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Green Mangrove Microparticle Enrichment Enhances Early Zoeal Phototaxis and Accelerates Megalopa Settlement in Mud Crab (*Scylla serrata*)

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ABSTRACT

Optimization of hatchery rearing protocols for the mud crab (*Scylla serrata*) requires an understanding of larval behavioral transitions and their underlying nutritional drivers. Phototaxis is a key behavioral indicator of larval vigor, swimming capacity, and settlement readiness across ontogeny. This study evaluated the ontogenetic trajectory of positive phototaxis in *S. serrata* larvae across six developmental stages (Zoea 1 to Megalopa) under dietary enrichment with green mangrove microparticles at four dosages: P0 (Control – 0 mg), P1 (5 mg), P2 (10 mg), and P3 (15 mg). The result revealed that One-way ANOVA demonstrated stage-specific sensitivity to mangrove microparticle dosage, with significant treatment effects observed at Zoea 1 ($p = 0.0080$) and Megalopa ($p = 0.0151$). In Zoea 1, enrichment with 10 mg (P2: $65.31 \pm 16.28\%$) and 15 mg (P3: $47.77 \pm 6.39\%$) significantly increased positive phototaxis compared to the control (P0: $22.53 \pm 13.32\%$). Positive phototaxis peaked across all treatments during Zoea 3 ($72.76\% - 86.44\%$). Upon metamorphosis to the Megalopa stage, a distinct behavioral inversion occurred: larvae enriched with 10 mg (P2: $29.98 \pm 5.81\%$) and 15 mg (P3: $21.94 \pm 10.55\%$) exhibited a marked decline in positive phototaxis compared to the control ($51.64 \pm 11.05\%$). In conclusion, green mangrove microparticle enrichment enhances early zoeal visual orientation through essential phytonutrient delivery and accelerates the behavioral transition from pelagic surface attraction to benthic habitat settlement at the Megalopa stage. A dosage of 10 to 15 mg is recommended in hatchery operations to improve larval quality and synchronize benthic settlement.

INTRODUCTION

The mud crab (*Scylla serrata*) is an economically vital marine crustacean widely cultivated across the Indo-Pacific region due to its high market value, rapid growth rate, and premium meat quality (Holme *et al.,* 2007; Ruscoe *et al.,* 2004). Despite significant advancements in commercial aquaculture, the mud crab industry continues to face bottlenecks stemming from inconsistent hatchery seed production and severe larval mortality during metamorphosis (Nghia *et al.,* 2007; Suprayudi *et al.,* 2004). Successful hatchery culture of *S. serrata* requires precise synchronization of environmental, nutritional, and behavioral conditions across six distinct larval developmental stages five planktotrophic zoeal stages

(Zoea 1 to Zoea 5) and one transitional post-larval stage (Megalopa) (Zeng & Naylor, 1996; Genodepa *et al.,* 2004).

Among sensory behaviors in decapod larvae, phototaxis the directional orientation and movement in response to a light stimulus serves as a primary behavioral mechanism governing vertical distribution, planktonic foraging efficiency, predator avoidance, and habitat selection (Forward, 1988; Epifanio, 1988). Early zoeal stages typically exhibit positive phototaxis, positioning themselves in photic upper water columns where prey density and temperature optimize metabolic growth (Forward, 1987; Cronin & Forward, 1988). As larvae progress through ontogeny, this light-oriented behavior undergoes physiological and neurological remodeling. Upon metamorphosing into the Megalopa stage, a dramatic behavioral inversion often occurs, wherein positive phototaxis diminishes or shifts toward light avoidance, driving the post-larvae downward to settle in complex benthic nursery habitats such as mangrove root systems (Forward & Rittschof, 1994; Webley & Connolly, 2007).

