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Moonlight-driven zooplankton migration shapes phytoplankton distribution in a tropical peatland pond

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Abstract. *Veronica E, Ardianor, Dohong S, Asi N, Afentina, Hanasia. 2025. Moonlight-driven zooplankton migration shapes phytoplankton distribution in a tropical peatland pond. Biodiversitas 26: 4746-4760.* The interaction between phytoplankton and zooplankton plays a vital role in regulating aquatic ecosystem dynamics. This study explored the vertical distribution of phytoplankton in relation to zooplankton abundance under varying lunar light conditions and assessed the influence of selected physicochemical parameters. The research was conducted in Beje Pond, Peat Techno Park (PTP), Universitas Palangka Raya, Central Kalimantan, Indonesia, with sampling performed at seven depth intervals (0-180 cm) every three days over a one-month period. A total of 20 phytoplankton species were identified, with seven dominant taxa consistently observed: *Chlamydomonas nivalis*, *Chlorogonium elongatum*, *Asterococcus superbus*, *Staurastrum tetracerum*, *Zygnema* sp., *Closterium praelongum*, and *Skeletonema costatum*. Phytoplankton abundance ranged from 810 to 2,232 cells/L, peaking during half-moon conditions. Zooplankton abundance reached a maximum of 765 ind/L during the ninth sampling under dim moonlight, with apparent temporal offset from phytoplankton peaks. This pattern suggests the possibility of zooplankton diel vertical migration modulated by lunar illumination. Principal Component Analysis (PCA) showed that Dissolved Oxygen (DO), temperature, and pH together accounted for 84.6% of the environmental variance. Spearman correlation analysis indicated significant positive correlations ($p < 0.05$) between DO and phytoplankton abundance ($r = 0.59$), and between phytoplankton and zooplankton ($r = 0.53$). No significant correlations were observed between pH and phytoplankton or between DO and zooplankton. While patterns suggest possible vertical variation linked to diel cycles and lunar phase, these findings remain correlative. Further integrative studies are recommended to investigate the ecological mechanisms driving these distributions in tropical peatland waters.

Keywords: Dynamic distribution, moonlight, phytoplankton, zooplankton

INTRODUCTION

Phytoplankton and zooplankton are fundamental components in maintaining the balance of aquatic ecosystems, particularly within food web structures where they play pivotal roles in energy transfer and nutrient cycling. Phytoplankton contributes nearly 50% of the Earth's annual oxygen production and are essential in the absorption of atmospheric carbon dioxide through photosynthesis (Jahan 2023; García-Oliva and Wirtz 2025). As primary producers, phytoplankton serve as the main energy source for zooplankton, which function as primary consumers in aquatic trophic network (Borics et al. 2021; Gao et al. 2024). Zooplankton regulate phytoplankton populations through grazing and facilitate the transfer of energy and nutrients to higher trophic levels. Their behavior significantly shapes phytoplankton dynamics, including vertical positioning in the water column (Hassan et al. 2017).

Among the most well-documented behaviors in zooplankton is Diel Vertical Migration (DVM), defined as the synchronized daily movement of organisms up to surface waters during the night to feed, and downward during the day to avoid visually hunting predators (Guerra et al. 2019; Retnaningdyah et al. 2024). The extent and depth of this migration are influenced by external cues, particularly lunar illumination, which enhances underwater visibility during full moon phases and thereby elevates predation risk (Last et al. 2016; Hobbs et al. 2021; Hernández-León et al. 2025). As a result, zooplankton may alter their vertical positioning during bright nights, affecting their grazing activity and interaction with phytoplankton communities.

While DVM is an active behavioral response, the vertical distribution of phytoplankton is governed by a combination of abiotic factors including light availability, temperature, oxygen levels, nutrient gradients as well as biotic interactions such as zooplankton grazing. Unlike zooplankton, phytoplankton are generally not capable of active vertical migration, and instead undergo passive redistribution due to turbulence, sinking, buoyancy regulation, and biotic pressure. Therefore, it is crucial to distinguish between active zooplankton DVM and passive

or abiotic-driven phytoplankton vertical stratification when analyzing depth-related community patterns. Previous research on lunar-influenced zooplankton migration has primarily focused on marine and polar systems (e.g., Arctic waters, the Mediterranean Sea) where photoperiod and predation pressure strongly govern DVM patterns (Darnis et al. 2017; Archibald et al. 2019; Guerra et al. 2019). However, little is known about how these mechanisms operate in tropical freshwater lentic systems, such as ponds and wetlands, particularly those in peatland environments with low light penetration and shallow water columns.

Tropical peatland waters in Central Kalimantan, Indonesia, are ecologically distinct due to their dark humic content, high acidity, and diel fluctuations in temperature and dissolved oxygen (Kunarso et al. 2022). These characteristics make them ideal for investigating the coupling between light-driven zooplankton behavior and phytoplankton distribution patterns. Yet, studies assessing how lunar illumination modulates these interactions in such environments remain scarce. This study aims to explore how lunar cycles influence zooplankton DVM and how this behavior subsequently affects the vertical distribution of phytoplankton in a tropical peatland pond. The research is guided by three ecological hypotheses: (i) Zooplankton abundance and vertical migration are modulated by lunar light intensity, with diminished surface presence expected during brighter moon phases due to increased predation risk; (ii) Phytoplankton vertical distribution is influenced by temporal grazing pressure from zooplankton, which fluctuates in accordance with DVM patterns; (iii) Abiotic factors such as Dissolved Oxygen (DO), temperature, and pH interact with biotic mechanisms to shape phytoplankton abundance and its depth-related distribution.

Field observations were conducted at Beje Pond, a man-made water body located in the Peat Techno Park (PTP), Universitas Palangka Raya, Central Kalimantan. This tropical peatland pond characterized by acidic, low-transparency waters and diel physicochemical gradients offers a natural setting for examining predator-prey interactions modulated by lunar cycles. The findings are expected to refine trophic interaction models and support ecosystem monitoring efforts in tropical peatland freshwater systems.

MATERIALS AND METHODS

Study area and study site

This research was conducted at Beje Pond, located within the Peat Techno Park (PTP) area of Universitas Palangka Raya, Central Kalimantan, Indonesia (Figure 1). The pond is a shallow, man-made water body typical of lowland tropical peatlands, characterized by organic-rich substrates and surrounded by peat swamp vegetation. The pond has a maximum depth of approximately 180 cm, allowing for the study of fine-scale vertical gradients within the water column. To support the interpretation of phytoplankton vertical distribution, water quality parameters including water temperature, pH, and DO were measured at each depth during every sampling event using a portable multiparameter water quality probe (APHA 2017). These parameters are essential to explain the ecological conditions that influence phytoplankton assemblages in peatland aquatic systems. Sample processing and analysis were conducted at the Aquatic Resources Management Laboratory, Department of Fisheries, Universitas Palangka Raya.

Procedures

Sampling methods

Phytoplankton sampling was performed at a single fixed station in Beje Pond at seven depth intervals: 0, 30, 60, 90, 120, 150, and 180 cm. Sampling was conducted exclusively at night, every three days, over a continuous one-month period (10 total sampling events). This design enabled high-resolution profiling of vertical phytoplankton distribution in relation to lunar illumination under stable nighttime conditions (Smith et al. 2024).

