

Article

Study of Growth and Survival of Four Wild-Caught Mud Crab Species (*Scylla* spp.) During Nursery and Grow-Out Phases

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Abstract

This study compared the survival and growth of four wild-caught mud crab species (*Scylla serrata*, *S. paramamosain*, *S. tranquebarica*, and *S. olivacea*) under controlled conditions. The experiment was divided into two stages: Stage I (crablet to juvenile) and Stage II (juvenile to adult). At the end of each stage, the sex ratio, survival rate (SR), body weight (BW), carapace width (CW), weight gain (WG), and average daily gain (ADG) were calculated. The results showed that *S. tranquebarica* had the highest cumulative survival (67.6%), whereas *S. serrata* recorded the lowest (38.6%). Growth performance varied among species and between sexes. Male *S. serrata* demonstrated the highest growth potential with a final CW (11.77 cm), BW (447.1 g), WG (428.61 g), and ADG (3.93 g/day). Conversely, *S. olivacea* exhibited the lowest overall growth performance in Stage II. Males of *S. serrata* and *S. paramamosain* showed superior final growth performance over females. Furthermore, *S. tranquebarica* showed phase-dependent growth acceleration, transitioning from the lowest growth in Stage I to the second highest in Stage II. Further studies are needed to evaluate *S. tranquebarica* as a potential alternative or complementary culture species to *S. serrata*.

Keywords: mud crab; growth comparison; weight gain; average daily gain; survival rate

Key Contribution: This study demonstrates significant species- and sex-specific variations in mud crab (*Scylla*) growth and survival, with *S. serrata* achieving the highest growth and the lowest survival, and males outperforming females in key species.



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1. Introduction

Mud crabs of the genus *Scylla*, including *S. serrata*, *S. paramamosain*, *S. tranquebarica*, and *S. olivacea*, are among the most economically important crustaceans in tropical and subtropical regions. These species are widely distributed from the Indian Ocean to the western Pacific, supporting fisheries and providing critical income for coastal communities [1]. Their rapid growth, high nutritional value, and broad environmental adaptability contribute to strong market demand and make them promising candidates for aquaculture development [2,3].

In response to increasing global demand for aquatic products, mud crab farming has expanded rapidly across Asia and is now recognized as a sector with significant potential

for large-scale production [4–6]. However, production efficiency remains constrained by several challenges. Survival rates in outdoor culture systems are often low, and large-scale hatchery technologies are still underdeveloped, resulting in continued reliance on wild-caught seed stock. This dependence introduces multiple limitations, including mixed-species composition, inconsistent seed quality, high size heterogeneity, elevated risks of pathogen transmission, increasing costs, and vulnerability to environmental changes [1]. Collectively, these factors reduce supply stability and hinder the expansion of mud crab aquaculture [7–9].

Understanding species-specific growth performance and survival is therefore essential for improving production efficiency. Previous studies have demonstrated that *Scylla* species differ significantly in growth rates, environmental tolerance, and nutritional requirements [10–12]. In addition, sex-based differences further influence aquaculture performance [13,14]. Following maturity, females allocate energy toward reproduction, affecting body weight (BW) and carapace width (CW) [15], whereas males often exhibit enhanced somatic growth associated with cheliped development [16]. These differences are closely linked to reproductive strategies and developmental patterns [8]. However, most studies have only examined individual species or controlled conditions, limiting direct comparisons across species and sexes under uniform culture environments.

To address this gap, the present study evaluates the growth performance and survival of four *Scylla* species under the same outdoor rearing conditions using wild-caught seed stock. The experiment was conducted in two phases: Stage I (crablet to juvenile) and Stage II (juvenile to adult). Specifically, this study aims to (1) analyze the species composition and sex ratios of wild-caught *Scylla* species (*S. serrata*, *S. paramamosain*, *S. tranquebarica*, and *S. olivacea*); (2) compare interspecific growth performance and survival under identical environmental conditions; and (3) assess sex-based differences in growth and survival within each species. The findings provide a foundation for improving species selection, stocking strategies, and sex-specific management in mud crab aquaculture and are expected to benefit the future crab farming industry.

2. Materials and Methods

2.1. Ethics Statement

Wild mud crabs (*Scylla*) were collected from the Linbian River estuary in Pingtung, Taiwan. They were not privately owned or protected in any way. The field studies did not include endangered or protected species. All experimental procedures on animals were in compliance with the guidelines of the Animal Protection Act of Taiwan (Ministry of Agriculture).

2.2. Experimental Organisms

Wild mud crab seed stock (megalopa) was collected from the Linbian River estuary in Pingtung, Taiwan (22°25′00″ N, 120°30′41″ E). Following collection, the larvae were transported to the Taixi Experimental Station of the Mariculture Research Center, Fisheries Research Institute, Ministry of Agriculture, Taiwan (23.7175° N, 120.1903° E). Within three hours after arrival, mud crab megalopae were separated from other organisms and debris collected from the wild for initial counting, weighing, and subsequent acclimation. Species and sex identification were not conducted during this initial sorting procedure.

2.3. Experimental Design

The larvae were reared under identical environmental and management conditions to enable comparative evaluation. The parameters for each aquaculture stage for lar-

vae, including duration (days), stocking and harvest counts, and mean CW and BW, are summarized in Table 1.

Table 1. Mean body weight (g) and carapace width (cm) of mud crabs (*Scylla* spp.) at different culture stages ($n = 10$).

Stages	Duration (Days)	Individual No.		Body Weight (g)		Carapace Width (cm)	
		Initial	Final	Initial	Final	Initial	Final
Acclimation (Megalopa to Crablet)	8	1000	855	0.0038 ± 0.0009	0.02 ± 0.0051	0.36 ± 0.0033	0.5 ± 0.07
Stage I (Crablet to Juvenile)	30	855	728	0.02 ± 0.0051	14.4 ± 2.02	0.56 ± 0.07	2.37 ± 0.07
Stage II (Juvenile to Adult)	109	728	392	14.4 ± 2.02	294 ± 103.6	2.37 ± 0.07	8.69 ± 2.09

2.3.1. Acclimatization Stage

The acclimatization stage involves rearing wild-caught megalopa to the crablet stage. This stage facilitates the assessment of health status and SR to ensure that subsequent formal trials are supported by a sufficient and representative sample size.

