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# Effects of different shelters on feeding, molting, survival, and growth of *Scylla paramamosain*

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Providing shelters is considered an effective method to prevent self-harm and improve the survival rate of *Scylla paramamosain*. In this study, four shelter groups—the shelters of which included fine sand, arched tiles, PVC pipes, and trapezoidal net cages—and one group without shelters were established to investigate the effects of shelters on *S. paramamosain* by calculating their feeding rate, molting rate, survival rate, and growth index. The results showed that the feeding rates of the fine sand and PVC pipe groups were greater than 12% and that the feeding rates of the arched tile and trapezoidal net cage groups were greater than 9%, while the feeding rate of the group without shelters was only 6.7%. The food conversion rates of both the fine sand and PVC pipe groups exceeded 21%. In contrast, the food conversion rate of the non-shelter group was the lowest at 14%. The molting rates of the fine sand and PVC pipe groups were the highest, reaching 29% in the later stages of the experiment, while the molting rate of the non-shelter group was only 19%. There was no significant difference in survival rates among the groups during the first 20 days of the experiment. However, on the 60th day, the survival rate of the fine sand group was 92%, while the non-shelter group had a survival rate of 79%. The experimental results showed that the incidence of cheliped injuries in the fine sand group was 16%, while it was 25% in the non-shelter group. During the daytime, the occupancy rate of burrows by the four shelter groups was 60–70%, while during the night, the occupancy rate of each shelter decreased to 40–50%, and there was no significant difference in occupancy rates among the shelter groups during the night. The weight and full carapace width of *S. paramamosain* in the fine sand and PVC pipe groups were significantly higher than those in the other groups ( $P < 0.05$ ), and the weight gain rate and specific growth rate of the fine sand and PVC pipe groups were significantly higher than those of the other groups ( $P < 0.05$ ). Research has shown that fine sand and PVC pipes, as shelters for *S. paramamosain*, can effectively prevent cannibalism, increase feeding rates and survival rates, and promote growth and molting. This study provides scientific guidance for the proper selection of shelters in the farming process of *S. paramamosain*.

## KEYWORDS

*Scylla paramamosain*, shelter, fine sand, arched tile, PVC pipe, plastic cage

# 1 Introduction

Mud crabs (*Scylla paramamosain*) are spread throughout the tropical and warm temperate regions of the Pacific, providing support for lucrative offshore fisheries in many countries (Keenan, 1999; Le Vay, 2001). In southern China, *S. paramamosain* has been widely cultivated (Zhao et al., 2015) and has become one of the most popular mud crab species. However, the output of *S. paramamosain* is far from meeting the increasing market demand; the market price is continuously high, and many key scientific and technological problems facing mud crab aquaculture have not been effectively solved. Therefore, it is urgent to increase the output of *S. paramamosain* by improving cultivation technology.

Intraspecific agonistic behavior-induced killing is one of the main causes of death in crustacean aquaculture, especially in the early larval and adult stages, due to the very high stocking densities in aquaculture ponds (Ye et al., 2011). Intraspecific self-harm in crustaceans may also be caused by a number of other factors, including living substrates and shelters (Kurihara and Okamoto, 1987; Moksnes et al., 1998). A crucial behavioral strategy for crustaceans is the selection of a suitable shelter for feeding and enemy defense (Nelson and Vance, 1979). After long-term environmental adaptation and evolution, crustaceans have developed certain behavioral characteristics, including a nocturnal lifestyle and the use of shelters (Tidau and Briffa, 2016). Therefore, shelter is critical for the survival and life activities of *S. paramamosain*.

Previous studies have indicated that shelters can effectively prevent aquatic organisms from killing each other (Moksnes et al., 1997; Catacutan, 2002). As a critical feature of aquaculture ponds, shelters not only provide protection for aquaculture animals but also serve as biological bait, thereby playing an instrumental role in the survival and growth of aquaculture animals (Douglas, 1976; Sloan and Bodungen, 1980). There are several common types of crustacean shelters, including substrates (e.g., rocks, sand, and bricks), burrows (e.g., cracks, holes, pipes, and perforated bricks), macrophytes, and sheets (e.g., onion bags and fiber cement) (Moksnes et al., 1998; Sáez-Royuela et al., 2001; González et al., 2011). In wild aquatic environments, seaweeds, filamentous algae, and shells are used by crabs as natural shelters, and these shelters help prevent crabs from killing each other (Heck and Thoman, 1981; Perkins-Visser et al., 1996).

The survival rate of mud crabs is higher when fine sand is used as a refuge compared to when there is no refuge (Fatihah et al., 2017). Additionally, Mirera and Moksnes (2013) found that using fine sand as a refuge for crabs can reduce intraspecific aggression by 50%. Studies have also shown that lobsters prefer to dwell in fine sand (Cobb, 1971). Using tiles as shelters can increase the abundance of crab populations (Sheehan et al., 2008). Moreover, related studies have found that placing tiles can alter the behavior of purple shore crabs, resulting in their higher aggregation (McGaw, 2001). After placing PVC pipes as shelters, the molting rate of crabs increased fivefold, and the spawning rate of female crabs also doubled (Beck, 1995). Additionally, Supriyono et al. (2017) found

that placing PVC pipes can increase the survival rate and yield of lobsters. Utilizing net cages for rearing post-larval *Macrobrachium rosenbergii* can enhance the survival rate of the larvae (Avillanos et al., 2019). Rodriguez et al. (2007) also found that the survival rate of mud crabs reared in net cages is significantly higher than those in earthen ponds.