The development and acuity of visual sensory organs in decapod larvae are heavily dependent on nutritional state (Cronin & Forward, 1988; Hamasaki *et al.,* 2002). Biosynthesis of retinoid chromophores and maintenance of the optic rhabdomere structure require dietary access to essential carotenoids, polyunsaturated fatty acids (PUFAs), and lipid-soluble antioxidants (Suprayudi *et al.,* 2004; Nghia *et al.,* 2007). In traditional hatchery settings, standard live feeds (such as *Brachionus rotundiformis* and *Artemia* nauplii) frequently lack the specialized phytochemical profile found in natural estuarine environments (Ruscoe *et al.,* 2004). Microparticles derived from green mangrove leaves (*Rhizophora* and *Avicennia* spp.) represent a rich source of bioavailable plant carotenoids, polyphenols, essential minerals, and dietary fibers that mimic natural estuarine detrital diets (Cannicci *et al.,* 2008). While mangrove microparticles have been explored for growth and nutritional enhancement in aquaculture, their direct influence on sensory organ functional development, stage-specific phototactic behavior, and benthic settlement dynamics remains unquantified.

Understanding how mangrove microparticle enrichment modulates phototactic response across ontogeny can provide critical insights into the physiological readiness and visual performance of hatchery-reared larvae. Therefore, this study aimed to quantify the ontogenetic trajectory of positive phototaxis in *S. serrata* larvae from Zoea 1 through Megalopa under varying dosages of green mangrove microparticle enrichment (0, 5, 10, and 15 mg), evaluate the dose-dependent effects of mangrove microparticles on early zoeal visual orientation and the behavioral switch governing Megalopa settlement and establish optimal enrichment dosages to enhance larval quality and settlement synchronization in commercial mud crab hatcheries.

METHOD

Preparation and Characterization of Green Mangrove Microparticles

Fresh, undamaged green leaves of mangrove (*Rhizophora mucronata*) were harvested from healthy estuarine stands. Leaves were thoroughly rinsed with distilled water to remove salt deposits and epibionts, air-dried under shaded conditions for 24 hours, and subsequently oven-dried at 45°C until reaching a constant weight. The dried tissue was finely pulverized using an electric stainless-steel mill and passed through a 45-µm mesh sieve to isolate microparticles suitable for ingestion by rotifers (*Brachionus rotundiformis*) and *Artemia* nauplii, as well as direct uptake by later zoeal stages.

The resulting green mangrove microparticles were stored in airtight, light-shielded desiccators at 4°C prior to live feed enrichment which could be seen in the fig 1. Biochemical characterization verified that the microparticle powder contained essential crude protein, bioavailable polysaccharides, natural carotenoid precursors (β-carotene and astaxanthin derivatives), and phenolic antioxidants.

Broodstock Management and Larval Rearing

Berried female mud crabs (*Scylla serrata*) were obtained from local estuarine waters and acclimated in 500-L circular fiberglass tanks equipped with recirculating, sand-filtered seawater. Water quality parameters during broodstock conditioning were maintained at:

- Temperature: 28.0 ± 1.0°C
- Salinity: 30 ± 1 ppt
- pH: 8.0 ± 0.2
- Dissolved Oxygen: > 5.5 mg L^{-1}
- Photoperiod: 12 h light: 12 h dark

Upon egg hatching, healthy, actively swimming Zoea 1 larvae displaying strong positive phototaxis were collected from the water surface using a fine mesh dip net (150 μm). Larvae were randomly distributed into twelve 50-L larval rearing tanks at an initial stocking density of 50 larvae L^{-1}.

Experimental Design and Dietary Treatments

The experiment was arranged in a Completely Randomized Design (CRD) comprising four dietary enrichment treatments with three replicates per treatment ($n = 3$):

- P0 (Control): Live feed enriched with 0 mg mangrove microparticles.
- P1: Live feed enriched with 5 mg L^{-1} mangrove microparticles.
- P2: Live feed enriched with 10 mg L^{-1} mangrove microparticles.
- P3: Live feed enriched with 15 mg L^{-1} mangrove microparticles.