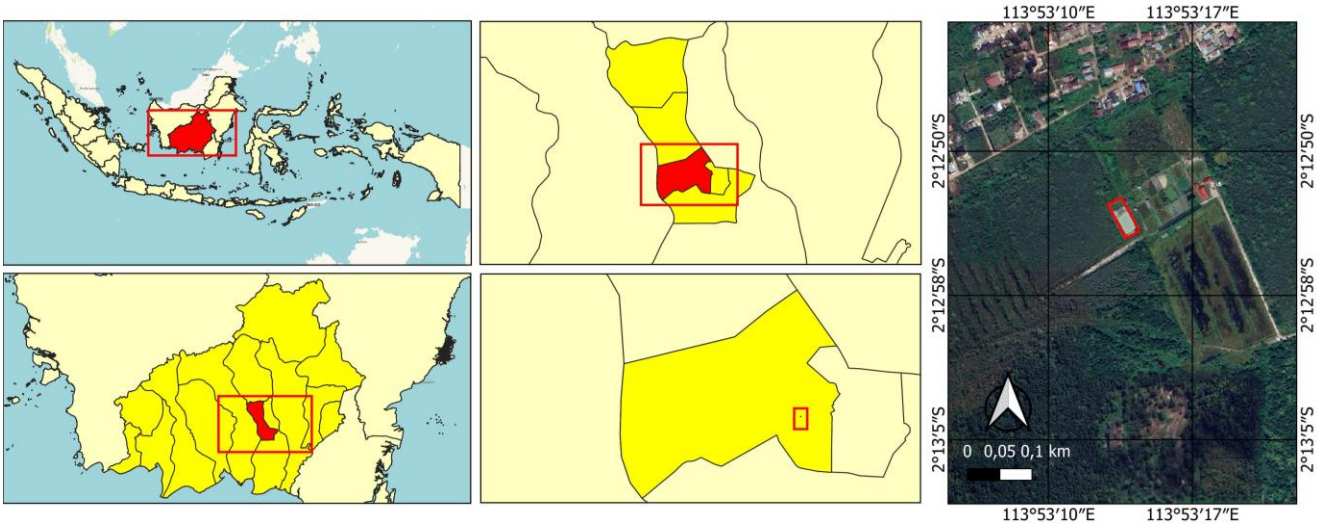

Figure 1. Map of the sampling locations in Beje Pond, Peat Techno Park (PTP), Universitas Palangka Raya, Central Kalimantan, Indonesia

At each depth, water was collected using a PVC pipe inserted to the designated depth. The water was pumped to the surface, and a 10-liter sample was filtered through a plankton net and preserved in 5% formalin for laboratory identification (Kostryukova et al. 2018). While DVM is best assessed through both day and night sampling, this study focused specifically on nighttime profiles to isolate the influence of moonlight variation across the lunar cycle. The limitation of not sampling during the daytime is acknowledged, and future studies are planned to incorporate full diel cycles and more frequent temporal sampling to assess short-term migratory patterns. In addition, environmental parameters including water temperature, pH, and DO were measured at each depth during every sampling event to support interpretation of phytoplankton vertical distribution.

Phytoplankton identification

The identification of phytoplankton was carried out through several stages. Microscope slides and cover glasses were first rinsed with distilled water and dried using tissue paper by wiping in a single direction to avoid surface damage. The phytoplankton samples were homogenized in film bottles, after which 1 mL was taken using a dropper pipette and placed onto a slide, then covered with a cover glass. Observations were performed systematically, starting from the upper left of the slide to the right, then moving downward to the edge of the slide, and continuing in a zig-zag pattern until the entire field of observation was examined. The number of phytoplankton individuals was counted in each field of view, and photographic documentation was conducted to support identification. Taxonomic identification of phytoplankton was performed using standard references, particularly Freshwater Algae (Bellinger and Sigee 2015; Wehr et al. 2015).

Phytoplankton abundance

The abundance of phytoplankton (N, cells/L) was estimated following (Fachrul 2008), where N is the phytoplankton abundance (cells/L), n is the number of individuals observed, Vr is the volume of water filtered (mL), V_o is the sample volume (L), and Vs is the volume of one pipette drop (mL):

$$N = (n \times Vr) / (V_o \times Vs)$$

Zooplankton abundance

The abundance of zooplankton (N, cells/L) was calculated using the Hardy formula (Hardy 1939), where N is the zooplankton abundance (cells/L), n is the number of individuals counted, S is the volume of filtered water (mL), a is the volume of water observed (mL), and V is the total water volume (L):

$$N = (n \times S) / (a \times V)$$

Diversity index

The diversity of biota species at the research site was computed using Simpson's Diversity Index formula (Krebs 1989). In this case, s is the number of species, n_i is the number of individual species observed, and N is the total number of individuals from all species:

$$1 - Ds = 1 - \Sigma [n_i(n_i - 1)] / [N(N - 1)]$$

Dominance index (D)

Following Odum (1998), the dominance index (D) was calculated using Simpson's formula (Krebs 1989). where D is the Simpson dominance index, n_i is the number of individuals of species i, and N is the total number of individuals across all species:

$$D = \Sigma [n_i(n_i - 1)] / [N(N - 1)]$$

Lunar phase and ambient light condition

To evaluate the potential influence of ambient light on diel vertical plankton distribution, sampling events were strategically aligned with distinct lunar phases. Events 1 through 6 occurred during moderate to high moonlight conditions, with estimated surface illuminance ranging from ~0.05 to 0.25 lux. In contrast, events 7 through 9 took place during waning crescent to new moon phases, with estimated illuminance falling below 0.03 lux. These variations were considered during data interpretation to assess light-related behavioral patterns in plankton communities. The absence of direct lux measurements constitutes a limitation of this study. Future investigations may benefit from deploying underwater light sensors to capture real-time nocturnal light gradients within the water column.

Although in situ measurements of light intensity (lux) were not performed during fieldwork, estimated surface illuminance values under cloudless conditions were approximated from published references on typical lux levels corresponding to lunar phases. Table 1 summarizes the lunar phases, qualitative moonlight brightness, and estimated illuminance values during each sampling event.

Data analysis

The vertical distribution and interrelationship between phytoplankton and zooplankton during nighttime sampling were analyzed using contour diagrams (depth-time isopleths) generated from abundance data collected at multiple depths and time intervals. Data analysis was conducted using R software version 4.2.0 (R Core Team 2021) with the Akima package version 0.6-3.4 (Akima and Gebhardt 2022) for interpolation. To explore relationships between environmental variables (temperature, DO, pH, and depth) and biological variables (phytoplankton and zooplankton abundance), Principal Component Analysis (PCA) was performed using the vegan package (version 2.6-4). The first two Principal Components (PC1 and PC2) were retained based on eigenvalues greater than 1 and their contribution to explaining overall variance. PCA biplots were used to visualize clustering patterns of environmental gradients and their associations with phytoplankton and zooplankton abundance across depth profiles.

Table 1. Summary of lunar phases and estimated light intensity during each sampling

Sampling no.	Moon image	Approximate lunar phase	Moonlight condition	Estimated illuminance (lux)
1		First Quarter (~50%)	Moderately bright	~0.05-0.10
2		Waxing Gibbous (~85%)	Bright	~0.10-0.20
3		Full Moon (100%)	Very bright	~0.25
4		Full Moon (100%)	Very bright	~0.25
5		Waning Gibbous (~85%)	Bright	~0.10-0.20
6		Last Quarter (~50%)	Moderately bright	~0.05-0.10
7		Waning Crescent (~20%)	Dim	~0.01-0.03
8		New Moon (0%)	Very dim/dark	< 0.01
9		Waxing Crescent (~10%)	Dim	~0.01

RESULTS AND DISCUSSION

Water quality parameters

Based on Table 2, the water quality parameters measured at the Beje Pond study site include temperature, pH, and DO. These parameters were measured at each sampling depth during every sampling event following standard procedures (APHA 2017). The measurement results show that the average water temperature is 28.86°C with a standard deviation of 0.77, indicating a relatively stable temperature at the site. The pH parameter has an average of 5.07 with a standard deviation of 0.41, suggesting that the water at Beje Pond tends to be acidic. Meanwhile, the average DO concentration is 2.59 mg/L with a standard deviation of 0.66, indicating a relatively low dissolved oxygen concentration.

