Journal of Applied Ichthyology

WILEY

RESEARCH ARTICLE OPEN ACCESS

Effect of Food Deprivation and Refeeding on Antioxidant Defense Status in Asian Sea Bass (*Lates calcarifer*)

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Received: 18 September 2025 | **Revised:** 25 February 2026 | **Accepted:** 2 March 2026

Academic Editor: Guido Pietroluongo

Keywords: antioxidant defense | *Lates calcarifer* | liver | muscle | refeeding | starvation

ABSTRACT

This study examined the impact of short-term starvation on oxidative stress and antioxidant defense mechanisms in juvenile Asian sea bass (*Lates calcarifer*). Juvenile fish (35 ± 9 g) were randomly allocated to 12 300 L fiberglass tanks (15 fish/tank) following acclimation. Experimental treatments (in triplicate) consisted of starvation periods of 2, 4, and 8 days, each followed by 16 days of refeeding, alongside a continuously fed control group. Fish were hand-fed a commercial diet to satiation twice daily. Liver and muscle tissues were sampled poststarvation and postrefeeding, following euthanasia with 2-phenoxyethanol. Growth performance; lipid peroxidation (malondialdehyde, MDA); and activities of key antioxidant enzymes, superoxide dismutase (SOD), catalase (CAT), and glutathione peroxidase (GPx) were assessed. Starvation significantly influenced weight gain, with the 8-day group exhibiting reduced growth compared to other treatments ($p < 0.05$). Antioxidant enzyme activities in muscle tissue remained unchanged across treatments; however, liver samples from the 8-day starvation group showed significant alterations in antioxidant indices ($p < 0.05$). These findings indicate that hepatic antioxidant defense is more responsive to starvation period than muscle tissue is and that starvation period of 8 days or longer may induce oxidative stress in the liver.

1 | Introduction

Fish, like many other animals, can withstand long periods of starvation. In aquaculture, despite the availability of food, several fish go through periods of starvation during stressful situations such as declining water quality and disease outbreaks. In aquaculture, fish often experience temporary fasting associated with handling, transfer, and transportation as part of routine husbandry practices, which may affect welfare and physiological status [1], as well as some diets that include food deprivation [2]. The adaptive capacity to withstand starvation and the evolutionary ability to restore homeostasis after refeeding vary significantly among fish species. These differences are influenced by factors such as the duration of food deprivation, environmental conditions, and the organism's metabolic and antioxidant defense strategies [3–5].

Fish are aerobic organisms that need oxygen to survive, but oxygen consumption leads to the formation of reactive oxygen species (ROS) that can damage biological molecules and eventually cause pathological conditions. It is believed that the most potentially harmful effects of oxygen are associated with these ROS that act as oxidants. An imbalance between oxidants and antioxidants is called oxidative stress [6]. The antioxidant defense system of an aerobic organism can prevent the production of free radicals, neutralize them, and repair the damage caused by them [7]. Enzymatic antioxidants such as catalase and glutathione peroxidase (GPx) convert H_2O_2 into H_2O, while other antioxidant systems scavenge free radicals and stabilize redox homeostasis. When these combined defenses fail to counter excessive prooxidant activity, hydrogen peroxide and other ROS accumulate, increasing oxidative stress [8].

Food deprivation has been reported to affect antioxidant defenses [3, 9–12]. Nevertheless, existing studies have largely focused on prolonged starvation, chronic nutritional stress, or single time-point measurements, providing limited insight into the early redox responses to short-term feed deprivation and the physiological dynamics of refeeding. In particular, the extent to which short-term starvation perturbs antioxidant defenses and whether refeeding rapidly restores redox homeostasis remains poorly understood. Therefore, the present study aimed to investigate the effects of short-term food deprivation followed by refeeding on oxidative stress indices and antioxidant defense responses in Asian seabass. By focusing on early redox adjustments rather than chronic starvation, this study provides physiologically relevant insights into how feeding interruptions influence oxidative balance in fish, with implications for both stress physiology and aquaculture management.

