



## DIEL CHANGES IN THE VERTICAL DISTRIBUTION OF DECAPODA LARVAE IN A TROPICAL ANTHROPIZED ESTUARY

### MUDANÇAS NICTEMERAIS NA DISTRIBUIÇÃO VERTICAL DE LARVAS DE DECÁPODES EM UM ESTUÁRIO TROPICAL ANTROPIZADA

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#### Resumo

Organismos planctônicos, incluindo larvas de crustáceos decápodes, comumente realizam migração vertical nictemeral como estratégia comportamental em ambientes estuarinos. Este estudo investigou a distribuição vertical, a variabilidade nictemeral e os padrões sazonais das larvas de decápodes em um estuário tropical eutrofizado e altamente antropizado (Estuário do Pina, Nordeste do Brasil). As larvas foram amostradas ao longo de um ciclo nictemeral completo, durante os períodos chuvoso (2016) e seco (2017), nas camadas superficial e próxima ao fundo. Foi detectada interação significativa entre o horário do dia e a profundidade (ANOVA;  $p < 0,05$ ). As densidades larvais na superfície permaneceram baixas durante o período diurno, mas aumentaram expressivamente à noite, enquanto as camadas próximas ao fundo não apresentaram variação nictemeral significativa. Diferenças relacionadas à profundidade foram observadas somente durante o dia, com maiores densidades larvais próximas ao fundo. Não foram detectadas diferenças sazonais significativas na abundância larval. A densidade larval apresentou correlação positiva com a salinidade ( $r_s = 0,41$ ;  $p = 0,01$ ), indicando que a intrusão marinha e a dinâmica das marés desempenham papel fundamental na estruturação da distribuição larval. Esses resultados confirmam a migração vertical nictemeral como um processo comportamental dominante, em curto prazo, na regulação da distribuição vertical das larvas de decápodes, provavelmente associado à evasão de predadores e ao transporte hidrodinâmico. A

persistência das larvas, apesar da intensa pressão antrópica, sugere certo grau de resiliência ecológica dependente da conectividade marinha. Este estudo destaca a relevância da dinâmica larval como indicadora do funcionamento estuarino e fornece subsídios úteis para a gestão de ecossistemas costeiros tropicais impactados.

*Palavras-chaves:* Conectividade costeira; Eutrofização; Transporte hidrodinâmico; Intrusão marinha; Ciclo nyctemeral; Ecologia do plâncton; Dinâmica de recrutamento; Gradiente de salinidade.

### **Abstract**

Planktonic organisms, including decapod crustacean larvae, commonly exhibit diel vertical migration as a behavioral strategy in estuarine environments. This study investigated the vertical distribution, diel variability, and seasonal patterns of decapod larvae in a eutrophic and highly anthropized tropical estuary (Pina Estuary, northeastern Brazil). Larvae were sampled over a complete nycthemeral cycle during the rainy (2016) and dry (2017) seasons at surface and near-bottom layers. A significant interaction between time of day and depth was detected (ANOVA;  $p < 0.05$ ). Larval densities at the surface were consistently low during daytime but increased markedly at night, whereas bottom layers showed no significant diel variation. Depth-related differences were observed only during the day, with higher larval densities near the bottom. No significant seasonal differences in larval abundance were detected. Larval density showed a positive correlation with salinity ( $r_s = 0.41$ ;  $p = 0.01$ ), indicating that marine intrusion and tidal dynamics play a key role in structuring larval distribution. These results confirm diel vertical migration as a dominant short-term behavioral process regulating the vertical distribution of decapod larvae, likely associated with predator avoidance and hydrodynamic transport. The persistence of larvae despite strong anthropogenic pressure suggests a degree of ecological resilience dependent on marine connectivity. This study highlights the relevance of larval dynamics as indicators of estuarine functioning and provides useful insights for the management of impacted tropical coastal ecosystems.

*Keywords:* Coastal connectivity; Eutrophication; Hydrodynamic transport; Marine intrusion; Nycthemeral cycle; Plankton ecology; Recruitment dynamics; Salinity gradient.



## Introduction

Estuaries are semi-enclosed coastal ecosystems located at river mouths, characterized by the dynamic interaction between freshwater discharge and marine waters. This interaction gives rise to steep physical and chemical gradients especially in salinity, temperature, turbidity, and nutrient availability which in turn promote high biological productivity and habitat heterogeneity (Pereira et al., 2010; Neto et al., 2021; Crump et al., 2024; He et al., 2025). Consequently, estuaries play a crucial ecological role as feeding grounds, nursery areas, and breeding sites for numerous aquatic organisms, including ecologically and economically important crustaceans and fish (Nagelkerken et al., 2015; Kumar et al., 2023; Bernard et al., 2025).