In this study, fine sand, arch-shaped tiles, PVC pipes, and trapezoidal net cages were selected as shelters for the indoor cultivation of *S. paramamosain*. The effects of each shelter on the survival, molting, feeding, and growth performance of *S. paramamosain* were compared. The research findings of this paper will provide practical information for aquaculture. Farmers can use the simple and practical techniques described in this paper to reduce the mortality rate of *S. paramamosain* and thereby increase their production.

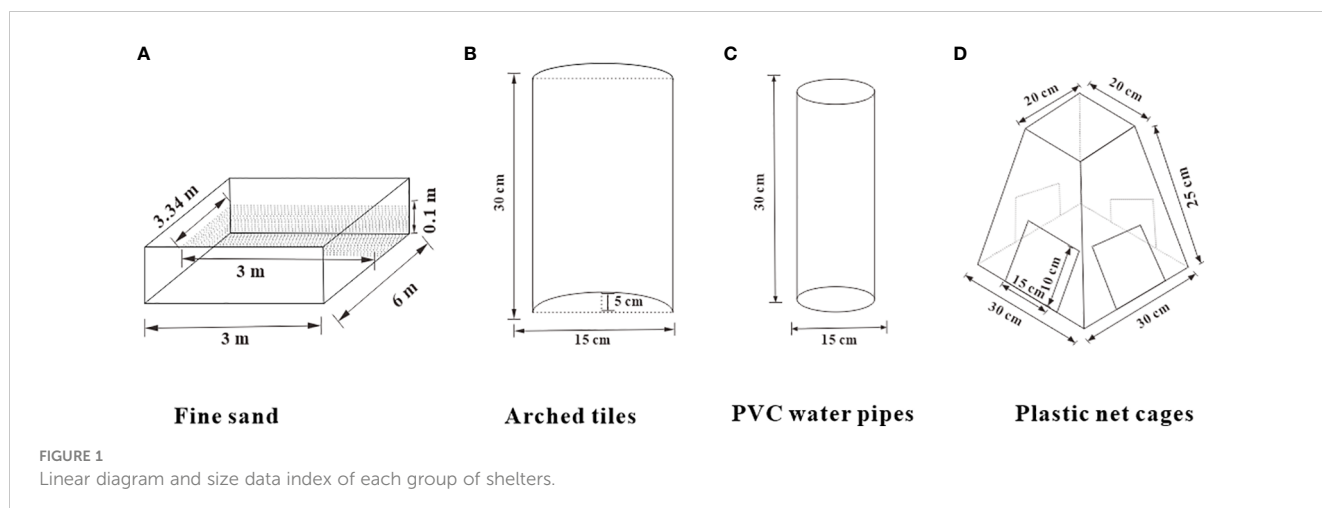
## 2 Materials and methods

### 2.1 Animal collection and maintenance

*S. paramamosain* specimens were procured from Ningbo Huada Haichang Aquatic Science and Technology Co., Ltd. (N:29°21', E:121°54') on May 31, 2021. A total of 450 crabs were acquired, boasting an average weight of 20 grams each. Subsequently, these crabs were transported to the indoor cultivation ponds of Shandong Haihong Industrial Group Co., Ltd. (N:37°54', E:118°89'). The facility was equipped with 15 experimental ponds and three reservoirs. Each pond measured  $6 \times 3 \times 1.5 \text{ m}^3$  in volume, accommodating 30 crabs per experimental pond.

### 2.2 Experimental design

There were a total of five experimental groups: fine sand, arched tiles, PVC water pipes, plastic net cages, and a control group with no shelter. Each group had three parallel replicates, with each replicate being a single pond. The volume of fine sand particles was less than 0.5 mm, and a  $10 \text{ m}^2$  section of each pond was covered with fine sand to a depth of 10 cm. The remaining  $8 \text{ m}^2$  of each pond was designated for bait feeding and sewage discharge. The arched tiles ( $30 \times 15 \times 5 \text{ cm}$ ) were arranged in a parabolic shape, and 40 tiles were placed in each pond. PVC pipes (15 cm in diameter and 30 cm in length) were also used, with 40 pipes placed in each pond. The plastic mesh cage was trapezoidal in shape, with a wider bottom and a narrower top, and it had the following dimensions: a bottom length  $\times$  width of  $30 \times 30 \text{ cm}^2$ , a top length  $\times$  width of  $20 \times 20 \text{ cm}^2$ , and a height of 25 cm. The trapezoid had openings measuring  $15 \times 10 \text{ cm}$  on all four sides (Figure 1). There were 40 mesh cages in each pond. The experiment lasted for 60 days, from June 1 to July 30, 2021. Every 10 days, the weight and growth indices of *S. paramamosain* were measured, and data on molting rate, survival rate, cheliped injury rate, shelter occupancy rate, and other indices were collected and analyzed.