Phytoplankton species

A total of 20 phytoplankton species from three classes were identified in Beje Pond, as listed in Table 3 and Figure 2. The class Zygnematophyceae accounted for the highest number of species (15 species), followed by Chlorophyceae (4 species) and Bacillariophyceae (1 species). Based on Table 1, several phytoplankton species were observed only during certain sampling periods. In contrast, *Chlamydomonas nivalis*, *Chlorogonium elongatum*, *Asterococcus superbus*, *Staurastrum tetracerum*, *Zygnema* sp., *Closterium praelongum*, and *Skeletonema costatum* were recorded consistently throughout all sampling periods. The continuous presence of these species suggests high adaptability to environmental variability and possible resistance to zooplankton predation.

Previous studies have shown that water quality parameters such as nutrient availability, temperature, and water flow significantly influence the abundance and composition of phytoplankton communities in aquatic ecosystems (Gao et al. 2024). Wu et al. (2019) also emphasized that underwater light intensity is a key factor affecting phytoplankton growth. Moreover, climate change has been shown to impact both phytoplankton biomass and species composition. For instance, in the northeastern East China Sea, seasonal variations in nitrogen and phosphorus concentrations shifted community dominance, with cryptophytes replacing diatoms during the winter of 2020 (Sun et al. 2022). Similarly, in the Western Antarctic Peninsula, increasing temperatures have led to enhanced phytoplankton biomass and prolonged bloom durations (Ferreira et al. 2024). Climate is therefore considered one of the primary drivers shaping global phytoplankton dynamics. In addition to abiotic factors, biotic interactions such as grazing by zooplankton also significantly affect phytoplankton abundance (Gao et al. 2024).

The consistent presence of certain phytoplankton species, such as *C. nivalis*, *C. elongatum*, *A. superbus*, and *S. costatum*, across all sampling periods suggests ecological resilience and adaptive flexibility. These species appear to sustain their populations despite fluctuations in environmental conditions, including variations in moonlight intensity that may influence both underwater illumination and predator behavior. Their resilience may result from physiological tolerance to changing light regimes or from rapid growth rates that compensate for grazing losses (Sun et al. 2022).

Furthermore, variation in species composition across sampling periods reflects dynamic responses to both abiotic stressors (e.g., temperature, dissolved oxygen, light availability) and biotic pressures (e.g., zooplankton grazing). The consistent recurrence of certain species, despite these pressures, suggests the presence of adaptive traits such as flexible pigment composition or behavioral adjustments (e.g., timing of vertical migration) to maximize photosynthetic efficiency while avoiding predation (Gao et al. 2024; Ferreira et al. 2024).

Table 2. The water quality parameters of study sites in Beje Pond, Peat Techno Park (PTP), Universitas Palangka Raya, Central Kalimantan, Indonesia

Parameters	Mean ± SD
Temperature (°C)	28.86 ± 0.77
pH	5.07 ± 0.41
DO (mg/L)	2.59 ± 0.66

Table 3. Phytoplankton species found in the Beje Pond, Peat Techno Park (PTP), Universitas Palangka Raya, Central Kalimantan, Indonesia

Class	Family	Genus	Species	Sampling Period								
				1	2	3	4	5	6	7	8	9
Chlorophyceae	Chlamydomonadaceae	*Chlamydomonas*	*Chlamydomonas nivalis* (F.A.Bauer) Wille	✓	✓	✓	✓	✓	✓	✓	✓	✓
Chlorophyceae	Haematococcaceae	*Chlorogonium*	*Chlorogonium elongatum* P.A.Dang.	✓	✓	✓	✓	✓	✓	✓	✓	✓
Chlorophyceae	Radiococcaceae	*Asterococcus*	*Asterococcus superbus* (Cienk.) Scherff.	✓	✓	✓	✓	✓	✓	✓	✓	✓
Chlorophyceae	Scenedesmaceae	*Ankistrodesmus*	*Ankistrodesmus fusiformis* Corda	✓	✓	✓	✓	✓	-	✓	-	✓
Zygnematophyceae	Desmidiaceae	*Cosmarium*	*Cosmarium botrytis* Menegh. ex Ralfs, 1848	-	✓	✓	✓	-	-	✓	-	✓
Zygnematophyceae	Desmidiaceae	*Cosmarium*	*Cosmarium contractum* Kirchn.	✓	✓	-	-	✓	-	-	✓	✓
Zygnematophyceae	Desmidiaceae	*Staurastrum*	*Staurastrum tetracerum* Ralfs	✓	✓	✓	✓	✓	✓	✓	✓	✓
Zygnematophyceae	Desmidiaceae	*Staurastrum*	*Staurastrum paradoxum* Meyen ex Ralfs	✓	✓	✓	✓	✓	✓	-	✓	-
Zygnematophyceae	Desmidiaceae	*Staurastrum*	*Staurastrum cuspidatum* Bréb. ex Ralfs	✓	-	-	✓	✓	✓	✓	✓	✓
Zygnematophyceae	Desmidiaceae	*Staurastrum*	*Staurastrum arctiscon* (Ehrenb.) P.Lundell	-	-	✓	-	✓	-	✓	-	✓
Zygnematophyceae	Desmidiaceae	*Micrasterias*	*Micrasterias rotate* (Grev.) Ralfs	-	-	-	-	-	✓	✓	-	✓
Zygnematophyceae	Desmidiaceae	*Micrasterias*	*Micrasterias mahabuleshwarensis* J.Hobson	-	✓	✓	-	✓	-	-	✓	✓
Zygnematophyceae	Desmidiaceae	*Euastrum*	*Euastrum ansatum* Ralfs	-	✓	-	-	-	-	✓	✓	✓
Zygnematophyceae	Desmidiaceae	*Euastrum*	*Euastrum insigne* Hassall ex Ralfs	-	✓	-	-	✓	-	✓	✓	✓
Zygnematophyceae	Gonatozygaceae	*Teilingia*	*Teilingia granulata* (J.Roy & Bisset) Bourr.	✓	-	-	✓	-	-	-	✓	✓
Zygnematophyceae	Zygnemataceae	*Haplotaenium*	*Haplotaenium indentatum* Kouwets, 1991	✓	✓	-	✓	-	✓	-	✓	✓
Zygnematophyceae	Zygnemataceae	*Zygnema*	*Zygnema* sp.	✓	✓	✓	✓	✓	✓	✓	✓	✓
Zygnematophyceae	Desmidiaceae	*Penium*	*Penium spirostriolatum* J.Barker	✓	✓	-	✓	-	✓	✓	✓	✓
Zygnematophyceae	Closteriaceae	*Closterium*	*Closterium praelongum* Bréb.	✓	✓	✓	✓	✓	✓	✓	✓	✓
Bacillariophyceae	Skeletonemataceae	*Skeletonema*	*Skeletonema costatum* (Greville) Cleve, 1873	✓	✓	✓	✓	✓	✓	✓	✓	✓