Despite their natural productivity, estuaries rank among the most vulnerable coastal environments due to intense anthropogenic pressures. Urban expansion, industrial development, untreated wastewater discharge, and hydrological alterations frequently degrade water quality and disrupt ecosystem functioning (Silva et al., 2016; Bordalo et al., 2018). These stressors can significantly affect biological communities, particularly planktonic assemblages, which respond rapidly to environmental changes and disturbances.

Port areas are among the most impacted zones within estuarine systems, as they concentrate multiple stressors such as dredging, vessel traffic, contaminant input, and habitat modification (Todd et al., 2015). In urbanized tropical estuaries, port-related activities often exacerbate eutrophication processes and disrupt trophic interactions, leading to biodiversity loss and reduced ecological resilience (Sant'Anna and Tundist, 1996; Santos et al., 2009; He et al., 2025). The Pina Estuary, adjacent to the Port of Recife, exemplifies a highly impacted ecosystem that is continuously affected by domestic and industrial effluents from surrounding urban areas.

Within the zooplankton, decapod crustacean larvae constitute a taxonomically diverse and ecologically relevant group, including the larval stages of crabs, shrimps, lobsters, and hermit crabs. Most decapod species exhibit planktonic larval stages that are ecologically distinct from their adult habitats and highly sensitive to abiotic factors such as salinity, temperature, and hydrodynamics (Martins and Calazans, 2003; Martin et al., 2014; Dias et al., 2018; Neumann-Leitão et al., 2021; Monteiro et al., 2024). These larvae are not only sensitive to environmental variation but also serve as bioindicators and hold socioeconomic importance for artisanal fisheries (Calumby et al., 2016; Longo, 2025).

A key behavioral strategy exhibited by many zooplanktonic organisms, including decapod larvae, is diel vertical migration (DVM). This behavior involves systematic vertical movements within the water column, generally characterized by nocturnal ascent and daytime descent, primarily in response to light intensity and predation risk (Hays, 2003; Longo, 2025). In estuarine environments, DVM may also interact with salinity gradients and tidal dynamics, influencing larval retention and dispersion (Melo et al., 2021; Monteiro et al., 2024). This behavior thus constitutes a key mechanism in regulating larval transport and population connectivity in estuarine systems.



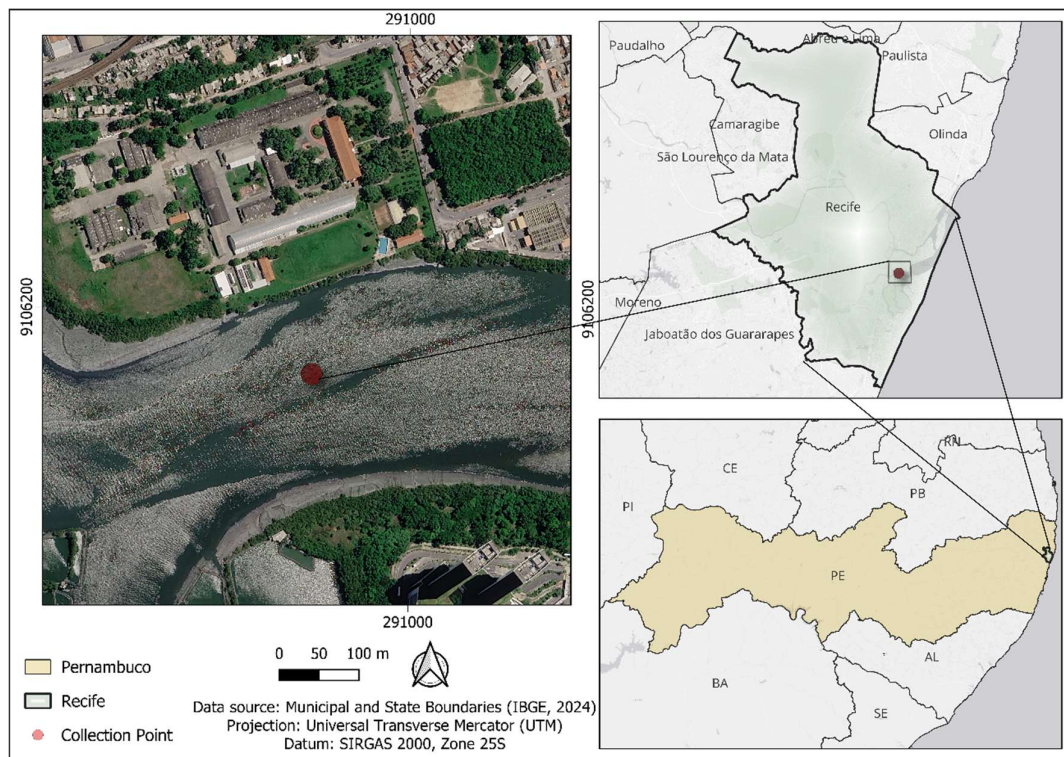


Given the complexity of these interactions in anthropogenically influenced estuaries, it is essential to understand how diel vertical migration and seasonal variability affect the distribution and abundance of decapod larvae. In this context, the present study investigates the diel vertical migration and seasonal variation of Decapoda larvae in the Pina Estuary, with the objective of assessing the influence of environmental factors on their vertical distribution patterns and abundance.