## 2.3 Aquaculture management

The *S. paramamosain* in all ponds were provided with an artificial compound bait feed (manufactured by Tianbang Food Co., Ltd.) at 8:00 a.m. and 5:00 p.m. Each pond received an equal amount of feed (25 g) during each feeding session. Additionally, six oxygen-infused stones were placed in each pond to ensure a continuous oxygen supply. Water was replaced every three days, any remaining bait was promptly removed, and water quality was consistently monitored.

## 2.4 Index measurement

Before weighing, the moisture was gently wiped off the body surface with a dry towel. Then, each crab was weighed with an electronic balance (accurate to 0.01 g), and the growth index was measured with a vernier caliper. The following formulas were used to calculate daily food intake rate (FI), food conversion efficiency (FCE), molting rate (MR), survival rate (SR), cheliped injury rate (CIR), shelter occupancy rate (SO), specific growth rate (SGR), weight gain rate (WGR), and condition factor (CF) (Holland et al., 1971; Breteler, 1975; Fotheringham, 1976; Ennis, 1984; Snyder and Chang, 1986; Savolainen et al., 2004; Mazumder et al., 2016):

$$F = FA - S \times R,$$

$$FI (\%/d) = F / [T \times (W_i + W_f) / 2] \times 100\%,$$

$$FCE (\%) = (W_f - W_i) / F \times 100\%,$$

$$MR (\%) = 100\% \times (N_q / N_i),$$

$$SR (\%) = 100\% \times (N_f / N_i),$$

$$CIR (\%) = 100\% \times (CI / TIN),$$

$$SO (\%) = 100\% \times (SN / TIN),$$

$$SGR (\%) = 100\% \times (InW_f - InW_i) / T,$$

$$WGR (\%) = 100\% \times (W_f - W_i) / W_i, \text{ and}$$

$$CF (g/cm^3) = 100 \times W / L^3.$$

In the above equations, F represents daily food intake (g), FA signifies feeding amount (g), S denotes the dissolution rate of residual bait, R corresponds to the weight of surplus feed (g), N<sub>q</sub> indicates the number of *S. paramamosain* molts, N<sub>f</sub> represents the final count of *S. paramamosain*, and N<sub>i</sub> indicates the initial number of *S. paramamosain*. Furthermore, CI represents the count of lost or damaged *S. paramamosain* chelipeds, TIN signifies the number of surviving *S. paramamosain* on the assessment day, SN denotes the number of *S. paramamosain* in the shelter, W<sub>f</sub> corresponds to the final weight of *S. paramamosain* (g), W<sub>i</sub> indicates the initial weight of *S. paramamosain* (g), T represents the duration of the culture period (days), W denotes the body mass of *S. paramamosain* (g), and L indicates the width of *S. paramamosain* (cm).

## 2.5 Data analysis

The experimental data were statistically analyzed using Excel 2010 and SPSS 22.0. All experimental data were expressed as mean values ± SD (mean values ± standard deviation). The normality of the data was tested using the Levene test in SPSS 22.0 software. One-way analysis of variance (ANOVA) was performed on all data using SPSS 22.0 software. After testing for the homogeneity of variances, the differences between means were assessed using independent samples *t*-test, with a *P*-value less than 0.05 considered statistically significant.

## 3 Results

### 3.1 Daily food intake rate and food conversion rate

A significant difference in food intake rate was observed between the shelter group and the non-shelter group (*P* < 0.05).

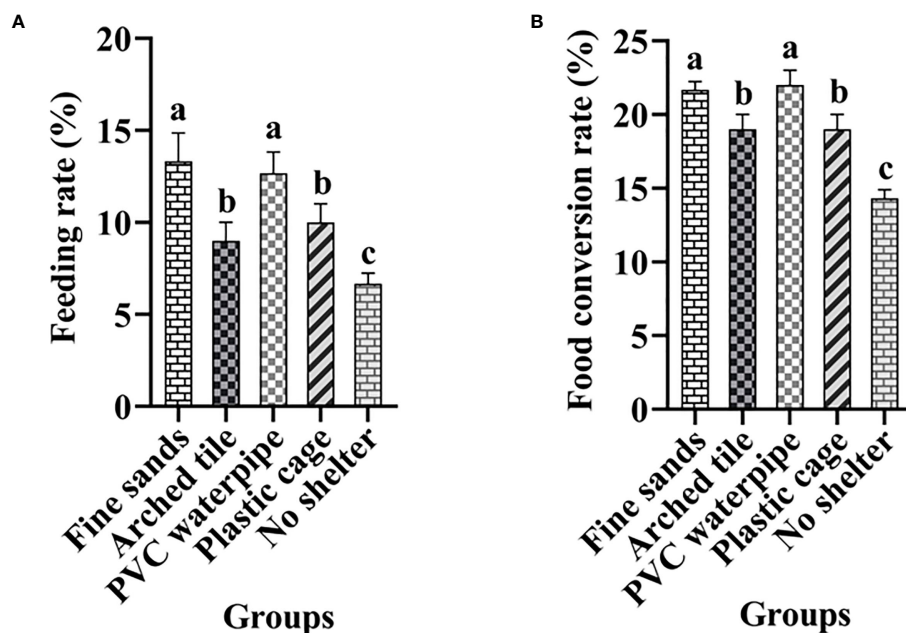


FIGURE 2

Analysis of the feeding rate (A) and the food conversion rate (B) of *Scylla paramamosain* under different shelter conditions (mean  $\pm$  SD; different letters indicate significant differences among groups).