2 | Materials and Methods

2.1 | Experimental Design

Two hundred and forty Asian seabass juveniles (mean weight 35 ± 9 g) were purchased and transferred to the laboratory. After two week of acclimatization, fish were randomly distributed into 16 300 L cylindrical polyethylene tanks ($n = 15$). Fish were hand-fed to satiation with a commercial Barramundi feed (SB303, Faradane Iran, 6 mm, Pr: 50%–52%, Fat: 11%–13%, Ash: 9%–13%, Moisture: 6%–8%) twice daily at 10:00 a.m. and 17:00 p.m. Salinity of water kept at 20 ± 1 ppt, and water change rate was 20%–50% daily. Water quality parameters including temperature, dissolved oxygen, ammonia, and pH were measured daily (Table 1). Four experimental groups were used in this study (each in triplicate): Control group (without food deprivation), Group 1 (2 days of food deprivation), Group 2 (4 days of food deprivation), and Group 3 (8 days of food deprivation), followed by 16 days of refeeding. The design of the study was in such a way that refeeding started on the same day in all groups. Sampling was done at the beginning of the experiment, after starvation and at the end of the refeeding period. All fish in each tank were weighed individually. Percentage weight gain calculated by standard formula [13].

During the study, all groups were hand-fed to satiation at 10:00 a.m. and 17:00 p.m. Sampling was done at the beginning of the experiment and at the end of the refeeding period. Three fish from each tank were randomly collected using a hand net and euthanized by a high dose of 2-phenoxyethanol. Then, the fish was dissected with a scalpel. The muscle and liver were removed and rinsed with distilled water. Tissues were homogenized with a ratio of 1:10 (w/v) in 100 mM potassium phosphate buffer, 100 mM potassium chloride, and 1 mM EDTA with a pH of 7.4. Then, the homogenized samples were centrifuged at 15,000x g for 30 min at 4°C and the supernatant was used to measure the activity of antioxidant enzymes [14]. The supernatant is captured and stored in −80°C until analysis.

2.2 | Biochemical Analysis

Antioxidant enzyme activity was investigated in muscle and liver homogenates. Catalase (CAT, E.C. 1.11.1.6) activity was determined in the homogenates by the decrease in absorbance at 240 nm ($e = 40\ \mathrm{M}^{-1}\cdot\mathrm{cm}^{-1}$) using 50 mM H_2O_2 as substrate [15]. Superoxide dismutase (SOD, E.C. 1.15.1.1) activity was determined as the degree of inhibition of cytochrome c reduction by O_2^- produced by the xanthine oxidase/hypoxanthine system at 550 nm, described by McCord and Fridovich [16]. The GPx (E. C. 1.11.1.9) activity was determined by the Ransel kit (Randox, Ireland) as described by company. The malondialdehyde (MDA) content of muscle and liver was assayed according to Buege and Aust [17]. Briefly, tissue homogenates were combined with a reaction mixture at a ratio of 1:2 (v/v) containing 15% (w/v) trichloroacetic acid, 0.375% (w/v) thiobarbituric acid, and 0.25 M hydrochloric acid and mixed thoroughly. The mixture was then incubated in a boiling water bath for 15 min. Following cooling to room temperature, samples were centrifuged at 1000x g for 10 min to remove precipitated material. The absorbance of the resulting clear supernatant was measured at 535 nm. The protein concentrations of the supernatant solutions were determined by the Biuret method, using bovine serum albumin (BSA) as the standard. All data are presented as mg protein/tissue.

2.3 | Data Analysis

Data are shown as mean ± SE. Means were analyzed by one-way analysis of variance (ANOVA) using SPSS 20 and Tukey's post hoc if a significant difference was indicated. $p < 0.05$ was the accepted significance level.

3 | Results

No mortality was recorded during either the starvation or refeeding phases of the experiment. Weight gain percentage exhibited an inverse relationship with the duration of starvation, as the lowest weight gain was seen in the group subjected to 8 days of fasting ($p < 0.05$; Figure 1).

