



Effect of mangrove leaf litter on shrimp (*Penaeus monodon*, Fabricius, 1798) growth and color

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ABSTRACT

Color, texture and flavor are all important determinants of seafood product quality and value. For shrimp, *Penaeus monodon*, one of the highest-priced shrimp species of the South-East Asia shrimp industry, dark tiger-striped coloration is a key product quality criterion. We evaluated the effects of leaf litter of the mangrove species *Avicennia officinalis* (AO), *Heritiera fomes* (HF), *Sonneratia apetala* (SA) and *S. caseolaris* (SC) on length, weight and body color of shrimp (*Penaeus monodon*) post-larvae (PL). Fifteen-day-old PL (weight: 0.01 g) were reared in 1100-L fiber-reinforced polyethylene tanks. Five treatments having three replications were conducted for four weeks. Four treatments received leaf litter of the four mangrove species and supplemental feeds and one control treatment was provided with supplemental feed only (FO). The pH, biological oxygen demand (BOD₅), chemical oxygen demand (COD) and phytoplankton and zooplankton biomass were lower, while total ammonia nitrogen (TAN) concentration were significantly higher in the FO treatment than in treatments including leaf litter. PL survival averaged 89% and only differed significantly between the SA and SC leaf litter treatments ($p < 0.05$). After 4 weeks of culture, larvae in the FO treatment had significantly shorter body and carapace length, lower body weight and a lower specific growth rate than larvae in the other treatments, while SA-reared larvae attained significantly greater length and weight than in the other leaf litter treatments. Shrimp body coloration and pattern with leaf litter treatments were significantly different from the FO treatment. SA-reared larvae at harvest were significantly darker in body color than larvae reared with other mangrove species. Shrimp value chain stakeholders preferred dark shrimp as an indicator of organic production and higher price. Mangrove leaf litter was found to enhance the production and color quality of black tiger shrimp and this technique can be applied in commercial shrimp aquaculture.

1. Introduction

Shrimp farming is widely practiced in coastal areas of tropical and subtropical countries (Viet Nguyen et al., 2020). It is one of the fastest growing economic activities and sources of foreign-exchange earnings for several developing countries in Asia and Latin America (He et al., 2021). Bangladesh is well known as a shrimp producing country in South-East Asia. The country earned about US\$ 494 million by exporting fish and shrimp in 2019–2020, more than 80% of which was from the

export of shrimp (DoF, 2021). Moreover, shrimp culture provides employment, income and food security to the rural people in the coastal areas where alternative livelihood options are very limited (Al-Mamun et al., 2021; Fox and Weisberg, 2019). Shrimp culture systems are diverse in Bangladesh, ranging from integrated rice–shrimp systems to semi-intensive systems (FAO, 2022). Semi-intensive and extensive systems are different in terms of management, production and disease occurrence (Islam et al., 2016). Extensive shrimp farming is commonly practiced in shallow ponds in the coastal zone, stocking shrimp

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post-larvae (PL) at low densities with no complementary feeding. To fertilize these ponds, some low cost inputs such as compost produced from agriculture and household plant and animal waste may be applied (Ariyati et al., 2019). Alam et al. (2021a; b (2022), Rejeki et al. (2019) and Ariyati et al. (2019) observed that mangrove leaf litter positively affects shrimp growth performance. Addition of mangrove leaf litter containing nutrients (carbon, nitrogen, phosphorus) enhances natural food production and improves the use efficiency of supplemental and commercial feed (Alam et al., 2021a; b, 2022). These results suggest that mangrove litter could play an important role in the production of organic shrimp which appeals to consumers for their high quality (Paul and Vogl, 2012; Dhar et al., 2019). Integrated shrimp mangrove farming is often referred to as organic aquaculture (Ahmed et al., 2018).

Growth rate is a key metric in fisheries and aquaculture. Individual growth performance is of great interest because of its importance to yield (Crane et al., 2019). Growth performance is also influenced by environmental conditions such as water temperature, diet, turbidity and water chemistry (Tacon et al., 2002; Shoup et al., 2007; Shoup and Lane, 2015; Crane and Einhouse, 2016). Like growth, the color pattern of shrimp is also important as it can be influenced by the type of production system and generates a price premium in some export markets (Wade et al., 2013; Rodriguez et al., 2017). The same also holds for fish species (Uribe et al., 2018). Considering consumer preferences, Parisenti et al. (2011) observed that a dark color in shrimp was more preferred by consumers than a pale color. Although the effect of mangrove restoration on shrimp performance is well documented, little information is available on the effects of leaf litter on phenotypic traits related to growth (e.g., total length, body length and carapace length) and body color.

