Effects of Compensatory Feeding after Starvation on Growth Performance, Serum Biochemical Indices, Digestive Enzymes and Antioxidant Enzyme Activities in Juvenile Megalobrama amblycephala during High Temperature Season: Postprint

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Abstract

This study aimed to investigate the effects of compensatory feeding following starvation during the hot season on growth performance, serum biochemical parameters, intestinal digestive enzyme activities, and hepatic antioxidant enzyme activities in juvenile Megalobrama amblycephala.

Full Text

Effects of Compensatory Feeding after Starvation on Growth Performance, Serum Biochemical Indices, Digestive Enzyme Activities, and Hepatic Antioxidant Enzyme Activities of Juvenile Blunt Snout Bream (Megalobrama amblycephala) in High Temperature Season

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Abstract: This study investigated the effects of compensatory feeding after starvation on growth performance, serum biochemical indices, intestinal digestive enzyme activities, and hepatic antioxidant enzyme activities of juvenile blunt snout bream (*Megalobrama amblycephala*) during the high temperature season. Five experimental groups were established with starvation periods of 0, 5, 10, 15, and 20 days, followed by 3 weeks of compensatory feeding, designated as S0 (control), S5, S10, S15, and S20 groups, respectively. The results demonstrated that: (1) The S10 group exhibited the highest final body weight, weight gain rate, specific growth rate, and feed efficiency ratio, with significantly increased daily feed intake and feed efficiency compared to the control group ($P<0.05$), indicating that compensatory growth in juvenile blunt snout bream was achieved through enhanced feeding rate and feed conversion efficiency. (2) Serum triglyceride levels in S5 and S10 groups were significantly lower than in other groups ($P<0.05$), while serum aspartate transaminase activity in S20 group was significantly higher than in all other groups ($P<0.05$), suggesting that prolonged starvation may cause liver damage. No significant differences were observed among groups in serum glucose, total protein, albumin, total cholesterol, or alanine aminotransferase activity ($P>0.05$). (3) After compensatory feeding, intestinal lipase activity in S15 group was significantly higher than in other groups ($P<0.05$), and intestinal protease activity in S20 group was significantly higher than in all groups except S5 ($P<0.05$), indicating that compensatory feeding after long-term starvation may enhance protein digestive capacity. (4) Hepatic superoxide dismutase (except in S5 and S20 groups) and catalase activities in compensatory feeding groups were significantly higher than in the control group ($P<0.05$), while hepatic glutathione peroxidase activity in S20 group was significantly lower than in other compensatory feeding groups ($P<0.05$), suggesting that long-term starvation may suppress the recovery of antioxidant capacity. In conclusion, juvenile blunt snout bream subjected to 10 days of starvation followed by 3 weeks of compensatory feeding achieved optimal compensatory growth effects during the high temperature season, with concurrent enhancement of immune and antioxidant capacity.

Keywords: blunt snout bream (*Megalobrama amblycephala*); compensatory feeding after starvation; growth performance; serum biochemical parameters; digestive enzyme; antioxidant enzyme

Introduction

In natural aquatic ecosystems, fish experience starvation stress or nutritional deficiency due to uneven food distribution, limited mobility, and other constraints caused by seasonal changes, climate fluctuations, and long-term ecological variations [1-2]. Under aquaculture conditions, intensive farming practices have exponentially pushed the productivity limits of cultured fish [3], and fish may also encounter starvation due to insufficient or uneven feeding or improper feeding strategies [4-5]. Fish possess certain physiological and ecological adaptations to starvation stress. After short-term starvation and subsequent refeeding, fish may exhibit faster growth than continuously fed individuals, a phenomenon known as compensatory growth. However, beyond certain limits, insufficient feed intake or declining physiological function can lead to digestive failure and loss of compensatory growth capacity [6-7].

Previous studies on compensatory growth in fish have reported on various freshwater species including Nile tilapia (*Oreochromis niloticus*) [8-9], gibel carp (*Carassius auratus gibelio*) [10], red crucian carp [11], and gilthead seabream (*Sparus aurata*) [12]. However, few studies have investigated compensatory growth in blunt snout bream (*Megalobrama amblycephala*), with only Qiao et al. [13] examining the effects of starvation and refeeding on growth, body composition, and intestinal digestive enzyme activities. Research has shown that high temperatures affect growth and feeding rates in blunt snout bream, potentially causing mortality under severe conditions. High temperature stress induces cellular stress responses, disrupts the antioxidant system, and reduces immune function, while prolonged exposure increases susceptibility to pathogens and dramatically decreases disease resistance [14-15]. Therefore, this study focused on whether compensatory growth occurs in blunt snout bream under high temperature conditions.