Megalopae were reared in indoor plastic tanks ($1.3 \times 1.3 \times 0.9$ m) with an effective water volume of 1.5 m^3 . Over an 8-day acclimatization period, larvae were stocked at a density of 591.7 ind./m^2 under a light intensity of 3000–5000 lux and dissolved oxygen (DO) levels of 6.53 mg/L . The larvae were fed minced mussel at 30% body weight once daily. At the end of the 8-day acclimation period, the surviving individuals had developed into first-stage crablets (CI). The crablets were then collected for survival counting, species identification, and sex determination. Species identification was based on external morphological characteristics of first-stage crablets, including distinguishable interspecific differences in the frontal median spines and chelipeds [17]. Sex identification was based on external sexual characteristics observable at the CI stage, including the presence or absence of female gonopores [18]. Ten individuals of each species were randomly sampled for BW and CW measurements.

2.3.2. Stage I: Crablet to Juvenile

The first experimental stage evaluated the growth from the crablet-to-juvenile phase. Healthy crablets were transferred to an outdoor concrete pond ($8 \text{ m} \times 4.4 \text{ m} \times 1.45 \text{ m}$) for a 30-day growth trial at a stocking density of 24.3 ind./m^2 (0.019 ind./L). The crablets were fed three times daily at a total daily feeding rate of 30% of their weight. The diet comprised minced mussel and commercial shrimp feed (0.4 mm) at a 3:1 ratio. Macroalgae were placed in the culture system as structural barriers. Following the 30-day period, all juveniles were collected for survival counting, species and sex identification, and subsequent culture procedures. Body weight (BW) was recorded in grams (g) using a digital balance (AUW220D, Shimadzu Corporation, Kyoto, Japan; minimum display: $0.1 \text{ mg}/0.01 \text{ mg}$), while carapace width (CW) was measured using vernier calipers (Mitutoyo Corporation, Kawasaki, Japan, $\pm 0.05 \text{ mm}$).

2.3.3. Stage II: Juvenile to Adult

This stage recorded the growth performance during the transition from juvenile to adult. At the initiation of this phase, juveniles collected from the previous stage were stocked into an outdoor earthen pond ($53.26 \text{ m} \times 20.20 \text{ m} \times 1.2 \text{ m}$) at an average density of 0.68 ind./m^2 for a 109-day grow-out period. The diet consisted of minced fish and commercial adult shrimp feed (3–4 mm) at a 7:3 weight ratio. Feeding was conducted once

daily, with the feeding rate adjusted based on growth and satiation, decreasing from 8% of the total biomass in the initial stage to 3% toward the end. Upon completion of the trial, all surviving crabs were collected to determine species distribution and sex ratios. Ten male and female individuals of each available species were subsequently sampled for measurements of BW and CW. These data were used to analyze growth, survival, and sex-based variations among the four *Scylla* species.

2.4. Water Source Preparation and Water Quality Monitoring

To maintain stable conditions, standardized water management and monitoring protocols were implemented across all experimental phases. During the acclimatization period, water quality parameters (temperature, salinity, and DO) were monitored with bottom siphoning and water exchange performed every two days. In Stage I, water quality was monitored weekly, with bottom siphoning and water exchange performed once every 5 days. For Stage II, water quality was also monitored weekly, and approximately 20% of the pond volume was replenished every 30 days to stabilize water levels and physicochemical properties. To mitigate the risk of exogenous pathogens, all supplemental seawater was disinfected with 10 mg/L sodium hypochlorite. This water was only introduced into the culture systems after verifying that residual chlorine had reached undetectable levels.

The temperature, salinity, and pH were monitored using a YSI ProDSS Multi-Parameter Water Quality Meter (Yellow Springs Instrument, Yellow Springs, OH, USA). Additionally, total ammonia nitrogen (TAN) and nitrite–nitrogen (NO_2^- -N) concentrations (mg/L) were determined using a Water Link Spin Touch photometer (LaMotte, Chestertown, MD, USA).

2.5. Survival Rates (SRs) and Growth Performance

The SR and growth performance calculation methods are as follows:

$$\text{Survival Rate (SR, \%)} = (\text{Nf}/\text{N0}) \times 100 \quad (1)$$

N0: Initial number of stocked individuals.

Nf: Final number of surviving individuals.

$$\text{Weight Gain (WG, g)} = \text{Wf} - \text{W0} \quad (2)$$

W0: Initial average weight of the stage.

Wf: Final average weight of the stage.

$$\text{Average Daily Gain (ADG, g/day)} = (\text{Wf} - \text{W0})/\text{T} \quad (3)$$

T: Duration of the experimental period, days.

2.6. Statistical Analysis

Statistical analyses were performed using Microsoft Excel 2019 and IBM SPSS Statistics 21.0. Data are presented as numbers and percentages. Directly measured variables, including BW and CW, are presented as mean $\pm$ standard deviation.

Differences in the observed survival proportions among the four *Scylla* species within each culture stage were evaluated using chi-square tests. When an overall chi-square test was significant, adjusted standardized residuals (ASRs) were examined to identify the species contributing to the observed differences. Growth measurements were analyzed separately for Stage I and Stage II. Initial and final BW and CW were independently compared among the observed species–sex groups using one-way analysis of variance (ANOVA), followed by Tukey's honestly significant difference (HSD) test. In Stage I, initial measurements were compared among eight species–sex groups, whereas final measurements were

compared among seven surviving groups because no female *S. tranquebarica* survived to the end of Stage I and Stage II. Initial and final measurements were obtained from independent random samples. The WG and ADG were considered descriptive group-level growth indices and were not subjected to inferential statistical testing. Statistical comparisons of BW and CW were therefore conducted at the level of sampled individuals and were interpreted as comparisons within the shared culture cohort.

