1 during the fasting period ($p<0.05$). These values significantly decreased by the end of the re-feeding period ($p<0.05$). Therefore, this study concludes that re-feeding after fasting resulted in partial compensatory growth in the European sea bass fingerlings examined.

Anahtar kelimeler:

Levrek
Dicentrarchus labrax
Antioksidan enzimler
Mineral madde
Açlık
Yeniden besleme
Telafi büyümesi

Avrupa Levreği Yavrularının (*Dicentrarchus labrax*) Açlık ve Yeniden Beslenmede Telafi Edici Büyüme Tepkisi ile Mineral ve Antioksidan Enzim Aktivitelerinin Belirlenmesi

Öz: Beslenme eksikliğinden sonra yeniden besleme döneminden sonra oluşan telafi büyümesi, balık çiftçiliğinin genel verimliliğini ve ekonomik uygulanabilirliğini önemli ölçüde etkileyebilir. Avrupa levreğinde (*Dicentrarchus labrax*) telafi edici büyümeyi anlamak, daha verimli besleme stratejilerine ve iyileştirilmiş balık sağlığına yol açabileceğinden su ürünleri yetiştiriciliği uygulamalarını optimize etmek için de önemlidir. Bu amaçla, bu çalışmada açlığın ve yeniden beslemenin levrek yavrularının büyüme performansı, mineral içeriği ve antioksidan enzim aktiviteleri üzerindeki etkileri değerlendirilmiştir. Deney, her biri üç tekrarlı beş uygulamayı içermektedir. Kontrol grubu (C) sürekli beslenirken, A1, A2, A3 ve A4 grupları bir, iki, üç ve dört hafta boyunca aç bırakılmıştır. Açlık döneminin ardından, tüm deneme grupları dört hafta boyunca günde iki kez doyuncaya kadar beslenmiştir. Denemenin sonunda, kontrol grubu açlık döneminde en iyi büyümeyi gösterirken, diğer grupların büyümesi açlık süresiyle azalma göstermiştir ($p<0,05$). Sonuç olarak, en yüksek spesifik büyüme oranı (SGR), yem dönüşüm oranı (FCR) ve hepatosomatik indeks (HSI) kontrol grubunda gözlenmiştir ($p<0,05$). Yeniden besleme döneminde potasyum (K) ve kalsiyum (Ca) düzeyleri açlık dönemine kıyasla önemli derecede azaldı. Ca, K, sodyum (Na) ve demir (Fe) oranları açlık döneminde yeniden besleme dönemine göre daha yüksek tespit edilmiştir. Dört hafta süren A4 grubu, her iki dönemde de kontrol uygulamasına kıyasla açlık döneminde en yüksek mineral içeriğine sahip bulunmuştur. Yeniden besleme döneminde kontrol uygulaması en düşük Ca, Fe, fosfor (P), manganez (Mn) ve çinko (Zn) düzeylerine sahip bulunmuştur ($p<0,05$). Süperoksit dismutaz (SOD), katalaz (CAT), glutatyon peroksidaz (GPx) ve lipid peroksidasyonu (LPO) dahil antioksidan enzim aktiviteleri, açlık döneminde A2, C ve A1 gruplarında en yüksek tespit edilmiştir ($p<0,05$). Bu değerler yeniden besleme döneminin sonunda önemli ölçüde azalmıştır ($p<0,05$). Bu nedenle, bu çalışma açlıktan sonra yeniden beslemenin incelenen levrek yavrularında kısmi telafi büyümesinin gözlendiği sonucuna varmaktadır.

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Introduction

In a certain period of their lives, all living organisims may encounter hunger that can lead to death due to seasonal reasons such as shortage of food resources or sudden temperature changes (McCue, 2010). The frequency and duration of these hunger periods in nature may differ seasonally (Ali et al., 2003; McCue, 2010). The term hunger is expressed as the ability of an animal to give up feeding opportunity after digestion through some hormonal or metabolic activities (Doucett et al., 1999). After this period, the biological term given to the rapid increase in the growth performance of living organisms with the start of feeding again is compensatory growth (Ali et al., 2003). Compensatory growth is also defined as growth in which an organism catches the weight of those whose growth has never decreased, following a period of limited growth or negative growth, usually resulting from low feed consumption (Hornick et al., 2000).

The effect of fasting period applied for certain periods in breeding conditions on nutrition, feed intake, feed conversion rate and growth has been studied in many fish species. While there is a rapid growth after re-feeding in some fish species exposed to fasting, it was determined by some researchers that the feed utilization rate did not change (Hayward et al., 2000). This mechanism has brought along a good feed conversion efficiency as well as rapid growth in some studies (Ali and Jauncey, 2004). This event is not only a theoretical issue but also commercially applicable, increasing feed conversion efficiency with growth (Wang et al., 2000). Previous studies have investigated various fish species, such as rainbow trout (*Oncorhynchus mykiss*), Atlantic salmon (*Salmo salar*), and Nile tilapia (*Oreochromis niloticus*), to understand the effects of fasting and re-feeding. In rainbow trout, fasting followed by re-feeding has been shown to enhance growth rates and improve feed conversion efficiency (Quinton and Blake, 1990). In Atlantic salmon, compensatory growth was observed with a significant increase in feed intake and growth rate upon re-feeding (Johansen et al., 2001). Similarly, Nile tilapia exhibited improved growth performance and feed utilization efficiency after a period of fasting and re-feeding (Ali et al., 2003). When comparing these findings to sea bass, it is observed that while the mechanisms of compensatory growth, such as increased feed intake and metabolic adjustments, are similar, the specific responses in growth performance and feed utilization may vary due to species-specific differences in metabolism and dietary requirements.