The shrimp sector produces primarily for export markets, and to a lesser extent for domestic markets. If consumers, domestic and in export countries, would recognize colored shrimp as organic, healthy and good quality, this can help to promote mangrove shrimp aquaculture. Therefore, the objective of this study was to assess the effects of leaf litter on these traits in shrimp PL culture and to explore color preference by various stakeholders in the shrimp sector.

2. Methodology

2.1. Selection of mangrove species

The mangrove species providing the leaf litter types used in this experiment were selected following Alam et al. (2021a, 2022) and Rahman et al. (2020).

2.2. Sample collection: mangrove leaf litter and shrimp PL

Naturally-fallen yellowish senescent leaves were collected from the selected mangrove species in the Sundarbans mangrove forest. The leaf traps were 2 by 2 m and installed beneath the trees during winter (November 2018-January, 2019). At regular intervals, the fallen leaves were recovered from the traps, separated according to species and prepared for the use in this experiment.

Specific pathogens free (SPF) shrimp PL of 15 days old with an average weight of 0.01 g were obtained from the Desh Bangla Shrimp Hatchery, Batiaghata, Khulna, Bangladesh. These were brought to the experimental site in oxygenated plastic bags provided with sufficient aeration. After arrival at the experimental site, the shrimp PLs were acclimatized by gradually adjusting the salinity and temperature to the conditions in the experimental rearing tanks, before releasing them.

2.3. Experimental design

The culture experiment was carried out at a farm located in Debhata, Satkhira at the northern rim of the Sundarbans mangrove area in Bangladesh. Culture was conducted under the ambient conditions in

which the rearing tanks were covered with a translucent plastic roofing that prevented large fluctuations in salinity due to heavy rain, while still maintaining the natural diurnal variation in light incidence. The experiment included five treatments, all receiving commercial feed (F) at 5% body weight per day. Four treatments received leaf litter of four different mangrove species (*Avecennia officinalis*: AO, *Heritiera fomes*: HF, *Sonneratia apetala*: SA and *S. caseolaris*: SC) and the remaining 5th treatment was a control treatment provided with feed only (F). All treatments were executed in triplicate, and the treatments were randomly assigned to the experimental rearing tanks.

The shrimp were reared in 1100-L fiber-reinforced polyethylene tanks containing 1000 L of brackish water (10 ppt) with a water depth of 0.9 m. Brackish water collected from a nearby canal was stocked in a pond and left to settle for one week. The top layer of that settled water was transferred to the experimental tanks through a 25 µm mesh size net to keep out large debris and predators, including their eggs and larvae, from the experimental tanks. Each tank was aerated using a single air stone (diameter 2 cm) connected to an air blower (RESUN, LP-100). Mangrove leaf litter was directly added in the culture tanks on day one at a concentration of 1 g/L (wet weight). This loading rate was standardized following Hai and Yakupitiyage (2005). On the same day, 100 shrimp PLs were stocked at a rate of 1 PL/10 L of water in each tank. The experiment was conducted for a four-week period and the water was not exchanged during this experimental period. The average shrimp body weight in the control treatment tanks was checked weekly to adjust the amount of feed administered during the next week. The experiment was terminated after four weeks, when all the shrimp were collected. Total biomass and number of shrimp per experimental tank were recorded at stocking and harvest. Shrimp survival, growth and color were assessed, recorded, and analyzed at the end of the experiment. Finally, a survey among shrimp value chain stakeholders was conducted to identify the shrimp color preference by the shrimp sector in Bangladesh.

2.4. Feeding the shrimp PL and FCR

The commercial “Titas Tiger” feed named “starter” was purchased from the Bismillah Feed Mills Limited, Mollahat, Bagerhat, Bangladesh. This feed is labeled as containing 12% moisture, 36% protein, 10% lipid, 7% fiber, 18% ash, 1.9% calcium and 1.7% phosphorus. It was applied in the tank at 5% BW of shrimp PL per day. The feeding table for all tanks was prepared weekly based on the average size and survival rate recorded in the control treatment tanks. The FCR per tank was calculated after harvesting as the total feed given (g wet weight) divided by total shrimp biomass gain (g wet weight) as described by Alam et al. (2022).

2.5. Water quality monitoring, data collection and record

Temperature, salinity, pH and dissolved oxygen (DO) in each tank were measured daily, biological oxygen demand (BOD₅) was measured weekly and chemical oxygen demand (COD) was measured once every two weeks. Procedures for sample collection, preparation and analysis were following the methods described in Alam et al. (2022).

2.6. Sampling and analysis of plankton

Phytoplankton and zooplankton samples were collected on day 1 and 28. Samples (15 L per sample) were collected at 9.00–11.00 hr from 3 points in each tank. Procedures for sample collection, preparation and analysis were following the method described in Alam et al. (2022).