Furthermore, there were significant differences among the shelter groups ( $P < 0.05$ ; see Figure 2). In particular, the feeding rates exceeded 12% in the fine sand and PVC water pipe groups, while the arch tile and plastic mesh box groups exhibited feeding rates exceeding 9%. However, the non-shelter group had a feeding rate of only 6.7%. The food conversion rates of the fine sand and PVC water pipe groups were significantly higher than those of other groups ( $P < 0.05$ ), with rates exceeding 21%. In contrast, the non-shelter group had the lowest food conversion rate, at only 14%.

### 3.2 Molting

Throughout the experiment, we collected data every 10 days and observed a significant difference in molting rates between *S. paramamosain* with and without shelter ( $P < 0.05$ ). Notably, the molting rates of *S. paramamosain* in the fine sand and PVC water

pipe groups were significantly higher than those in the arch tile and plastic net cage groups ( $P < 0.05$ ). At each sampling point, the fine sand group exhibited the highest molting rates, while the group without shelter had the lowest. Furthermore, we found that the longer the culture period, the greater the molting rate of *S. paramamosain*, as shown in Table 1.

### 3.3 Survival and cheliped injury rates

During the first 20 days of the trial (as shown in Table 2), we observed no statistically significant differences in survival rates among the groups. However, as the trial period extended, differences in survival rates among the groups became more pronounced. At the conclusion of the 60-day trial, we found that the *S. paramamosain* survival rate was highest in the fine sand group, followed by the PVC water pipe group. In contrast, the group without shelter exhibited the lowest survival rate.

TABLE 1 The molting rates (MR, mean  $\pm$  SD) of *S. paramamosain* throughout the experiment.

Time	Fine sand	Arched tile	PVC water pipe	Plastic cage	No shelter
Day 10	12.00 $\pm$ 1.73 <sup>a</sup>	9.00 $\pm$ 1.73 <sup>ab</sup>	8.00 $\pm$ 1.73 <sup>abc</sup>	5.67 $\pm$ 2.31 <sup>bc</sup>	4.33 $\pm$ 2.31 <sup>c</sup>
Day 20	13.33 $\pm$ 3.51 <sup>a</sup>	11.00 $\pm$ 1.73 <sup>ab</sup>	14.33 $\pm$ 2.31 <sup>a</sup>	11.00 $\pm$ 1.73 <sup>ab</sup>	5.67 $\pm$ 2.31 <sup>b</sup>
Day 30	15.67 $\pm$ 2.31 <sup>a</sup>	14.33 $\pm$ 2.31 <sup>ab</sup>	17.00 $\pm$ 0.00 <sup>a</sup>	15.67 $\pm$ 2.31 <sup>a</sup>	7.00 $\pm$ 0.00 <sup>b</sup>
Day 40	22.00 $\pm$ 2.00 <sup>a</sup>	15.67 $\pm$ 2.31 <sup>bc</sup>	20.00 $\pm$ 3.00 <sup>ab</sup>	17.67 $\pm$ 2.08 <sup>ab</sup>	10.00 $\pm$ 3.00 <sup>c</sup>
Day 50	27.00 $\pm$ 4.00 <sup>a</sup>	23.00 $\pm$ 3.00 <sup>ab</sup>	25.67 $\pm$ 2.31 <sup>a</sup>	19.00 $\pm$ 3.46 <sup>b</sup>	16.33 $\pm$ 3.06 <sup>b</sup>
Day 60	29.33 $\pm$ 5.13 <sup>ab</sup>	25.33 $\pm$ 1.53 <sup>bc</sup>	29.67 $\pm$ 2.08 <sup>a</sup>	21.67 $\pm$ 2.31 <sup>cd</sup>	19.00 $\pm$ 1.73 <sup>d</sup>

Different superscript letters in the same line indicate significant differences among groups ( $P < 0.05$ ).

TABLE 2 The survival rates (SR, mean  $\pm$  SD) of *S. paramamosain* throughout the experiment.