## Material and Methods

### Study Area

Sampling was conducted at a fixed station located in the Pina Basin Estuary, northeastern Brazil ( $8^{\circ}04'56.28''$  S,  $34^{\circ}53'51.79''$  W; Figure 1). The estuary is formed by the confluence of the Capibaribe, Tejiþiþ, Jordão, and Pina rivers and lies adjacent to the Port of Recife, within the urban area of Recife, Pernambuco, Brazil (Sant'Anna and Tundisi 1996). The regional climate is characterised by a dry season from September to February ( $<100$  mm month<sup>-1</sup>) and a rainy season from March to August ( $>200$  mm month<sup>-1</sup>) (Sant'Anna and Tundisi 1996).



**Figure 1.** Location map of the Pina Estuary, Recife, Pernambuco, Brazil.

### Sampling and samples treatment

Sampling was performed at three-hour intervals over a complete 24-hour cycle during the rainy season (August 2016) and dry season (February 2017), coinciding with spring tide conditions. Abiotic parameters (temperature, salinity, depth) were measured using a CastAway mini-CTD, while water samples for dissolved oxygen and chlorophyll-a were collected with a 2 L Niskin bottle.

Decapod larvae were collected through horizontal subsurface and near-bottom tows. Subsurface tows employed a 500  $\mu\text{m}$  conical-cylindrical plankton net (60 cm diameter), while bottom tows used a 500  $\mu\text{m}$  closing net (30 cm diameter). A digital flowmeter (General Oceanics, Model 2030) was attached to each net to calculate filtered volume. Tows were conducted at 2 knots for approximately 10 minutes. Samples were preserved in 4% formaldehyde, buffered with sodium tetraborate.

Samples with high larval abundance were subsampled using a plankton splitter until ~300 individuals were obtained. Larvae were sorted and counted under a stereomicroscope. Samples with fewer than 300 individuals were analyzed in full. A subset of 20 individuals per sample was measured to estimate biovolume ( $\text{mm}^3 \text{m}^{-3}$ ) using stereometric approximations.

Dissolved oxygen ( $\text{ml L}^{-1}$ ) was determined by the Winkler method (Grasshoff et al., 1983). Chlorophyll-a ( $\text{mg m}^{-3}$ ) was quantified by filtering water samples through GF/C filters, extracting pigments in 90% acetone at  $-18^\circ\text{C}$  for 24 h, and measuring absorbance at 630, 645, 665, and 750 nm with a spectrophotometer. Concentrations were calculated following Parsons and Strickland (1963). Trophic status was classified as oligotrophic ( $<1 \text{ mg m}^{-3}$  chlorophyll-a) or eutrophic ( $>1 \text{ mg m}^{-3}$ ).

### **Data analysis**

Larval densities were standardized to individuals per cubic meter ( $\text{ind. m}^{-3}$ ). The differences in density and biovolume were tested across diel period and depth using a two-way ANOVA to assess the interaction between diel period and depth to verify if potential differences in the decapod larvae density between surface and bottom samples have any influence of diel period. The Shapiro-Wilk test was used to verify normal distribution of errors of the anova model, and the Bartlett test was used to verify homocedasticity. Post hoc comparisons were performed by means of a Tukey's HSD test. The differences between seasonal periods were tested with t-tests.

Relationships between larval density and environmental variables were examined using the Pearson correlation, with log-transformed density values, and the significance of the correlations were tested with the Pearson correlation test. Significant correlations were further explored with linear regression. A correlation matrix based Principal Component Analysis (PCA) was performed with data standardized to zero mean and unit variance.

All analyses were conducted in R (version 4.0, R Core Team, <https://cran.r-project.org>), within the integrated development environment RStudio (version 1.3, <https://www.rstudio.com>), and in Python (Python Software Foundation, Python Language Reference v. 3.13, [www.python.org](http://www.python.org)), within the integrated development environment PyCharm (version 2025.1.2, [www.jetbrains.com/pycharm/](http://www.jetbrains.com/pycharm/)).