In muscle tissue, the activities of CAT, SOD, and GPx showed a general decrease following the refeeding period compared to poststarvation levels; however, these changes were not statistically significant between experimental groups ($p > 0.05$). Similarly, MDA level in muscle tissue remained stable throughout the experimental period, with no significant differences observed either between experimental groups or sampling times ($p > 0.05$; Figure 2).

In contrast, liver tissue exhibited a more pronounced response to the duration of starvation. SOD activity increased significantly at the end of the starvation period, peaking in the 8 day starvation group, which showed significantly higher values compared to the other groups ($p < 0.05$; Figure 2). Following refeeding, SOD activity declined across all treatments, returning to baseline levels by the end of the experimental period.

TABLE 1 | Water quality parameters during the period of study.

Temperature (°C)	Dissolved oxygen (mg/L)	Ammonia (mg/L)	pH
27.5 ± 0.5	7.5 ± 0.65	0.2 ± 0.5	8.5 ± 0.1

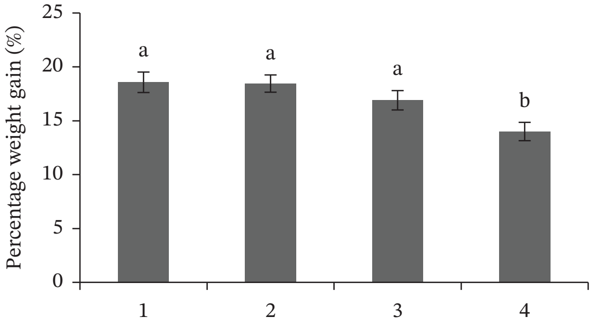

FIGURE 1 | The effect of short-term starvation and refeeding on the percentage weight gain in Asian seabass in different experimental groups. Different letters indicate changes compared to the control group ($p < 0.05$). 1: control group, 2: 2 days fasting, 3: 4 days fasting, 4: 8 days fasting.

A similar trend was observed for CAT and GPx activities in the liver (Figure 3). Both enzymes demonstrated significantly elevated activities in the 8 day starvation group at the end of the fasting period ($p < 0.05$), followed by a reduction to basal levels after refeeding, with no significant differences among treatments at the end of the experimental period ($p > 0.05$).

The MDA value in the liver also increased with prolonged starvation, reaching the highest levels in the 8 day starvation group. However, this increase was not statistically significant when compared to the control group ($p > 0.05$, Figure 3).

4 | Discussion

Weight gain percentage decreased in Asian seabass by increase in starvation period. Diminishment in weight caused by starvation could be related to decrease in availability of nutrient resources in *Acipenser persicus* [18]. Food deprivation causes degradation of endogenous lipids, glycogen, and proteins in an arrangement to preserve the homeostasis and driving weight loss [19]. Yang et al. [20] reported that starvation led to decrease in final weight in Yangtze sturgeon (*Acipenser dabryanus*).

Based on our findings, antioxidant enzyme activities in the muscle tissue of Asian seabass remained unchanged across all experimental treatments throughout the study period. In contrast, hepatic antioxidant enzyme activities increased significantly following 8 days of starvation compared with the other treatments ($p < 0.05$). However, enzyme activities in the liver returned to levels comparable to the control after refeeding, with no significant differences observed among groups ($p > 0.05$).

Simultaneous increases in CAT and GPx activities are generally interpreted as evidence of elevated intracellular hydrogen peroxide production [21]. Consistent with this interpretation, Bayir et al. [9] reported that both total and partial food deprivation enhanced ROS production in the liver and gills of brown trout (*Salmo trutta*). Similarly, starvation-induced increases in ROS generation have been documented in *Sparus macrocephalus* [22] and *Pseudosciaena crocea* [23].

