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Effects of different predator stress on vulnerability to predation and the underlying physiological and behavioral mechanisms of this vulnerability in juvenile qingbo (*Spinibarbus sinensis*)

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ABSTRACT

Differences in the early life history would have a profound influence on the survival of the animal during the later life stages. We aimed to examine the effect of predator stress on vulnerability to predation in fish and the possible underlying behavioral and physiological mechanisms of this vulnerability. For this, we selected juvenile qingbo (*Spinibarbus sinensis*) as the prey and its natural predator, the southern catfish (*Silurus meridionalis*), as the predator. The juvenile qingbo were reared together with free predators (lethal group), caged predators (non-lethal group), and without predators (control group) for 4 weeks at 25 ± 0.5 °C. After predator acclimation, predation mortality was evaluated to understand the potential difference in vulnerability to predation among these treatments when prey fish from each treatment group was cultured together with the predator. To investigate the possible physiological and behavioral mechanisms of this vulnerability, we measured the following parameters under the same environmental conditions: metabolic response parameters such as routine metabolic rate (*RMR*), maximum metabolic rate (*MMR*), and metabolic scope ($MS = MMR - MS$); routine activity level determined by measuring the total movement distance, percentage of time spent moving or hiding, and average velocity while moving; fast-start escape performance determined by measuring the response latency, maximum swimming speed (V_{max}), and maximum acceleration (A_{max}). Both the lethal and non-lethal group fish exhibited significantly lower predation mortality, greater boldness (as suggested by the percentage of time spent hiding), and shorter response latency of fast-start response compared to those of the control group. Furthermore, the lethal group exhibited higher activity level, as evidenced by the increased amount of time spent moving at higher average speed and higher *RMR*. However, neither the fast-start parameters (V_{max} and A_{max}) nor the maximum metabolic capacity (*MMR* and *MS*) of the two predator-stress groups differed from those of the control group. These results suggest that the *S. sinensis* cultured under predation stress was less vulnerable to predators because of shorter response latency and more explorative routine activities. However, the increase in spontaneous activity and enhanced alertness resulted in further energy expenditure in qingbo. Thus, the plasticity in physiology and behavior in qingbo may be one of the main anti-predator strategies that can increase the survival rate of this fish species under predator stress conditions.

1. Introduction

Predation is one of the key factors governing patterns (e.g., energy and information) in natural systems, and experimental manipulations of predator have shown that they have important effects on prey populations [1]. Similarly, changes in predation pressures have dramatic influences on virtually all aspects of an animal's physiology, behavior, morphology and even life-history traits [2]. To evade the predator, prey usually increase the detective activities to the predator and alter their anti-predator defenses of behavior, morphology and life history [3]. Upon encountering a predator, prey animals may show dramatic changes in their behavior by fleeing or seeking refuge, which results in subtle changes in habitat choice and alterations in the timing of foraging [4]. Different experiences of the life history in the species have profound effects on the growth, reproductive patterns and longevity of the prey [5–7]. Surviving in the environments of different predator pressure, fish individuals possess their optimum fitness, and face the various challenges and generate new adaptive traits under the dramatic alterations of their habitat.

Generally, fish that have been exposed to predators often have stronger anti-predator responses than predator-naive prey [8–12]. Furthermore, predator-encountered experience can improve the escape ability of prey by inducing alterations in behavior, morphology, physiology and even life histories [4,13–16]. For example, compared to prey in an environment without predators (or lower predator stress), the

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presence of predators (or higher predation stress) results in higher concentrations of adrenaline and cortisone [17], higher respiratory and metabolic responses [18,19], improved fast-start escape performance [20], increased spontaneous movements, increased boldness and higher vigilance [21,22]. These studies have focused on the physiological and behavioral responses to changes in predation stress [23–25]. However, whether such responses can reduce the vulnerability to predation and the corresponding underlying physiological and behavioral mechanisms of this vulnerability remains unclear.

Therefore, the aims of this study were to examine the effects of different predation intensities on escape ability of prey and to determine the underlying physiological and behavioral mechanisms. To achieve these aims, we selected the juvenile qingbo (*Spinibarbus sinensis*) and its natural predator, the southern catfish (*Silurus meridionalis*), as the prey and predator, respectively. The qingbo is a common commercial fish which widely distributed in the Yangtze River of China, while the southern catfish is an ambush and carnivorous predator in the same water body. These two fish species are important components of the food chain in the Yangtze River. The experimental incubated qingbo, which did not experience with any predator pressure, were reared without predators (the control group), with a caged southern catfish predation threat (the non-lethal group) or with predators (the lethal group) at 25 ± 0.5 °C for a period of 28 d. After the acclimation, the variables of the different treatment groups, including predator mortality, metabolic responses, fast-start performance and routine spontaneous activities, were evaluated to provide beneficial data for the fundamental research of the fish physiology and ecology.

