Effects of Shell Length and Shucking of *Ruditapes philippinarum* on Growth and Energy Allocation of *Scylla paramamosain*

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Abstract [**Objectives**] To evaluate the effects of shell length and shucking of *Ruditapes philippinarum* on *Scylla paramamosain*. [**Methods**] Feeding different-sized mud crabs with shucked or unshelled *R. philippinarum* of various shell lengths for 60 d, their growth performance and energy allocation patterns were evaluated. [**Results**] Survival rates were high across all treatments, with only sporadic mortality observed during the experiment. When fed unshelled clams, the weight gain rate and specific growth rate of smaller crabs were significantly higher than those of larger crabs, showing a clear decreasing trend with increasing initial body mass. Crabs with an initial mass of 3.86 g allocated significantly less energy to growth than those with an initial mass of 49.83 g. Crabs with an initial mass of 49.83 g had a significantly lower proportion of energy lost in molting than those with an initial mass of 260.41 g. Crabs with an initial mass of 3.86 g had a significantly higher proportion of energy lost in feces than those with initial masses of 182.48 and 260.41 g. No significant differences were found in the proportions of energy allocated to nitrogen excretion and metabolic consumption. When crabs within an initial mass range of 202.76 –210.25 g were fed with clams of different shell lengths, no significant differences were observed in their growth performance or energy allocation indicators. Feeding shucked versus unshelled clams to crabs of different initial sizes resulted in significant differences in growth performance based on the crab's initial size, but the removal of clam shells had no significant effect. As the initial mass of the crabs increased, the proportion of energy lost through molting increased significantly, while the proportion lost in feces decreased significantly. However, whether the clams were removed or not had no significant impact on the crabs' energy allocation indicators. [**Conclusions**] The initial body mass of the crabs significantly influences growth performance and energy allocation across different treatments, whereas clam shell length and shell removal have minor effects.

Key words *Scylla paramamosain*, *Ruditapes philippinarum*, Shucking, Growth, Energy allocation

0 Introduction

The mud crab (*Scylla paramamosain*) is the primary species of mud crabs distributed along China's coastal waters and the most important crab in aquaculture, accounting for over 90% of China's farmed mud crab production[1]. The diet of wild mud crabs mainly consists of marine-derived detritus, mollusks, crustaceans, fish, *etc.*, with the significance of different food sources varying greatly across regions[2-3]. In coastal mudflats and shallow seas, bivalves constitute a major component of the mud crab's diet[2-3], and they are frequently used as feed in mud crab aquaculture[2, 4-5]. In mud crab farming, low-value bivalves are often fed whole with shells, which may impose additional energy expenditure on the crabs during consumption, potentially altering their energy allocation patterns.

Energy allocation patterns are key parameters reflecting the utilization of feed and environmental adaptation in the *S. paramamosain*. Reports on energy allocation in *S. paramamosain* are relatively scarce, though energy budget models for larvae at different developmental stages have already been established[6-8]. The energy allocation in juvenile mangrove crabs (*Scylla serrata*) was investigated in a study examining the effects of different fishmeal-to-soybean protein ratios[9]. Energy allocation models for juvenile *S. paramamosain* during the overwintering period, fed with low-value fish, shrimp, shellfish, and polychaeta were established[10]. Response of energy metabolism in juvenile *S. paramamosain* to temperature fluctuations were studied[11-12]. In contrast, research on energy metabolism and allocation has been more systematic for the Chinese mitten crab (*Eriocheir sinensis*), the most important crab species in freshwater aquaculture in China, and the swimming crab (*Portunus trituberculatus*), the most significant crab in marine aquaculture[13-21]. In energy budget studies of these crab species, the Manila clam (*R. philippinarum*) has been used as feed, but only shucked clam meat was provided[10, 13]. Since the shell-crushing ability of crabs depends on species and individual size, the additional energy expenditure required to break shells may influence feeding preferences of crabs for bivalves in both natural and cultured environments. To investigate the impact of consuming shucked clams on the energy allocation of *S. paramamosain*, we conducted experiments using both shucked and unshelled Manila clams as feed, examining the effects of different crab sizes and clam shell lengths on the growth and energy allocation patterns of *S. paramamosain*.