In the present study, antioxidant enzyme activities increased after 8 days of starvation compared with the control group, whereas in *Sparus macrocephalus* a comparable elevation in antioxidant activity was observed after only 3 days of food deprivation [22]. In contrast, prolonged fasting in *Oncorhynchus mykiss* resulted in decreased CAT and GPx activities, which have been attributed to reduced enzyme synthesis and enhanced lipid peroxidation under extended nutritional stress [24]. Conversely, Guderley et al. [25] reported increased hepatic GPx and glutathione S-transferase (GST) activities in starved Atlantic cod (*Gadus morhua*), indicating activation of antioxidant defenses in response to fasting.

Differences in antioxidant responses among tissues and enzymes under food deprivation have also been widely reported. For instance, Antonopoulou et al. [26] observed no significant changes in antioxidant enzyme activities in the liver or white muscle of European seabass (*Dicentrarchus labrax*), while activities of SOD, CAT, and GPx increased in the intestine. Similarly, in rock bream (*Oplegnathus fasciatus*), short-term starvation upregulated hepatic sod and cat expression, whereas gpx expression remained unchanged [27]. Such variability among studies may reflect differences in species, tissue-specific metabolic roles, and the duration of food deprivation, particularly when the starvation period is insufficient to disrupt existing redox equilibrium or establish a new physiological steady state [28].

Increased activity of CAT and GPX simultaneously represents increased production of H_2O_2 throughout the cell [21]. Bayir et al. [9] reported that total or partial food deprivation enhances the production of ROS in the liver and gills of brown trout (*Salmo trutta*). Moreover, enhanced ROS rates have been reported as a consequence of starvation in *Sparus macrocephalus* [22] and yellow croaker (*Pseudosciaena crocea*) [23].

In this study, the activity of antioxidant enzyme increased 8 days after starvation in comparison to the control, but in *Sparus macrocephalus,* this increase in antioxidant enzymes activity was recorded 3 days after starvation [22]. In *Oncorhynchus mykiss* activity of CAT and GPx decreased due to the increase in fasting time. These could be related to decrease in enzyme synthesis and also an increase in lipid peroxidation [24]. Also, fasting leads to an increase in GPX and GST activities in the liver of the starved Atlantic cod, *Gadus morhua* [25]. They also found that food deprivation leads to increased GPX and GST activity in the liver of starving Atlantic cod.

Differences in the response of different organs to the effect of food deprivation on antioxidant defense have been shown in different studies. In European seabass, *Dicentrarchus labrax*, no change in liver and white muscle antioxidant enzyme activity was recorded, while in intestine, activity of SOD, CAT, and GPX increased [26]. Differences in the response of antioxidant enzymes to food deprivation have also been reported. For example, in rockbream, *Oplegnathus fasciatus*, expression of *sod* and *cat* genes in the liver increased following short-term starvation, while expression of *gpx* did not change [27]. The difference in the results obtained could be related to the period of study that was not enough to break the existing equilibrium or create a new equilibrium [28].

MDA, a secondary product of lipid peroxidation, is commonly used as an indicator of oxidative damage to membrane lipids [29]. However, it should be noted that MDA reflects lipid peroxidation specifically and may not fully represent oxidative damage to other macromolecules or overall cellular redox status. In the