2.7. Physical and life history metrics/variables/ characteristics

2.7.1. Survival and growth

The survivability of PL was monitored twice every day. The shrimp PLs were harvested after 28 days. The survival rate, individual body

weight gain (IWG) and specific growth rate (SGR) were calculated following Busacker et al. (1990) as described by Alam et al. (2022).

At the same time, 15 PLs from each experiment unit were anaesthetized in an ice bath and then a photograph of each PL was made by using a digital camera (Canon D5126621) after placing it on a laminated graph paper. All photos were taken under the day-light condition at the same place and time. From the raw images (Fig. 1), total length (TL), body length (BL), and carapace length (CL) were measured using the ImageJ software (version 1.50i). TL (from tip of the rostrum to tip of the telson), BL (from post orbital border of the carapace to the tip of telson) and CL (from posterior margin of orbit to posterior edge of carapace) were measured following Rebello et al. (2014).

2.7.2. Color pattern

Before taking photographic image, the body color of each juvenile shrimp was observed carefully and recorded. Then the color patterns of each shrimp from different treatments were re-evaluated from the captured raw images. In this study, the shrimp displayed three different distinct colorations which were referred to as Dark (dark greenish-blue), Grey-blue and Pale (light grey/transparent) (Fig. 2). The percentage occurrence of animals displaying these three overall color variants was calculated for each tank and used for comparison between treatments.

2.8. Color preference by stakeholders

After informing stakeholders of the color outcomes of the experiment on juvenile shrimp, a survey was done among shrimp producers, local consumers and exporters to ask about their color preferences. The producers were in turn divided into two groups: mangrove farmers (who have naturally grown mangroves in their farms) and non-mangrove farmers, making for a total of 4 groups. For each stakeholder categories, 25 persons were randomly selected for the survey. They were asked to indicate their shrimp color preference and the reason of their color preference as well as their opinion if the color of fresh shrimp did or did not influence their client's product appreciation, and if so, for which reason.

2.9. Statistical analyses

All analyses were done using R version 4.0.2 (R Development Core Team, 2020). R-packages used including onewaytests, car, ggplot2, multcomp, FSA, gmodels, rcompanion, vcdExtra and PerformanceAnalytics. The assumptions of normality and homogeneity were tested using Shapiro-Wilk test and Levene's test (Dag et al., 2018). A univariate analysis of variance (ANOVA) model was applied when a variable followed the assumptions of normality (Fox and Weisberg, 2019), followed by the Tukey multiple comparison test (Hothorn et al., 2008). The Kruskal-Wallis (K-W) test was applied to a variable when transformations failed to give a normal distribution, followed the Dunn multiple comparisons test (Ogle et al., 2020). In both models, 'feeding types' were included as the independent variable, while an individual

growth metrics (except color pattern) was incorporated as the dependent variable. Since 'color pattern' is a categorical variable, Pearson's chi-squared was applied (Mangiafico, 2020; Warnes et al., 2018) to explore the differences in body color among different feeding groups. A mosaic plot was made to display the color variation among different feeding groups (Friendly, 2017). In order to assess the relation between growth performance and plankton biomass (both phytoplankton and zooplankton), the correlation test was performed (Peterson and Carl, 2020).

3. Results

3.1. Water quality

The analysis revealed significant differences in water quality parameters between treatments except for the parameters DO and NO₂-N (Table 1). Tanks receiving only feed had significantly lower pH, BOD₅, phytoplankton and zooplankton biomass, and higher TAN concentrations than the treatments also receiving leaf litter (Table 1). Among the leaf litter treatments, the highest BOD₅, phytoplankton and zooplankton biomass was observed with SA leaf litter, while these parameters were lowest with HF leaf litter. Results with the AO and SC leaf litter treatments were not significantly different for any of the water quality parameters except BOD₅ (Table 1). The temperature for all treatments ranged between 27.8 °C to 28.1 °C and did not differ significantly between treatments.

It was not possible for us to identify phytoplankton to species level except for the green algae *Closterium tumidum*. Most of the zooplankton were also identified at genus level, except for the copepod *Acartia tonsa*. These two plankton species were numerically most abundant species of phytoplankton and zooplankton, respectively.

3.2. Survival and growth of shrimp PL

At the end of the experimental period (28 days) there were significant differences ($p < 0.05$) in percentage survival between treatments where SA-F had the highest survival rate and SC-F the lowest (Table 2). In terms of exoskeletal and growth related parameters, analysis showed that PL in the FO treatment realized a smaller TL, BL, CL, IWG and SGR than in the other treatments. Among the leaf litter treatments, shrimp cultured with SA leaf litter performed best (Table 2). Though the TL reached by the PL was similar for the treatment with HF and SC, the IWG and SGR were higher in the SC-F treatment than in the HF-F treatment (Table 2).