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1 Materials and methods

1.1 Experimental facilities Plastic boxes (50 cm × 40 cm × 40 cm) were used as culture containers in the experiment. Before use, the plastic boxes were soaked in potassium permanganate for 6 h, then rinsed, and then 20 cm sand filtration seawater was added. An air stone was placed in each culture box, and air was continuously filled to maintain the dissolved oxygen content not less than 5.0 mg/L.

1.2 Seawater for experiment The seawater used in the experiment was filtered by three grades of sand and then disinfected by ultraviolet irradiation. The seawater salinity ranges from 26 to 30, the pH ranges from 7.9 to 8.3, and the dissolved oxygen content is not less than 5.0 mg/L.

1.3 Source and cultivation of juvenile crabs The experimental *S. paramamosain* were derived from the fifth-stage juveniles provided by Guangxi Marine Research Institute Co., Ltd. These juveniles were initially nursed (a process literally known as "Biaocu" in Chinese) and then cultured in aquaculture ponds. According to the experimental requirements, crabs of various sizes were captured at different times, and healthy individuals were selected as experimental specimens.

1.4 Diets preparation *R. philippinarum* was selected as a representative food source. Prior to the experiment, the clams were collected from local tidal flats and acclimatized in sand-filtered seawater for 24 h before use. The clams were shucked, and soft tissues were offered as feed.

1.5 Experimental design A total of three experiments were conducted: (i) Energy allocation of different sizes of *S. paramamosain* fed with shucked and unshelled clams; (iii) Differences in energy allocation of *S. paramamosain* fed with shucked versus unshelled clams; (iii) Energy allocation of *S. paramamosain* feed different sizes of unshelled clams.

1.5.1 Energy allocation of different-sized *S. paramamosain* fed with shucked clams. A total of 150 *S. paramamosain*, comprising 30 individuals each from five different average body weight groups, were captured. Each crab was weighed and recorded. Subsequently, one crab was placed into each aquaculture tank for the farming experiment. A total of 75 aquaculture tanks were used for this 60-d farming experiment.

1.5.2 Differences in energy allocation of different-sized *S. paramamosain* fed with shucked versus unshelled clams. A total of 200 *S. paramamosain* were captured, comprising 50 individuals each from four different average body weight groups. From each weight group, 30 uniform and healthy individuals were selected and randomly assigned to either the shucked clam diet treatment or the unshelled clam diet treatment. One crab was placed in each aquaculture tank, and a total of 120 tanks were used for this 60-d farming experiment.

1.5.3 Energy allocation of *S. paramamosain* fed with clams of different sizes. A total of 80 *S. paramamosain* with an average body mass of about 200 g were captured. From these, 60 uniform and healthy individuals were selected and randomly assigned to four dietary treatments with different sizes of clams. One crab was placed in each aquaculture tank, and a total of 60 tanks were used for this 60-d farming experiment.

During the experimental period, a diet leaching experiment was designed. Six replicates each of prepared shucked clams and unshelled clams were weighed based on their soft tissue content (C_{wet}, each containing approximately 100 g of soft tissue) and then dried to constant weight in a 60 ℃ oven. Another six replicates were weighed and immersed in seawater-filled containers for 22 h. After immersion, the samples were collected, soaked in distilled water for 15 min, rinsed three times with distilled water, dried to constant weight at 60 ℃ (C_{dry}), and finally stored in a desiccator.