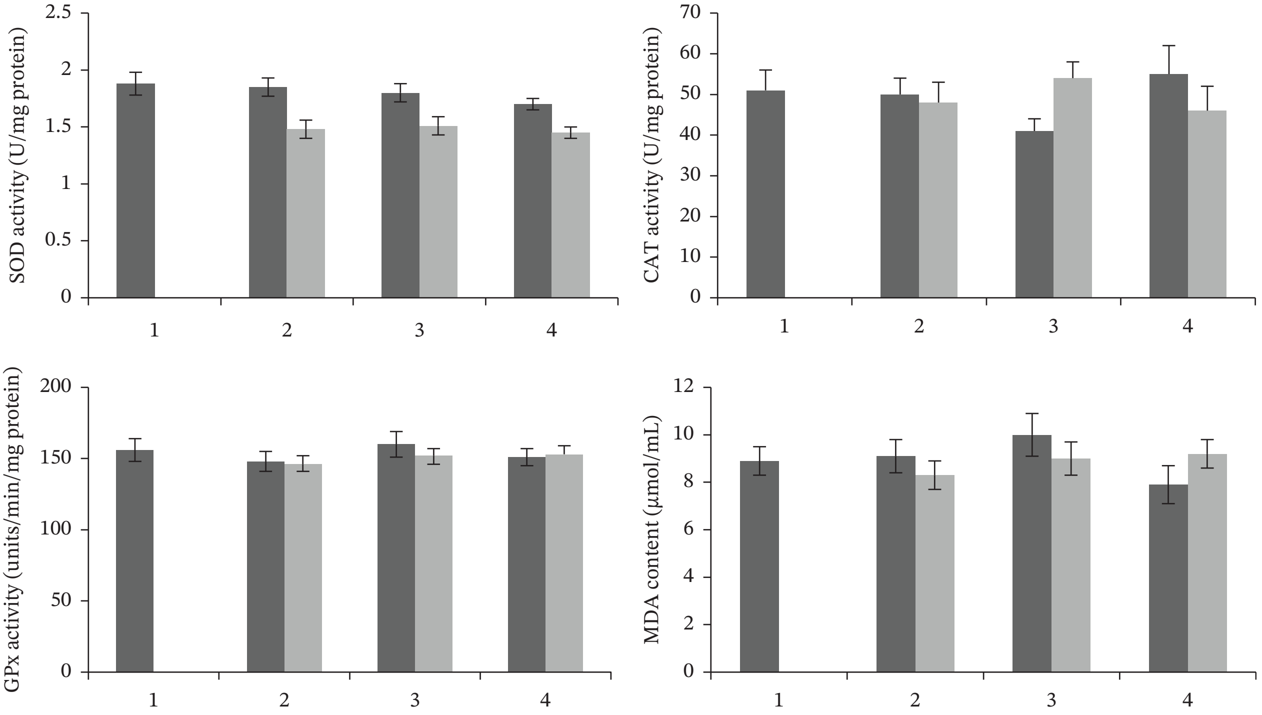

FIGURE 2 | The effect of short-term starvation and refeeding on the antioxidant defense in Asian seabass muscle tissue in different experimental groups. 1: control group, 2: 2 days fasting, 3: 4 days fasting, 4: 8 days fasting.

present study, no significant changes in muscle MDA content were observed among the experimental groups ($p > 0.05$). Similarly, a decrease in lipid peroxidation has been reported in *Oncorhynchus mykiss* under starvation, suggesting that reduced metabolic activity and depletion of muscle energy reserves may limit ROS generation in this tissue [24]. In addition, white muscle is predominantly anaerobic and receives lower blood supply and oxygen availability compared with metabolically active organs