Blunt snout bream, also known as Wuchang fish, belongs to the family Cyprinidae, subfamily Cultrinae. With a long aquaculture history, this species is valued for its delicious meat, rapid growth, and high survival rate, making it an important economically cultured freshwater fish in China [16-17]. Previous studies have documented changes in blood biochemical indices of blunt snout bream under starvation [18]. This experiment investigated whether compensatory feeding after starvation could achieve dual benefits of rapid growth and enhanced immune function in juvenile blunt snout bream during high temperature season, providing reference for scientific feeding strategies.

1.1 Experimental Design

Juvenile blunt snout bream were obtained from the Nanquan Fishery Farm of the Freshwater Fisheries Research Center, Chinese Academy of Fishery Sciences, with an initial average body weight of (22.03$±$0.04) g. Based on previous studies [1,19-21], experimental fish were subjected to starvation periods of 0, 5, 10, 15, and 20 days, followed by 3 weeks of compensatory feeding, forming five groups designated as S0 (control), S5, S10, S15, and S20. Each group had three replicates with 18 fish per replicate, with stocking details shown in Table 1 . Prior to the formal experiment, fish were acclimated for 2 weeks using commercial feed (32% protein, 6% lipid) from Tongwei Company to adapt to the culture environment, and were fasted for 24 hours before the trial began.

The experimental system consisted of 200 L circular plastic tanks containing 140 L recirculating water, with continuous 24-hour aeration. Dissolved oxygen concentration was maintained at 5.4-6.8 mg/L, water temperature at (32.98$±0.36)°*C*, *pHat*7.7±$0.2, and ammonia nitrogen concentration below 0.1

mg/L. During the compensatory feeding period, fish were fed to satiation three times daily (08:00, 12:00, 16:00) with commercial feed from Tongwei Company, with slow feeding until no further feeding activity was observed.

Throughout the experiment, fish swimming behavior, feeding activity, and physical condition were monitored daily. Any dead fish were removed, counted, and weighed, with necropsy performed to observe pathological changes in internal organs. Daily feed intake and remaining feed were recorded.

1.2 Sample Collection

At the end of the feeding trial, fish were fasted for 24 hours before sampling. Fish in each tank were counted and weighed. Three fish were randomly selected from each tank, anesthetized with MS-222, and immediately subjected to caudal vein blood collection using a syringe. Blood samples were centrifuged at 7,500 r/min for 5 min at 4 °C to separate serum, which was stored at -80 °C for subsequent analysis. Following blood collection, fish were dissected to obtain intestinal and liver samples, which were stored at -20 °C for further analysis.

1.3 Index Measurement

The following parameters were calculated: weight gain rate (WG), specific growth rate (SGR), feed efficiency ratio (FER), daily feed intake (DFI), hepatosomatic index (HSI), viscerosomatic index (VSI), condition factor (CF), and survival rate (SR):

Weight gain rate (%) = 100 × (Wt - W0) / W0
Specific growth rate (%/d) = 100 × (ln Wt - ln W0) / t
Feed efficiency ratio = (Wt - W0) / F
Daily feed intake (g/d) = F / t
Hepatosomatic index (%) = 100 × Wh / Wb
Viscerosomatic index (%) = 100 × Wv / Wb
Condition factor (%) = 100 × Wb / L^3
Survival rate (%) = 100 × Nt / N0

Where: W0 = initial average body weight (g); Wt = final average body weight (g); t = feeding duration (d); F = average total feed intake per fish (air-dry basis) (g); Wh = final liver weight per fish (g); Wv = final viscera weight per fish (g); Wb = final body weight per fish (g); L = final body length per fish (cm); N0 = initial fish number; Nt = final fish number.

Serum glucose (GLU), total protein (TP), albumin (ALB), triglycerides (TG), cholesterol (TC) levels, and activities of alkaline phosphatase (ALP), alanine aminotransferase (ALT), and aspartate transaminase (AST) were measured using an automatic biochemical analyzer with reagent kits purchased from Shenzhen Mindray Bio-Medical Electronics Co., Ltd.

Intestinal and liver samples were homogenized separately with 84% physiological saline at a 9:1 mass-to-volume ratio to prepare 10% homogenates. The homogenates were centrifuged at 3,000 r/min for 10 min at 4 °C, and the supernatants were aliquoted for determination of intestinal amylase (AMS), lipase (LPS), protease (PTS) activities, and hepatic superoxide dismutase (SOD), catalase (CAT), and glutathione peroxidase (GPX) activities. All enzyme activities were measured using commercial assay kits purchased from Nanjing Jiancheng Bioengineering Institute.

1.4 Data Processing

Experimental data were analyzed using one-way ANOVA in SPSS 19.0 statistical software. Differences were considered significant at $P<0.05$, and Duncan' s multiple range test was used for post-hoc comparisons when significant differences were detected. Results are presented as mean ± standard error (SE).