The FCR in all treatments was very low, ranging between 0.20 and 0.46 and significantly different between treatments. Shrimp in rearing tanks with leaf litter realized a better FCR than animals in the FO treatment (Table 2).

3.3. Coloration

The relative frequencies of the three different body color categories differed between treatments (Pearson's chi-squared test: $\chi^2 = 95.46$, $p < 0.001$). After the experimental period, 100% of the shrimp in the FO treatment were pale colored which was a higher percentage ($p < 0.001$) than for shrimp in HF-F (56%), SC-F (47%), SA-F (31%) and AO-F (22%) treatments (Fig. 3a). On the other hand, shrimp in the AO-F treatment were 67% grey-blue colored (Fig. 3a) which was higher ($p < 0.001$) than the percentage of grey-blue shrimp in the HF-F (29%), SA-F (29%) and FO (0%) treatment and similar to shrimp in the SC-F (49%, $p > 0.05$). In the SA-F treatment, 40% of the shrimp had the dark body color, which was higher ($p < 0.001$) than the percentage of dark body colored shrimp in the HF-F (16%), AO-F (11%), SC-F (4%) and FO (0%) treatments (Fig. 3a). The most striking overall difference was between shrimp cultured with mangrove and those without mangrove (FO). The latter were uniformly pale in color (Fig. 3b).

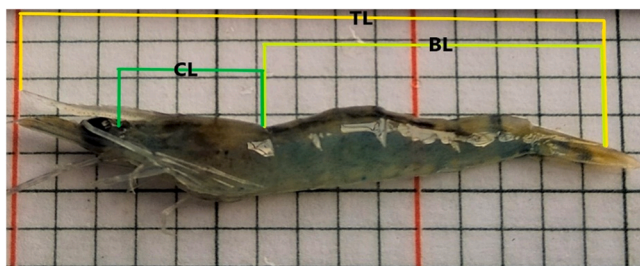


Fig. 1. Different types of length measured in *P. monodon*; TL: Tip of the rostrum to tip of the telson; BL: Post orbital border of the carapace to tip of the telson; CL: Post orbital border of the carapace to posterior edge of carapace.



Fig. 2. Categories of different color patterns found in experimental shrimp PL such as dark, grey-blue and pale.

Table 1

Average water quality parameter values measured in shrimp PL rearing tanks during a four-week culture period provided with leaf litter from four different mangrove species and supplemental feed.

Water parameters	Feeding types					S.E. M	p-value
	AO-F	HF-F	SA-F	SC-F	FO		
DO (mg/L)	5.36	5.34	5.35	5.34	5.38	0.01	ns
pH	7.87 ^b	7.87 ^b	7.92 ^b	7.90 ^b	7.77 ^a	0.01	**
BOD ₅ (mg/L)	2.37 ^c	1.86 ^a	2.67 ^d	2.15 ^b	1.82 ^a	0.09	**
TAN (mg/L)	0.23 ^a	0.27 ^{ab}	0.17 ^a	0.20 ^a	0.50 ^b	0.04	**
NO ₂ -N (mg/L)	0.47	0.3	0.53	0.5	0.23	0.04	ns
Zooplankton (ind./ml)	6.7 ^{ab}	5.0 ^{ab}	8.3 ^b	5.0 ^{ab}	4.8 ^a	0.53	*

Values are presented as mean. Treatments with no letter in common are significantly different ($p < 0.05$). P value is expressed as a symbol ($p < 0.01$: **, $p < 0.05$: *, ns: not significant). AO-F = *Avicennia officinalis* leaf litter and feed; HF-F = *Heritiera fomes* leaf litter and feed; SA = *Sonneratia apetala* leaf litter and feed; SC = *Sonneratia caseolaris* leaf litter and feed; FO = Feed Only.

Table 2

Shrimp performance observed in controlled condition in tanks with different leaf litter mangrove species and supplemental feed.