The effects of nutritional factors on the physiological and health of fish have been comprehensively studied, but feeding frequency may also affect fish's antioxidant ability and immunity (Garcia and Villarroel, 2009; Sheikhzadeh et al., 2012). Ding et al. (2017) reported that malnutrition not only causes oxidative damage but also results in immunosuppression. The effects of oxidative stress resulting from the disruption of prooxidant-antioxidant balance in living organisms due to any stress factor can be eliminated with the help of antioxidant substances that strengthen the antioxidant defense system. Changes in the activities of SOD, CAT and GPx, which are the main enzymatic antioxidants, can be used as an indicator of oxidative stress (Ekambaram et al. 2014). These enzymes provide defense against the damage caused by reactive oxygen species (ROS) in living systems and cells are well protected by these antioxidant enzymes (Altan et al., 2005).

Many stressors in the animal world are universal because of the similarity of the basic needs of animals. Social interaction requirements such as non-optimal environmental conditions (temperature, oxygen, etc.), malnutrition, sunlight, openness to predators and the need to determine the area are defined as universal stressors. Fish and other aquatic organisms are exposed to more stress factors than land animals. This is due to the fact that homeostasis mechanisms are highly dependent on the environmental conditions in which they operate (Harper and Wolf, 2009). Looking at today's conditions, it can be said that the environment in which fish live is under threat of change (due to reasons such as climate change). Therefore, just as there is always a risk of fish fasting under natural conditions, there is also a risk for aquaculture. Aquaculture is not only carried out offshore but also in coastal areas, where hatcheries and earthen ponds are commonly established. Inaccessibility to aquaculture systems due to weather conditions, lack of food, malnutrition, technical problems, and other factors can lead to periods of fasting for fish in both settings. Therefore researchers have started to focus on this topic recently. Also, there is no research regarding the effect of fasting and re-feeding on the mineral matter in sea bass.

Sea bass is a fish with high economic value and can easily adapt to climatic conditions. It is carnivorous and feeds on shrimp, crabs, worms, and fish in nature, therefore it has a wide range of feeding habits. Sea bass, which is highly able to gain live weight, is also preferred by consumers for its meat quality, an important criterion in farming. Its rich vitamin, mineral, and trace element content holds special importance in healthy nutrition. These fish have a high probability of starving in nature and farming. Therefore, in the present study, the changes in growth performance, mineral content, antioxidant enzyme activities, and lipid peroxidation activities of sea bass after fasting and re-feeding period were examined, and the contributions of these changes to compensatory growth were investigated. It also hypothesized how physiological and biochemical changes affect compensatory growth in sea bass and how re-feeding after a period of starvation would lead to significant improvements in growth and health markers. This research is novel in its comprehensive approach and is expected to contribute valuable insights into optimizing feeding strategies for sustainable aquaculture practices, enhancing both the economic viability and health of cultured sea bass.

Material and Methods

Animals, experimental conditions and water parameters

The experiment was carried out in Sinop University Fisheries and Aquaculture Faculty Research and Application Center. Sea bass (300 fish) provided from a commercial sea bass farm (Kızılırmak Su Ürünleri Inc., Samsun/Turkey) were used. The transport of fish was carried out with water-filled and ventilated transport tanks. The fish brought to the research center were stocked in 3-ton tanks, and they were acclimatized to the experimental conditions by taking them for a 2-week feeding period with commercial sea bass feed. After acclimatization, fish (weight ~32.09±0.07 g) were fasted for a day, weighted and randomly distributed into 120-L rectangle glass aquaria in a recirculation seawater system.

Fish were maintained under a stress-free conditions during the experimental period. The water quality parameters of the recirculated system were measured daily; temperature (21.11 ± 0.05°C), dissolved oxygen (DO) (7.08±0.01 mg/L), pH (8.14±0.05) and salinity (19.65±0.06‰) did not change significantly between treatments during the experiment. A recirculated system consisting of 15 tanks and five sump filter systems was established. Mechanical, chemical and biological filtration were provided thanks to the continuous water circulation and filter materials in the sump filter system. Aeration was realized by two air stones placed in the sump filter system.

Experimental design and feeding

The experiment was designed with three replications using a total of 270 sea bass fingerlings in 15 square tanks with 18 fish in each tank for eight weeks. The experiment was divided into two phases: fasting (weeks 0-4) and re-feeding (weeks 5-8). All treatments were fed commercial sea bass pellets, with their approximate composition, mineral content, and amino acid composition detailed in Table 1. Throughout the experiment, the control treatment (C) was fed commercial diets twice daily until satiation. The other four treatments underwent varying fasting periods: fish in treatments A1 (one week fasting), A2 (two weeks fasting), A3 (three weeks fasting) and A4 (four weeks fasting) were starved for one, two, three, and four weeks, respectively.

From weeks 5 to 8, fish in the control treatment (C) and the fasting treatments A1, A2, A3 and A4 were fed twice a day until satiation. To remove unnecessary food and feces, the tanks were regularly siphoned. Approximately 10% of the total water volume was replaced daily throughout the experiment. The fish were weighed every 15 days to monitor growth performance. They were kept under a natural light regime, and tank aeration was provided by an air pump.

Sampling

Sampling was done in the 4th and 8th weeks of the study. During these weeks, a total of 6 fish from each group (2 fish from each tank) were sampled. First, the length and weight measurements of the sampled fish were measured. During these weighing and measuring processes, in order to prevent the fish from being damaged by mechanical effects and from getting stressed and to make accurate measurements, the fish were stunned in benzocaine solution (50 mg/lt). The weighed fish were taken to experimental tanks that were cleaned and water was added after being separated in a separate tank that was continuously ventilated and contained clean water. The weighing process was carried out in the early morning hours when the fish were hungry and since the fish were not fed on the weighing days, these days were not included in the experimental period. Then, the abdomen was dissected, the gastrointestinal organs and liver were removed. The liver was weighed to determine the hepatosomatic index (HSI) and placed in small storage bags. For enzyme analysis, the livers were transported to the laboratory in a cold chain and stored at -20°C in sucrose until analysis. The fish meat, after being cleaned of bones and skins, was weighed, homogenized, and stored at -80°C for biochemical composition, amino acid, and mineral matter analysis.