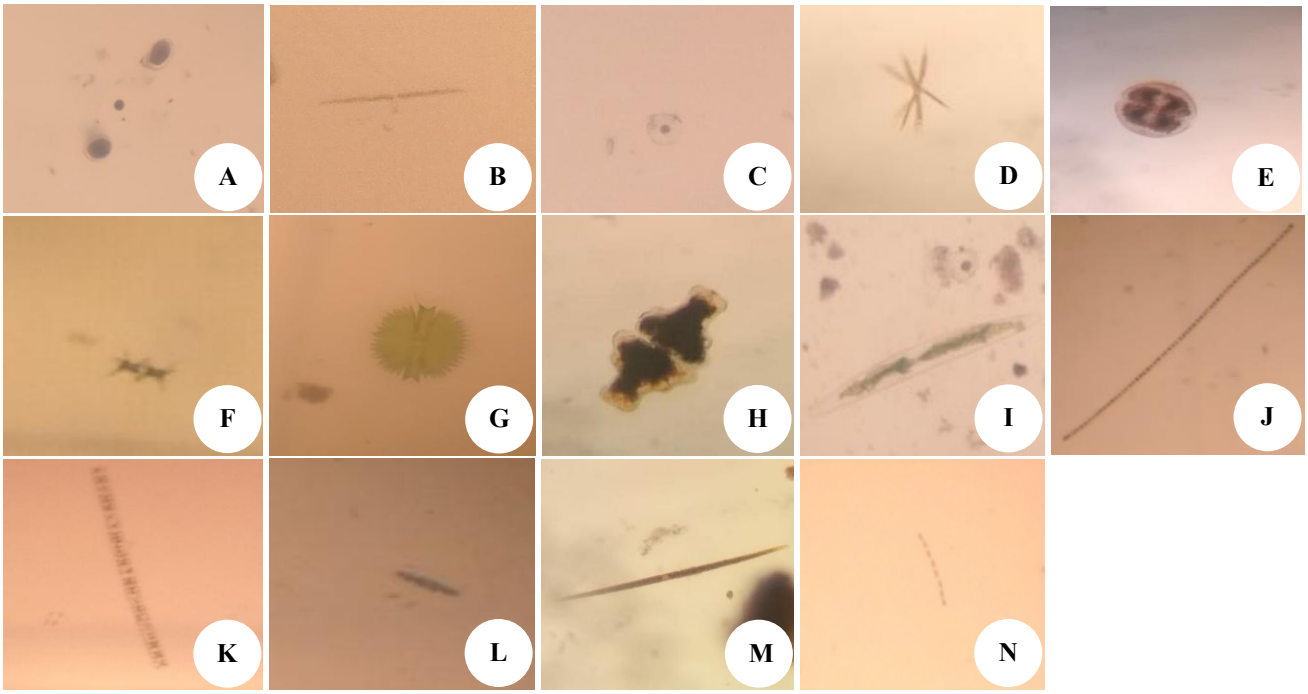

Figure 2. Phytoplankton species found in the Beje Pond, Peat Techno Park (PTP), Universitas Palangka Raya, Central Kalimantan, Indonesia. A. *Chlamydomonas* sp.; B. *Chlorogonium* sp.; C. *Asterococcus* sp.; D. *Ankistrodesmus* sp.; E. *Cosmarium* sp.; F. *Staurastrum* sp.; G. *Micrasterias* sp.; H. *Euastrum* sp.; I. *Haplotaenium* sp.; J. *Teilingia* sp.; K. *Zygnema* sp.; L. *Penium* sp.; M. *Closterium* sp.; N. *Skeletonema* sp.

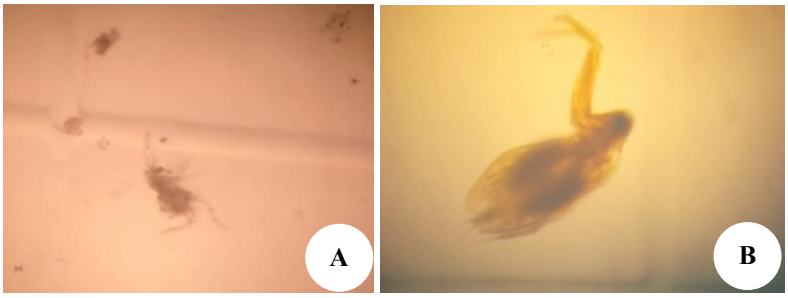

Figure 3. Zooplankton species found in the Beje Pond, Peat Techno Park (PTP), Universitas Palangka Raya, Central Kalimantan, Indonesia. A. *Moina micrura*; B. *Diaphanosoma* sp.

These patterns indicate that phytoplankton in Beje Pond exhibit both species-specific environmental tolerances and adaptive behavioral strategies that promote ecological stability under fluctuating lunar conditions. In essence, the lunar cycle indirectly influences community structure by modifying light availability and predator activity, to which phytoplankton respond either through resilience or by altering their dominance strategies (Petrusevich et al. 2020; Ursella et al. 2021).

Species-level identification was limited by the resolution of light microscopy and the lack of molecular data. Although many taxa were confidently assigned to species level, others (e.g., *Zygnema* sp.) were identified only to the genus level due to morphological ambiguity or absence of reproductive structures. These limitations are common in phytoplankton studies conducted in remote tropical regions without access to advanced imaging or genetic tools. Nonetheless, genus-level identifications still provide valuable ecological insight when interpreted in the context of known trait-based behaviors.

Phytoplankton and zooplankton abundance

The zooplankton species identified in Beje Pond were *Diaphanosoma* sp. and *M. micrura,* as listed in Table 4 and Figure 3. As shown in Figure 4, phytoplankton abundance ranged from 810 to 2232 ind/L, while zooplankton abundance ranged from 327 to 765 ind/L. The highest phytoplankton abundance (2232 ind/L) was recorded during the first sampling period and coincided with the half-moon phase, whereas the lowest was observed during the fifth sampling. In contrast, the highest zooplankton abundance (765 ind/L) was found during the ninth sampling, when the moon was in the waning phase, while the lowest abundance occurred during the seventh sampling.

Table 4. Zooplankton species found in the Beje Pond, Peat Techno Park (PTP), Universitas Palangka Raya, Central Kalimantan, Indonesia

Class	Family	Genus	Species	Sampling Period								
				1	2	3	4	5	6	7	8	9
Cladocera	Moinidae	*Moina*	*Moina micrura* Kurz, 1875	✓	-	-	✓	✓	-	-	✓	✓
Cladocera	Sididae	*Diaphanosoma*	*Diaphanosoma* sp.	✓	✓	✓	✓	✓	✓	✓	✓	✓

Changes in plankton abundance in Beje Pond are likely influenced by moonlight intensity, which affects predator fish behavior and triggers behavioral responses in zooplankton. Hernández-León et al. (2025) reported that increased moonlight enhances underwater visibility, improving the hunting efficiency of visually oriented predatory fish. Consequently, fish become more active in surface foraging under bright moonlight, causing zooplankton to migrate to deeper water layers to avoid predation. Similarly, Hobbs et al. (2021) demonstrated that zooplankton perform diel vertical migration in response to increased visual predation risk during intense moonlight, resulting in decreased zooplankton abundance near the surface. Conversely, under low moonlight intensity, predation pressure decreases, enabling zooplankton to ascend to surface waters where their abundance increases (Ursella et al. 2021). Low moonlight also reduces predator activity, allowing zooplankton to exploit phytoplankton-rich surface layers with minimal risk.

Figures 5-10 present the distribution patterns of three dominant species in relation to depth and moonlight. Figures 5, 7, and 9 illustrate depth-time isopleth graphs, while Figures 6, 8, and 10 show species' vertical distribution. Figure 5 displays the depth-time isopleths for *C. elongatum* (phytoplankton), *Diaphanosoma* sp. (zooplankton), and *M. micrura* (zooplankton). *Chlorogonium elongatum* was consistently distributed at depths of 0-60 cm from the first to ninth sampling period. The highest abundance of this species (at 0 cm depth) was recorded during the seventh, eighth, and ninth sampling, when the moon was in its waning phase. Despite low moonlight, *C. elongatum* remained dominant near the surface. This suggests that *C. elongatum* and *A. superbus* may prefer moonlight intensities that support photosynthesis, which likely enhances survival and foraging efficiency.