Parameters	Feeding types (n = 100 shrimp PL per tank)					S.E. M	p-value
	AO-F	HF-F	SA-F	SC-F	FO		
Survival (%)	86 ^{ab}	93 ^{ab}	94 ^b	85 ^a	88 ^{ab}	1.15	*
Total length (TL; cm)	2.77 ^{bc}	2.63 ^b	2.92 ^c	2.71 ^b	2.23 ^a	0.03	**
Body length (BL; cm)	1.86 ^{bc}	1.76 ^b	1.97 ^b	1.80 ^b	1.48 ^a	0.02	**
Carapace length (CL; cm)	0.90 ^{bc}	0.86 ^b	0.95 ^c	0.91 ^{bc}	0.73 ^a	0.01	**
Individual weight gain (IWG; g)	0.32 ^c	0.25 ^b	0.37 ^d	0.30 ^c	0.17 ^a	0.01	**
Specific growth rate (SGR; g bw d ⁻¹)	14.9 ^c	14.0 ^b	15.4 ^d	14.7 ^c	12.7 ^a	0.09	**
Feed conversion ratio (FCR)	0.24 ^b	0.30 ^c	0.20 ^a	0.26 ^{bc}	0.46 ^d	0.02	**

Presented values are presented as the mean. Means in each rows sharing different superscript letter are significantly different according to Tukey HSD test ($p > 0.05$). P value is expressed as a symbol ($p < 0.001$: **, $p < 0.05$: *). AO-F = *Avicennia officinalis* leaf litter and feed; HF-F = *Heritiera fomes* leaf litter and feed; SA = *Sonneratia apetala* leaf litter and feed; SC = *Sonneratia caseolaris* leaf litter and feed; FO = Feed Only.

3.4. Correlations between phenotypic traits and primary productivity

There were significant positive correlations among different physical and life history parameters traits (Fig. 4). The total length (TL) and weight gain (WG) were significantly and positively correlated with both zooplankton and phytoplankton (Fig. 4).

3.5. Color preference by the stake-holders

The highest percentages of persons with in each stakeholders categories preferred dark colored shrimp followed by grey-blue colored shrimp. No stakeholders gave preference to pale colored shrimp (Table 3).

All of the queried exporters (100%) indicated that shrimp color had an important effect on selling price even though they did not give an indication of the magnitude of the price difference between colored and pale shrimp. High percentages of mangrove farmers (36%) and local consumers (60%) also indicated that color influences price. In contrast, 100% of non-mangrove farmers, 64% mangrove of mangrove-farmers and 40% of local consumer said that color does not influence shrimp selling price (Fig. 5).

When asking how color could affect selling price, the majority of farmers did not answer. However, all categories of stakeholders mentioned colored shrimp as a criteria of freshness. The majority exporters associated darker colored shrimp to freshness, while others considered dark color an indicator of organically grown or a higher buyer's demand (Fig. 6).

4. Discussion

4.1. Water quality

The experiment found significant differences between treatments for water quality parameters. DO is one of the most important limiting factors for shrimp PL reared with mangrove leaf litter (Nga et al., 2006). Mangrove leaf litter loading at excessive concentrations depleted DO in the water of shrimp culture tanks (Hai and Yakupitiyage, 2005; Nga et al., 2006). However, mangrove leaf litter with aeration and at a loading rate of 1 g/L did maintain a good DO level as observed by Alam et al. (2021a, 2021b) and Hai and Yakupitiyage (2005), as was also the case in this experiment.

The pH concentration in our experiment did not differ significantly between the various leaf litter treatments, but was significantly lower in the FO treatment (Table 1). This finding is consistent with some other studies (Deano and Robinson, 1985; Marschner and Noble, 2000; Hai and Yakupitiyage, 2005; Alam et al., 2021a; b, 2022) that demonstrated that leaf litter can lower pH in shrimp culture. However, in all cases, the