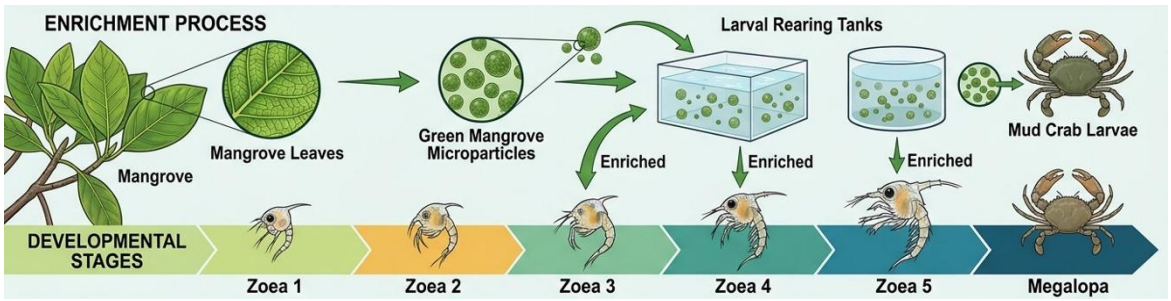


Fig 1 Enrichment process or crab larva

The feeding schedule was adapted according to larval developmental stage:

1. **Zoea 1 – Zoea 2:** Fed L-type rotifers (*Brachionus rotundiformis*) at a density of 15–20 individuals mL^{-1}, pre-enriched for 6 hours with the corresponding treatment dosage of mangrove microparticles.
2. **Zoea 3 – Zoea 5:** Fed a combination of rotifers (10 ind mL^{-1}) and newly hatched *Artemia* nauplii (3–5 ind mL^{-1}), pre-enriched with the designated microparticle concentrations.
3. **Megalopa:** Fed enriched *Artemia* nauplii (5–8 ind mL^{-1}) alongside minced fresh mussel meat.

Fifty percent of the water in each rearing tank was exchanged daily with fresh, UV-sterilized seawater, and mild aeration was provided continuously to maintain suspended microparticle distribution.

Phototaxis Behavioral Bioassay

Phototactic behavioral assays were conducted at each larval developmental stage (Zoea 1, Zoea 2, Zoea 3, Zoea 4, Zoea 5, and Megalopa) within 12 hours following the completion of molting.

A custom-designed, horizontal acrylic bioassay trough (60 cm length × 10 cm width × 10 cm depth) was utilized for the phototaxis trials fig 2. The trough was marked into two equal compartments:

- **Light Zone:** Positioned adjacent to a directional cold-white LED light source (500 lux; ~ 10 μmol m^{-2} s^{-1}).
- **Dark/Neutral Zone:** Shielded from direct illumination using opaque black acrylic barriers.

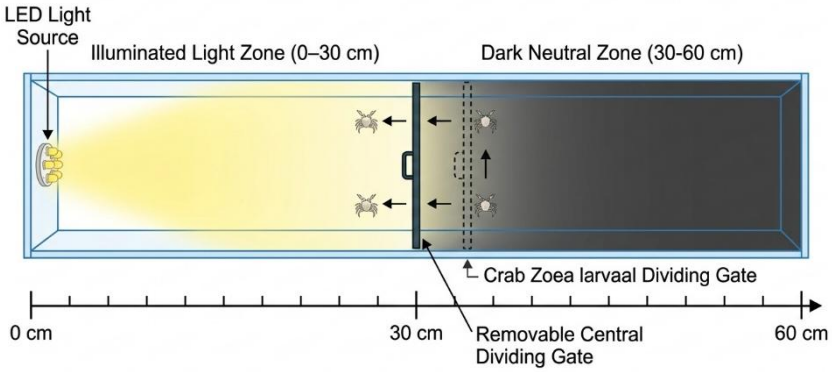


Fig 2. Schematic illustration of the horizontal acrylic bioassay

For each trial, 30 active larvae were randomly sampled from a replicate tank and placed into the center of the bioassay trough filled with filtered seawater (30 ppt, 28°C). Larvae were allowed to dark-acclimate for 10 minutes under ambient dark conditions. Following dark adaptation, the LED light source was switched on for 10 minutes. At the conclusion of the exposure period, the central dividing gate was closed, and the number of larvae located within the illuminated zone was recorded.