1.6 Management of *S. paramamosain* culturing experiment The experiment was conducted between May and October 2022 without active water temperature control. The recorded water temperature range during this period was 25 ℃ – 31 ℃. *S. paramamosain* were fed once daily at 16:00. Two hours prior to each feeding, 100% of the water was exchanged. The clams to be fed to each tank were weighed and recorded before being provided. The daily feeding ration was adjusted based on the remaining bait observed before the next day's water exchange to ensure a slight excess of feed. Throughout the farming period, regular checks were conducted for any crab mortality, and such instances were promptly recorded.

1.7 Sample collection Six replicate samples (approximately 100 g each) of each bait type were randomly collected immediately after preparation. These samples were dried to constant weight in a 60 ℃ oven and then stored in a desiccator.

Residual bait from each culture tank was collected 2 h prior to daily feeding. The samples were rinsed with purified water, drained, placed in sealed bags, and stored at – 20 ℃. At the end of the experiment, all residual bait samples were dried to constant weight at 60 ℃ and stored in a desiccator.

Feces from each tank were siphoned onto an 80-mesh sieve screen prior to daily water exchange. The collected feces were transferred to beakers and stored at – 20 ℃. Upon completion of the experiment, all fecal samples were dried to constant weight at 60°C and stored in a desiccator.

Molting was monitored daily at 08:00 and 18:00. Any molted exoskeletons found were immediately collected, rinsed with purified water, and placed in sealed bags (one bag per tank). These were recorded and stored at – 20 ℃. After the experiment, all exuviae were counted, weighed, dried to constant weight at 60 ℃, and stored in a desiccator.

Initial crab samples were obtained by collecting five replicates from the remaining crabs after experimental subjects were selected. Each replicate consisted of three crabs. These were counted, weighed, initially stored at – 20 ℃, then dried to constant weight at 60 ℃ and stored in a desiccator.

At the end of the experiment, following a 24 h fasting period, each crab was treated as an individual sample. After being weighed and placed in sealed bags, the samples were stored at −20 ℃, then dried to constant weight at 60 ℃ and stored in a desiccator.

1.8 Sample processing Upon completion of the farming experiment, all samples were dried to constant weight. Subsequently, they were pulverized using a small electric grinder and sieved through a 60-mesh screen. The resulting powder was stored in a desiccator as prepared samples for subsequent analysis.

1.9 Sample analysis Sample nitrogen content was determined using the micro-Kjeldahl method, and crude protein content was calculated by multiplying the nitrogen content by 6.25. The energy content of the samples was measured with a PARR 6400 oxygen bomb calorimeter (PARR Instrument Company, USA). The acid-insoluble ash (AIA) content in the feed and feces was determined according to the method described by Atkinson et al[22]. All measurements were performed in triplicate, and the average value was taken as a result.

1.10 Data calculation The formulas for calculating the mass growth rate (*MGR*, %) and the specific growth rate (*SGR*, %) of the *S. paramamosain* were as follows:

$$MGR = 100 \times (M_{t2} - M_{t1}) / M_{t1}$$

$$SGR = 100 \times \ln (M_{t2}/M_{t1}) / (t_2 - t_1)$$

where t_1 and t_2 represent different experimental time points, M_{t1} and M_{t2} represent the body mass of *S. paramamosain* at the corresponding time points, and *I* represent the food intake during the period from t_1 to t_2. In this experiment, *MGR*, *SGR* and *FCE* expressed by dry matter, protein and energy were calculated according to the crude protein content and energy content of the samples, which were expressed as *MGR-D*, *MGR-P*, *MGR-E*, *SGR-D*, *SGR-P*, *SGR-E*, *FCE-D*, *FCE-P* and *FCE-E*, respectively. The relevant parameters in the energy budget formula were calculated according to the method of the literature[23]:

$$IE = Id \times GEd$$

$$GRE = FCe - ICe$$

$$FE = Fd \times GEf$$

$$EE = Ed \times GEe$$

$$UE + ZE = (UN + ZN) \times 24.83$$

$$ME = IE - GRE - FE - EE - (UE + ZE)$$

where *IE*, *GRE*, *FE*, *EE*, *UE + ZE* and *ME* denote ingestion energy, growth energy, fecal energy, exuviae energy, excretion energy and metabolic energy, respectively. *Id*, *Fd*, *Ed*, *GEd*, *GEf* and *GEe* represent the amount of dry matter ingested, the amount of dry matter in feces, the amount of dry matter in exuviae, the energy content of food, the energy content of feces, and the energy content of exuviae, respectively. *FCe* and *ICe* represent the energy of the *S. paramamosain* at the end of the experiment and the energy of the *S. paramamosain* at the beginning of the experiment. *UN + ZN* represents the nitrogen excreted through urine and gills, while *UE + ZE* represents the energy loss of nitrogen excretion. The energy loss of 1 g nitrogen excretion was calculated according to the parameter 24.83 kJ given by Elliott[24]. The calculation method of *UN + ZN* was based on the literature[25−26]:

$$UN + ZN = IN - GN - FN - EN$$

where *IN*, *GN*, *FN* and *EN* separately denote ingestion nitrogen, growth nitrogen, fecal (excretion) nitrogen and ecdysis nitrogen. The calculation method of F_N and E_N was as follows:

$$F_N = I_N \times (100 - DR_N) / 100$$

$$F_E = I_E \times (100 - DR_E) / 100$$

where DR_N and DR_E represent the apparent digestibility of nitrogen and energy of *S. paramamosain*s to diets, and they can be determined by acid-insoluble ash method[22]:

$$DR_N = 100 \times [1 - (N_{feces}/N_{diet}) \times (AIA_{diet}/AIA_{feces})]$$

$$DR_E = 100 \times [1 - (GE_{feces}/GE_{diet}) \times (AIA_{diet}/AIA_{feces})]$$

where N_{feces} and N_{diet} represent the nitrogen content of the feces and diet, GE_{feces} and GE_{diet} represent the energy content of the feces and diet, and AIA_{diet} and AIA_{feces} represent the acid-insoluble ash content of the diet and feces.

1.11 Statistical analysis Data is expressed as mean ± standard error (M ± SE). Statistical analyses were performed using SPSS version 11.5 software. One-way analysis of variance (ANOVA) was employed to compare numerical indices among *S. paramamosain* of different treatments, including body mass, molting-related parameters, energy intake, energy allocated to growth, exuviae, feces, and metabolism. Differences among treatments were analyzed using Duncan's multiple range test.

Percentage data, such as body weight gain rate, specific growth rate, and the allocation proportions of ingested energy to growth, exuviae, feces, excretion, and metabolism, were subjected to arcsine square root transformation ($\sin^{-1}\sqrt{x}$) prior to ANOVA. When the data met assumptions of normality and homogeneity of variances, one-way ANOVA was applied, with $P < 0.05$ considered statistically significant. In cases of heterogeneous variances, the non-parametric Kruskal − Wallis test was used, with the same significance threshold of $P < 0.05$.

2 Results and analysis

2.1 Growth and energy distribution of different sizes *S. paramamosain* fed with shucked clams In the experiment where shucked clams were fed, only one crab each from the groups with average body masses of 49.83 and 260.41 g died during the experimental period, resulting in survival rates exceeding 90% for all groups. The body mass gain rate and specific growth rate (*SGR*) of smaller crabs were significantly higher than those of larger crabs, showing a clear decreasing trend with increasing initial body mass (Table 1). The smallest crabs achieved a mass gain rate of 896.37%, whereas the largest crabs only increased in mass by 34.30%. The *SGR* was 3.83 %/d for the smallest crabs, but only 0.49% per day for the largest crabs.