## **Results**

### **Abiotic Data**

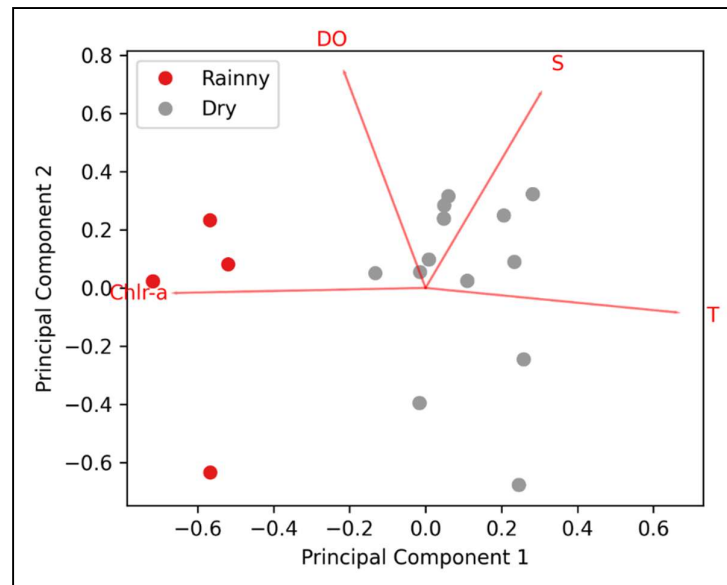


Dissolved oxygen values varied between 1.17 mg L<sup>-1</sup> (day, surface/bottom, low tide, dry season) and 4.01 mg L<sup>-1</sup> (day, surface, flow tide, rainy season). Chlorophyll-a ranged between 0.02 mg m<sup>-3</sup> (day, surface, flow tide, dry season) and 1.99 mg m<sup>-3</sup> (day, surface, ebb tide, rainy season). Temperature ranged between 27°C (night and day, surface, flow tide and high tide, rainy season) and 30°C (day, surface, low tide, dry season). Salinity values varied between 25.14 (day, surface, low tide, rainy season) and 37.07 (night, bottom, high tide, dry season).

The first two axes of the principal component analysis explained 85% of the variance in the dataset (Table 1). A seasonal gradient in the distribution of the samples was observed in the ordination (Figure 2) with samples from the rainy period associated with higher chlorophyll-a values and lower temperature values. Samples from the dry season were associated with higher temperature and salinity values.

**Table 1.** Eigenvalues, explanation percentages, and main hydrological variables in each axis of the principal components analysis.

| Axis | Eigenvalue | Explanation | Cumulative explanation | Main variables |
|------|------------|-------------|------------------------|----------------|
| 1    | 2.18       | 53.0%       | 53.0%                  | Chl-a, Temp    |
| 2    | 1.30       | 31.6%       | 84.6%                  | DO, Sal        |
| 3    | 0.54       | 13.2%       | 97.8%                  |                |
| 4    | 0.09       | 2.2%        | 100.0%                 |                |



**Figure 2.** Principal Components Analysis ordination presenting hydrological variables, and seasonal periods gradients in the samples.