Time	Fine sands	Arched tile	PVC water pipe	Plastic cage	No shelter
Day 10	100 $\pm$ 0 <sup>a</sup>	98.67 $\pm$ 2.31 <sup>a</sup>	98.67 $\pm$ 2.31 <sup>a</sup>	97.33 $\pm$ 2.31 <sup>a</sup>	97.33 $\pm$ 2.31 <sup>a</sup>
Day 20	98.67 $\pm$ 2.31 <sup>a</sup>	97.33 $\pm$ 2.31 <sup>a</sup>	98.67 $\pm$ 2.31 <sup>a</sup>	96 $\pm$ 0 <sup>a</sup>	93.33 $\pm$ 2.31 <sup>a</sup>
Day 30	97.33 $\pm$ 2.31 <sup>a</sup>	96 $\pm$ 0 <sup>a</sup>	96 $\pm$ 0 <sup>a</sup>	94.67 $\pm$ 2.31 <sup>ab</sup>	92 $\pm$ 0 <sup>b</sup>
Day 40	94.67 $\pm$ 2.31 <sup>a</sup>	93.33 $\pm$ 2.31 <sup>a</sup>	92.33 $\pm$ 3.51 <sup>ab</sup>	89 $\pm$ 1 <sup>b</sup> <sup>c</sup>	85 $\pm$ 1 <sup>c</sup>
Day 50	93.33 $\pm$ 2.31 <sup>a</sup>	90.00 $\pm$ 1.00 <sup>bc</sup>	91.00 $\pm$ 1.73 <sup>ab</sup>	88.33 $\pm$ 1.15 <sup>cd</sup>	83.33 $\pm$ 1.53 <sup>d</sup>
Day 60	92.33 $\pm$ 3.51 <sup>a</sup>	85.67 $\pm$ 0.58 <sup>b</sup>	91.00 $\pm$ 1.73 <sup>a</sup>	83.33 $\pm$ 1.53 <sup>bc</sup>	79.00 $\pm$ 3.61 <sup>c</sup>

Different superscript letters in the same line indicate significant differences among groups ( $P < 0.05$ ).

Throughout the experiment, we observed an increase in the cheliped injury rate of *S. paramamosain* across all groups, as shown in Table 3. Specifically, between the 10th and 30th day of the trial period, we found no significant difference in cheliped injury rates among the groups. However, from day 30 to day 60, we observed the highest *S. paramamosain* cheliped injury rate in the non-shelter group, followed by the plastic cage group. In contrast, the fine sand and PVC water pipe groups exhibited the lowest cheliped injury rates.

### 3.4 Shelter occupancy

The behavior of *S. paramamosain*, specifically their movement in and out of shelters, was meticulously documented and examined during both daytime and nighttime throughout the trial duration. At the conclusion of the study, the pertinent data were gathered and analyzed. The findings revealed that *S. paramamosain* exhibited a shelter-occupancy rate of 60–70% during daylight hours, whereas the occupancy rate at night fell to 40–50%. Notably, significant differences in daytime occupancy rates were observed among various shelters ( $P < 0.05$ ), while no such significant disparities were detected in nighttime occupancy rates (Figure 3).

### 3.5 Growth

After the experiment, we examined the growth indices of *S. paramamosain*. Our findings showed significant differences in weight between the shelter and non-shelter groups, as well as

among different types of shelters ( $P < 0.05$ ). Specifically, *S. paramamosain* weight was highest in the fine sand group (122 g) and the PVC water pipe group (120 g), while the group without shelter had the lowest weight (only 100 g). Additionally, we observed significant differences in full carapace width, carapace width, carapace length, and body height among the different groups ( $P < 0.05$ ) (refer to Figure 4).

Following the 60-day trial period, substantial disparities in *S. paramamosain* weight gain and specific growth rate were observed between the shelter and non-shelter groups, as well as among various shelter types ( $P < 0.05$ ). The weight gain rate and specific growth rate of *S. paramamosain* reached their peak in the PVC water pipe group, while the lowest rates for weight gain and specific growth were recorded in the non-shelter group. No significant differences were detected in the condition factor between the shelter and non-shelter groups or among the different shelter types (Table 4).

## 4 Discussion

Owing to its delectable flavor, abundant nutritional content, and favorable economic impact, *S. paramamosain* has emerged as a crucial aquaculture species in China (Xu et al., 2020). Although the *S. paramamosain* industry has experienced rapid growth in recent years, it has faced numerous challenges that demand immediate attention, such as high self-injury rates and low survival rates during breeding (Ut et al., 2007). In this study, we aimed to tackle the high rate of self-harm during the *S. paramamosain* breeding process. To this end, we established four shelter groups

TABLE 3 The cheliped injury rates (CIR, mean  $\pm$  SD) of *S. paramamosain* throughout the experiment.