Significant differences were observed in the energy allocation to growth, exuviae, and feces among *S. paramamosain* of different sizes fed clams, while no significant differences were found in the proportions of energy used for nitrogen excretion and metabolic expenditure (Table 2). The proportion of energy allocated to growth ranged from 23.70% to 29.49%. *S. paramamosain* with an initial body mass of 3.86 g allocated a significantly lower proportion of energy to growth compared to those with an initial mass of 49.83 g. The proportion of energy lost through exuviae ranged from 1.84% to 3.16%. Crab with an initial body mass of 49.83 g had a significantly lower proportion of energy loss from exuviae than those with an initial mass of 260.41 g. The proportion of energy lost through fecal excretion ranged from 7.08% to 9.83%. *S. paramamosain* with an initial body mass of 3.86 g had a significantly higher proportion of energy loss in feces compared to those with initial masses of 182.48 and 260.41 g.

Table 1 Growth of *Scylla paramamosain* fed with shucked clams

Initial Body mass//g	Survival rate//%	Final Body mass//g	MGR//%	*SGR*//%/d
3.86 ± 0.92^{a}	100.00	38.46 ± 3.47^{a}	896.37 ± 24.73^{d}	3.83 ± 0.39^{d}
49.83 ± 1.86^{b}	93.33	99.74 ± 7.12^{b}	100.16 ± 3.21^{c}	1.16 ± 0.18^{c}
115.26 ± 5.57^{c}	100.00	182.16 ± 7.18^{c}	58.04 ± 4.63^{b}	0.76 ± 0.26^{b}
182.48 ± 9.71^{d}	100.00	292.88 ± 8.44^{d}	60.50 ± 2.77^{b}	0.79 ± 0.22^{b}
260.41 ± 8.28^{e}	93.33	349.72 ± 8.69^{e}	34.30 ± 3.36^{a}	0.49 ± 0.23^{a}

NOTE In the same row, values without same superscript letter were significantly different from each other. The same below.

Table 2 Energy allocation of *Scylla paramamosain* fed with shucked clams

Initial body mass//g	Growth//%	Exuviae//%	Feces//%	Excretion//%	Metabolism//%
3.86 ± 0.92	23.70 ± 1.84^{a}	2.56 ± 0.14^{ab}	9.83 ± 0.45^{b}	4.51 ± 0.15^{a}	59.40 ± 1.40^{a}
49.83 ± 1.86	29.49 ± 4.33^{b}	1.84 ± 0.62^{a}	8.86 ± 1.39^{ab}	4.51 ± 0.88^{a}	55.30 ± 7.70^{a}
115.26 ± 5.57	28.36 ± 7.03^{ab}	2.29 ± 0.45^{ab}	8.04 ± 1.65^{ab}	3.97 ± 0.71^{a}	57.34 ± 6.91^{a}
182.48 ± 9.71	27.79 ± 7.21^{ab}	2.72 ± 0.67^{ab}	7.60 ± 1.59^{a}	4.45 ± 0.57^{a}	57.43 ± 5.60^{a}
260.41 ± 8.28	26.70 ± 6.86^{ab}	3.16 ± 0.58^{b}	7.08 ± 1.50^{a}	3.94 ± 0.52^{a}	59.13 ± 5.69^{a}

2.2 Growth and energy distribution of *S. paramamosain* fed with different sizes of clams When *S. paramamosain* with an initial body mass ranging from 202.76 to 210.25 g were fed with clams of different shell lengths, survival rates remained high across all treatments. Only crabs fed clams with a shell length of 2.68 cm had a mortality event, resulting in a survival rate of 93.33%, while all other treatments achieved a 100% survival rate (Table 3). No significant differences were observed in growth performance among crabs fed clams of different shell lengths. Final body mass, body mass growth rate, and *SGR* throughout the experimental period were highly consistent across all treatments.