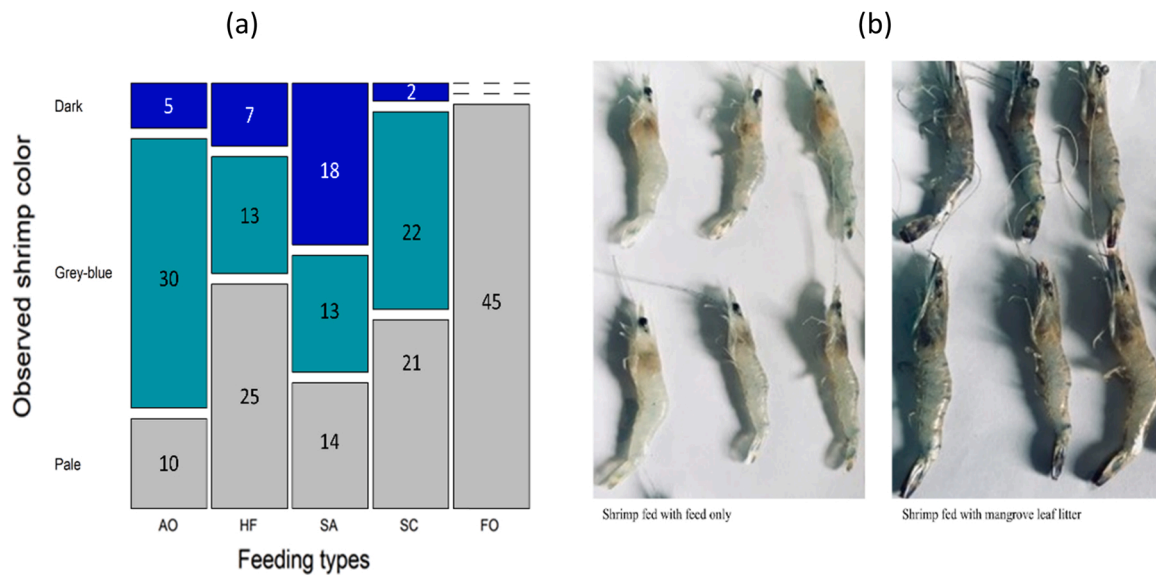


Fig. 3. (a-b). (a) The mosaic plot showing overall color variation among different treatments ($n = 45$ for each treatment with 15 for each replication). Numbers within each treatment bar within each color category indicate the number of shrimp that were found in that particular color category for that treatment. (b) Comparison of overall color of harvested juvenile shrimp reared with feed and mangrove leaf litter.

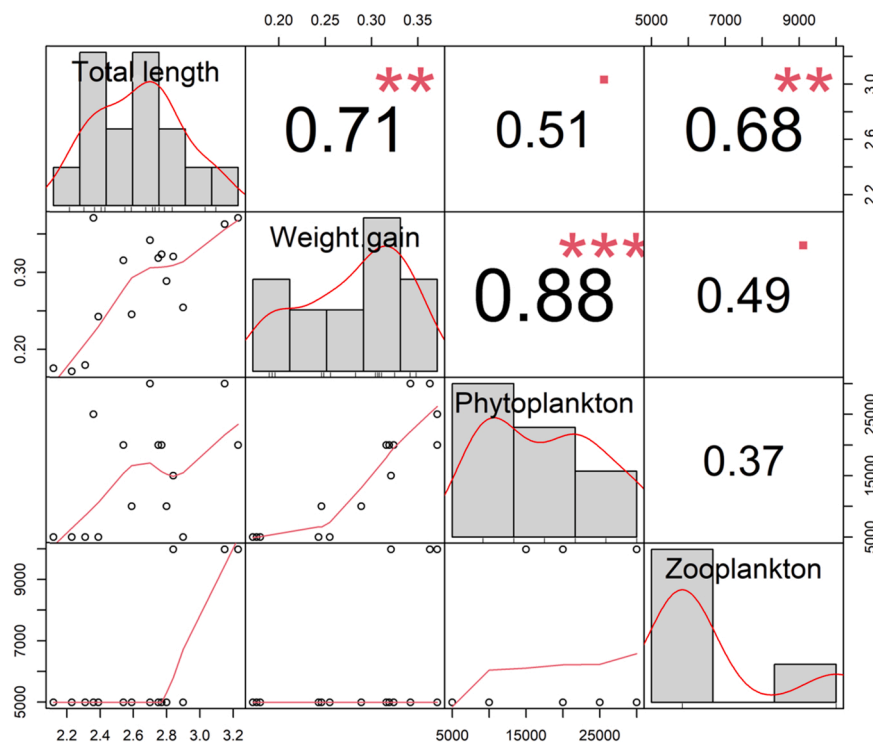


Fig. 4. Correlations between total length and weight gain with the primary productivity during the experiment. Here, the variable full names are: Total length (cm); Weight gain (g); Phytoplankton biomass (inds/ml). and Zooplankton biomass (inds/ml) with the values given on the x and y axes. Correlation coefficients (r) are indicated with numeric values, while significance levels (p) are denoted by asterisks (* <0.05 , ** <0.01 , *** <0.001).

pH ranged between 7.5 and 8.0 and did not adversely affect shrimp performance as it was within the known safe operational range (7.5–9.0) for shrimp PL (FAO, 1986).

In all treatment tanks, both TAN and $\text{NO}_2\text{-N}$ remained within acceptable limits (TAN: 1 mg/L; $\text{NO}_2\text{-N}$: 0.5 mg/L) as described by Banrie et al. (2012). The N-input load was higher in leaf litter supplemented tanks than in FO tanks, which can be expected to causing a higher release of TAN in leaf litter tanks. However, contrary to expectations, the TAN concentration was higher in the FO treatment.

We speculate that this may have been due to the leaf litter stimulating the sequestration of ammonia into natural food (plankton), lowering the TAN concentration in the water column (Ebeling et al., 2006).