Time	Fine sand	Arched tile	PVC water pipe	Plastic cage	No shelter
Day 10	4.40 $\pm$ 1.91 <sup>bc</sup>	7.73 $\pm$ 1.96 <sup>ab</sup>	3.30 $\pm$ 0.00 <sup>c</sup>	5.50 $\pm$ 1.91 <sup>abc</sup>	9.97 $\pm$ 3.35 <sup>a</sup>
Day 20	6.77 $\pm$ 0.29 <sup>a</sup>	7.00 $\pm$ 0.17 <sup>a</sup>	7.97 $\pm$ 2.02 <sup>a</sup>	8.10 $\pm$ 2.25 <sup>a</sup>	9.53 $\pm$ 2.38 <sup>a</sup>
Day 30	9.04 $\pm$ 2.16 <sup>a</sup>	12.67 $\pm$ 2.36 <sup>a</sup>	10.01 $\pm$ 2.27 <sup>a</sup>	13.63 $\pm$ 2.55 <sup>a</sup>	15.81 $\pm$ 0.87 <sup>a</sup>
Day 40	10.93 $\pm$ 2.29 <sup>b</sup>	12.50 $\pm$ 0.50 <sup>ab</sup>	12.10 $\pm$ 3.85 <sup>ab</sup>	13.50 $\pm$ 1.32 <sup>ab</sup>	17.87 $\pm$ 1.67 <sup>a</sup>
Day 50	13.67 $\pm$ 1.15 <sup>c</sup>	15.80 $\pm$ 1.39 <sup>bc</sup>	13.33 $\pm$ 1.53 <sup>c</sup>	16.67 $\pm$ 1.53 <sup>ab</sup>	20.00 $\pm$ 1.00 <sup>a</sup>
Day 60	16.00 $\pm$ 1.00 <sup>c</sup>	17.67 $\pm$ 1.15 <sup>b</sup>	15.33 $\pm$ 0.58 <sup>c</sup>	21.33 $\pm$ 2.52 <sup>a</sup>	25.67 $\pm$ 2.89 <sup>a</sup>

Different superscript letters in the same line indicate significant differences among groups ( $P < 0.05$ ).



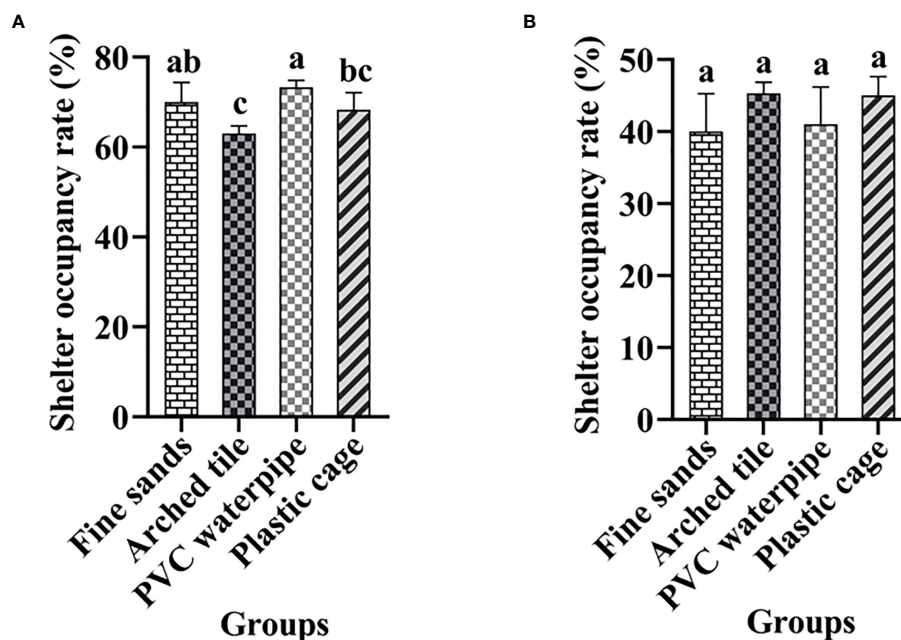


FIGURE 3 Artificial shelter occupancy (%) of *S. paramamosain* during the daytime (A) and nighttime (B) over 60 days (mean  $\pm$  SD; Different letters indicate significant differences among groups).

and one group without shelter to ascertain if shelter availability mitigated self-harm rates. Prior research has indicated that shelters offer camouflage and refuge for *S. paramamosain*, consequently preventing self-harm and predation (Ye et al., 2011). In this study, we observed that *S. paramamosain* rapidly retreats to its shelter to feed upon capturing prey, thereby preventing intraspecific food competition. Moreover, the feeding rates of the shelter groups were significantly higher than that of the non-shelter group, indicating that shelters played a critical role in promoting *S. paramamosain* feeding. Therefore, shelters not only reduce conflict among *S. paramamosain* but also decrease the energy expenditure required for vital activities, ultimately increasing the energy available for molting and growth.

Shelter is among the most critical ecological factors affecting the living conditions of aquatic animals, as it offers a suitable habitat and an escape mechanism from natural enemies (Moksnes et al., 1998). Crustaceans, known for their territorial and aggressive behavior, frequently engage in combat (Dingle and Caldwell, 1969). Numerous studies have shown that cheliped injuries significantly affect the physiological ecology of crustaceans, impacting aspects such as food intake, survival, immunity, growth, reproduction, and resistance to enemy damage (Smith, 1992; Frisch and Hobbs, 2011; Quintino and Estepa, 2011). During or immediately after molting, shrimps and crabs are soft and possess limited mobility, rendering them susceptible to intraspecific attacks (Polis, 1981). Consequently, shrimps and crabs tend to molt in relatively concealed locations (Moksnes et al., 1997). Our experimental data indeed revealed that *S. paramamosain* molt more swiftly in indoor pools with shelter compared to those without shelter, and that molting rates are higher in pools offering better concealment. For instance, as