Table 3 Growth of *Scylla paramamosain* fed with clams of different sizes

Shell length of clam//cm	Initial body mass//g	Survival rate//%	Final body mass//g	MGR//%	*SGR*//%/d
2.05 ± 0.09	205.38 ± 2.33	100	312.50 ± 12.47^{a}	52.16 ± 3.74^{a}	0.70 ± 0.13^{a}
2.68 ± 0.12	210.25 ± 1.86	93.33	318.16 ± 11.55^{a}	51.32 ± 4.89^{a}	0.69 ± 0.17^{a}
3.37 ± 0.15	208.82 ± 2.81	100	317.40 ± 17.32^{a}	52.00 ± 2.93^{a}	0.70 ± 0.21^{a}
4.13 ± 0.20	202.76 ± 9.33	100	306.37 ± 14.13^{a}	51.10 ± 5.48^{a}	0.69 ± 0.16^{a}

Feeding *S. paramamosain* with clams of different shell lengths had no significant effect on their energy allocation (Table 4). The proportion of energy allocated to growth across different treatments ranged from 29.32% to 31.78%, while the proportion of energy consumed by metabolism ranged from 54.80% to 57.24%. The sum of these two components accounted for approximately 86% of the ingested energy. The proportions of energy lost through exuviae, feces, and nitrogen excretion were relatively consistent across all treatments.

Table 4 Energy allocation of *Scylla paramamosain* fed with different sizes of clams

Shell length of clam//cm	Growth//%	Exuviae//%	Feces//%	Excretion//%	Metabolism//%
2.05 ± 0.09	31.78 ± 4.09^{a}	2.92 ± 0.70^{a}	5.98 ± 1.31^{a}	4.52 ± 0.38^{a}	54.80 ± 8.79^{a}
2.68 ± 0.12	31.44 ± 3.82^{a}	2.38 ± 0.46^{a}	6.28 ± 0.98^{a}	4.93 ± 0.47^{a}	54.97 ± 6.71^{a}
3.37 ± 0.15	30.09 ± 6.88^{a}	2.39 ± 0.71^{a}	6.94 ± 1.61^{a}	4.03 ± 0.67^{a}	56.55 ± 7.57^{a}
4.13 ± 0.20	29.32 ± 5.77^{a}	2.74 ± 0.55^{a}	6.51 ± 1.22^{a}	4.19 ± 0.77^{a}	57.24 ± 7.73^{a}

2.3 Growth and energy distribution of *S. paramamosain* fed with shucked and unshelled clams *S. paramamosain* of different initial body masses were fed with shucked or unshelled clams. During the experiment, except for one crab death in two treatment groups, the survival rate of *S. paramamosain* in all other treatments was 100% (Table 5). The body mass growth rate of *S. paramamosain* decreased significantly with increasing initial body mass. However, whether the clams were fed with shells or not did not have a significant impact on the body mass growth rate. Crabs fed with shucked clams showed only slightly lower body mass growth rate compared to those fed with unshelled clams. The *SGR* of *S. paramamosain* also decreased significantly with increasing initial body mass. Similarly, whether the clams were shucked or unshelled had no significant effect on *SGR*, though crabs fed with shucked clams exhibited a slightly higher *SGR* than those fed with with shucked clams.

Table 5 Growth of *Scylla paramamosain* fed with shucked and unshelled clams

Diets	Initial body mass // g	Survival rate // %	Final body mass // g	MGR // %	*SGR* // %/d
Clam	52.05 ±2.33	100	103.26 ±5.28^{a}	98.39 ±4.35^{c}	1.14 ±0.14^{c}
Unshelled clam	49.83 ±1.86	93.33	99.74 ±7.12^{a}	100.16 ±3.21^{c}	1.16 ±0.18^{c}
Clam	113.13 ±2.81	100	172.85 ±8.33^{b}	52.79 ±2.97^{b}	0.71 ±0.24^{b}
Unshelled clam	115.26 ±5.57	100	182.16 ±7.18^{b}	58.04 ±4.63^{b}	0.76 ±0.26^{b}
Clam	180.36 ±4.51	100	283.10 ±6.29^{c}	56.96 ±3.66^{b}	0.75 ±0.18^{b}
Unshelled clam	182.48 ±9.71	100	292.88 ±8.44^{c}	60.50 ±2.77^{b}	0.79 ±0.22^{b}
Clam	263.67 ±6.20	100	353.79 ±9.17^{d}	34.18 ±4.21^{a}	0.49 ±0.17^{a}
Unshelled clam	260.41 ±8.28	93.33	349.72 ±8.69^{d}	34.30 ±3.36^{a}	0.49 ±0.23^{a}