2. Materials and methods

2.1. Experimental animals and acclimation

Experimental juvenile qingbo (4–8 g, $n = 240$) and southern catfish (20–26 g, $n = 8$) were obtained from local farmers (Hechuan district, Chongqing) and kept in dechlorinated, fully aerated 25 ± 0.5 °C water tanks (approximately 250 L) for three weeks before the experiments. The prey and predator were separately raised. All juvenile qingbo, which were predator naive before the experiment, were individually marked with passive integrated transponders (PIT) for observation of fish behavior using PIT antenna systems [26]. The fish were fed to satiation with a commercial diet once daily at 09:00 h. The chemical composition of the formulated diet was 41.2 ± 0.9% protein, 8.5 ± 0.5% lipid, 25.7 ± 1.2% digestible carbohydrate and 12.3 ± 0.4% ash. The southern catfish were fed to satiation with cutlets of freshly killed loach (*Misgurnus anguillicaudatus*) once daily at 09:00 h. Uneaten food and feces were removed with a siphon 1 h after feeding. All tanks were replaced approximately by 10% of total water volume everyday. The water temperature was maintained at 25.0 ± 0.5 °C, and the oxygen content of the water was maintained above 7.0 mg/L. The tanks were kept under a natural light cycle.

2.2. Experimental design

After the acclimation, all tests were performed at a water temperature of 25 ± 0.5 °C. At the beginning of the experiment, body mass and body length were measured after the fish were slightly anesthetized with neutralized tricaine methanesulfonate (MS-222, 50 mg/L). These selected fish (5.88 ± 0.08 g, 6.52 ± 0.04 cm) were similar in the body mass and body length with a good healthy condition. The fish were randomly assigned to 3 groups: the non-predator group (control group without predators, $n = 30$), non-lethal predator group (fish reared with the predation threat of 'non-lethal' caged southern catfish, $n = 30$) and lethal predator group (fish reared with direct predation by southern catfish, $n = 70$ at the beginning of the test). Because not all of the experimental fish could be held in one tank during the experimental period, similar physical conditions, including water temperature and dissolved oxygen levels, were maintained in the different tanks, and the fish density was kept the same by adjusting the rearing water volume, thus ensuring that the differences among different experimental groups were a reflection of treatment rather than tank variation.

Fish were reared for 4 weeks under the same conditions as in the acclimation period. All fish prey of three groups were fed to satiation with the same commercial diet once a day. The caged southern catfish in the non-lethal group were fed to satiation with freshly killed loach once three day, whereas those in the lethal group only fed on qingbo. After the 4 week' growth experiment, the body mass and body length of the qingbo were measured after slight anesthetization with MS-222 (50 mg/L) to evaluate the metabolism, behavior and predation mortality using randomly selected fish. The water temperature, dissolved oxygen level and light cycle of all tanks (length × width × height, 1.5 m × 0.6 m × 0.5 m) were kept the same as those during the acclimation period.

2.3. Experimental procedure

2.3.1. Metabolism

The metabolism parameters of present study included routine metabolic rate (*RMR*), maximum metabolic rate (*MMR*) and metabolic scope ($MS = MMR - RMR$). Ten experimental fish were selected from each of the treatment groups. For the measurement of *RMR*, each fish was placed individually in the respirometer chamber and allowed to acclimate for 48 h. On the following two days, the oxygen consumption rate ($\dot{M}O_2$) of individual fish was measured at 09:00, 15:00 and 21:00 by using an oxygen meter (HQ_{20}, Hach Company, Loveland, CO, USA). Six measurement data were averaged for the *RMR* of each fish. The fish were used again for the measurement of *MMR* by the chasing method. Briefly, the experimental fish were chased to exhaustion with a hand net in a circular trough (Φ outside = 56 cm, Φ inside = 33 cm, water depth = 15 cm) and suffered a reflux with an approximate water velocity of 60 cm/s. The whole exercise process usually lasted within 5 min [27]. After the exhaustion, each fish was immediately placed into a respirometer chamber and $\dot{M}O_2$ of each fish was measured for an interval of one minute during a recovery period of 5 min. The flow rate of water through the respirometer chamber was measured by collecting the water outflow from each tube. The water flow rate of the respirometer chamber was approximately 0.6/L, and 99% of the water was replaced within 1 min in the 0.1 L chamber [28]. Therefore, the first measurement of $\dot{M}O_2$ was made 1 min after the fish was placed in the chamber. Maximal $\dot{M}O_2$ was usually observed immediately (1–2 min) after the fish was placed in the chamber and could be used as the *MMR* of experimental fish. The following formula was used to calculate the $\dot{M}O_2$ (mg/kg/h) of individual fish:

$$\dot{M}O_2 = \Delta O_2 \times v/m$$

where $\dot{M}O_2$ presents the metabolic rate of the experimental fish under different physiological status (resting or after exhaustion), ΔO_2 is the difference in the oxygen concentration (mg/L) between the experimental chamber and the control chamber (chamber without fish), v is the water flow rate in the experimental chamber (L/h) and m is the body mass of the fish (kg).

2.3.2. Fast-start performance

The fast-start performance of experimental fish was examined by the self-made device [29]. According to a previous study [30], the center-of-mass (CM) were marked in the place which account for a 44.3% of the body length from lip. Ten experimental fish were randomly selected from each of the treatment groups. A small white plastic ball (diameter: 1 mm) was attached to the dorsal side of each fish at the CM position determined by a pilot experiment after the fish was slightly