Results

2.1 Effects of Compensatory Feeding after Starvation on Growth Performance of Juvenile Blunt Snout Bream in High Temperature Season

The effects of compensatory feeding after starvation on growth performance are shown in Table 1 . Survival rate was 100% in all groups. With equal compensatory feeding duration, final body weight, specific growth rate, weight gain rate, and feed efficiency ratio initially increased then decreased with prolonged starvation duration, with S10 group showing the best performance. This group achieved the highest final body weight (55.58 g), specific growth rate (6.10%/d), weight gain rate (151.65%), and feed efficiency ratio (0.98), significantly higher than all other groups ($P<0.05$). Viscerosomatic index in S10 and S15 groups was significantly higher than in S0 group ($P<0.05$), with no significant differences between other starvation-refeeding groups and S0 group ($P>0.05$). Hepatosomatic index in S15 group was significantly higher than in S0, S5, and S10 groups ($P<0.05$), but not significantly different from S20 group ($P>0.05$). Condition factor showed no significant differences among all groups ($P>0.05$).

2.2 Effects of Compensatory Feeding after Starvation on Serum Biochemical Indices of Juvenile Blunt Snout Bream in High Temperature Season

The effects on serum biochemical indices are presented in Table 2 . With equal compensatory feeding duration, serum TG levels in S5 and S10 groups were significantly lower than in all groups except S20 ($P<0.05$). Serum ALP activity in S10 group was significantly higher than in S0 group ($P<0.05$), with no significant differences from other starvation-refeeding groups ($P>0.05$). Serum AST activity was highest in S20 group, significantly higher than in all other groups ($P<0.05$). No significant differences were observed among groups in serum GLU, TP, ALB, TC levels, or ALT activity ($P>0.05$).

2.3 Effects of Compensatory Feeding after Starvation on Intestinal Digestive Enzyme Activities of Juvenile Blunt Snout Bream in High Temperature Season

The effects on intestinal digestive enzyme activities are shown in Table 3 . With equal compensatory feeding duration, intestinal LPS activity was highest in S15 group, significantly higher than in all other groups ($P<0.05$), while other starvation-refeeding groups showed no significant differences from S0 group ($P>0.05$). Intestinal PTS activity in S20 group was significantly higher than in all groups except S5 ($P<0.05$), with no significant differences between other starvation-refeeding groups and S0 group ($P>0.05$). Intestinal AMS activity remained stable with no significant differences among all groups ($P>0.05$).

2.4 Effects of Compensatory Feeding after Starvation on Hepatic Antioxidant Enzyme Activities of Juvenile Blunt Snout Bream in High Temperature Season

The effects on hepatic antioxidant enzyme activities are presented in Table 4 . With equal compensatory feeding duration, hepatic SOD (except in S5 and S20 groups) and CAT activities in all starvation-refeeding groups were significantly higher than in S0 group ($P<0.05$). Hepatic GPX activity in S20 group was significantly lower than in other starvation-refeeding groups ($P<0.05$).

Discussion

3.1 Effects of Compensatory Feeding after Starvation on Growth Performance of Juvenile Blunt Snout Bream in High Temperature Season

Compensatory growth in fish can be categorized into four types based on compensation magnitude: hyper-compensation, full compensation, partial compensation, and no compensation [22-23]. The occurrence and extent of compensatory growth are determined by comparing body weight and specific growth rate between continuously fed control groups and compensatory feeding groups over the same period [24]. Studies have shown that fish exhibit reduced feed intake and decreased energy allocation to growth during high temperature seasons, resulting in slower growth under thermal stress [25-26]. Our results indicate that S10 group displayed optimal growth performance with hyper-compensatory growth effects, while other starvation-refeeding groups achieved full compensatory growth. These findings align with previous studies: rainbow trout (*Salmo gairdneri*) showed hyper-compensatory growth with higher weight gain after cyclic starvation-feeding for 3 weeks compared to continuously fed controls [27]; GIFT Nile tilapia (*Oreochromis niloticus*) exhibited full compensatory growth after 5 days starvation followed by 15 days refeeding, but only partial compensation after 10 or 15 days starvation with equivalent refeeding duration [28]. Conversely, short-term feed restriction (within 3 weeks) failed to induce compensatory growth in Atlantic cod (*Gadus morhua*) [29].

The physiological mechanisms underlying compensatory growth remain inconclusive. Starved fish may achieve enhanced growth through increased feed intake, reduced metabolic expenditure, or improved feed conversion efficiency, thereby increasing net energy available for growth [30-31]. In this study, both daily feed intake and feed efficiency ratio were high in S10 group, suggesting that these fish enhanced growth by simultaneously increasing appetite and improving feed conversion, consistent with mechanisms reported in Pacific salmon (*Oncorhynchus* spp.) [32] and gibel carp [33]. Other starvation-refeeding groups achieved compensatory growth primarily through increased feed intake, similar to observations in Siberian sturgeon (*Acipenser baerii*) [19]. Therefore, the conditions, magnitude, and mechanisms of compensatory growth may depend on starvation duration and method, as well as species, fish size, and experimental conditions.