Amino acid analysis of fish feed

Agilent Technologies/6460 Triple Quad LC-MS/MS Liquid Chromatography Mass/Mass Spectrometer was performed for amino acid analysis; 5 separate standard, internal standard, mobile phases, reagents, chromotographic separation and mass detection parameters are developed using the Jasem LC-MS/MS amino acid analysis kit (Pt Berca Niaga Medica/Indonesia) with updated sample preparation including acid hydrolysis procedure (Bilgin et al., 2018).

Mineral matter analysis of fish fillets

Element analysis was determined in the laboratories of Sinop University Scientific and Technological Researches Center (SUBITAM). Analyses (Se, P, Zn, Ca, Na, K, Mg, Mn, Co and Fe) were performed by wet digesting of the samples in HNO_3/H_2O_2. 0.5 g of the sample from the homogenous sample was placed in the 90 ml heat and pressure-resistant dried or lyophilized teflon containers of the microwave device. The sample was treated with 7 ml of 65% HNO_3 suprapur purity and 1 ml of 30% H_2O_2 suprapur purity before being broken up in the necessary microwave program. Up to 50 mL of ultrapure water was filled into the containers and read on the ICP-MS (inductively coupled plasma/optical emission spectrometer).

Analytical procedures of antioxidant enzymes

At the end of fasting and re-feeding periods, fish liver samples were taken to determine the activity of antioxidant enzymes such as SOD, CAT, GPx and LPO. All samples were stored at −80 °C until analysis. After thawing, liver samples were washed with sterile physiological saline, dried with filter paper, and homogenized in a Potter-Elvehjem homogenizer with approximately 1 g liver sample and inserted in a homogenization medium (0.25 M sucrose, 0.5 mM EDTA and 10 mM Tris-HCl; pH 7.4) for

4°C centrifugation, 20000 g for 45 minutes (Hisar et al., 2009). The supernatant was isolated after centrifugation and used for enzyme activity assays. In the analysis, SOD was determined using the SIGMA 19160-1KT-F SOD Assay Kit; catalase activity was determined using the Cayman 707002 Catalase Assay Kit; glutathione peroxidase activity was determined using the Cayman 703102 Glutathione Peroxidase Assay Kit; and lipid peroxidation was determined using the Cayman 10009055 TBARS Assay Kit. All these methodologies have been carried out following the guidance of the manufacturer.

Statistical analysis

Results were presented as mean±SE. The data collected at the conclusion of the study were analyzed using one-way analysis of variance (ANOVA), and Tukey's multiple comparisons procedure was used to determine the significance level of differences within and between groups (IBM SPSS 21). The relationships between fillet and diet fatty acids were evaluated by regression analysis. The tables and figures were created using the MS Office 2010 program. Prior to statistical analysis, arcsine square root transformations of percentage data were performed to ensure homogeneity of variances. When $p<0.05$, differences were deemed significant.

Results

Amino acid and mineral matter contents of fish feeds

The commercial sea bass feed used in the study contained 46% crude protein and 19% crude lipid. It was rich in minerals, including Calcium (Ca, 22897.07 mg/kg), Potassium (K, 8346.08 mg/kg), and Phosphorus (P, 15207.15 mg/kg). The feed also included essential amino acids such as histidine (1.47%), isoleucine (1.42%), leucine (3.73%), lysine (3.31%), methionine (0.90%), phenylalanine (2.15%), taurine (2.09%), and valine (1.90%) (Table 1). The essential amino acid profiles of the experimental diets meet the requirements for the sea bass (NRC, 1993). All the essential amino acids for growth were found in the diets. The amino acid composition of the experimental diet is shown in Table 1.

Table 1. Biochemical composition, mineral matter contents and amino acid composition of commercial sea bass pellets used in the study

Biochemical composition (% wet weight)	NRC (1993)	Mineral matters (mg/kg)	NRC (1993)	Essential Amino Acids (g/100g)	NRC (1993)	Non-essential Amino Acids (g/100g)	NRC (1993)
Crude protein 46	45-55	Calcium (Ca) 22897.07	12000-20000	Histidine 1.47	0.8-1.2	Alanine 2.90	3.0-4.5
Crude lipid 19	10-20	Iron (Fe) 312.94	50-100	Isoleucine 1.42	1.2-1.8	Aspartic acid 4.23	4.5-6.5
Ash 10	<12	Potassium (K) 8346.08	9000-12000	Leucine 3.73	1.8-2.5	Glutamic acid 6.43	6.5-10.0
Fiber 1.7	-	Magnesium (Mg) 1781.65	500-1000	Lysine 3.31	2.5-3.5	Glycine 2.93	4.0-6.0
		Sodium (Na) 3123.82	2000-4000	Methionine 0.90	0.9-1.2	Serine 2.52	2.0-3.5
		Phosphorus (P) 15207.15	7000-12000	Phenylalanine 2.15	1.2-1.8	Tyrosine 1.24	0.9-1.3
		Manganese (Mn) 55.71	10-30	Threonine 2.09	1.2-1.8		
		Zinc (Zn) 150.96	30-50	Valine 1.90	1.4-2.0		
		Cobalt (Co) 2.13	-	Arginine 2.69	1.8-2.5		
		Selenium (Se) 1.35	0.15-0.3				
		Ca/P 1.51	1.33-1.67				

Growth performance

The best growth during the fasting period was in the control group, growth in other groups decreased according to the degree of fasting (Figure 1). As a result of the first weighing of the fish with the same average initial weights on the 15th day, a slight decrease was determined in all groups including the control. The control group showed a rapid recovery and growth rate dollowing a decline after day 15th. A1 and A2 groups also showed a recovery after the decline on day 15th, but they did not grow as fast as the control group. Groups A3 and A4 also showed growth after the decline on day 15th, but the recovery was not as strong as the other groups. At the end of the study,

treatments were ranked as control>A1>A2>A3>A4 with respect to observed growth rates.