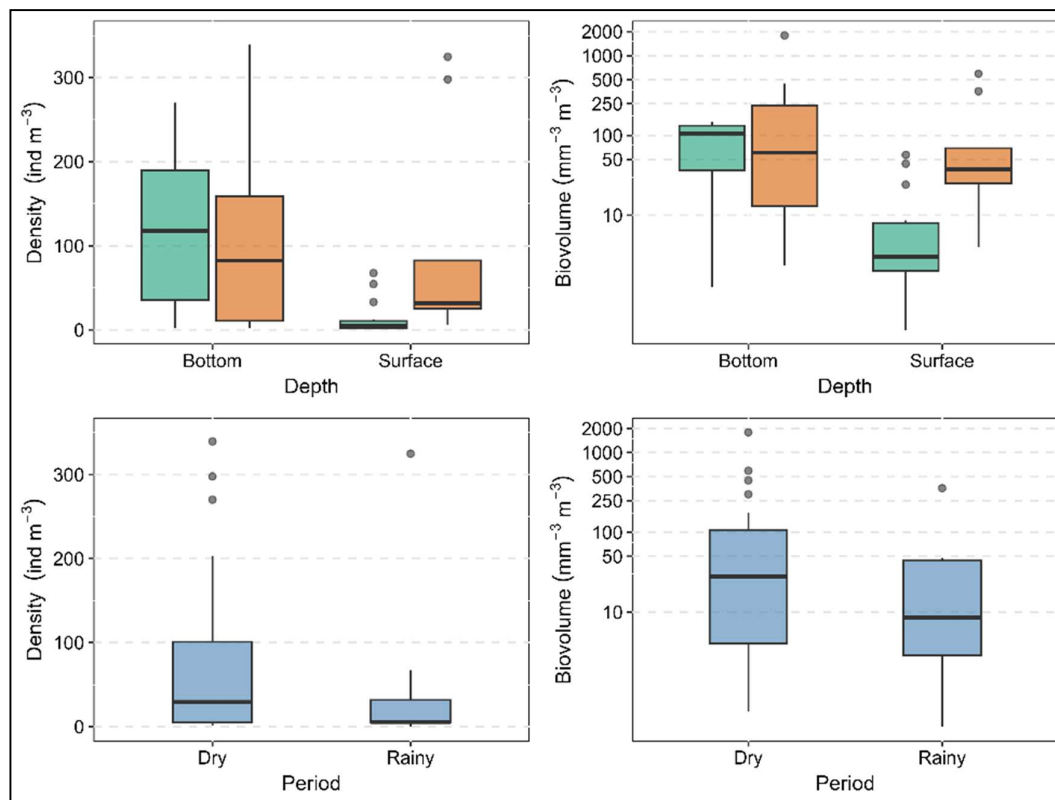
### **Decapod larvae**

Larval densities ranged from 0.42 ind. m<sup>-3</sup> (morning, surface, rainy season, flood tide) to 2737.5 ind. m<sup>-3</sup> (night, bottom, dry season, ebb tide). A significant interaction between time of day and depth was detected (two-way ANOVA;  $p < 0.05$ ; Figure 3). Surface densities were consistently low during the day (0.42–67.5 ind. m<sup>-3</sup>; mean  $14.3 \pm 21.6$  ind. m<sup>-3</sup>) but increased significantly at night (6–324 ind. m<sup>-3</sup>; mean

93.5  $\pm$  125.5 ind. m<sup>-3</sup>; Tukey;  $p < 0.05$ ) (Table 2). No diel differences were observed in bottom layers (Tukey;  $p > 0.05$ ), although a non-significant decreasing trend was noted. Daytime comparisons revealed significantly higher densities at the bottom than at the surface (Tukey;  $p < 0.05$ ). No seasonal differences were detected (t-test;  $p > 0.05$ ).

**Table 2.** Decapod larvae density variation (ind m<sup>-3</sup>) in the surface and bottom samples of day and night samples.

|       |         | Minimum | Maximum | Mean  | Standard Deviation |
|-------|---------|---------|---------|-------|--------------------|
| Day   | Surface | 0.42    | 67.5    | 14.3  | 21.6               |
|       | Bottom  | 2.04    | 270.0   | 121.3 | 105.5              |
| Night | Surface | 6.03    | 324.6   | 93.5  | 125.5              |
|       | Bottom  | 2.25    | 2737.5  | 397.1 | 804.0              |



**Figure 3.** Boxplot of the total density (ind m<sup>-3</sup>) and total biovolume (mm<sup>3</sup> m<sup>-3</sup>) of decapod larvae in the Pina Estuary in relation to different depths (surface and bottom) and day period (green boxes represent diurnal samples, and orange boxes represent the nocturnal samples), as well as in relation to season (rainy and dry seasons). Biovolume scale is logarithmic.