3.2 Effects of Compensatory Feeding after Starvation on Serum Biochemical Indices of Juvenile Blunt Snout Bream in High Temperature Season

Serum biochemical indices serve as important indicators for evaluating nutritional health status and environmental adaptation in fish, reflecting physiological condition and metabolic function [34]. Glucose is an essential fuel for most tissues, and under normal conditions, blood glucose concentration is dynamically regulated by the nervous and endocrine systems [35], making its stability crucial for normal life activities [36-37]. The absence of significant differences in serum GLU levels among all groups suggests that blunt snout bream adaptively regulated glucose homeostasis to maintain normal physiological functions during starvation and compensatory feeding.

Serum TG plays an important role in lipid metabolism [38]. The significantly lower TG levels in S5 and S10 groups indicate physiological activities related to endogenous lipid transport mechanisms, indirectly suggesting that fish extensively mobilized body fat to supplement energy for accelerated growth after compensatory feeding. This phenomenon has been observed in black seabream (*Acanthopagrus schlegeli*) juveniles [39]. ALP is an important metabolic regulator involved in phosphate group transfer and calcium-phosphorus metabolism, playing a crucial role in nutrient absorption [40]. The highest ALP activity in the group with optimal growth performance supports this theory. ALT and AST are important aminotransferases widely present in mitochondria [41], closely related to protein metabolism. The highest serum AST activity in S20 group suggests potential liver cell damage and increased membrane permeability, leading to substantial AST leakage into the bloodstream, indicating that prolonged starvation may cause organic changes in the liver.

3.3 Effects of Compensatory Feeding after Starvation on Intestinal Digestive Enzyme Activities of Juvenile Blunt Snout Bream in High Temperature Season

Under feed restriction or nutritional deficiency, fish must regulate various enzyme activities to improve utilization efficiency of stored nutrients for survival [42-43]. If starvation duration is not excessive and the digestive system remains functionally intact, sensory stimulation during compensatory feeding triggers central nervous system signals to digestive glands [44-45], resulting in rapid increases in digestive enzyme secretion to levels comparable to or even exceeding those of continuously fed fish, reflecting compensatory feeding and digestive capacity [46]. In this study, increased intestinal LPS activity in starvation-refeeding groups accelerated lipid energy supply, consistent with previous findings that blunt snout bream primarily utilizes fat as an energy source during starvation [13,18], and similar to results in Chinese sucker (*Myxocyprinus asiaticus*) [19] and Jian carp (*Cyprinus carpio* var. Jian) [47].

However, S20 group showed lower intestinal LPS activity but higher PTS activity, possibly because prolonged starvation depleted fat reserves and forced the fish to utilize protein as an energy source, thereby enhancing protein digestion capacity after refeeding. Studies have reported that Japanese seabass (*Lateolabrax japonicus*) sequentially mobilized muscle fat followed by protein during starvation, with tissue protein showing a recovery trend after refeeding [48]. Similarly, black seabream utilized body fat and protein sequentially during starvation, primarily relying on protein catabolism for survival [39]. The type and sequence of mobilized body reserves during starvation depend on starvation severity, fish size, and species, while the priority of energy allocation for reserve restoration after compensatory feeding also varies.

3.4 Effects of Compensatory Feeding after Starvation on Hepatic Antioxidant Enzyme Activities of Juvenile Blunt Snout Bream in High Temperature Season

Both starvation stress and high temperature stress can induce excessive reactive oxygen species (ROS) production in fish. The increased activities of hepatic SOD and CAT in starvation-refeeding groups (except S5 and S20) suggest enhanced antioxidant capacity to eliminate ROS and protect the body from oxidative damage, consistent with results from cyclic starvation-refeeding studies in Jian carp [41]. Research on Sydney rock oyster (*Saccostrea glomerata*) demonstrated that hepatic SOD and CAT activities were suppressed during starvation but increased after refeeding, emphasizing the important influence of stress duration on enzyme activities [53]. The lowest hepatic GPX activity in S20 group suggests that prolonged starvation may lead to failure of antioxidant defense, increasing cellular sensitivity to oxidative damage. The underlying mechanisms of how compensatory feeding after starvation affects hepatic antioxidant enzyme activities in juvenile blunt snout bream remain unclear and require further investigation at the molecular level.

In conclusion, juvenile blunt snout bream subjected to 10 days of starvation followed by 3 weeks of compensatory feeding during the high temperature season achieved optimal compensatory growth through enhanced feed intake and feed efficiency, with concurrent improvement in antioxidant capacity.

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