Although fish weights increased rapidly after the re-feeding period, the best growth was determined in the control group as there was no full compensatory growth. Accordingly, the highest SGR, FCR and HSI were also in the control group (Table 2). HSI was quite low in groups A2 (fasting for two week), A3 (fasting for three week) and A4 (fasting for four week) during the fasting period. HSI values increased when re-feeding was started ($p<0.05$).

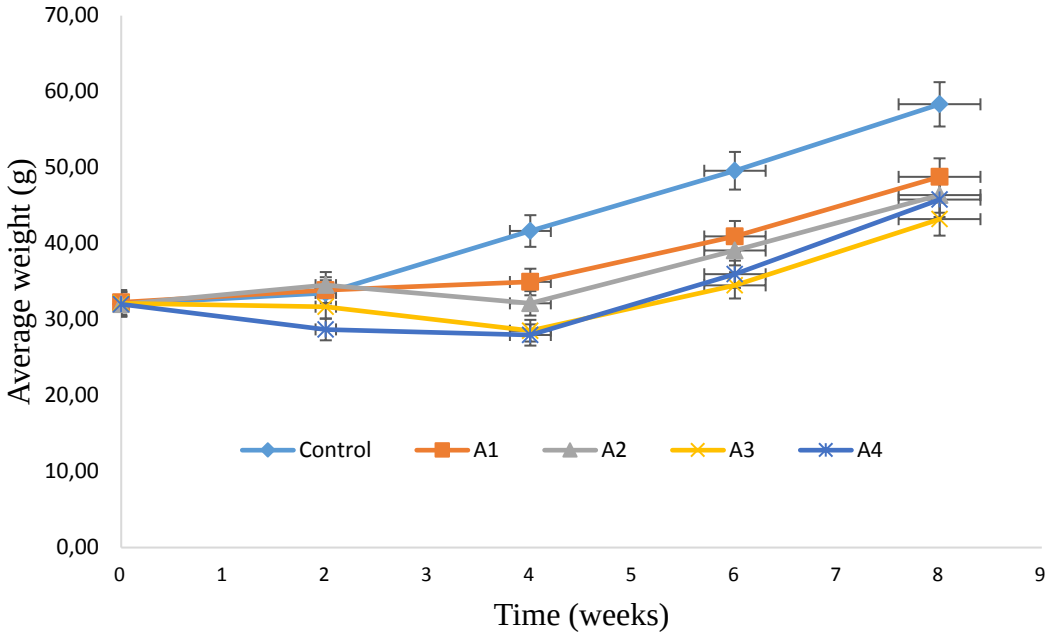

Figure 1. Changes in the average weight of fish during the study period

Table 2. Growth and feed utilization of sea bass fingerlings fed with fasting (week 0 to 4) and re-feeding (week 5 to 8) for 8 weeks.

	Treatments				
	Control	**A1**	**A2**	**A3**	**A4**
Initial weight (g)	32.03±0.02^{a}	32.28±0.19^{a}	32.01±0.38^{a}	32.13±0.18^{a}	32.01±0.14^{a}
Weight (0-4 weeks; g)	41.66±1.05^{a}	34.95±0.82^{b}	32.14±0.78^{c}	29.07±0.11^{d}	27.98±0.26^{e}
Lenght (0-4 weeks; cm)	15.62±0.22^{a}	15.38±0.22^{a}	15.12±0.17^{a}	15.15±0.23^{a}	14.98±0.22^{a}
Final weight (5-8 weeks; g)	58.33±2.96^{a}	48.79±2.85^{b}	46.38±1.11^{c}	43.21±1.34^{d}	45.79±2.02^{c}
Final length (cm)	17.69±0.05^{a}	16.73±0.39^{b}	16.49±0.06^{b}	16.13±0.13^{b}	16.39±0.23^{b}
Weight gain (g)	26.30±2.97^{a}	16.51±2.90^{b}	14.37±1.26^{c}	11.08±1.62^{d}	13.78±2.14^{c}
SGR (g day^{-1})	1.07±0.13^{a}	0.74±0.15^{b}	0.66±0.07^{c}	0.53±0.04^{d}	0.64±0.11^{c}
Daily feed intake	24.08±0.77^{a}	18.40±0.75^{b}	14.94±0.19^{c}	14.98±0.19^{c}	11.90±0.62^{d}
FCR	1.37±0.12^{d}	2.03±0.30^{b}	2.12±0.30^{b}	1.84±0.48^{c}	2.82±0.74^{a}
HSI (0-4 weeks; %)	1.75±0.26^{a}	1.17±0.06^{b}	0.80±0.06^{c}	0.70±0.59^{d}	0.82±0.07^{c}
HSI (5-8 weeks; %)	1.72±0.21^{c}	1.65±0.12^{d}	1.82±0.15^{b}	1.87±1.71^{a}	1.76±0.19^{c}

Data are reported as mean ± standard errors of three replicates (3). Means with different superscript letter in a row are significantly different ($p<0.05$). SGR:Specific Growth Rate,,FCR: Feed Conversion Ratio, HSI: HepatosomaticIndex

Mineral matter contents of fish fillets

Comparisons of fillet mineral matter contents (mg/kg) during the fasting period (week 0 to 4) and re-feeding period (week 5 to 8) of sea bass fingerlings are shown in Table 3. In the fasting period, calcium, potassium, sodium and iron ratios were more dominant than the re-feeding period. The A4 group (fasting for four week) had the highest mineral content during the fasting period compared to the control group of both periods. In the re-feeding period, the lowest calcium, iron, phosphorus, manganese and zinc were in the control group, the other groups had slightly higher values.