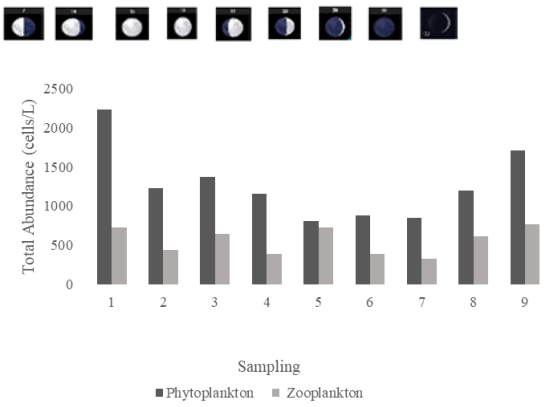

Figure 4. Phytoplankton and zooplankton abundance in Beje Pond, Peat Techno Park (PTP), Universitas Palangka Raya, Central Kalimantan, Indonesia

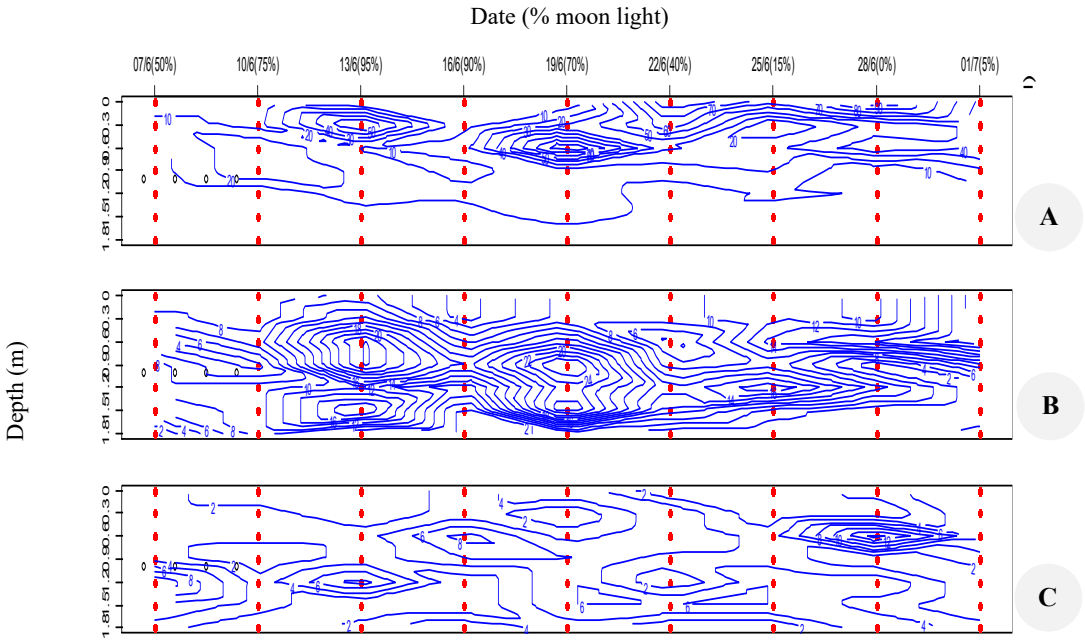

Figure 5. Depth-time isopleth of: A. *C. elongatum,* B. *Diaphanosoma* sp., and C. *M. micrura*

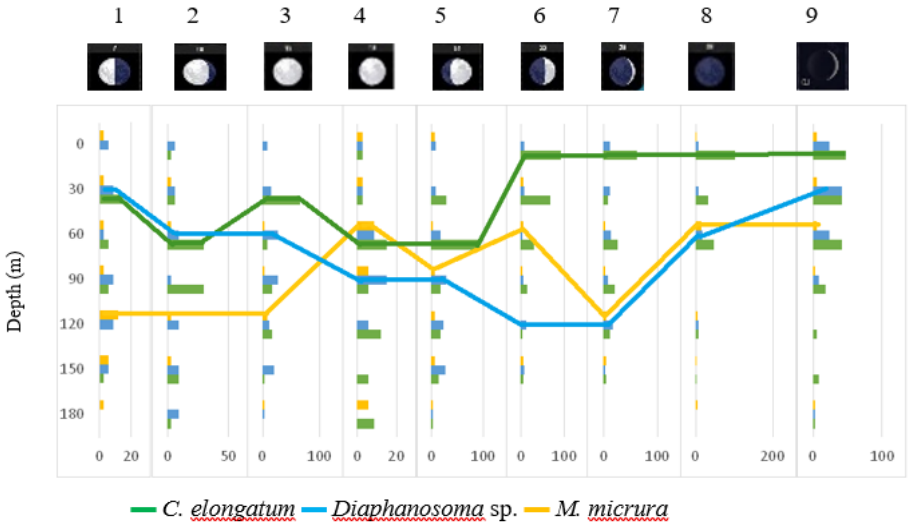

Figure 6. Vertical distributions of *C. elongatum*, *Diaphanosoma* sp., and *M. micrura*

In contrast, *Diaphanosoma* sp. and *M. micrura* exhibited vertical migration in response to changing moonlight. During bright moon phases (sampling 1-3), both species occupied deeper layers (approximately 1.2-1.5 m), likely as a strategy to avoid visually hunting predators. However, during dim moon phases (sampling 8 and 9), they moved upward toward the surface, utilizing reduced predation risk to feed on surface phytoplankton, such as *C. elongatum*.

Figure 6 illustrates the vertical distribution of *C. elongatum*, *Diaphanosoma* sp., and *M. micrura* across sampling periods and depths. The highest abundance of *C. elongatum* was observed during the eighth sampling event (102 cells/L), while the lowest was recorded in the fourth sampling (15 cells/L). *Diaphanosoma* sp., peaked in the fifth sampling (30 cells/L) and showed the lowest abundance during the first and second samplings (9 cells/L). *Moina micrura* reached its maximum abundance in the eighth sampling (15 cells/L) and its minimum in the second sampling (3 cells/L). These distribution patterns are likely influenced by predation pressure from fish, which exhibit increased surface activity during bright moon phases, prompting zooplankton to avoid upper water layers (Murphy et al. 2023). The observed DVM patterns appear to be driven by a combination of moonlight intensity, food availability, and predation risk (Petrusevich et al. 2020). Unlike zooplankton, which have longer generation times, phytoplankton populations can respond more rapidly to favorable environmental conditions through accelerated cell division.

A similar phenomenon was observed in Figure 7, which illustrates the vertical distribution of *A. superbus*, *Diaphanosoma* sp., and *M. micrura*. In this case, *A. superbus* was generally found at intermediate depths, while *Diaphanosoma* sp. and *M. micrura* showed a more even distribution across various depths. During the first sampling, conducted under a half-moon phase, *A. superbus* exhibited its highest abundance at a depth of 150 cm. However, in subsequent observations, its peak distribution shifted to shallower depths, including 120, 30, and 90 cm, indicating a change in its vertical migration pattern over time. Notably, during the sixth and seventh sampling periods, *A. superbus* was observed near the surface (0 cm depth), suggesting a clear upward migration pattern influenced by moonlight phases.

The vertical distribution patterns of *A. superbus*, along with the zooplankton species *Diaphanosoma* sp. and *M. micrura*, at different depths are shown in Figure 8. The highest abundance of *A. superbus* (300 cells/L) was recorded at 150 cm depth during third sampling, which coincided with bright moonlight. In contrast, its lowest abundance (3 cells/L) was found in eight sampling at the same depth, during a dim moonlight phase. A similar trend was observed in *C. elongatum*, which showed low abundance in Sampling 1 likely due to intensive zooplankton grazing during low moonlight conditions. This suggests that zooplankton activity, particularly under reduced illumination, may contribute to the decreased abundance of phytoplankton such as *A. superbus* through grazing pressure.

Figures 9 and 10 illustrate the vertical distribution over time (depth-time isopleths) and abundance of three species: *S. costatum* (phytoplankton), *Diaphanosoma* sp., (zooplankton) and *M. micrura* (zooplankton). *Skeletonema costatum* was more frequently observed at deeper depths, particularly between 90 and 120 cm, especially during the full moon phase (100% moonlight). Its increased abundance and broader distribution at deeper layers during the full moon suggest that high moonlight intensity may influence its vertical migration. This species was most abundant in first to third sampling events, which coincided with bright moon phases, and was consistently present within the water column. However, its abundance declined during the fourth to sixth sampling events and increased again in the seventh and eighth samplings, which coincided with dim moonlight conditions. The highest abundance of *S. costatum* during these phases was recorded at the surface (0 cm depth).