The positive phototaxis index was calculated as follows:

$$\text{Positive Phototaxis (\%)} = \left(\frac{N_{\text{light}}}{N_{\text{total}}}\right) \times 100$$

where N_{light} is the number of larvae retrieved from the light zone and N_{total} is the total number of larvae evaluated per assay ($N_{\text{total}} = 30$). All bioassays were executed in triplicate for each treatment group across all six ontogenetic stages.

Statistical Analysis

All numerical data were verified for normality using the Shapiro-Wilk test and for homogeneity of variance using Levene's test ($p > 0.05$). Stage-specific differences in positive phototaxis across dietary treatment doses (P0, P1, P2, P3) were analyzed using One-Way Analysis of Variance (ANOVA). Where significant main effects were detected ($p < 0.05$), Fisher's Least Significant Difference ($LSD_{0.05}$) post-hoc test was performed for pairwise mean comparisons. Statistical calculations were executed using Python. All values are reported as Mean $\pm$ Standard Deviation (SD).

RESULT AND DISCUSSION

Results

Ontogenetic Trajectory and Dose-Dependent Influence of Mangrove Microparticles

The positive phototactic response of mud crab (*Scylla serrata*) larvae exhibited distinct stage-specific sensitivity to dietary enrichment with green mangrove microparticles across ontogeny from Zoea 1 to Megalopa could be seen the table 1 and fig 3. One-way Analysis of Variance (ANOVA) confirmed that mangrove microparticle dosage significantly influenced positive phototaxis during the early Zoea 1 stage ($F_{(3,8)} = 8.191$, $p = 0.0080$) and the post-larval Megalopa stage ($F_{(3,8)} = 6.545$, $p = 0.0151$). Homogeneity of variance across all developmental stages was verified using Levene's test ($p > 0.05$).

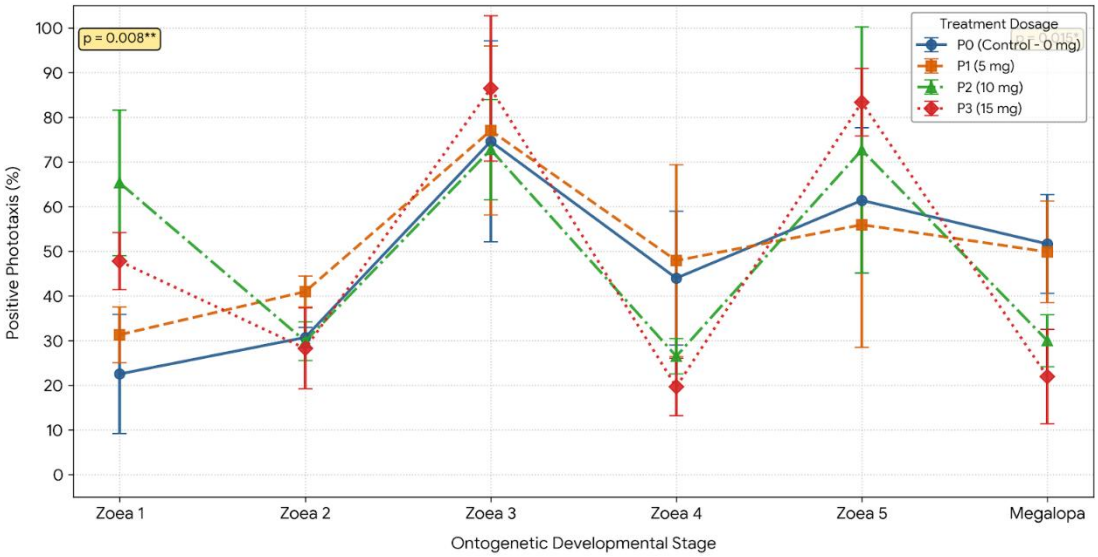


Fig 3 Ontogenetic Trajectory phototactic response of mud crab (*Scylla serrata*) larvae