Table 3. Comparisons of fillet mineral matter contents (mg/kg) during fasting period (week 0–4) and re-feeding period (week 5–8) of sea bass fingerlings

	Treatments				
	Control	**A1**	**A2**	**A3**	**A4**
Fasting period (mg/kg; week 0-4)					
Calcium	1391.88±5.79^{c}	823.01±2.96^{e}	1104.22±4.27^{d}	1465.66±1.37^{b}	1860.47±4.51^{a}
Iron	7.65±0.54^{c}	8.19±1.07^{b}	6.65±0.64^{d}	10.20±0.94^{a}	4.83±0.52^{e}
Potassium	3044.18±4.36^{c}	2612.03±3.09^{e}	2874.93±3.98^{d}	3150.80±2.22^{b}	5403.33±3.28^{a}
Magnesium	322.26±4.61^{b}	310.35±3.54^{c}	319.87±5.11^{c}	337.96±2.91^{b}	357.60±2.96^{a}
Sodium	400.33±4.60^{c}	401.02±3.66^{c}	443.70±3.70^{b}	455.29±2.44^{b}	527.40±2.82^{a}
Phosphorus	2453.91±4.54^{d}	2831.07±3.19^{c}	2869.16±4.09^{c}	3238.18±2.99^{b}	3509.70±2.89^{a}
Manganese	0.70±0.11^{a}	0.53±0.07^{c}	0.57±0.06^{bc}	0.60±0.07^{b}	0.61±0.11^{b}
Zinc	6.76±0.64^{b}	7.09±0.97^{b}	6.95±0.71^{b}	6.81±0.78^{b}	7.56±0.99^{a}
Selenium	0.25±0.02^{a}	0.25±0.02^{a}	0.25±0.01^{a}	0.26±0.00^{a}	0.26±0.02^{a}
Re-feeding period (mg/kg; week 5-8)					
Calcium	201.35±1.17^{e}	304.47±0.78^{d}	511.88±2.81^{b}	398.42±1.96^{c}	841.53±3.22^{a}
Iron	5.69±0.07^{e}	7.97±0.05^{d}	32.39±0.18^{a}	15.88±0.11^{b}	14.16±0.04^{c}
Potassium	1739.88±1.75^{a}	1798.09±2.05^{a}	1669.62±1.82^{b}	1683.15±2.31^{b}	1695.59±1.61^{b}
Magnesium	289.31±1.76^{b}	307.48±1.05^{a}	306.86±1.61^{a}	281.94±1.24^{b}	304.38±1.46^{a}
Sodium	545.76±2.39^{a}	377.54±1.15^{b}	334.89±1.39^{c}	356.40±1.52^{bc}	352.98±1.67^{bc}
Phosphorus	2349.48±1.81^{c}	2581.99±1.50^{b}	2481.07±1.92^{c}	2481.57±1.99^{c}	2863.49±2.12^{a}
Manganese	0.28±0.01^{d}	0.36±0.01^{c}	0.89±0.01^{a}	0.76±0.01^{b}	0.73±0.01^{b}
Zinc	5.29±0.10^{b}	5.39±0.06^{b}	6.39±0.09^{a}	5.55±0.09^{b}	5.93±0.07^{a}
Selenium	0.22± 0.01^{a}	0.22±0.01^{a}	0.24±0.01^{a}	0.22±0.01^{a}	0.20±0.01^{a}

Data are mean ± SE. Means with different superscript letter in a column are significantly different ($p<0.05$)

Antioxidant enzyme activities of fish

In this study, antioxidant enzyme activities (SOD, CAT, GPx, LPO) were evaluated to determine the effects of experimental treatments (Figure 2). In all groups, SOD, CAT, GPx and LPO activities, which were high during the fasting period (especially in the A2 group), decreased during the re-feeding period except for A4 group.

SOD activities determined on the fasting and re-feeding periods in Table 4. The highest SOD activity was recorded in A2 group (76.23±1.97 U/mg protein), whereas, the lowest was in A4 group fish (30.16±1.84 U/mg protein) on the fasting period. On the re-feeding period, the highest SOD value was in A2 and A4 groups. On the other hand, control group fish had lowest SOD activity ($p<0.05$). Lipid peroxidation (LPO) was examined in liver tissues of fish. LPO results determined on the fasting and re-feeding periods are presented in Table 4. On the fasting period, the highest LPO value was in A1 group fish. On the other hand, control, A2 and A3 groups fish had the

lowest muscle LPO ($p<0.05$). During the re-feeding period, A3 group had the highest LPO value and it decreased significantly in fish of all the experimental groups and control ($p<0.05$). Highest GPx activity was observed in A1 and A3, on the fasting period ($p<0.05$). There were no significant differences in GPx values between control and experimental groups on the re-feeding period ($p>0.05$). In terms of CAT, the highest value was in the control group on the fasting period (Table 4). The lowest value was estimated in A2 on the same period. On the re-feeding period, fish of all experimental groups were significantly higher than that of the control ($p<0.05$).