3. Results

3.1. Water Quality Analysis

Water quality was monitored throughout the acclimatization phase and the two subsequent experimental cultivation stages. The monitored parameters included temperature, salinity, DO, pH, TAN, and nitrite concentrations. Fluctuations in these parameters were observed over the experimental period, driven by the synergistic effects of seasonal transitions, feeding frequencies, and the distinct environmental conditions of each culture system. Overall, water temperature gradually increased across the successive stages, with mean values recorded at 28.40 ± 0.11 °C during the acclimatization phase, 30.02 ± 0.35 °C in Stage I, and 30.10 ± 0.46 °C in Stage II. Salinity followed a similar slight upward trend throughout the study, with values of 30.25 ± 0.05 psu during the acclimatization phase, 31.5 ± 0.05 psu in Stage I, and 32.19 ± 1.11 psu in Stage II.

DO levels were recorded at 6.53 ± 0.23 mg/L during acclimatization, increased to 7.90 ± 0.06 mg/L in Stage I, and remained stable at 7.56 ± 0.27 mg/L through Stage II. The pH was relatively stable across all phases, remaining slightly alkaline; mean pH values were 8.19 ± 0.07 in the acclimatization phase, 8.24 ± 0.12 in Stage I, and 8.10 ± 0.41 in Stage II.

TAN concentrations remained below the detection limit during the acclimatization phase, while the mean values of Stage I and Stage II were 0.13 ± 0.26 mg/L and 0.16 ± 0.25 mg/L, respectively. Nitrite–nitrogen (NO_2^- -N) displayed a progressive upward trend throughout the study, increasing from 0.02 ± 0.03 mg/L during acclimatization to 0.04 ± 0.06 mg/L in Stage I and 0.06 ± 0.05 mg/L in Stage II.

3.2. Survival Rate (SR)

The overall SRs for the four *Scylla* species across both experimental stages are presented in Table 2. In Stage I, all four species maintained high overall SR. *S. olivacea* exhibited the highest survival (91.0%), whereas *S. serrata* displayed the lowest survival (79.1%). Meanwhile, *S. paramamosain* (83.3%) and *S. tranquebarica* (88.2%) did not show a significant difference.

Table 2. Survival rates (%) of four *Scylla* species across two culture stages.

Stages	<i>S. serrata</i>	<i>S. paramamosain</i>	<i>S. tranquebarica</i>	<i>S. olivacea</i>	Total
I	79.10 ^b	83.30 ^{ab}	88.20 ^{ab}	91.00 ^a	85.14
II	48.70 ^b	52.60 ^{ab}	76.70 ^a	55.80 ^{ab}	53.84
Final	38.60 ^b	43.80 ^{ab}	67.60 ^a	50.80 ^a	45.84

Note: Different superscript letters within the same row indicate statistically significant differences among species ($p < 0.05$), based on chi-square tests followed by comparisons of adjusted standardized residuals.

In Stage II, SRs across all species decreased markedly, and interspecific differences became more pronounced. *S. tranquebarica* recorded the highest SR (76.7%), whereas *S. serrata* still showed the lowest survival (48.7%). Meanwhile, *S. paramamosain* (52.6%) and *S. olivacea* (55.8%) showed no significant differences.

At the end of the experiment, *S. tranquebarica* showed the highest overall SR (67.6%), while *S. serrata* had the lowest overall SR (38.6%). Additionally, the SRs of *S. olivacea* and *S. paramamosain* were 50.8% and 43.8%, respectively.

3.3. Abundance and Sex Ratio

The abundance, percentage (%), and sex ratio (%) of the four *Scylla* species across all cultivation stages are summarized in Table 3. Since all individuals were sourced from wild-caught crablets, the interspecific variation in abundance during the acclimatization phase might reflect the natural population structure. *S. olivacea* was the most dominant species throughout the study, with 321, 292, and 163 individuals recorded during the acclimatization phase, Stage I, and Stage II, respectively. In contrast, *S. tranquebarica* exhibited the lowest abundance across all three stages (34, 30, and 23 individuals). The ranking of species proportions remained consistent across stages: *S. olivacea* > *S. paramamosain* $\approx$ *S. serrata* > *S. tranquebarica*.

Table 3. Population individuals, percentages, and sex ratios between females (F) and males (M) of four *Scylla* species at different culture stages.

Stages		<i>S. serrata</i>	<i>S. paramamosain</i>	<i>S. tranquebarica</i>	<i>S. olivacea</i>
Acclimation	No. (%)	249 (29.12)	251 (29.36)	34 (3.98)	321 (37.54)
	F:M (%)	51.0/49.0	49.8/50.2	11.8/88.2	52.6/47.4
I	No. (%)	197 (27.06)	209 (28.71)	30 (4.12)	292 (40.11)
	F:M (%)	51.8/48.2	53.1/46.9	0.0/100.0	52.7/47.3
II	No. (%)	96 (24.49)	110 (28.06)	23 (5.87)	163 (41.58)
	F:M (%)	52.1/47.9	52.7/47.3	0.0/100.0	50.9/49.1

Regarding sex ratios, *S. serrata*, *S. paramamosain*, and *S. olivacea* maintained a balanced ratio near 1:1. However, *S. tranquebarica* displayed a significant male bias: females accounted for only 11.8% of the population during acclimatization and were entirely absent (0%) in Stage I and Stage II.

3.4. Growth

3.4.1. Stage I

Growth varied significantly among species and sexes during Stage I (Table 4). While no significant differences were found in initial weight (IW) and initial CW across all groups, final body weight (FW) displayed distinct variation, with a statistically significant margin of 5.93 g between the highest and lowest recorded values. Male *S. serrata* attained the highest FW (18.49 ± 0.42 g), significantly surpassing all other groups. Meanwhile, the lowest FW values were recorded in female *S. paramamosain* (12.56 ± 0.68 g) and male *S. tranquebarica* (12.56 ± 0.88 g), with no significant difference observed between these two groups. The overall FW hierarchy for Stage I was as follows: male *S. serrata* > female *S. olivacea* > male *S. paramamosain* $\approx$ female *S. serrata* $\approx$ male *S. olivacea* > male *S. tranquebarica* $\approx$ female *S. paramamosain*.