observed in this study, fine sand shelters enable the crab to bury its entire body. Fine sand grains are small yet non-sticky, providing high air permeability and a loose texture that facilitates easy hiding for the crab. This aligns with prior studies demonstrating that fine sand can serve as a shelter for crustaceans, and that fine-sand shelters enhance crustacean safety due to their potent concealment properties (Richards, 1992; Mirera and Moksnes, 2013). Thus, fine sand, as a shelter for *S. paramamosain*, is characterized by strong concealment, high air permeability, and elevated comfort. Numerous studies have examined the use of PVC water pipes as shelters for crustaceans and fish (Supriyono et al., 2017; Rahman et al., 2020), showing that PVC water pipes significantly improve crustacean molting rates, growth rates, and fecundity (Beck, 1995; Sáez-Royuela et al., 2001; Balasundaram et al., 2004). The PVC water pipes employed in this study were of suitable length and height for adult *S. paramamosain* crabs, offering excellent concealment and ample space for movement. *S. paramamosain* moved freely within the PVC water pipes and were relatively safe. Thus, the advantages of residing in a refuge include the following: first, the crab can hide under the refuge during molting, minimizing the risk of intraspecific attack; and second, as the crab typically restricts its activity to its own territory and adjacent areas for effective territorial defense, the frequency of intraspecific contact, and consequently intraspecific conflict, is reduced.

The survival rates and yields of *S. paramamosain* were enhanced by providing artificial shelters in aquaculture ponds. Our experimental data revealed that the survival rates of all four shelter groups exceeded 80%. In fact, the presence of shelters considerably reduced fighting and cannibalism among *S. paramamosain* compared to the group without shelters. However, among the four shelter groups, the survival rates of the fine sand group and the PVC