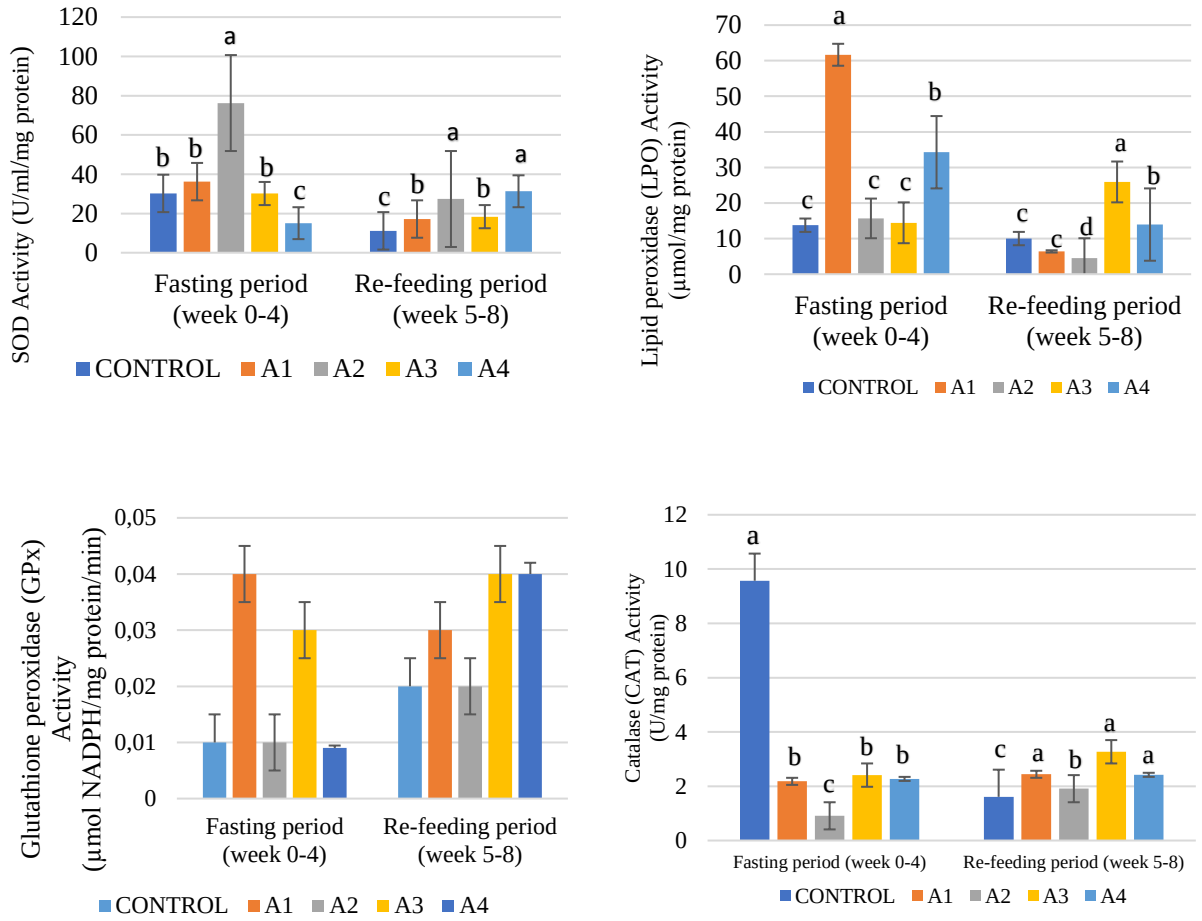

Figure 2. Changes in Superoxide Dismutase (SOD), Catalase (CAT), Lipid Peroxidase (LPO) and Glutathione Peroxidase (GPx) activity of sea bass fingerlings fed with fasting (week 0 to 4) and re-feeding (week 5 to 8) for 8 weeks.

Table 4. Antioxidant enzyme activities of sea bass fingerlings fed with fasting (week 0 to 4) and re-feeding (week 5 to 8) for 8 weeks.

Groups	Antioxidant Enzyme Acitvities			
	SOD	**LPO**	**GPx**	**CAT**
Fasting period (week 0-4)				
Control	30.21±1.96^{b}	13.78±1.23^{c}	0.01±0.01^{a}	9.57±1.10^{a}
A1	36.21±1.67^{b}	61.67±1.43^{a}	0.04±0.02^{a}	2.18±1.63^{b}
A2	76.23±1.97^{a}	15.68±1.09^{c}	0.01±0.01^{a}	0.91±0.10^{c}
A3	30.16±1.84^{b}	14.45±0.67^{c}	0.03±0.01^{a}	2.41±0.18^{b}
A4	15.05±1.52^{c}	34.28±0.22^{b}	0.01±0.01^{a}	2.27±1.81^{b}
Re-feeding period (week 5-8)				
Control	11.14±1.91^{c}	10.02±0.28^{c}	0.02±0.01^{a}	1.61±0.27^{c}
A1	17.16±1.80^{b}	6.42±0.49^{c}	0.03±0.01^{a}	2.44±1.81^{a}
A2	27.36±1.93^{a}	4.53±0.05^{d}	0.02±0.01^{a}	1.91±0.79^{b}
A3	18.37±1.56^{b}	25.94±1.17^{a}	0.04±0.03^{a}	3.27±1.24^{a}
A4	31.30±1.09^{c}	13.95±1.18^{b}	0.04±0.01^{a}	2.42±0.58^{b}

Data are mean ± SE. Means with different superscript letter in a row are significantly different ($p<0.05$)

Discussion and Conclusion

Fish can absorb minerals not only through food digestion but also by ingesting seawater and through exchanges between body tissues such as skin and gill membranes. Ca is readily absorbed from seawater, while freshwater contains low levels of calcium. However, most feedstuffs, especially those derived from animal proteins, are rich in Ca, indicating that calcium deficiency in fish caused by nutrient deficiencies is very unlikely. Conversely, both seawater and freshwater have minimal P content, making P levels in feeds and feed ingredients nutritionally very important (Anonymous, 2024a,b). It is well known that maintaining a favourable Ca and P balance is vital for fish, as it is for many vertebrates. The recommended ratio in fish feed is 1:1 or 1:1.5 (Martinéz-Valverde et al., 2000).Burrow et al. (2020) emphasized the physiological importance of Ca and P and stated that these minerals are essential for growth and energy production. In their study, Ca/P ratio was found to be 1.51 mg/kg. It was also reported that phosphorus supplementation to the diets of Atlantic salmon (*Salmo salar*) reared in seawater increased growth, improved feed utilisation and supported bone mineralisation (Akyurt, 1994).

Factors affecting the growth of fish in the feedback process after the fasting period are the amount of consumed feed, the quality of feed, and the water temperature (Ali et al., 2003; Eroldoğan et al., 2006; Pérez-Jiménez et al., 2007; Türkmen et al., 2012). Also, during periods of nutrient deprivation, the activation of body energy reserves to sustain life processes in fish, leads to a loss of body weight (Gisbert et al., 2011). Although partial compensatory growth (Morales et al., 2004; Mozanzadeh et al., 2017) and full compensatory growth (Pascual et al., 2003; Taravat et al., 2019), were reported, overcompensation growth is rare (Yılmaz, 2012). Adaklı and Taşbozan (2015) reported that short-term fasting and multiple cycles showed partial compensatory growth in sea bass. A partial compensatory growth was determined in the current study. Some similar results were obtained in studies on feeding patterns with different fish species (Eroldoğan et al., 2006; Mozanzadeh et al., 2017). Several studies have shown that compensatory fish growth is likely to be related to the length and impact of dietary restrictions imposed before re-feeding (Ali et al., 2003; Mozanzadeh et al., 2017). Applying different fasting and re-feeding protocols in sea bream juveniles (*Sparus aurata*) showed partial growth after feeding during the cycle period and even until satiation for 3 more weeks. Some degree of compensation was also achieved during the re-feeding period, but the best growth rate and SGR were reported in the control group (Eroldoğan et al., 2006).