Similarly, male *S. serrata* had the highest final CW (2.45 ± 0.09 cm), significantly larger than all other cohorts. Conversely, the lowest CW values were observed in female *S. olivacea* (2.31 ± 0.04 cm) and male *S. olivacea* (2.31 ± 0.02 cm). The other species showed high similarities in CW for Stage I.

Weight gain (WG) and average daily weight gain (ADG) mirrored these trends. Male *S. serrata* exhibited the highest WG (18.46 g) and ADG (0.61 g/day) among the observed groups. The lowest WG and ADG were consistently observed in female *S. paramamosain* and male *S. tranquebarica*. These data indicate that male *S. serrata* and female *S. olivacea*

possess superior growth potential during Stage I, suggesting that both species and sex strongly influenced the growth of *Scylla* crab during the early juvenile phase.

Table 4. Comparison of growth parameters between females (F) and males (M) of four *Scylla* species in Stage I.

Sex	<i>S. serrata</i>		<i>S. paramamosain</i>		<i>S. tranquebarica</i>		<i>S. olivacea</i>	
	F	M	F	M	F	M	F	M
Initial BW	0.03 ± 0.01 ^a	0.03 ± 0.01 ^a	0.02 ± 0.005 ^a	0.03 ± 0.003 ^a	0.02 ± 0.01 ^a	0.02 ± 0.01 ^a	0.03 ± 0.003 ^a	0.03 ± 0.003 ^a
Initial CW	0.56 ± 0.01 ^a	0.56 ± 0.03 ^a	0.55 ± 0.01 ^a	0.55 ± 0.01 ^a	0.55 ± 0.01 ^a	0.55 ± 0.01 ^a	0.56 ± 0.01 ^a	0.56 ± 0.00 ^a
Final BW	13.87 ± 0.59 ^c	18.49 ± 0.42 ^a	12.56 ± 0.68 ^d	14.12 ± 0.65 ^c	-	12.56 ± 0.88 ^d	15.40 ± 0.52 ^b	13.78 ± 0.83 ^c
Final CW	2.39 ± 0.08 ^{ab}	2.45 ± 0.09 ^a	2.35 ± 0.04 ^{bcd}	2.38 ± 0.06 ^{abc}	-	2.42 ± 0.03 ^{ab}	2.31 ± 0.04 ^d	2.31 ± 0.02 ^{cd}
WG	13.84	18.46	12.53	14	-	12.4	15.37	13.77
ADG	0.46	0.61	0.4	0.46	-	0.41	0.52	0.47

Note: Body weight (BW, g); carapace width (CW, cm); weight gain (WG, g); average daily gain (ADG, g/day). Initial and final BW and CW are presented as mean ± standard deviation ($n = 10$ per available group). Different lowercase letters within the same row indicate significant differences among the groups ($p < 0.05$). “-” indicates that no female *S. tranquebarica* survived to the end of Stage I.

3.4.2. Stage II

During Stage II, interspecific and sex-based variations in BW, growth rates, and carapace development became markedly more pronounced than those observed in Stage I. The magnitude of divergence in growth indicators expanded in Stage II, revealing distinct disparities in morphological size and growth potential among species (Table 5). Male *S. serrata* achieved the highest FW of 447.1 ± 66.6 g, significantly outperforming all other species and sex cohorts. Conversely, male and female *S. olivacea* displayed the lowest growth performance, with weights of 178.6 ± 23.43 g and 154.67 ± 5.95 g, respectively, showing no significant difference between them.

Table 5. Comparison of growth parameters between females (F) and males (M) of four *Scylla* species in Stage II.

Sex	<i>S. serrata</i>		<i>S. paramamosain</i>		<i>S. tranquebarica</i>		<i>S. olivacea</i>	
	F	M	F	M	F	M	F	M
Initial BW	13.87 ± 0.59 ^c	18.49 ± 0.42 ^a	12.56 ± 0.68 ^d	14.12 ± 0.65 ^c	-	12.56 ± 0.88 ^d	15.40 ± 0.52 ^b	13.78 ± 0.83 ^c
Initial CW	2.39 ± 0.08 ^{abc}	2.45 ± 0.09 ^a	2.35 ± 0.04 ^{bcd}	2.38 ± 0.06 ^{abc}	-	2.42 ± 0.03 ^{ab}	2.31 ± 0.04 ^d	2.31 ± 0.02 ^{cd}
Final BW	316 ± 48 ^{bc}	447.1 ± 66.6 ^a	282.1 ± 50.1 ^c	316.89 ± 60.87 ^{bc}	-	364 ± 12.79 ^b	178.6 ± 23.43 ^d	154.67 ± 5.95 ^d
Final CW	9.26 ± 0.31 ^c	11.77 ± 0.67 ^a	8.34 ± 0.06 ^d	9.03 ± 0.65 ^c	-	10.63 ± 0.55 ^b	5.95 ± 0.40 ^e	5.90 ± 0.34 ^e
WG	302.13	428.61	269.54	303.67	-	351.15	162.87	140.87
ADG	2.77	3.93	2.47	2.78	-	3.22	1.49	1.29

Note: Body weight (BW, g); carapace width (CW, cm); weight gain (WG, g); average daily gain (ADG, g/day). Initial and final BW and CW are presented as mean ± standard deviation ($n = 10$ per available group). The initial measurements for Stage II correspond to the end of Stage I. Different lowercase letters within the same row indicate significant differences among the groups ($p < 0.05$). The “-” indicates that no female *S. tranquebarica* survived to the end of Stage I.

Final CW also mirrored these trends. Male *S. serrata* showed the highest CW (11.77 ± 0.67 cm), significantly exceeding all other groups. Meanwhile, both sexes of *S. olivacea* were significantly smaller than all other cohorts (5.95 ± 0.40 cm and 5.90 ± 0.34 cm), with no significant variance between them.