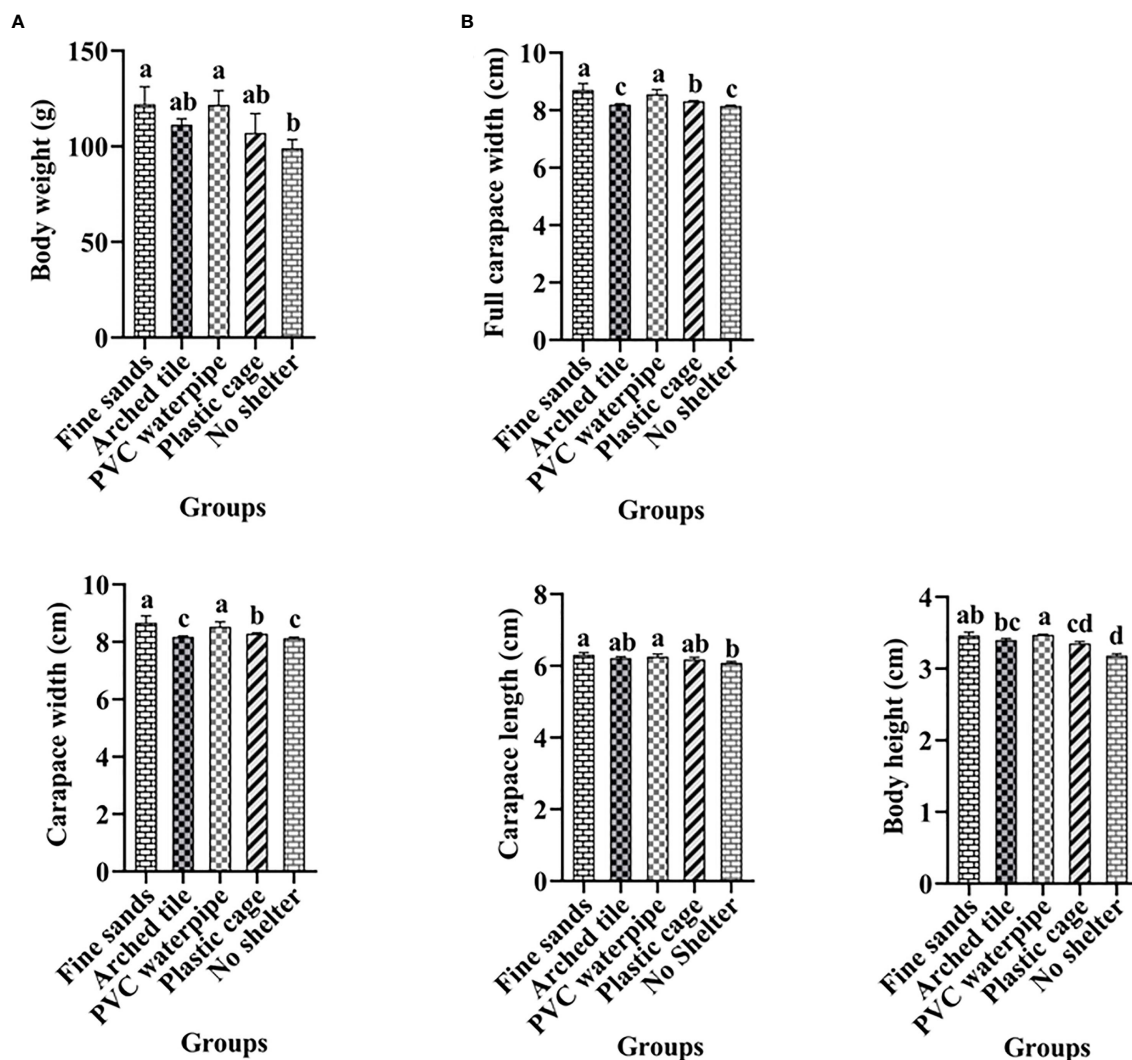


FIGURE 4 Analysis of growth indices of *S. paramamosain* under different shelter conditions after the experiment (mean ± SD; Different letters indicate significant differences between groups).

water pipe group were significantly higher than those of the tile group and the plastic cage group. The chelate injury rate was also substantially lower in the fine sand and PVC water pipe groups, suggesting that these shelter types more effectively decreased the disability rate and improved *S. paramamosain* survival rates. Moreover, we observed that *S. paramamosain* autonomously entered the shelter, especially during daytime, and remained concealed under or within the shelter for extended periods. When confronted with an invading conspecific, *S. paramamosain* exhibited

a threatening posture (elevating the body and extending the double cheliped) to deter and repel the intruder. Similar conspicuous territory-defense behaviors have also been observed in other aquatic animals (Tian et al., 2012; Guo et al., 2015).

Throughout the trial, the shelter occupancy rates of *S. paramamosain* were analyzed. We discovered that over 70% of *S. paramamosain* remained in the shelter during the day. However, only 40% of *S. paramamosain* entered the shelter at night. A similar behavioral pattern (i.e., hiding during the daytime and emerging at

TABLE 4 Analysis of weight gain rate (WGR), specific growth rate (SGR), and fitness index (CF) of *S. paramamosain* under different shelter conditions.

	Fine sand	Arched tile	PVC water pipe	Plastic cage	No shelter
WGR (%)	510.00 ± 45.83 <sup>a</sup>	456.67 ± 15.28 <sup>ab</sup>	517.33 ± 46.11 <sup>a</sup>	435.00 ± 50.74 <sup>ab</sup>	395.00 ± 22.91 <sup>b</sup>
SGR (%)	2.97 ± 0.15 <sup>ab</sup>	2.83 ± 0.06 <sup>abc</sup>	3.03 ± 0.12 <sup>a</sup>	2.73 ± 0.15 <sup>bc</sup>	2.63 ± 0.06 <sup>c</sup>
CF (g/cm <sup>3</sup> )	0.187 ± 0.014 <sup>a</sup>	0.203 ± 0.004 <sup>a</sup>	0.196 ± 0.021 <sup>a</sup>	0.187 ± 0.017 <sup>a</sup>	0.184 ± 0.011 <sup>a</sup>

Different superscript letters in the same line indicate significant differences among groups (P < 0.05).

night) was also reported in *Portunus trituberculatus* (He et al., 2017). *S. paramamosain* occupancy rates during the daytime varied significantly among the shelter types. The fine sand and PVC water pipe groups exhibited the highest occupancy rates during the day, whereas the arch tiles demonstrated the lowest occupancy rates. During the nighttime, there were no significant differences in occupancy rates among the groups. This may be attributed to *S. paramamosain* typically emerging for feeding at night.

The growth index of each *S. paramamosain* group was assessed after the 60-day trial period. *S. paramamosain* with shelter exhibited significantly higher growth indices compared to those without shelter. However, there were also notable differences in growth index among the shelter groups: the fine sand group and the PVC water pipe group displayed significantly higher growth indices than the arch tile group and the plastic net cage group. The weight gain rate and specific growth rate of *S. paramamosain* were also highest in the fine sand group and the PVC water pipe group. Nevertheless, there were no significant differences in the condition factor index among the groups. Our results demonstrated that access to shelter stimulated *S. paramamosain* feeding, enabling the crabs to accumulate more energy. With sufficient energy, *S. paramamosain* will molt and grow (He et al., 2017). Consequently, the presence of suitable shelters benefits *S. paramamosain* feeding and molting, ultimately promoting growth.

## 5 Conclusion

This study elucidates the effects of different types of shelters on the survival, molting, feeding, and growth performance of *S. paramamosain*, revealing that fine sand and PVC pipes are more conducive to enhancing these parameters. Therefore, during the cultivation of *S. paramamosain*, placing fine sand or PVC pipes as shelters can be beneficial in reducing aggression and increasing survival rates.

## Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

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## Author contributions

DZ: Methodology, Software, Data curation, Writing-Original draft preparation. LL: Conceptualization, Methodology, Writing-Reviewing and Editing, Funding acquisition. XH: Formal analysis, Visualization, Investigation. WF: Investigation, Validation. YF: Software, Validation. YL: Supervision. CW: Project administration, Supervision.

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## Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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