Table 1. Positive phototactic response (%) of mud crab (*Scylla serrata)* larvae across six ontogenetic stages

Larval Stage	P0 (Control) (%)	P1 (5 mg) (%)	P2 (10 mg) (%)	P3 (15 mg) (%)
Zoea 1	22.53 ± 13.32^{b}	31.32 ± 6.24^{b}	65.31 ± 16.28^{a}	47.77 ± 6.39^{a}
Zoea 2	30.71 ± 2.28^{b}	40.97 ± 3.47^{a}	29.86 ± 4.34^{b}	28.22 ± 9.04^{b}
Zoea 3	74.60 ± 22.50^{a}	77.01 ± 18.93^{a}	72.76 ± 11.23^{a}	86.44 ± 16.26^{a}
Zoea 4	43.98 ± 14.98^{ab}	47.91 ± 21.49^{a}	26.50 ± 3.95^{ab}	19.64 ± 6.44^{b}
Zoea 5	61.39 ± 16.25^{a}	55.95 ± 27.45^{a}	72.67 ± 27.51^{a}	83.36 ± 7.55^{a}
Megalopa	51.64 ± 11.05^{a}	49.86 ± 11.36^{a}	29.98 ± 5.81^{b}	21.94 ± 10.55^{b}

Early-Stage Response (Zoea 1–2)

In Zoea 1, larvae enriched with 10 mg green mangrove microparticles (P2) achieved the highest positive phototactic index ($65.31 \pm 16.28\%$), followed by the 15 mg dose (P3: $47.77 \pm 6.39\%$).

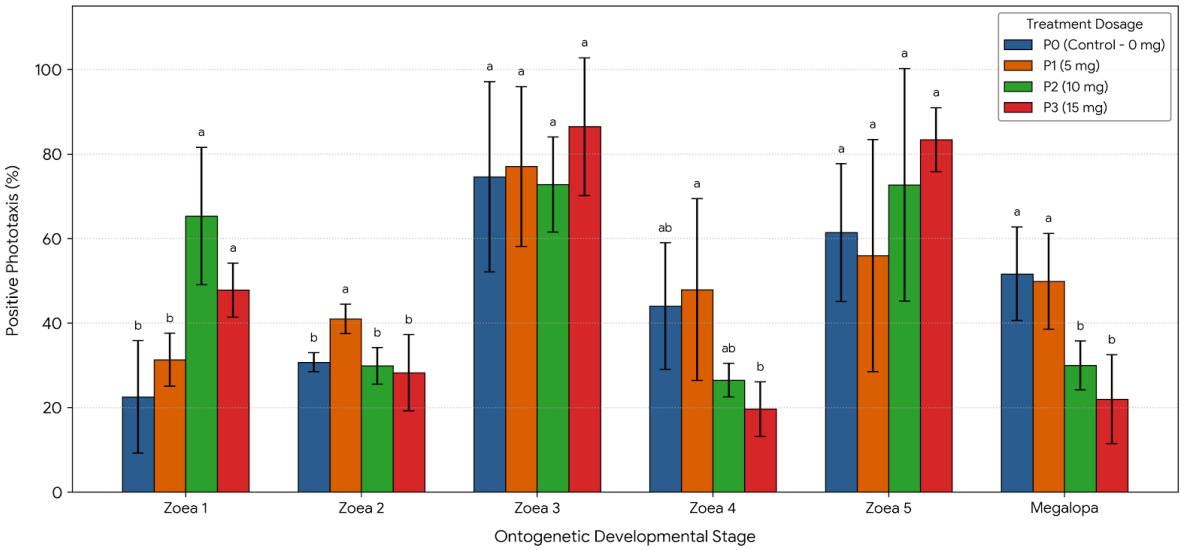


Fig 4. Positive phototactic response (%) of Scylla serrata larvae across treatments