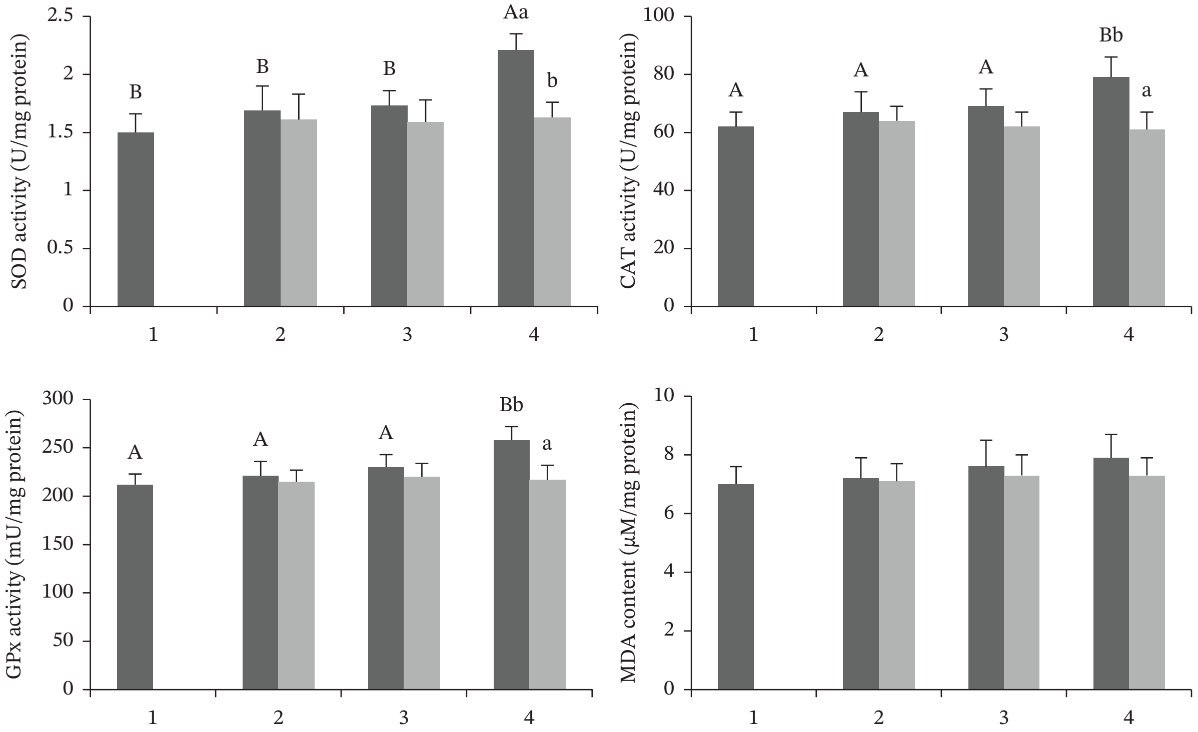

FIGURE 3 | The effect of short-term starvation and refeeding on the antioxidant defense in Asian seabass liver tissue in different experimental groups. Capital letters represents significant differences between the control group and other experimental groups, while small letters indicate significant differences in each group. ($p < 0.05$). 1: control group, 2: 2 days fasting, 3: 4 days fasting, 4: 8 days fasting.

such as the liver [30], which may further constrain lipid peroxidation processes.

Despite increased antioxidant enzyme activities in the liver, MDA levels remained unchanged across treatments. This suggests that the upregulation of antioxidant defenses was sufficient to counterbalance prooxidant processes and prevent excessive lipid peroxidation. While increases in hepatic MDA following food deprivation have been reported in *Umbrina cirrose* [31], *Sparus aurata* [32], and *Mesopotamichthys sharpeyi* [11], species-specific differences in metabolic regulation and antioxidant capacity likely explain these contrasting outcomes. For example, starvation in *Coilia nasus* has been shown to upregulate hepatic lipid catabolism while simultaneously suppressing antioxidant capacity, leading to elevated MDA accumulation [33]. Collectively, these findings indicate that MDA responses to starvation are highly context-dependent and should be interpreted alongside antioxidant enzyme activity to provide a more comprehensive evaluation of oxidative status.

Our results showed that short-term starvation did not increase ROS production in the muscle of Asian sea bass; however, in the liver, 8 days of starvation led to an oxidant-prooxidant imbalance but did not affect MDA content. The present findings should be interpreted with consideration of certain limitations. Although key antioxidant enzymes were quantified, additional antioxidant components such as GR, GST, GSH, and nonenzymatic antioxidants were not assessed. Future studies incorporating a broader suite of redox biomarkers, together with direct measurements of reactive oxygen species, would provide a more comprehensive understanding of antioxidant strategies and oxidative balance during nutritional stress in Asian seabass.

Author Contributions

Marjan Norouzi: investigation and statistical analysis. Emel Armashi: investigation. Preeta Kochanian: supervision and design of study. Ali Shariari: biochemical analysis. Amirparviz Salati: preparing draft.

Funding

There is no funding to report.

Ethics Statement

The authors confirm that the ethical policies of the journal, as noted on the journal's author guidelines page, have been adhered to, and the appropriate ethical review committee approval has been received. The US National Research Council's guidelines for the Care and Use of Laboratory Animals were followed.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data will be available on request.

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