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Feeding frequency affects stress, innate immunity and disease resistance of juvenile blunt snout bream *Megalobrama amblycephala*

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ABSTRACT

This study aimed to evaluate the effects of feeding frequency on stress, innate immunity and disease resistance of juvenile blunt snout bream *Megalobrama amblycephala* (average weight: 9.92 ± 0.06 g). Fish were randomly assigned to one of six feeding frequencies (1, 2, 3, 4, 5 and 6 times/day) following the same ration size for 8 weeks. After the feeding trial, fish were challenged by *Aeromonas hydrophila* and cumulative mortality was recorded for the next 10 days. Daily gain index of fish fed 3–5 times/day was significantly higher than that of the other groups. High feeding frequencies induced significantly elevated plasma levels of both cortisol and lactate. Fish fed 3–4 times/day exhibited relatively low liver catalase and glutathione peroxidase activities as well as malondialdehyde contents, but obtained significantly higher reduced glutathione levels and post-challenged haemato-immunological parameters (include blood leukocyte and erythrocyte counts as well as plasma lysozyme, alternative complement, acid phosphatase and myeloperoxidase activities) compared with that of the other groups. After challenge, the lowest mortality was observed in fish fed 4 times/day. It was significantly lower than that of fish fed 1–3 times/day, but exhibited no statistical difference with that of the other groups. In conclusion, both low and high feeding frequencies could cause oxidative stress of juvenile *M. amblycephala*, as might consequently lead to the depressed immunity and reduced resistance to *A. hydrophila* infection. The optimal feeding frequency to enhance growth and boost immunity of this species at juvenile stage is 4 times/day.
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1. Introduction

The growth of fish is largely governed by a number of factors, including food type, ration size, feeding frequency, food intake and its ability to absorb nutrients [1]. Among these, feeding frequency should be given high priority due to the fact that the survival and growth of fish at the early life stages is tightly regulated by feeding regimes [2]. Optimizing feeding frequency may not only improve the production efficiency by enhancing growth performance [3], but also minimize feed wastage, thus leading to improvement in culture environment [2] and/or reduction in size heterogeneity [1,3]. Considering this, the influence of feeding frequency on fish growth has been extensively investigated during the past few decades. However, the optimal feeding frequency for fish has generally been determined based on growth performance and body composition. Its potential effects on health status and welfare have while received little attention. Nowadays, consumers demand responsible aquaculture practices to provide "welfare friendly" products. Accordingly, considerable concerns have risen about managing protocols to safeguard the welfare of farmed fish [4]. If feeding frequency affects the stress and health condition of fish, great caution must be exercised when designing feeding strategies in practical aquaculture, since poor welfare usually lead to undesirable fish quality and low production efficiency [4,5]. Thus, it is quite necessary that health status is taken into account when evaluating the optimum feeding frequency for fish beside the growth. This is acceptable both economically and ethically, and would warrant the economic viability of fish production.

To date, there is relatively little information on whether or not feeding frequency could affect the stress and immune functions of fish [6]. According to a latest review, feeding could be one of the biggest stressors for fish under farming conditions, since they are challenged with artificial diets and feeding strategies which are quite different from that in their natural environment [4]. Hence, a wrong choice of feeding regime would not only result in poor growth performance and feed utilization of fish [1–3], but also

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would increase its stress levels [5,6]. Since stress is a potential cause of increased susceptibility to disease, it is now generally accepted that a better understanding of the relations between stress and the immune system will improve our knowledge of fish health and welfare in practical aquaculture [7]. However, the behavioral dynamics of fish differ among seemingly similar stocks, as consequently creates variations in stress levels within the same treatment, thus emphasizing the complexity of fish stress study [1,3,8]. In previous studies, an enhanced innate immunity of fish has been commonly described under acute stress [9], whereas deleterious effects have been observed as a consequence of chronic and/or repeated acute stress [5,6]. Since feeding is a punctual event, it might be a repeated acute stressor for fish [4], as would inevitably bring some harmful effects like immunosuppressions and reduced disease resistance to fish [5,6]. Therefore, feeding frequency can undoubtedly influence the health status of fish. However, due to the fact that relevant literature is quite limited, the correlations between feeding frequency and immune responses of fish still remains poorly understood.

So far, the effects of nutritional factors on the antioxidant defenses of fish have been extensively investigated. However, whether or not feeding regimes could affect the oxidative status of fish is still unknown. In a previous study, it was reported that various biological and non-biological factors in practical aquaculture might cause oxidative stress of fish [10]. Since feeding could be one of the biggest stressors for fish, it would undoubtedly affect the physiological state of fish [4], as might consequently lead to the alteration of oxidative status. Recently, it has been shown that oxidative stresses might render fish susceptible to different diseases [10]. This might suggest a close connection between oxidative status and immune responses of fish, as is still poorly understood. Therefore, oxidative stress should also be considered when designing feeding strategies in farming conditions and assessing the welfare state of cultured fish.