Post-hoc analysis ($LSD_{0.05} = 21.52\%$) confirmed that P2 and P3 were statistically comparable to each other but significantly higher ($p < 0.05$) than the 5 mg treatment (P1: $31.32 \pm 6.24\%$) and the unenriched control (P0: $22.53 \pm 13.32\%$). At Zoea 2, phototactic intensity moderated overall; the 5 mg dosage (P1) yielded the highest mean response ($40.97 \pm 3.47\%$), significantly outperforming the control P0 ($30.71 \pm 2.28\%$), P2 ($29.86 \pm 4.34\%$), and P3 ($28.22 \pm 9.04\%$).

Mid-to-Late Larval Stages (Zoea 3–5)

During Zoea 3, positive phototaxis peaked across all treatment groups, ranging from $72.76 \pm 11.23\%$ in P2 (10 mg) to $86.44 \pm 16.26\%$ in P3 (15 mg). No significant differences were observed between treatments ($F_{(3,8)} = 0.354$, $p = 0.7880$). Zoea 4 displayed a transient reduction in phototaxis across all groups, with P1 maintaining the highest positive phototaxis ($47.91 \pm 21.49\%$), significantly higher than P3 ($19.64 \pm 6.44\%$, $p < 0.05$). By Zoea 5, positive phototaxis recovered substantially across all groups, peaking in the 15 mg enriched group (P3: $83.36 \pm 7.55\%$) and 10 mg group (P2: $72.67 \pm 27.51\%$), although differences among dosages remained non-significant ($F_{(3,8)} = 0.974, p = 0.4514$).

Settlement Stage (Megalopa)

Upon metamorphosis to the Megalopa stage, a distinct behavioral switch occurred. Unenriched control larvae (P0: $51.64 \pm 11.05\%$) and low-dose enriched larvae (P1: $49.86 \pm 11.36\%$) retained moderate positive phototaxis. Conversely, Megalopa enriched with higher doses of green mangrove microparticles (P2 [10 mg]: $29.98 \pm 5.81\%$ and P3 [15 mg]: $21.94 \pm 10.55\%$) demonstrated a pronounced reduction in positive phototaxis ($p = 0.0151$).

Discussion

Bioactive Mechanisms of Mangrove Microparticles in Early Larval Phototaxis (Zoea 1–2)

The enhancement of positive phototaxis in Zoea 1 under moderate-to-high green mangrove microparticle enrichment (10 mg [P2] and 15 mg [P3]) underscores the critical nutritional and physiological role of mangrove-derived phytonutrients in early decapod development (Holme *et al.,* 2007; Ruscoe *et al.,* 2004). Green mangrove (*Rhizophora* and *Avicennia* spp.) microparticles are rich in natural carotenoids, polyphenols, essential trace minerals, and bioavailable polysaccharides (Cannicci *et al.,* 2008). Early zoeal stages possess developing compound eyes that rely on dietary pigments specifically β-carotene and astaxanthin precursors for retinoid chromophore synthesis and rhabdomere structural integrity (Cronin & Forward, 1988; Suprayudi *et al.,* 2004).

By providing antioxidant protection and essential lipid precursors, mangrove microparticles reduce photo-oxidative stress within rapidly dividing ocular tissues and optimize rhodopsin signal transduction pathways (Forward, 1988; Hamasaki *et al.,* 2002). This bioenergetic enhancement enables newly hatched Zoea 1 larvae to exhibit stronger phototactic orientation toward illuminated surface waters, maximizing encounter rates with planktonic prey (Forward, 1987; Epifanio, 1988). The transient peak observed at Zoea 2 under the 5 mg treatment (P1) suggests a lower threshold requirement for lipid maintenance as larvae undergo initial cuticle molting prior to secondary neural consolidation (Nghia *et al.,* 2007).