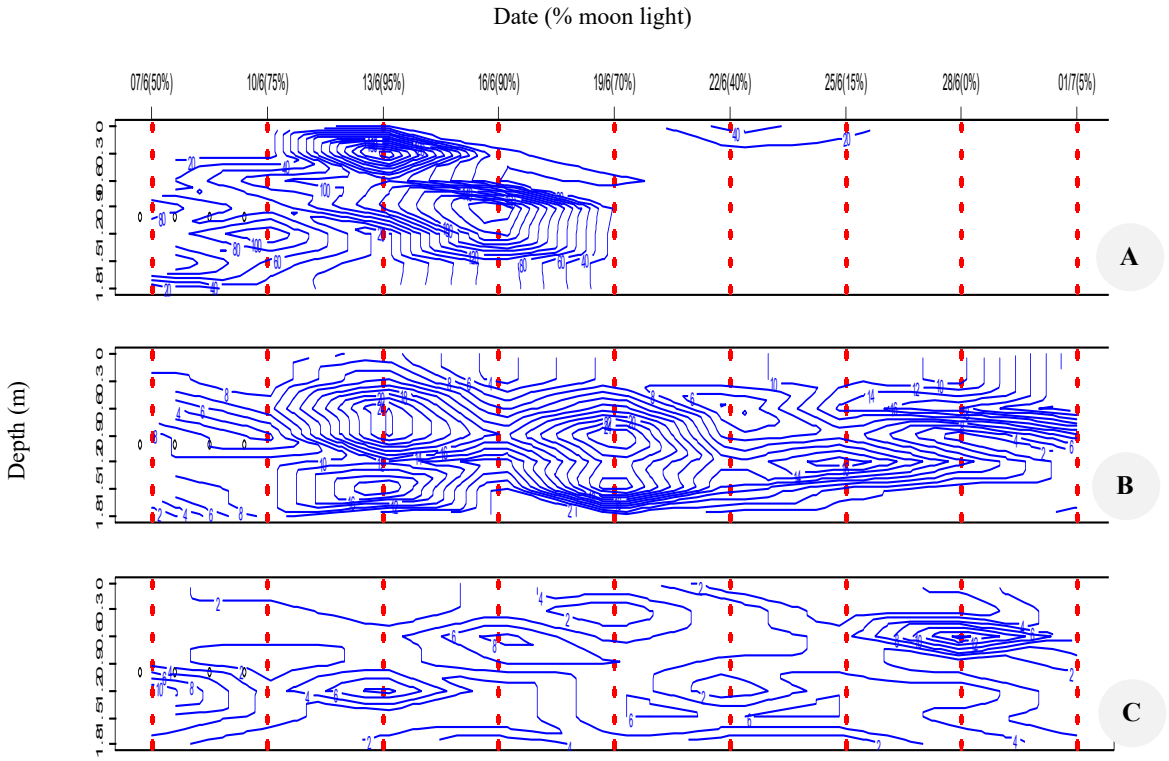

Figure 7. Depth-time isopleth of: A. *A. superbus*, B. *Diaphanosoma* sp., and C. *M. micrura*

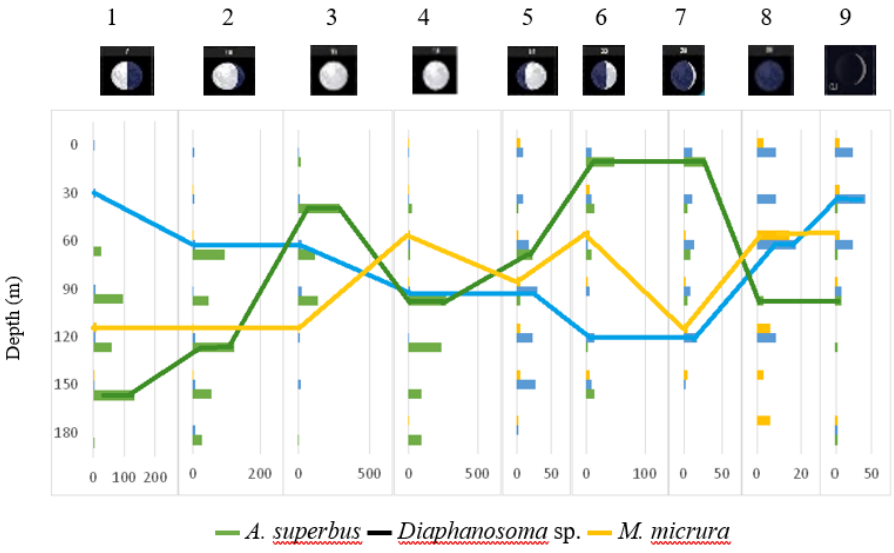

Figure 8. Vertical distribution of *A. superbus, Diaphanosoma* sp., and *M. micrura*

In contrast, *Diaphanosoma* sp. and *M. micrura* were more dominant in in the upper layers of the water column. *Diaphanosoma* sp. was commonly found at depths of 60-90 cm, particularly during the half-moon phase (50% moonlight), whereas *M. micrura* was more frequently observed at 30-60 cm. The highest abundance of *M. micrura* (33 cells/L) was recorded during the first and eighth sampling events, both conducted under new moon conditions (0% moonlight), whereas the lowest abundance (12 cells/L) occurred during the second sampling. Furthermore, *Diaphanosoma* sp. showed a clear tendency to migrate to deeper layers during bright or full moon phases (Figure 10). These results suggest that the vertical distribution of both species is influenced by lunar phase and moonlight intensity, with each species demonstrating distinct depth preferences under varying nocturnal light conditions. These patterns are consistent with previous findings indicating that moonlight regulates species-specific DVM in zooplankton (Last et al. 2016; Guerra et al. 2019).

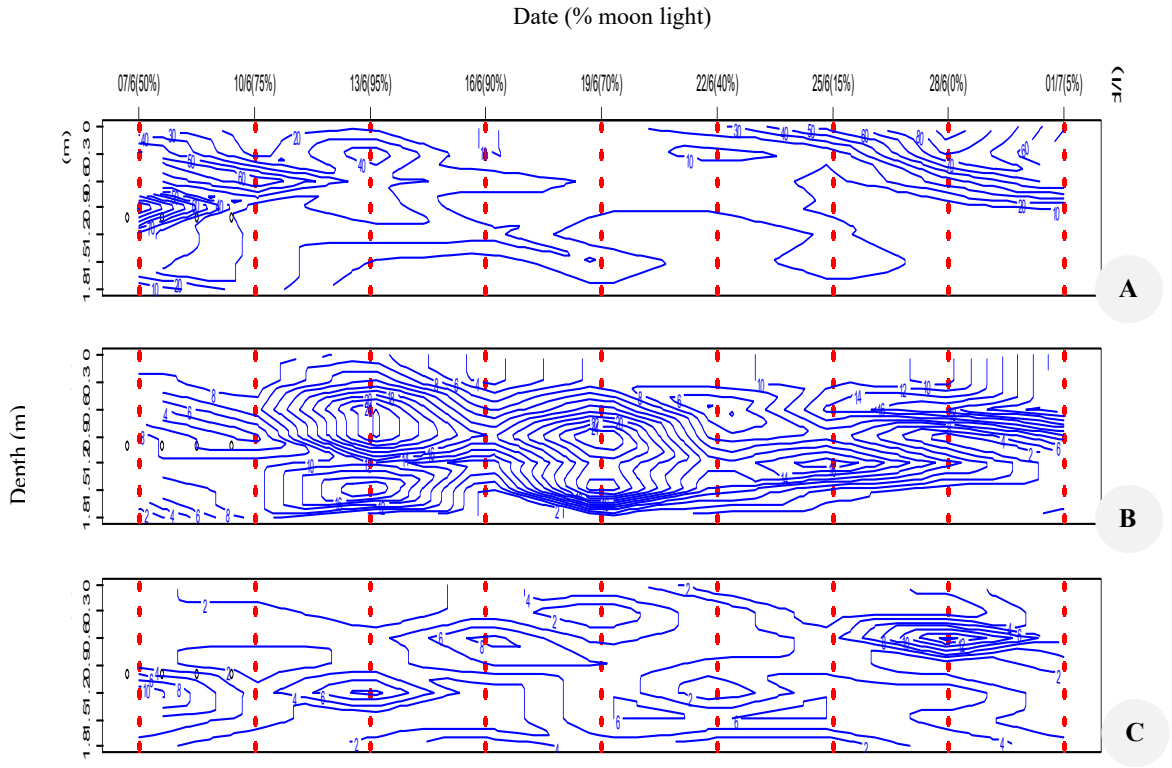

Figure 9. Depth-time isopleth of: A. *S. costatum*, B. *Diaphanosoma* sp., and C. *M. micrura*