Regarding WG, male *S. serrata* showed superior performance (428.61 g) among the observed groups. In contrast, both sexes of *S. olivacea* yielded the lowest WG values (162.87 g for females and 140.87 g for males). The ADG followed a similar pattern to WG. Male *S. serrata* achieved the highest ADG at 3.93 g/day among the observed groups. Consistent with other metrics, both sexes of *S. olivacea* recorded the lowest ADG values (1.49 g/day and 1.29 g/day). High similarities in ADG were observed between sexes and among the other species.

4. Discussion

4.1. Water Quality

Throughout the acclimatization phase and the two subsequent experimental stages, all water quality parameters were within the optimal range for mud crab cultivation. Previous studies have demonstrated that water temperature significantly influences the physiological responses, growth performance, survival, and sex ratios of juvenile *S. paramamosain* [9]. Specifically, a temperature range of 28–30 °C has been identified as optimal for the growth, molting frequency, and survival of juvenile *Scylla* species. In comparison, extreme temperatures (below 24 °C or above 32 °C) can induce physiological stress, resulting in growth retardation, gill deformities, and skewed sex distributions [9]. In the present study, water temperature ranged between 28.4 and 30.1 °C, aligning with the established thermal optima for mud crab development.

Previous research has shown that *S. serrata* is highly sensitive to pH fluctuations, making it a critical bioindicator for assessing the impacts of ocean acidification. Ling [19] reported significantly lower growth and survival of *S. serrata* at pH 7.5 than at pH 8.1, demonstrating the importance of suitable pH conditions for juvenile crab development. In the present study, the pH remained stable between 8.14 and 8.24, consistent with the optimal conditions required for mud crab growth.

Collectively, DO (6.53–7.90 mg/L), salinity (30.25–32.19 psu), TAN (0.13–0.16 mg/L), and nitrite (0.02–0.06 mg/L) remained within biologically acceptable ranges for the cultured *Scylla* species.

4.2. Survival Rates (SRs)

Survival in mud crab culture may be influenced by species-specific biological traits, environmental conditions, and husbandry practices [20].

Providing adequate shelter structures can effectively mitigate competition and cannibalism, whereas excessive stocking densities often precipitate a decline in survival. Dietary quality and environmental stability dictate water quality and disease susceptibility; nutritional deficiencies often result in incomplete molting, subsequently triggering high mortality rates [21]. During the early juvenile stages, mud crabs possess immature immune systems, rendering them highly vulnerable to pathogenic infections. Consequently, stringent biosecurity measures and proactive disease prevention are essential strategies for enhancing survival [21].

In the present study, SR varied significantly among species during Stage I, with the highest value observed in *S. olivacea* (91.0%) and the lowest in *S. serrata* (79.1%) (Table 2). Because all four species were exposed simultaneously to the same environmental fluctuations within the shared culture system, these fluctuations alone cannot fully explain the observed interspecific differences in survival. Rather, the observed variation may reflect species-specific tolerance to environmental fluctuations, together with other biological and husbandry-related factors. Although all four species were maintained under the same culture environment, water quality management, husbandry practices, feeding frequency, and feed types during each culture stage, their initial abundance, sex composition, and relative proportions within the polyculture population were not equivalent. Interspecific competition and predatory or cannibalistic interactions may also have influenced the observed survival and growth patterns. Therefore, the observed interspecific differences should not be attributed solely to inherent species-specific biological traits, but should be interpreted as comparative performance under the polyculture conditions used in the present study. Conversely, Masum et al. [22] demonstrated that juvenile *S. olivacea* often experience physiological instability similar to other *Scylla* species, frequently leading to high mortality. Specifically, in Bangladesh cultivation trials, the highest mortality rates

were observed between the megalopae and C1 juvenile stages, with average mortality reaching 84.02% and total survival from Z1 to C1 ranging from only 0.67% to 3.17%. Despite these low baseline figures, Masum et al. [22] demonstrated that reducing megalopae stocking density from 15 ind./L to 3.75 ind./L could enhance survival to approximately 11%, underscoring the critical role of density-dependent factors in early development. In contrast, the stocking density employed during the acclimatization phase of this study (megalopa to crablet) was only 0.66 ind./L, significantly lower than the densities reported in the literature. This conservative density may have mitigated cannibalism and likely provided a safer environment for molting. In the present study, *S. olivacea* exhibited the highest SR during Stage I (91.0%). Previous studies have reported that *S. olivacea* inhabits low-salinity and fluctuating intertidal environments [21]; however, the present study did not directly evaluate species-specific tolerance to individual environmental variables.

On the other hand, *S. serrata* exhibited the lowest SR (79.1%) during Stage I. A previous monoculture study reported a significant increase in the survival of *S. serrata* from 31% to 98% by reducing density from 3.0 ind./m² to 0.5 ind./m² [21]. Therefore, the relatively lower survival observed in this trial may be related to density-induced stress and interspecific interactions within the polyculture system, rather than the species' inherent survival potential.

It should also be noted that stocking density was expressed differently between the two experimental stages because they represented different developmental and culture phases. Stage I (crablet to juvenile) was conducted in a concrete nursery pond, with a stocking density of 0.019 ind./L (24.3 ind./m²), whereas Stage II (juvenile to adult) was conducted in an outdoor earthen grow-out pond at 0.68 ind./m². These differences reflect changes in crab body size and culture system between the two stages and may have resulted in different density-related stressors and individual interactions. This consideration may be particularly relevant to *S. serrata*, which exhibited relatively low survival during both stages and for which survival has been reported to vary with stocking density [21].

Cannibalism is widely recognized as a primary constraint on SR within *Scylla* aquaculture. Previous studies found that *S. serrata* crablets are exceptionally vulnerable, with cannibalism-induced mortality reaching up to 60% within a few days immediately following molting [23]. The incidence of such behavior increased significantly when stocking densities were excessive, structural shelters were inadequate, or size heterogeneity among individuals increased. During both the juvenile and grow-out phases, frequent agonistic interactions and autotomy (limb loss) often precipitate sharp declines in survival, a phenomenon particularly pronounced in semi-intensive pond systems. Previous studies indicate that these mortality drivers (high density, lack of refugia, and disparate growth rates) can be mitigated through precise density control and the provision of artificial habitats or shelters [24].