There were significant differences in the proportion of energy loss in exuviae and feces among *S. paramamosain* of different sizes, but whether the clams fed to them were shucked or unshelled had no significant effect on the energy allocation indicators of the crabs (Table 6). The proportion of energy allocated to growth in *S. paramamosain* ranged from 26.70% to 30.03%, showing a slight decreasing trend with increasing initial body mass, though the difference was not statistically significant. As the initial body mass of the crabs increased, the proportion of energy lost in exuviae increased significantly, while the proportion lost in feces decreased significantly. Metabolic consumption and energy allocated to growth were the two largest components of energy allocation, together accounting for approximately 85% of the energy consumed.

Table 6 Energy allocation of *Scylla paramamosain* fed with shucked and unshelled clams

Diets	Initial body mass // g	Growth // %	Exuviae // %	Feces // %	Excretion // %	Metabolism // %
Clam	52.05 ±2.33	30.03 ±3.39^{a}	1.70 ±0.35^{a}	9.37 ±1.44^{b}	4.07 ±0.92^{a}	54.83 ±8.70^{a}
Unshelled clam	49.83 ±1.86	29.49 ±4.33^{a}	1.84 ±0.62^{a}	8.86 ±1.39b	4.51 ±0.88^{a}	55.30 ±7.70^{a}
Clam	113.13 ±2.81	28.91 ±6.97^{a}	1.75 ±0.58^{a}	8.63 ±1.73^{ab}	3.39 ±0.54^{a}	57.32 ±5.81^{a}
Unshelled clam	115.26 ±5.57	28.36 ±7.03^{a}	2.29 ±0.45^{ab}	8.04 ±1.65^{ab}	3.97 ±0.71a	57.34 ±6.91^{a}
Clam	180.36 ±4.51	29.14 ±7.03^{a}	2.19 ±0.68^{ab}	7.02 ±1.66^{a}	3.97 ±0.61^{a}	57.68 ±5.69^{a}
Unshelled clam	182.48 ±9.71	27.79 ±7.21^{a}	2.72 ±0.67^{b}	7.60 ±1.59^{ab}	4.45 ±0.57^{a}	57.43 ±5.60^{a}
Clam	263.67 ±6.20	27.57 ±6.98^{a}	2.71 ±0.72^{b}	6.62 ±1.38a	3.44 ±0.55^{a}	59.66 ±5.63^{a}
Unshelled clam	260.41 ±8.28	26.70 ±6.86^{a}	3.16 ±0.58^{b}	7.08 ±1.50^{a}	3.94 ±0.52^{a}	59.13 ±5.69^{a}

3 Discussion

3.1 Growth and energy distribution of different size *S. paramamosain*

The energy allocation patterns of farmed crustaceans determine their growth rates and economic benefits and therefore have garnered widespread attention. Energy allocation models have been established for various marine and freshwater farmed crustaceans. Environmental factors affecting crustacean metabolism, such as temperature, salinity, light, and pH, may lead to changes in energy allocation patterns[27-31]. Variations in feed composition and nutrients directly influence the digestion, absorption, and metabolism of crustaceans, making them major factors affecting energy allocation patterns[28, 31-35].