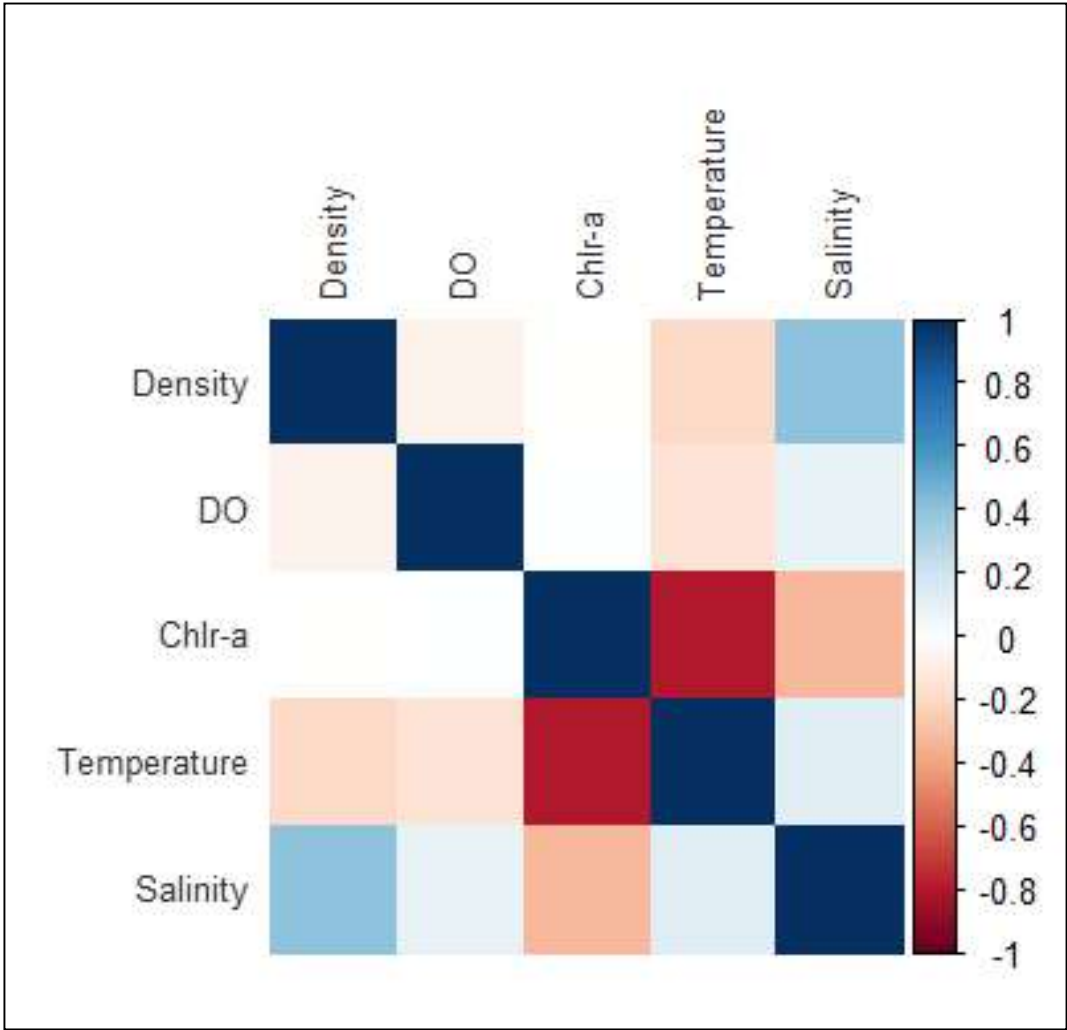
Biovolume values ranged from 0.365 mm<sup>3</sup> m<sup>-3</sup> (daytime, surface, rainy season) to 1790.33 mm<sup>3</sup> m<sup>-3</sup> (night, bottom, dry season) (Figure 3). No interaction between depth and time of day was observed (two-way ANOVA;  $p > 0.05$ ). However, surface biovolume was significantly higher at night compared to daytime (ANOVA;  $p < 0.01$ ).



Bottom biovolume tended to exceed surface values, though this difference was marginal (ANOVA;  $p = 0.05$ ). No seasonal differences were detected (t-test;  $p > 0.05$ ). Larval densities correlated positively with salinity ( $r = 0.41$ ; Spearman;  $p < 0.05$ ; Figure 4; Table 3), indicating higher concentrations under stronger marine influence (Figure 5).