During Stage II, *S. tranquebarica* exhibited the highest observed SR (76.7%) among the four species. However, because the initial abundance of *S. tranquebarica* was substantially lower ($n = 34$) than those of the other species, this survival pattern should be interpreted with caution and may not fully represent the broader survival performance of the species. Conversely, *S. serrata* appeared to encounter significantly higher environmental or agonistic pressures under identical cultivation conditions, resulting in the lowest observed SR. Syafaat et al. [25] reported an SR of only 22% for *S. tranquebarica* by the third month of cultivation, yet concluded that its farming remained economically viable. In the present study, *S. tranquebarica* exhibited an SR of 76.7% during Stage II. However, because cannibalistic behavior was not directly quantified and the *S. tranquebarica* cohort had a relatively small initial sample size, the factors contributing to its higher observed survival cannot be conclusively determined. A pooled survival analysis across all four species revealed an

SR of 85.14% during Stage I (crablet to juvenile) and 53.84% during Stage II (juvenile to adult), resulting in a cumulative survival of 45.84% (Table 2). The high survival observed in Stage I is likely attributable to the brief duration of the phase (30 days) and the small morphological size of the individuals. Although cannibalism remained a factor, the combination of moderate stocking density, feed availability, and the provision of oyster shell substrates as complex refugia effectively minimized individual competition and agonistic encounters. Conversely, the marked decline in survival during Stage II stems from the extended cultivation period, where increased body size and expanded foraging ranges heightened intraspecific competition, mating-related aggression, and feeding-related conflicts. These observed patterns align with Shelley and Lovatelli [26], who emphasized that enhancing habitat complexity and ensuring consistent dietary provision are critical strategies for mitigating mortality in mud crab aquaculture.

This study used a polyculture system with wild-caught seed stock of four *Scylla* species, resulting in survival outcomes that markedly differ from existing monoculture literature. Previous studies, such as [21], noted that monoculture of *S. serrata* juveniles consistently maintained an SR exceeding 70% under optimized management. Similarly, Fatimah et al. [27] reported a lower SR (59.26%) for *S. tranquebarica* reared at a density of 0.225 ind./L with sand substrate. Furthermore, Jangid et al. [23] found that juvenile *S. serrata* in monoculture, stocked at 0.149 ind./L and fed at 10–12% BW daily, achieved only 50% SR without shelters. However, when synthetic shelters such as frayed ropes and PVC pipes were provided, the SR increased to 65% and 71.7%, respectively. In contrast, the present study achieved a significantly higher cumulative SR of 85.14% during the equivalent juvenile (Stage I). This improvement might be associated with the implementation of a substantially lower stocking density (0.019 ind./L), increasing the daily feeding ration to 30% BW (satiation feeding), and introducing macroalgae as natural barriers. These findings suggest that variations in survival are multi-factorial, driven by the interplay of stocking densities, feeding regimes, and the structural complexity of the environment.

Pronounced sex-based growth differences were observed during Stage II. Males of *S. serrata* and *S. paramamosain* consistently exhibited higher FW and ADG than the females. For example, male *S. serrata* reached an FW of 447.1 g, whereas females attained 316.0 g (Table 5). This aligns with Shi et al. [16], who reported that male crabs direct more energy into heavy structures such as chelipeds and carapace. Consequently, at a comparable CW, males tend to attain a higher total body mass. In contrast, female crabs direct their energy toward reproduction (abdomen) to support future egg incubation. Therefore, the higher weights and growth rates seen in male crabs reflect these different energy strategies.

4.3. Growth Performance

The growth parameters for all four *Scylla* species during Stage I are summarized in Table 4. Experimental data revealed no significant differences in initial body weight (IW) and initial CW among the species. This uniformity indicates that the subsequent growth variations observed across the stages were likely driven by species- and sex-specific growth potential or other biological factors rather than by discrepancies in initial individual size.

By the conclusion of Stage I, distinct growth disparities in FW and final CW emerged across species and sexes. Male *S. serrata* attained the highest CW (2.45 cm), which was approximately 1.06-fold and 1.04-fold higher than that of *S. olivacea* (2.31 cm) and female *S. paramamosain* (2.35 cm), respectively. These data indicate that interspecific and sex-based variations in growth begin to manifest during this early phase. Notably, the variance in CW across groups was relatively marginal compared to weight, suggesting that CW may be a less sensitive indicator of growth differentiation during early developmental stages. The experimental results revealed a pronounced sex effect, with males of both *S. serrata*

and *S. paramamosain* exhibiting superior growth performance. Moreover, interspecific differences were clearly evident, with male *S. serrata* demonstrating the most prominent growth potential among all cohorts.

Upon progressing to Stage II, the growth disparities among the four *Scylla* species widened significantly, with interspecific and sex-based variations becoming increasingly pronounced (Table 5). Male *S. serrata* consistently maintained the highest growth rate throughout this phase, followed by male *S. tranquebarica*, while other cohorts exhibited markedly slower growth. These results suggest that species and sex remain decisive factors influencing growth performance beyond the early juvenile stage. Furthermore, the divergence in weight-related metrics during Stage II was greater than that of CW when compared to Stage I. This reinforces the observation that, across both developmental phases, body weight is a more sensitive and reliable indicator for monitoring the growth, differentiation, and physiological potential of various mud crab species and sexes.

Experimental results from both Stage I and Stage II indicate that male *S. serrata* consistently exhibit superior growth performance compared with females, a trend that aligns with the existing literature. Ruscoe et al. [28] also found that in seawater pond monocultures, male *S. serrata* exhibit a distinct growth advantage; specifically, juveniles reared at 30 °C and 10–20 ppt salinity can achieve a specific growth rate (SGR) of approximately 16%/day. Despite variations in experimental design, duration, and environmental parameters between studies, the overarching results remain consistent: the growth performance of male *S. serrata* is generally superior to that of other *Scylla* species and, in most instances, surpasses that of female *S. serrata* [28]. Furthermore, [16] observed that juvenile *S. serrata* (initial weight ~2 g) stocked at a density of 5 ind./m² reached FW exceeding 500 g after an 8.6-month pond culture period. Consistent with our findings, the final mean weights of males were significantly higher than those of females at harvest.