As an important species in mariculture, the energy utilization of feed by *S. paramamosain* has also been widely studied. However, comparative research on energy allocation changes across different growth stages has been lacking. This experiment found that, even when fed the same diet of shucked *R. philippinarum*, the body weight growth rate of small-sized crabs over 60 d was dozens of times higher than that of large-sized crabs. Yet, the proportion of consumed energy allocated to growth was significantly lower in small-sized crabs. This indicates that the high growth rate of small-sized crabs is achieved through a higher feeding rate rather than higher food energy conversion efficiency.

In this experiment, the proportion of energy allocated to growth in *S. paramamosain* ranged from 23.70% to 29.49%. This is lower than the 34.99% reported for *S. serrata* in the late molting stage[35], but comparable to the range observed in the *E. sinensis*[31]. It is also similar to the growth energy proportions reported for the Chinese shrimp (*Fenneropenaeus chinensis*)[28, 30], the Pacific white shrimp (*Litopenaeus vannamei*)[29, 33], and the black tiger shrimp (*Penaeus monodon*)[32]. The proportion of energy allocated to growth in the freshwater oriental river prawn (*Macrobrachium nipponense*) could vary from 20.5% to 59.7% under different temperatures[27]. Shrimp also exhibit significant changes in energy allocation patterns under different environmental conditions and when fed different diets[28, 31-35], indicating substantial plasticity in the energy allocation patterns of crustaceans.

Similar to other animals, the metabolic rate per unit body mass in crustaceans gradually decreases with individual growth, while the individual metabolic rate increases at a decelerating pace[36-39]. Changes in metabolic intensity and food intake during individual growth may lead to variations in energy allocation patterns[36]. For example, juvenile *Pandalus borealis* invest more energy in growth than adults[36]. However, this experiment found that the smallest-sized *S. paramamosain* allocated less energy to growth than larger-sized crabs. This is likely because the molting frequency of small-sized crabs is significantly higher than that of larger crabs[40-41]. Frequent molting leads to greater energy consumption, which may be the main reason for the lower proportion of energy allocated to growth in small-sized *S. paramamosain*. This experiment also observed a higher proportion of energy lost in feces in small-sized crabs, possibly due to their higher feeding rate and weaker digestive capacity. Overall, except for the smallest size group, no significant differences in energy allocation patterns were observed among the larger-sized *S. paramamosain*.

3.2 Effects of shucking of *R. philippinarum* on the energy allocation of *S. paramamosain* Crabs expend a certain amount of energy in preying on and processing hard-shelled bivalves, leading to differences in the energy efficiency of consuming bivalves of different sizes, which influences the crab's size selectivity[42]. However, this experiment found that whether the *R. philippinarum* were shucked or unshelled had no significant impact on the energy allocation patterns of the *S. paramamosain*. This is likely because, for the *S. paramamosain*, the energy consumed in crushing the clam shells is minimal compared to the energy contained in the clam flesh. This experiment also revealed that the energy allocation patterns of the *S. paramamosain* did not change significantly after consuming *R. philippinarum* of different shell lengths. This further indicates that the energy expenditure required to crush the clam shells constitutes an extremely small proportion of the crab's total daily energy metabolism and is insufficient to influence its long-term energy allocation patterns.

4 Conclusions

The survival rate of *S. paramamosain* fed with *R. philippinarum* is remarkably high, and their growth rate is relatively fast, indicating that *R. philippinarum* serve as a high-quality feed for *S. paramamosain*. After consuming *R. philippinarum*, the energy intake of *S. paramamosain* is primarily allocated to growth and daily metabolism, with minimal energy loss through feces, molting, and nitrogen excretion. Smaller-sized *S. paramamosain* may exhibit reduced energy allocation toward growth, potentially due to frequent molting leading to higher energy loss. The size of the variegated clams and whether they are shelled do not significantly alter the energy allocation patterns of the *S. paramamosain*, suggesting that the energy expended in crushing the clam shells constitutes only a negligible portion compared to the energy gained from feeding or the energy consumed in daily metabolism.

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