The higher nutrient loading in the leaf litter treatment tanks than in the FO treatment tanks, supported the production of new biomass, likely by means of biofilm formation as described by Gatune et al., (2012, 2014) and affected BOD_5 , pH, TAN and $\text{NO}_2\text{-N}$ concentrations in the tanks (Alam et al., 2021a).

The nutrients released from decomposing leaf litter enhanced the

Table 3

Outcomes of Pearson's chi-squared test to explore the preference of different stakeholders (n = 25 for each categories) for various shrimp colors.

Stakeholders	Percent of stake-holders preferred shrimp color			χ^2	p
	Dark	Grey-blue	Pale		
MF	76	24	0	19.82	< 0.001
NMF	80	20	0	19.14	< 0.001
LC	52	48	0	21.15	< 0.001
Exporter	64	36	0	20.85	< 0.001

The values are presented as percentage mean. MF: mangrove farmer; NMF: Non-mangrove farmer; LC: Local consumer.

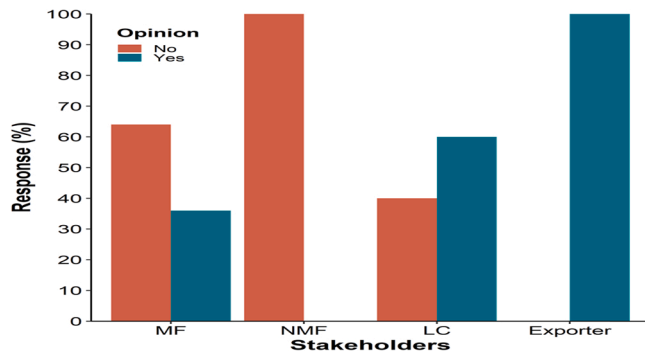


Fig. 5. The perception of different stakeholder groups on the existence of an effect of fresh shrimp color on product selling price. MF: Mangrove farmer; NMF: Non-mangrove farmer; LC: Local consumer.

shrimp culture food web, as documented presence of higher numbers of phytoplankton and zooplankton in leaf litter treatment tanks than in FO treatment tanks (Alam et al., 2021a, 2021b). Similar to Alam et al. (2021a), tank receiving SA leaf litter had the highest concentrations of both phytoplankton and zooplankton, while HF leaf litter resulted in the lowest concentrations (Table 1). The most abundant phytoplankton species, *Closterium tumidum* and zooplankton species, *Acartia tonsa* identified in leaf litter treatment in this study were also identified by Alam et al. (2021b) at the study with similar species of mangrove leaf litter. In addition, as in our experimental culture system, *Closterium tumidum* and *Acartia tonsa* are also common species reported in mangrove estuaries (Scwamborn et al., 2002; Satpati et al., 2013; Magalhaes et al., 2015).

4.2. Shrimp PL survival, growth and coloration

Decomposing mangrove leaf litter is an important direct or indirect food to shrimp PL, but an excessive loading rate can become detrimental (Hai and Yakupitiyage, 2005; Nga et al., 2006). In our experiment, mangrove leaf litter at a loading rate of 1 g/L did not negatively affect shrimp survival, consistent with the results by Alam et al. (2021a).

The growth performance of shrimp PL in terms of IWG, SGR, TL, BL and CL was much better with leaf litter than without leaf litter (Table 2), benefitting from synergy between leaf litter and supplemental feed (Alam et al., 2021b). In the leaf litter treatments, the highest performance in terms of TL, BL, CL, IWG and SGR was observed in SA-F treatment and the lowest in the HF-F treatment. This has been suggested to be associated with the higher BOD₅ and rate of decomposition of SA leaf litter (Alam et al., 2021a), as the microorganisms responsible for decomposition and biofilm formation are an important natural food for shrimp PL (Gatune et al., 2012, 2014). The higher number of phytoplankton and zooplankton in tanks fed leaf litter and feed than in fed tanks only also supported the higher growth performance. Phytoplankton and zooplankton are nutritive natural foods in shrimp nursery systems (Porchas-Cornejo et al., 2010; Thong, 2017).

While the positive effects of mangrove leaf litter on shrimp have been described by others before, most significant the present study was our findings of major shrimp color differences between treatments. In our experiments, mangrove leaf litter influenced shrimp coloration in addition to growth performance, whereas pelleted food alone yielded only pale shrimp (Fig. 4a, b). Possibly, carotenoids specially astaxanthin, and chlorophyll in chloroplasts of mangrove leaf litters (Dhankhar et al., 2012; Banerjee et al., 2017; Cadiz et al., 2021) influenced the body color in shrimp (Wade, 2013; Rodriguez et al., 2017). The much lower levels of natural phytoplankton and zooplankton developing in culture tanks fed only pelleted feed gave little or no color to shrimp. When consumed by larger zooplankton, like copepods, which in turn are eaten by the shrimp, this enhanced shrimp color pigmentation (Ananthi et al., 2011; de Carvalho and Caramujo, 2017).