Our findings also demonstrate that male *S. tranquebarica* exhibits rapid growth, achieving the second-highest FW in Stage II across all four species, surpassed only by male *S. serrata*. These observations align with research by Syafaat et al. [25], which compared the growth performance of juvenile *S. olivacea* and *S. tranquebarica* and found that the latter attained significantly higher final weights. Consistent with their conclusions, our study confirms that the final weight of male *S. tranquebarica* exceeds that of both sexes of *S. olivacea*. These results highlight *S. tranquebarica*'s rapid growth characteristics and substantial commercial aquaculture potential.

Compared to other species, both sexes of *S. olivacea* exhibited a lower growth pattern. This species recorded the lowest FW, WG, and ADG, and this disparity became particularly pronounced during Stage II, indicating that *S. olivacea* possesses an inherently slower growth rate during the middle and late stages of culture. In addition, *S. olivacea* typically inhabits mangrove intertidal zones and brackish estuaries with low, fluctuating salinity. While this suggests a strong ability to adapt to varying salt levels, the species generally shows lower growth (FW, ADG, and SGR) compared to other *Scylla* species. This pattern may be associated with its early sexual maturity. Because it matures at a smaller size and a younger age, *S. olivacea* shifts its energy from body growth to reproduction sooner, which limits its size during the later stages of culture [29].

It is hypothesized that the growth disparities observed during Stage II are primarily driven by density-dependent stress and intensified cannibalism as body size increases. While species like *S. olivacea* exhibited lower growth performance under these conditions, *S. serrata* and *S. tranquebarica* demonstrated superior adaptability and feeding efficiency, maintaining robust growth within the same environment. These findings align with the prevailing preference for *S. serrata* aquaculture across Southeast Asia. Its exceptional growth rates and high market valuation have established it as the foundational species for

mud crab industries in the region [30,31]. Furthermore, the rapid growth potential of *S. tranquebarica* suggests it could serve as a valuable alternative or complementary species for intensive production systems.

S. paramamosain has become a dominant species in Southeast Asian aquaculture, largely due to its optimal balance between growth and survival. Data from Table 5 indicate that males exhibited steady growth during Stage II, reaching an FW of 316.89 ± 60.87 g and an ADG of 2.78 g/day, while females reached only 282.1 ± 50.1 g and 2.47 g/day. Although its growth rate was lower than that of *S. serrata* and *S. tranquebarica*, the performance of male *S. paramamosain* was comparable to female *S. serrata* and significantly exceeded the growth trajectory of *S. olivacea*.

When evaluating aquaculture potential, the trade-off between survival and growth is a critical determinant of production efficiency. Across all stages, *S. serrata* exhibited the highest growth performance but consistently showed the lowest SR in the present study. This pattern may be attributed to its pronounced cannibalistic behavior and high mortality risk. As reported by Alberts-Hubatsch et al. [1], *S. serrata* is particularly vulnerable to conspecific attacks during molting, resulting in elevated mortality throughout the juvenile and grow-out phases. Similarly, Paran et al. [32] demonstrated that even in controlled cage or pond systems, SRs may decline substantially due to cannibalism. These findings explain why this species, despite its high growth potential, may be associated with increased culture risk.

In contrast, *S. paramamosain* maintained stable survival throughout the culture period, consistently higher than *S. serrata*. While *S. paramamosain* did not rank highest in any individual growth metric, it exhibited neither the high mortality rates of *S. serrata* nor the growth constraints seen in *S. olivacea*. This balanced performance, combined with its environmental adaptability, supports *S. paramamosain*'s suitability for a wide range of culture systems, from extensive to intensive ponds. As noted by Oniam et al. [33], *S. paramamosain* remains a preferred species due to its abundance, high market value, and the reliable balance between growth and survival.

4.4. Sex-Based Variation in Growth Performance Across *Scylla* Species

This study utilized a mixed-sex polyculture of *Scylla* species, and the results demonstrated sex-related differences in growth performance among species. Male mud crabs generally exhibited greater growth than females across the developmental stages (Tables 4 and 5). These data provide a critical empirical basis for optimizing aquaculture management and advancing sex-oriented selective breeding programs. Specifically, the overall WG in male *S. serrata* and *S. paramamosain* consistently exceeded that of their female counterparts at both stages, establishing a robust trend of sex-based variations in growth. These observations align with Triño et al. [34], who evaluated all-male, all-female, and mixed-sex cultivation systems for *S. serrata* and concluded that all-male cohorts achieve significantly higher FW than all-female groups.

The experimental results demonstrate that male *S. serrata* maintains a significant growth advantage through Stage II, followed by male *S. paramamosain*, both exhibiting a clear “males > females” growth hierarchy. Research indicates that during the growth process, male crabs typically exhibit higher consumption rates and prioritize energy allocation toward somatic WG and muscle development. In contrast, as females approach the pre-reproductive stage, a portion of their metabolic energy is progressively diverted toward gonadal development, resulting in a decelerated growth rate [35]. Lovatelli et al. [21] specifically selected males as experimental subjects due to their superior growth rates and enhanced disease resistance. Their findings further suggest that while males allocate their energy reserves to biomass accumulation, females must balance the competing ener-

getic demands of both somatic growth and reproductive maturation. These physiological distinctions provide critical insights for the development of future sex-oriented breeding strategies and optimized aquaculture management protocols. While the growth patterns observed provide a valuable baseline, the results for *S. tranquebarica* should be interpreted with particular caution. The initial sample size of this species was relatively limited ($n = 34$) and already showed a strongly male-biased sex composition during acclimation, with females and males accounting for 11.8% and 88.2%, respectively. Because the number of females was limited at the outset and no females survived to the end of Stage I, the growth performance recorded for *S. tranquebarica* in Stage II was derived entirely from male individuals. These findings should instead be interpreted within the context of the limited and predominantly male wild-caught sample used in the present study and generalized to the species level with caution. Further study is suggested to collect more representative samples of both sexes to further evaluate sex-ratio patterns and sex-related growth differences in *S. tranquebarica*.