Blunt snout bream (*Megalobrama amblycephala*) is an economically important herbivorous carp in China. In recent years, aquaculture of this fish at the juvenile stage has been restrained greatly by growth retardation, immunosuppression and high mortality caused by inappropriate feeding regimes, resulting in great economic loss. Therefore, it is quite urgent to investigate the correlations between feeding regimes and health status of this species. Bearing this in mind, the present study was conducted to evaluate the effects of feeding frequency on stress response, oxidative status and innate immunity of juvenile blunt snout bream. The data obtained here may provide some new insights into the immunomodulation of fish via feeding regime manipulations.

2. Materials and methods

2.1. Fish and the feeding trial

Juvenile blunt snout bream were obtained from the Fish Hatchery of Yangzhou (Jiangsu, China). Prior to the experiment, fish were reared in several floating net cages (2 × 1 × 1 m, L:W:H) for 2 weeks to acclimate to the experimental conditions. After the conditioning period, fish of similar size (average weight: 9.92 ± 0.06 g) were randomly distributed into 24 floating net cages (1 × 1 × 1 m, L:W:H) at a rate of 30 fish/cage. Then, fish were hand-fed for 8 weeks using a practical diet produced in our laboratory. This diet was formulated to satisfy the nutrient requirements of this species at juvenile stage according to our previous studies [11,12]. Formulation and proximate composition of the experimental diet was presented in Table 1. Fish were fed at a ration of 8% of the body weight per day for the first 4 weeks and 6% for the remaining 4 weeks. According to our previous study [11], this ration size could ensure the satiation of this species and minimize the feed waste.

Table 1
Formulation and proximate composition of the experimental diet.

Ingredients	(%)	Proximate composition	(%, Dry matter basis)
Fish meal	5.0	Crude protein	31.8
Soybean meal	30.0	Crude lipid	6.9
Cottonseed meal	15.0	Gross energy (MJ/kg)	18.6
Rapeseed meal	15.0		
Fish oil: soybean oil (1:1)	4.0		
Wheat bran	12.0		
Wheat middlings	11.0		
α-Starch	5.0		
$Ca(H_2PO_4)_2$	1.8		
Premix[a]	1.0		
Salt	0.2		

[a] Premix supplied the following minerals (g/kg) and vitamins (IU or mg/kg): $CuSO_4 \cdot 5H_2O$, 2.0 g; $FeSO_4 \cdot 7H_2O$, 25 g; $ZnSO_4 \cdot 7H_2O$, 22 g; $MnSO_4 \cdot 4H_2O$, 7 g; Na_2SeO_3, 0.04 g; KI, 0.026 g; $CoCl_2 \cdot 6H_2O$, 0.1 g; Vitamin A, 900000 IU; Vitamin D, 200000 IU; Vitamin E, 4500 mg; Vitamin K_3, 220 mg; Vitamin B_1, 320 mg; Vitamin B_2, 1090 mg; Niacin, 2800 mg; Vitamin B_5, 2000 mg; Vitamin B_6, 500 mg; Vitamin B_{12}, 1.6 mg; Vitamin C, 5000 mg; Pantothenate, 1000 mg; Folic acid, 165 mg; Choline, 60000 mg.

Feed amount was adjusted once every two weeks based on its growth rate reported previously [11,12]. Keeping the daily rations identical, differential feeding frequencies were chosen as the variable [2,3,6]. A total of six feeding frequencies (1, 2, 3, 4, 5 and 6 times/day) were adopted in this study. Each feeding frequency was tested randomly in four replicates. Fish were fed with utmost care at each meal to ensure that all feed was eaten. The initial body weight (g) for different treatments is presented as follows: 8.82 ± 0.08, 8.84 ± 0.09, 8.89 ± 0.10, 8.83 ± 0.06, 9.03 ± 0.04 and 8.79 ± 0.08. The feeding frequency and schedule followed in different treatments are presented in Table 2.

Cages were anchored approximately 5 m from the side of an outdoor pond (100 × 40 m) with an average water depth of 2 m. There was 3 m between cages. And one third of the pond water was changed weekly to ensure good water quality. Fish were held under natural photoperiod condition throughout the feeding trial. Water temperature ranged from 25 to 28 °C, pH fluctuated between 7.2 and 7.4, dissolved oxygen was maintained above 5.0 mg/L, and total ammonia nitrogen and nitrite was kept less than 0.2 and 0.005 mg/L, respectively, during the feeding trial.

2.2. Sampling and analysis

2.2.1. Sampling

At the end of the feeding trial, fish were starved for 24 h to evacuate the alimentary tract contents prior to sampling. 6 fish from each replicate with a total of 24 fish from each treatment were randomly selected and anesthetized in diluted MS-222 (tricaine methanesulfonate, Sigma, USA) at the concentration of 100 mg/L. Blood was quickly drawn from the caudal vein using heparinized syringes, then transferred immediately to heparinized capillary

Table 2
Daily feeding frequency and time for juvenile blunt snout bream during the feeding trial.

Feeding frequency (times/day)	Feeding time
1	17:00
2	07:00 and 17:00
3	07:00, 12:00 and 17:00
4	07:00, 10:00, 14:00 and 17:00
5	07:00, 09:30, 12:00, 14:30 and 17:00
6	07:00, 09:00, 11:00, 13:00, 15:00 and 17:00

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