**Table 3.** Spearman correlations and associated p-values for decapod larvae density and abiotic variables.

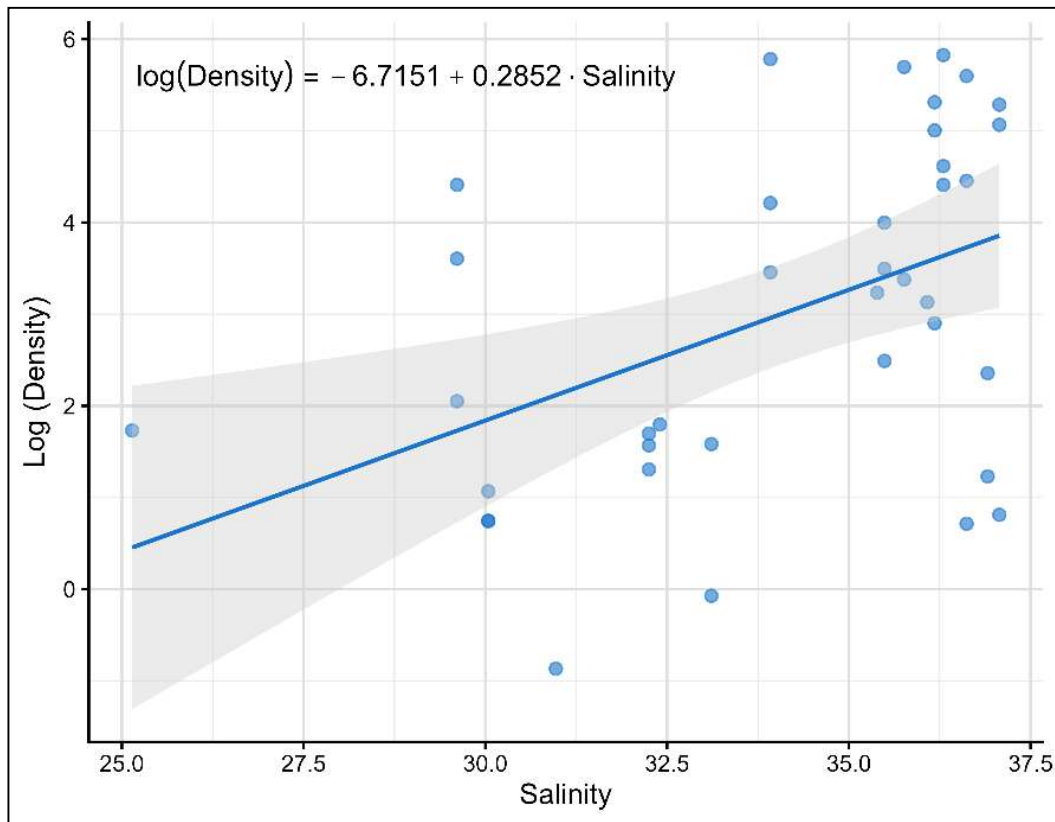
|             | Salinity | Chlorophyll-a | Dissolved Oxygen | Temperature |
|-------------|----------|---------------|------------------|-------------|
| Coefficient | 0.41     | -0.01         | -0.06            | -0.19       |
| p-value     | 0.01     | 0.97          | 0.62             | 0.16        |



**Figure 4.** Correlogram of spearman correlations between decapod larvae density and abiotic variables.







**Figure 5.** Correlation between decapod density and salinity in the Pina Estuary.

## Discussion

### ***Salinity, temperature and hydrodynamic control***

Salinity and temperature acted as the primary abiotic drivers structuring the vertical and temporal distribution of decapod larvae in the Pina estuary. The positive relationship between larval density and salinity highlights the strong dependence of early larval stages on marine water intrusion, reflecting physiological constraints related to limited osmoregulatory capacity during initial development (Charmantier, 1998; Anger, 2003). Recent studies conducted in large tropical estuarine systems further confirm salinity as the main predictor of decapod larval distribution, reinforcing its central role in controlling larval survival and spatial patterns (Lima et al., 2019; Monteiro et al., 2024; Bernard et al., 2025).

Salinity emerged as the main abiotic factor associated with larval density, while temperature contributed to seasonal environmental variation, whereas reduced salinity associated with freshwater discharge during rainy periods may limit larval persistence in inner estuarine areas (González-Gordillo and Rodríguez, 2003; Sterza and Fernandes, 2006). Similar patterns have been observed in Amazonian estuaries, where salinity gradients regulate larval retention and export processes, evidencing the interaction between physiological tolerance and hydrodynamic forcing (Lima et al., 2019).

Tidal dynamics reinforced this pattern by modulating salinity and controlling larval transport within the estuary. Flood tides increased marine influence and coincided with higher larval densities, suggesting that continuous larval supply from

adjacent coastal waters plays a central role in sustaining estuarine populations (Christy and Morgan, 1998; Melo et al., 2021). Conversely, ebb tides were associated with lower salinity and reduced larval abundance, likely due to dilution effects and increased advective export, a common feature of tide-dominated estuaries (Pereira et al., 2010).

Although temperature varied less markedly, higher values during the dry season may enhance reproductive activity and larval release, strengthening the combined influence of hydrological and thermal conditions on larval dynamics (Silva et al., 2003; Luppi et al., 2003). Recent analyses of decapod larval communities under changing climatic and environmental conditions corroborate the sensitivity of larval assemblages to temperature salinity interactions (Monteiro et al., 2024).

### ***Role of chlorophyll-a, dissolved oxygen and eutrophication***

Chlorophyll-a and dissolved oxygen influenced larval distribution indirectly by reflecting trophic conditions and ecosystem metabolism. Elevated chlorophyll concentrations during the rainy season indicate nutrient enrichment driven by continental runoff and urban effluents, a typical feature of highly anthropized tropical estuaries such as the Pina system (Sant'Anna and Tundist, 1996; Santos et al., 2009; Melo et al., 2021). Increased primary production may enhance secondary productivity, improving food availability for planktonic larvae and supporting higher survival rates (Lucas et al., 1999; Neumann-Leitão et al., 2021).