4.5. Correlation Between Survival and Growth Performance

The experimental results demonstrate that *S. serrata* consistently recorded the lowest SR among the four studied species across both Stage I and Stage II. Conversely, it exhibited the greatest weight gain in both phases, underscoring its exceptional growth potential despite its relatively low survival rate. This phenomenon is hypothesized to stem from the species' high levels of agonistic behavior, intense territoriality, and aggressive competition for spatial resources, which are likely to elevate mortality under the applied stocking density. To unlock the full potential of *S. serrata* as a high-value aquaculture species, future management strategies should focus on mitigating intraspecific interference and cannibalism. Proposed interventions include increasing the complexity of three-dimensional shelters, diversifying and increasing the frequency of feeding regimes, and optimizing pond architecture such as implementing compartmentalized structures. By minimizing individual encounters and agonistic interactions, *S. serrata* holds significant potential to become the optimal candidate for production-oriented mud crab aquaculture.

In addition to cannibalism, the contrasting growth and survival performance of *S. serrata* may also be considered from the perspective of energy allocation. Previous studies on mud crabs have suggested sex-related differences in energy allocation, with females requiring additional energy for gonadal development, which may partly contribute to differences in somatic growth between sexes [35]. Rapid somatic growth and the development of structures such as the chelipeds may therefore involve considerable energetic investment. In crustaceans, immune activation also substantially increases the demand for energy and metabolic substrates, indicating a close relationship between metabolic status and immune function [36]. Moreover, environmental stressors can impose additional metabolic costs associated with maintaining homeostasis and may affect immune defense [37]. From this perspective, the high growth performance observed in *S. serrata* may be associated with greater energetic investment in somatic growth and cheliped development, potentially resulting in trade-offs with other maintenance or defense functions. Further studies incorporating physiological and immunological measurements would help clarify the role of energy allocation in the growth–survival patterns observed in *S. serrata*.

S. tranquebarica exhibited the second-highest SR during Stage I, despite having the lowest WG among the four species. This suggests robust viability during the early crablet stage but with a relatively conservative growth rate. However, upon progressing to Stage II, its SR rose to the highest among all species, and its growth performance accelerated to become the second highest, surpassed only by *S. serrata*. This phase-dependent shift indicates that *S. tranquebarica* may employ a compensatory or late-onset growth strategy,

demonstrating substantial economic potential during the mid-to-late grow-out phases. Nonetheless, given the relatively small initial sample size of *S. tranquebarica* ($n = 34$), the observed survival and growth patterns should be interpreted with caution. Further studies using larger and more balanced sample sizes are needed to confirm the performance and commercial potential of this species.

S. paramamosain displayed the second-lowest performance in both survival and WG across Stage I and Stage II of the four studied crab species. While its growth and survival metrics were not as prominent as those of its congeners, the data remained relatively stable throughout the experimental period. This stability suggests that in practical aquaculture operations, *S. paramamosain* is unlikely to cause significant fluctuations in overall yield or market value due to extreme deficiencies in survival or growth rates. Consequently, it can be characterized as a robust and reliable species for commercial cultivation.

In contrast, *S. olivacea* achieved a peak SR of 91% in Stage I, the highest among all cohorts, while maintaining the second-highest growth rate. Upon entering Stage II, although its survival remained the second highest (55.80%), its growth performance decelerated to the lowest among the four species. These findings characterize *S. olivacea* as a species with exceptional physiological resilience and early-stage viability, though its long-term growth potential appears to be more constrained compared to its congeners.

This study represents the first comprehensive comparison of growth trajectories and survival dynamics across distinct developmental phases among four *Scylla* species. The results provide critical baseline data for mud crab aquaculture, serving as a scientific framework for optimizing husbandry management and species selection. The collective results indicate that the survival and growth rates of mud crabs are significantly influenced by a complex interplay of species-specific traits, body size, and sex. The profitability of mud crab farming depends entirely on the balance between growth rates and survival percentages. While rapid growth is desirable, it often entails higher mortality risks that can undermine total yield. Conversely, a strategy prioritizing stable, high survival, even with moderate growth rates, can enhance overall productivity through the cumulative biomass of the surviving population. Consequently, the strategic insights provided by this research are essential for achieving the dual goals of economic optimization and long-term sustainability in mud crab aquaculture development.

5. Conclusions

The results showed that *S. tranquebarica* had the highest cumulative SR at the end of the study, whereas *S. serrata* consistently exhibited the lowest survival. The survival of *S. olivacea* and *S. paramamosain* remained intermediate, with limited fluctuations in ranking across different stages. In terms of growth, male *S. serrata* exhibited the highest WG in both Stage I and Stage II. Conversely, *S. paramamosain* (both sexes) occupied lower-to-middle growth rankings with minimal variation across stages. Notably, *S. tranquebarica* displayed a low growth ranking in Stage I but showed a marked upward shift in Stage II. In conclusion, *S. serrata* demonstrated the highest growth potential but faced the highest mortality risks, whereas *S. tranquebarica* showed a comparatively favorable combination of survival and Stage II growth performance under the conditions of the present study. However, the results for *S. tranquebarica* were based on a relatively limited and predominantly male wild-caught sample. Further studies are needed to evaluate *S. tranquebarica* as a potential alternative culture species to *S. serrata*. *S. paramamosain* proved to be a stable and consistent species for cultivation. These results provide a critical empirical foundation for future precision aquaculture management strategies tailored to species, sex, and developmental stages.

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Abbreviations

The following abbreviations are used in this manuscript:

ADG	Average Daily Gain
ASRs	Adjusted Standardized Residuals
BW	Body Weight
CW	Carapace Width
DO	Dissolved Oxygen
FW	Final Body Weight
IF	Initial Body Weight
SGR	Specific Growth Rate
SR	Survival Rate
TAN	Total Ammonia Nitrogen
WG	Weight Gain

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