Compensatory growth is a complex phenomenon influenced by various mechanisms, including metabolic adjustments and increased feed intake efficiency. After a period of starvation, fish often exhibit a hyperphagic response upon re-feeding, consuming more food than during normal feeding periods. This increased feed intake can lead to accelerated growth rates as the fish efficiently utilize the available nutrients to catch up on the lost growth

(Ali et al., 2003; Johansen et al., 2001). Additionally, metabolic adjustments, such as enhanced protein synthesis and reduced energy expenditure during the re-feeding period, play a crucial role in facilitating compensatory growth (Won and Borski, 2013). These mechanisms enable fish to not only regain lost weight but also improve their overall physiological condition, contributing to better growth performance and health outcomes. Graynoth and Taylor (2000) applied restricted feeding for 33 days in two species of eels (*Anguilla australis* and *A. dieffenbachii*) which were then fed to satiation for 10 days and determined that compensatory growth occured at the end of the experiment. Mozanzadeh et al. (2017) reported that with the same nutritional regimen (1-day fasting, 2 days re-feeding) in sobaity seabream (*Sparidentex hasta*) showed full compensatory growth. This suggests that fasting and re-feeding cycles provide a species-specific response. Again, Taravat et al. (2019) reported that after the re-feeding period, groups with food deprivation showed full compensatory growth and from the results sobaity seabream had the ability to maintain optimal growth after periods of food deprivation and re-feeding. Pérez-Jiménez et al. (2007), who subjected sea bass to a 9-day fasting period followed by 12 days of re-feeding with diets containing 42% (42P) and 50% (50P) protein, reported that fish experienced rapid metabolic adjustments to both fasting and re-feeding, and that no significant differences in growth performance, feed intake and feed efficiency were observed between groups. Türkmen et al. (2012) concluded that sea bass responds rapidly to cyclical fasting and re-feeding and that the 25% restricted feeding rate is insufficient to induce a compensatory growth response in sea bass.

The majority of fish species rely on their body's protein and lipid reserves when they are starved, and research on the significance of glycogen as an energy reserve has produced conflicting findings (Hemre et al., 2002; Furné et al., 2012). The main site of glycogen accumulation in fish is the liver. The cases of liver enlargement have been reported as a result of intense glycogen accumulation (Hemre et al., 2002). In the current study, low HSI in the fasting groups (A1, A2, A3, and A4) supported lipid utilization for metabolic energy. Our results are consistent with the observations for several fish species in which rapid regeneration of liver reserves in re-feeding. This demonstrates the importance of the liver during short-term fasting and restricted feeding regimes (Ali and Jauncey, 2004; Pérez-Jiménez et al., 2007). This might be the result of consuming more feed in the early stages of re-feeding in order to replenish muscle glycogen stores quickly and to recover energy (Black and Love, 1986). According to Liu et al. (2022), after seven days of re-feeding, the majority of the starvation-induced alterations in the immune system, gut microbiota, liver transcriptome, and enzyme activity in golden pompano (*Trachinotus ovatus*) progressively returned to normal. Because a species' eating habits influence how it responds metabolically to nutrient scarcity, carnivorous fish—which naturally feed less than omnivorous and herbivorous fish—are more adapted to this environment than other fish species (Furné et al., 2012). Given their carnivorous nature, sea bass juveniles in our study may have chosen to segregate intraperitoneal lipids for various metabolic uses, such as foraging (Eroldoğan et al., 2006).

Fish meat is an important source of minerals despite being high in digestible protein. While K, Na, Cl, Mg, P and Ca contents are higher, Fe, Zn, Cu and I contents are lower (Martinéz-Valverde et al., 2000). These components are also crucial for many aspects of fish metabolism. They give fish bones their strength and toughness. They are primarily involved in the neurological and endocrine systems, as well as in preserving the osmotic equilibrium with the water environment, in bodily fluids. They are parts of blood pigments, enzymes, and other organic substances. They also have a role in metabolic processes related to energy transport (New, 2021). Various studies have shown that the trace mineral content in fish is affected by various factors such as fish size (Yildiz, 2008), sexual maturity (Roy and Lal, 2006; Yildiz, 2008), food sources (Roy and Lal, 2006) and environment (Yamashita et al., 2006). In the present study, there were no significant size variations among all groups and not all fish were sexually mature. All environmental conditions such as salinity, temperature, dissolved oxygen and pH were optimal for these fish species. Only the factors of food deprivation and re-feeding, which were included in the study, were different. Different things happened to each group depending on the circumstances. Fish utilize their endogenous reserve to obtain the energy required to sustain essential functions (brain function, breathing, controlling mineral balance, etc.) and drastically cut energy expenditure from protein conversion in order to survive during periods of unfavorable feeding conditions (Salem et al., 2007). Depending on the species, this response necessitates metabolic adjustments (Wang et al., 2006). Furthermore, fish age or nutritional state are two variables that affect intra-specific modifications unique to these circumstances (Furné et al., 2012). During the fasting period, the highest mineral contents were found in the A4 group (fasting for four week). This suggested that fish tend to store minerals as a response to fasting.