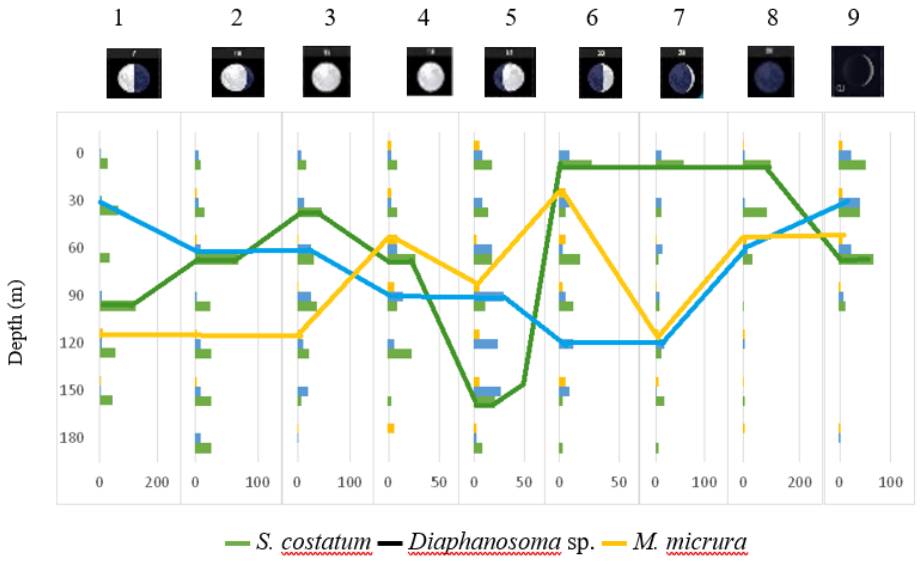

Figure 10. Vertical distribution of *S. costatum, Diaphanosoma* sp., and *M. micrura*

The observed shifts in vertical distribution and abundance of both phytoplankton and zooplankton across lunar phases suggest that the plankton community in Beje Pond exhibits a combination of adaptive behavioral strategies and ecological resilience. Zooplankton species such as *Diaphanosoma* sp. and *M. micrura* clearly demonstrate DVM, descending during bright moon phases to evade predation by visually oriented fish. This behavior reflects plasticity essential for survival under fluctuating predation pressures (Ursella et al. 2021; Petrusevich et al. 2020).

Phytoplankton such as *C. elongatum, A. superbus,* and *S. costatum* show resilience across depths and lunar phases, suggesting strong physiological or behavioral adaptability. For instance, *A. superbus* shifted upward during low light periods, while *S. costatum* displayed deeper migration under full moons, possibly to reduce surface grazing or optimize photosynthesis. Such vertical adjustments support the notion of ecological flexibility (Hernández-León et al. 2025). Moonlight intensity, therefore, emerges as a secondary ecological driver, indirectly influencing plankton

distribution by modulating light availability and predator activity. This highlights the simultaneous operation of top-down (predation) and bottom-up (light, nutrient) controls in shaping aquatic communities (Gao et al. 2024; Ferreira et al. 2024).

The vertical distribution patterns observed in certain phytoplankton species may be influenced by their ecological traits. For example, *C. elongatum* and *C. nivalis* are flagellated, motile green algae capable of vertical repositioning to optimize light acquisition and avoid grazers. *Asterococcus superbus* tends to form colonies, which may offer partial protection against predation and enhance buoyancy. Meanwhile, *S. costatum*, a diatom, is non-motile but forms chains that increase drag and reduce sinking speed, potentially explaining its deeper presence during bright moon phases. These traits, including flagella-based motility, colony formation, and morphological adaptations for buoyancy regulation, contribute to species-specific vertical patterns in response to environmental gradients.

Ultimately, the persistence of certain species and predictable migration patterns indicate ecological stability and finely tuned adaptive mechanisms. However, long-term disruptions such as artificial light pollution or climate anomalies could destabilize this balance, altering community structure and trophic interactions. These findings emphasize that plankton are not passive organisms but active agents navigating environmental pressures through evolved survival strategies.

Nutrient concentrations such as nitrogen and phosphorus are known to strongly influence phytoplankton biomass, productivity, and vertical distribution. However, in the present study, no direct measurements of dissolved inorganic nutrients (e.g., nitrate, phosphate, ammonium) were conducted due to logistical constraints and limited access to field-based chemical analysis equipment.

This constitutes a limitation in fully disentangling the drivers of phytoplankton vertical structuring, as nutrient gradients, along with light and grazing pressure, can significantly influence phytoplankton dynamics. Therefore, the observed vertical patterns in phytoplankton abundance should be interpreted with caution and understood primarily in relation to physical and light-related factors. Future studies that incorporate concurrent nutrient profiling would provide a more comprehensive understanding of the ecological mechanisms underlying plankton stratification in this system.

Beyond nutrient gradients, other abiotic factors may also contribute to variability in plankton vertical distribution. Factors such as wind-induced turbulence, precipitation, and convective mixing may have influenced vertical stratification and the behavioral patterns observed in this study. Surface wind and rainfall events can disrupt thermal layering and redistribute plankton along the vertical axis, potentially obscuring DVM signals typically attributed to variations in lunar illumination or predator avoidance. Notably, the absence of direct measurements of wind speed, rainfall intensity, and water column turbulence represents a methodological limitation. To better distinguish biologically mediated vertical movements from physically induced mixing processes, future investigations should incorporate high-resolution meteorological data and in situ hydrodynamic profiling to quantify and account for the effects of abiotic disturbances.

The temporal overlap in vertical distribution patterns between dominant zooplankton (e.g., *Diaphanosoma* sp., *M. micrura*) and phytoplankton species (e.g., *C. elongatum*, *S. costatum*) may suggest an interaction shaped by DVM and differential grazing pressure under variable moonlight conditions. In tropical freshwater systems, zooplankton are known to migrate vertically in response to lunar illumination and predation risk, often altering their grazing impact on surface-dwelling phytoplankton (Last et al. 2016; Guerra et al. 2019). However, the presumed coupling between zooplankton migration and phytoplankton abundance in the present study should be interpreted with caution, as direct evidence of trophic interaction or synchronized movement is lacking. Rather than concluding a causal relationship, these observations highlight a potentially significant but understudied ecological mechanism that warrants further experimental validation, particularly in shallow, light-sensitive tropical systems.

Diversity of phytoplankton and zooplankton

The Shannon-Wiener diversity index (H′) values for phytoplankton in Beje Pond ranged from 0.567 to 0.901, while the values for zooplankton ranged from 0.697 to 0.788 (Figure 11). These levels indicate moderate ecological diversity, generally suggesting a relatively balanced and functioning aquatic ecosystem, though not free from ecological pressures (Odum 1998).