Dissolved oxygen followed similar seasonal trends, likely regulated by photosynthetic activity and hydrodynamic mixing (Santos et al., 2009). The positive association between larval density and oxygen suggests that well-oxygenated conditions favor larval persistence, particularly in eutrophic systems where hypoxia may occur episodically (Silva et al., 2016). Recent studies emphasize that nutrient-driven changes in primary production can rapidly alter trophic coupling and zooplankton dynamics in anthropogenically impacted estuaries (Crump and Bowen, 2024; Bernard et al., 2025).

### ***Diel vertical migration as a behavioral mitigation mechanism***

A pronounced diel vertical migration pattern was observed, with larvae occupying surface waters at night and deeper layers during daytime. This behavior is widely recognized as an adaptive strategy that reduces predation risk from visually oriented predators while allowing larvae to exploit surface waters for feeding and horizontal transport under reduced light conditions (Morgan, 1995; Hovel and Morgan, 1997; Christy and Morgan, 1998).

Recent community-level studies of decapod larvae continue to support the importance of vertical distribution patterns as a key mechanism modulating larval exposure to environmental gradients and transport processes, even in highly dynamic coastal systems (Carreton et al., 2022). In eutrophic and turbid estuaries such as the Pina, diel vertical migration may also function as a behavioral mechanism that mitigates exposure to unfavorable conditions, including high temperatures, reduced



dissolved oxygen, and elevated contaminant concentrations near the surface during daylight hours (Clark, 2001; Silva et al., 2016).

The association of higher larval densities with nighttime flood tides further supports the role of vertical migration in enhancing estuarine retention. Synchronizing upward movement with flood tides likely promotes landward transport while reducing export losses, reinforcing population maintenance within estuarine nursery areas (Morgan and Christy, 1997; Neumann-Leitão et al., 2008).

### ***Seasonal stability and implications for larval retention***

Despite marked seasonal variation in environmental conditions, no significant seasonal differences in larval density were detected. This apparent stability suggests that short-term behavioral processes, particularly diel vertical migration combined with tidal dynamics, exert a stronger influence on larval distribution than seasonal forcing (Silva et al., 2003; Neumann-Leitão et al., 2008). Similar stability in larval abundance has been reported in recent studies, even under scenarios of environmental variability, highlighting the buffering role of behavioral strategies and continuous marine larval supply (Monteiro et al., 2024).

Such stability is particularly relevant in urbanized estuaries, where hydrological regimes and water quality are heavily modified. The persistence of decapod larvae under these conditions indicates a degree of ecological resilience, although this resilience likely depends on sustained marine connectivity and adequate hydrodynamic exchange (Nagelkerken et al., 2015; Bernard et al., 2025).

### ***Implications for fisheries and coastal management***

Decapod larvae represent the early life stages of ecologically and economically important species, many of which support artisanal and small-scale fisheries along the Brazilian coast (Calumby et al., 2016; Santana et al., 2018). Understanding their vertical and temporal distribution is therefore essential for predicting recruitment success and population connectivity (Nagelkerken et al., 2015).

The strong dependence on salinity, tidal dynamics, and behavioral synchronization observed in this study suggests that alterations to freshwater discharge, dredging activities, and port operations may directly affect larval supply and retention in the Pina estuary (Sant'Anna and Tundist, 1996; Santos et al., 2009). Recent syntheses highlight that zooplankton responses to anthropogenic disturbance can precede broader ecosystem shifts, reinforcing their value in monitoring and management programs (Crump and Bowen, 2024; Bernard et al., 2025).

Monitoring diel vertical migration patterns and larval abundance may thus provide an effective tool for assessing ecosystem functioning and detecting early signs of degradation in anthropogenically impacted estuaries (Silva et al., 2016; Bernard et al., 2025).



## Conclusion

This study demonstrated that decapod larvae in the Pina estuary exhibit a clear diel vertical migration pattern, with higher surface densities at night and increased occupation of deeper layers during daytime, likely as a strategy to reduce predation risk. Larval abundance was positively correlated with salinity, highlighting the importance of marine intrusion and tidal dynamics in structuring larval distribution, while no significant seasonal differences were detected.

These results indicate that short-term behavioral processes, particularly diel vertical migration coupled with estuarine hydrodynamics, exert a stronger influence on larval distribution than seasonal variability in this eutrophic and highly anthropized estuary. The persistence of decapod larvae under such conditions suggests a degree of ecological resilience that depends on sustained marine connectivity.

Given the sensitivity of decapod larvae to abiotic gradients, their vertical and temporal distribution represents a valuable indicator of estuarine functioning. Integrating larval dynamics with hydrodynamic modeling and long-term monitoring may provide important insights for assessing ecosystem health, predicting recruitment success, and supporting management strategies in impacted tropical coastal systems.

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