Ontogenetic Physiological Climax and Visual Remodeling (Zoea 3–5)

The uniform surge in positive phototaxis during Zoea 3 ($\geq 72.76\%$) across all experimental groups marks a major ontogenetic developmental threshold in *S. serrata* (Zeng & Naylor, 1996). At mid-zoeal ontogeny, rapid expansion of the optic neuropils, lamina ganglionaris, and lobula complex significantly enhances visual acuity and swimming power

(Cronin & Forward, 1988). The peak positive phototaxis observed at Zoea 3 represents an evolutionary strategy that keeps larvae in photic surface layers where microzooplankton prey densities are highest (Forward, 1988; Epifanio, 1988).

The temporary decline at Zoea 4 followed by recovery at Zoea 5 reflects metabolic reorganization prior to final larval metamorphosis (Genodepa *et al.,* 2004; Holme *et al.,* 2007). During late zoeal stages, metabolic reserves are directed toward hepatopancreas lipid accumulation and organ differentiation (Suprayudi *et al.,* 2004). High-dose microparticle supplementation (15 mg [P3]) sustained the highest phototactic response at Zoea 5 (83.36%), indicating that phytochemical enrichment meets the metabolic demands of the final zoeal molt (Nghia *et al.,* 2007).

Settlement Behavioral Switch and Ecological Adaptation in Megalopa

The significant drop in positive phototaxis observed in Megalopa reared under higher mangrove microparticle dosages (10 mg [P2] and 15 mg [P3]) reflects an accelerated behavioral transition from pelagic planktotrophy to benthic settlement (Forward & Rittschof, 1994; Webley & Connolly, 2007). Metamorphosis into the Megalopa stage requires a functional switch from surface light attraction to negative phototaxis or light avoidance, driving post-larvae downward toward protective mangrove roots, benthic detritus, and estuarine nursery habitats (Zeng & Naylor, 1996; Webley & Connolly, 2007).

Nutritional enrichment with 10–15 mg green mangrove microparticles provides critical biochemical triggers such as optimal lipid storage and phytonutrient reserves that signal physiological readiness for substrate selection (Genodepa *et al.,* 2004; Holme *et al.,* 2007). In contrast, Megalopa in the control (P0) and low-dose (P1) groups retained elevated positive phototaxis (51.64% and 49.86%). This delayed behavioral switch indicates nutritional deficiency or developmental lagging, forcing under-nourished post-larvae to remain longer in the photic pelagic zone searching for food (Forward & Rittschof, 1994). Supplementing live feeds with 10 mg to 15 mg of green mangrove microparticles accelerates visual switch behavior, promoting timely benthic settlement and improving survival during hatchery metamorphosis (Ruscoe *et al.,* 2004; Webley & Connolly, 2007).

CONCLUSION

This study demonstrates that green mangrove microparticle dietary enrichment exerts a significant, stage-specific influence on the ontogenetic phototaxis and behavioral settlement dynamics of mud crab (*Scylla serrata*) larvae. Microparticle enrichment significantly improves early zoeal visual orientation, with dosages of 10 mg/L (P2) and 15 mg/L (P3) increasing positive phototaxis in Zoea 1 larvae. Across mid-to-late zoeal development, phototaxis reaches an ontogenetic peak at Zoea 3. maintaining strong surface attraction during pelagic planktotrophy. Crucially, higher microparticle supplementation accelerates the post-larval behavioral switch during metamorphosis into the Megalopa stage. Enriched Megalopa (10-15 mg/L) exhibit a distinct reduction in positive phototaxis ($< 30\%$) compared to controls (51.64%), signaling timely nutritional readiness and driving the transition from pelagic photic attraction to benthic downward settlement toward estuarine microhabitats. Supplementing live feeds with 10 to 15 mg/L of green mangrove microparticles is recommended to enhance early larval quality, optimize phototactic foraging efficiency, and synchronize Megalopa benthic settlement, ultimately improving post-larval survival and nursery yield.

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