Although similar results were determined among mineral matter compositions in all groups during the re-feeding period, the calcium and phosphorus ratio was significantly lower than the values determined during the fasting period in all groups. Considering that calcium is an important mineral for bone development, it suggested that fish may have used these minerals effectively in bone development. In addition, calcium and phosphorus are physiologically critical minerals that are particularly necessary for growth and energy production (Burrow et al., 2020), suggesting that fish may have stored these minerals during the fasting period. Sodium is a mineral that is part of the carbohydrate and amino acid transport mechanism. Potassium balances the effects of sodium and ensures that fluid levels remain within a certain range. It also helps the proper functioning of body systems, including heart, muscle and bone health. (Akyurt, 1994).

Fish defense mechanisms that either completely eradicate or significantly restrict the spread of infections are involved in the antioxidant enzyme activities of fish (Blazer, 1992). The rise in antioxidant enzyme activity has been viewed by many scientists as a defense mechanism against oxidative stress (Thomas, 2000). According to Florescu et al. (2019), the activities of the enzymes SOD and CAT are thought to be biological indicators of oxidative stress, and an increase in SOD activity could be brought on by an increase in intracellular superoxide radicals (Cheng et al., 2007). Furthermore, oxidative stress resulting from a reduction in oxygen consumption varies among fish species and could be caused by a decrease in activity as a means of preserving body energy during times of food scarcity (Glass, 1968). In our study, activities specific to SOD and CAT increased in the liver of fish that were exposed to the fasting period compared to the re-feeding period. Therefore, excessive ROS production due to fasting, precisely O_2- and H_2O_2, may have triggered an increase in both SOD and CAT activities in the liver. Antonopoulou et al. (2013), contrary to the current study results, reported that there was no significant change in antioxidant enzyme levels in sea bass liver, and that there were significant changes in antioxidant enzyme levels (SOD and CAT) in other tissues they examined (red muscle, intestine and white muscle). Furthermore, in both *Sparus aurata* (Pascual et al., 2003) and *Dentex dentex* (Morales et al., 2004), dietary restriction has been shown to considerably improve antioxidant enzyme activities such as SOD, glutathione reductase, glutathione peroxidase, and CAT. Nonetheless, following a 12-week fast, there has been evidence of elevated CAT activity in the liver of Atlantic cod (Guderley et al., 2003). According to Bayir et al. (2012), antioxidant enzyme activity increased when brown trout (*Salmo trutta*) were deprived of nutrients, and re-feeding did not always result in antioxidant enzyme activity control values. In a similar vein, it was observed that following seven days of undernutrition, the expression of SOD and CAT genes in the liver and gills of *Labeo rohita* fingerlings was considerably elevated, downregulated after three days of re-feeding, and returned to basal levels after eight days of re-feeding (Dar et al., 2019). Growth, biochemical indices, and oxidative stress measures, including as total antioxidant capacity, CAT, and SOD, were all impacted by starving and re-feeding in a study conducted on golden pompano (*Trachinotus ovatus*) (Liu et al., 2022).

When hunger and fasting stress are present, oxidative stress production in fish is typically linked to an increase in LPO levels (Furné et al., 2009). The results, which were consistent with previous research, demonstrated that the fasting phase significantly increased LPO in the liver compared to control fish and that the re-feeding period caused oxidative stress based on LPO levels. In contrast to what we found, Florescu et al. (2019) observed that during the fasting phase and the re-feeding period that followed, the levels of LPO in stellate sturgeon (*Acipenser stellatus*) rose. Sakyi et al. (2020), in line with our research, found that Nile tilapia (*Oreochromis niloticus*, Linnaeus 1758) had a decrease in LPO levels during the re-feeding phase.

According to Zeng et al. (2016), one of the key antioxidant enzymes in the fish antioxidant defense system is GPx. In contrast to the control group, Wang et al. (2019) discovered that GPx levels in the tissues (gill, liver, spleen, and kidney) of *Schizothorax wangchiachii* were not significantly impacted by varying food restriction and re-feeding regimens. Although the fish in the current study were stressed out by fasting, the detrimental consequences of this stress were largely offset by re-feeding, so there was no discernible difference in the liver GPx levels between the treatments. In contrast, as re-feeding time rose, antioxidant enzyme levels such as SOD, CAT, and LPO dropped. These findings suggest that oxidative stress in European sea bass may occur from extended fasting. According to research by Furné et al. (2012), oxidative stress indicators were still present in the liver tissue and red blood cells of rainbow trout (*Oncorhynchus mykiss*) and sturgeon (*Acipenser naccarii*) after a protracted fasting period of 72 days and a 60-day re-feeding phase. Variations in species responses, life history phases, culture conditions, duration and degree of food availability, and the particular tissues tested can all be responsible for the observed disparities in the results (Antonopoulou et al., 2013).

The current research results confirm that a fasting and re-feeding regimen can serve as a viable alternative nutritional strategy in aquaculture for European sea bass (*Dicentrarchus labrax*) in low salinity conditions (‰19). The observed partial compensatory growth, along with significant fluctuations in mineral content and antioxidant enzyme activities, suggests that fish can adapt to periods of feed deprivation followed by re-feeding in these specific conditions. However, the impact on fish health and long-term performance indicates that these regimens must be carefully managed. Future studies should focus on optimizing fasting and re-feeding protocols at low salinity levels to minimize stress, ensure optimal growth, and maintain the nutritional and physiological well-being of the fish. These efforts will contribute to the sustainable and economical production of this valuable species in aquaculture under low salinity conditions.

Conflict of Interest

No potential conflict of interest was reported by the authors.

Author Contributions

Seval Dernekbaşı designed the work. Seval Dernekbaşı, Dilara Kaya Öztürk realised the work. Dilara Kaya Öztürk carried out the laboratory studies. Keriman Yürüten Özdemir performed antioxidant enzymes analyses. Ismihan Karayücel and Seval Dernekbaşı analysed the data and interpreted the results. All authors were involved in the setup and finalisation of the experiment.

Ethical Statement

This experiment was carried out according to the ethical principles of animal experiments established by Sinop University Animal Experiments Control Council and the current legislation approved by the Local Animal Use Ethics Committee (Protocol 12/2019).

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