Among all stakeholder groups interviewed, their response indicated shrimp with dark color as an evidence of organic and fresh shrimp and stimulating buyer's demand which might add special value to promote the reintroduction of mangroves into the shrimp culture systems. Shrimp labeled as organic are preferred by consumers (Paul and Vogl, 2012; Dhar et al., 2019), and a majority of consumers link color to freshness (Parisenti et al., 2011). This means that mangrove leaf litter not only enhances natural food availability to shrimp culture but also results in a higher percentage of dark colored shrimp, which will be of higher demand because they are more appealing to consumers. This can be used as an additional incentive to promote mangrove-shrimp aquaculture.

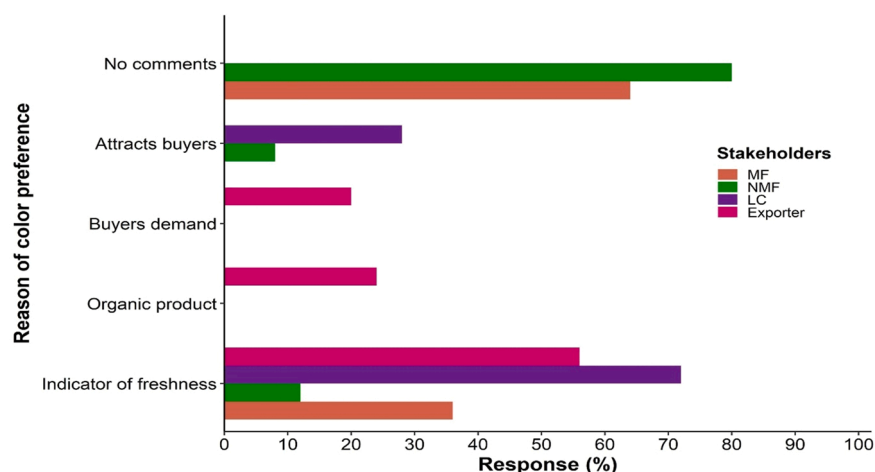


Fig. 6. The responses by stake-holders about the reason of preference for colored shrimp.

5. Conclusions and recommendations

Color, texture and flavor are all important determinants of seafood product quality and value. Shrimp is a valuable export item and its growth performance and quality are important. For the black tiger shrimp, *P. monodon*, one of the highest-priced shrimp species of the South-East Asia shrimp industry, dark tiger-striping are a key product quality criterion. At the same time, mangroves remain underutilized and leaf litter represents a major opportunity for shrimp aquaculture (Alam et al., 2021a, 2021b, 2022). Therefore, the present study underlines the importance of mangrove shrimp co-management, not only from an ecological point of view but also from an economic point of view. Finally, for a sustainable form of aquaculture reconciling mangrove restoration with intensification of shrimp aquaculture, we recommend further research on:

- the optimal number of mangrove trees and the mangrove species coverage proportion to associate with shrimp culture ponds, as it is known that excessive leaf litter loading and excess organic matter in the tank or pond can be detrimental to shrimp culture (Hai and Yakupitiyage, 2005; Rejeki et al., 2019);
- the long-term effects of leaf litter during the full life cycle of shrimp so that leaf litter concentrations may be adjusted appropriately during the course of the culture cycle;
- the integration of recent research findings and insights into tailor-made, sustainable management strategies for mangrove-shrimp aquaculture in different settings, in the cognizance that mangroves can bring a multitude of benefits to shrimp and fish production in terms of sustainability (Bosma et al., 2016).

CRediT authorship contribution statement

Md. Iftakharul Alam: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Writing – original draft. **Sanjida Yeasmin:** Data curation, Data analysis, Investigation, Methodology (parts). **Mst. Muslima Khatun:** Data curation, Data analysis, Writing – review & editing. **Md. Moshir Rahman:** Data curation, Data analysis, Writing – review & editing. **Moin Uddin Ahmed:** Funding acquisition, Project review & editing administration, Writing – review & editing, Resources. **Adolphe O. Debrot:** Funding acquisition, Project administration, Supervision, Writing – review & editing. **Md. Nazmul Ahsan:** Funding acquisition, Project administration, Writing – review & editing. **M.C.J. Verdegem:** Conceptualization, Data curation, Formal analysis, Project administration, Supervision, Writing – review & editing, Validation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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