The highest phytoplankton diversity was observed during the ninth sampling period (0.901), indicating a peak in species evenness and richness likely influenced by favorable environmental conditions, such as moderate nutrient concentrations and water temperature. Conversely, the lowest phytoplankton diversity (0.567) occurred during the fourth sampling period, possibly reflecting eutrophic stress or the early stages of species dominance. This aligns with observations by Zhou et al. (2018), who noted that nutrient enrichment often reduces diversity across tropical seas and alters phytoplankton community structure, demonstrating that species-specific responses to environmental disturbances can drive both vertical and compositional shifts.

For zooplankton, diversity remained within a narrower range (0.697-0.788), indicating a stable trophic response and adaptability to seasonal and lunar-driven environmental changes. The higher diversity during the seventh sampling may reflect an increase in available phytoplankton as food resources and reduced predation risk under dimmer moonlight conditions (Ursella et al. 2021). Moderate diversity values in both groups suggest that Beje Pond may exhibit mesotrophic characteristics, with nutrient levels sufficient to support productivity but without signs of acute degradation or harmful algal blooms. The continuous presence of several dominant species (e.g., *C. nivalis*, *Zygnema* sp., *S. costatum*) throughout the study further supports the notion of environmental tolerance and resilience within this ecosystem (Sun et al. 2022; Ferreira et al. 2024).

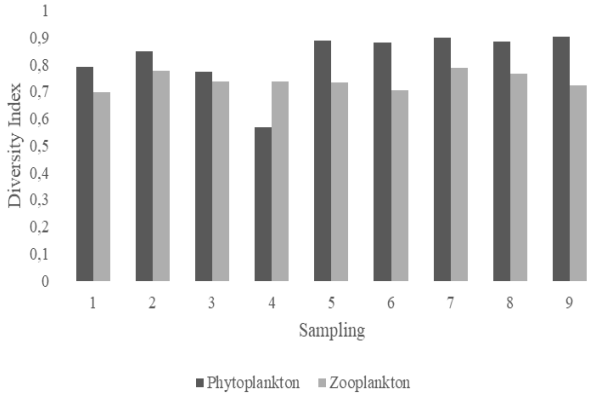

Figure 11. Diversity index of phytoplankton and zooplankton

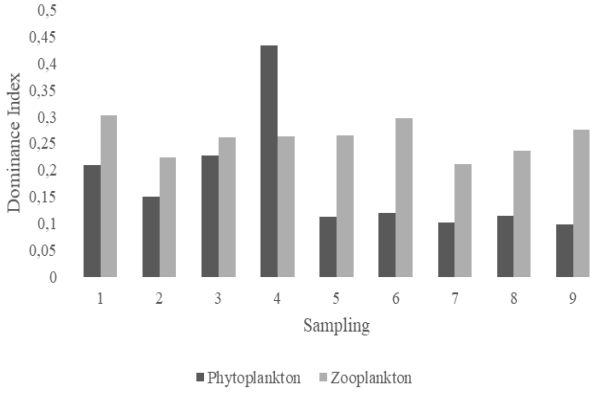

Figure 12. Dominance index of phytoplankton and zooplankton

Dominance index (D) of phytoplankton and zooplankton

The dominance index (Simpson's D) for phytoplankton ranged from 0.099 to 0.433, while that of zooplankton ranged from 0.212 to 0.303 (Figure 12). A low D value indicates even community structure and low dominance, while higher values suggest increasing control by a few species, often linked with ecosystem stress or eutrophication (Odum 1998). The highest dominance index for phytoplankton (0.433) was recorded during the fourth sampling period, coinciding with the lowest diversity value and suggesting a temporary ecological imbalance. This condition may reflect the proliferation of a few fast-growing taxa favored by sudden increases in nutrient availability, potentially linked to runoff or internal nutrient cycling. Recent research in tropical urban lakes supports this pattern. For example, Martins et al. (2024) observed that lakes with elevated nutrient concentrations and turbidity had higher dominance of few taxa and lower rarity. Such dominance can be a precursor to Harmful Algal Blooms (HABs) if environmental conditions persist.

In contrast, the lowest phytoplankton dominance (0.099) was recorded during the ninth sampling, supporting the view of a more evenly distributed and stable community at that time. Zooplankton dominance values were generally lower and more stable, indicating a broad distribution among species and a less pronounced response to nutrient or predation shifts. These findings suggest that the zooplankton community structure is more resilient and less prone to opportunistic dominance.

The consistently low to moderate D values in both phytoplankton and zooplankton imply that Beje Pond maintains a degree of ecological stability, though periods of increased phytoplankton dominance hint at potential vulnerability to trophic disturbance or climate-induced variability (Ferreira et al. 2024; Gao et al. 2024). Regular monitoring of these indices is essential to detect early warning signs of ecological shifts or bloom formation.

Relationship between physicochemical parameters and phytoplankton and zooplankton abundance

To better understand the interaction between environmental conditions and plankton abundance, a Principal Component Analysis (PCA) was conducted using three physicochemical parameters: temperature, pH, and Dissolved Oxygen (DO), alongside the abundance of phytoplankton (Nf) and zooplankton (Nz). The PCA results (Figure 13) revealed that the first two principal components (PC1 and PC2) accounted for a cumulative 62.8% of the total variance in the dataset. Specifically, PC1 explained 38.6%, capturing the main gradient of physicochemical variability, while PC2 explained 24.2%, which mostly reflected biological variation.

The loading values showed that temperature (0.543), pH (0.539), and DO (0.579) were strongly and positively loaded on PC1, indicating that this component represents a productivity gradient driven by environmental factors. Both phytoplankton (Nf) and zooplankton (Nz) abundance had moderate positive loadings on PC1 (0.236 and 0.154, respectively), suggesting that increases in temperature, pH, and DO tend to support higher plankton productivity. These findings are consistent with those of Weinstock et al. (2022), who emphasized the role of DO in supporting phytoplankton photosynthesis, and Garcia-Corral et al. (2017), who noted that optimal temperature levels enhance zooplankton metabolism.

PC2, in contrast, showed high negative loadings for Nf (−0.714) and Nz (−0.683), indicating that this axis reflects biological structuring, potentially influenced by grazing pressure, resource competition, or diel vertical migration. The distinction between PC1 and PC2 suggests that while environmental conditions are crucial in shaping overall abundance, biotic interactions likely modulate the community composition and vertical distribution of plankton (Petrusevich et al. 2020; Gao et al. 2024).

The PCA biplot also revealed a clustering pattern among sampling units. For instance, samples such as 1, 15, 36, and 43 clustered closer to environmental vectors, indicating periods of stronger physicochemical influence but relatively lower plankton abundance. Conversely, samples 26, 28, 32, and 59 were more aligned with the vectors for Nf and Nz, suggesting periods of enhanced biological productivity—possibly linked to favorable environmental conditions or reduced predation during waning moon phases.

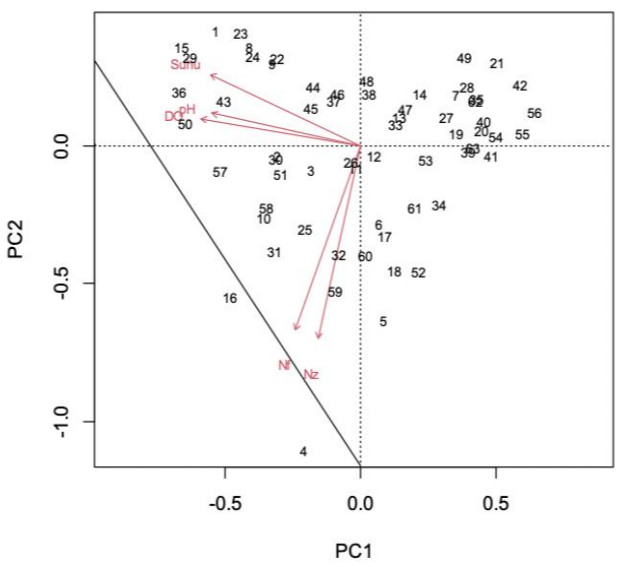

Figure 13. The physicochemical parameters (temperature, pH, and DO) and the abundance of phytoplankton (Nf) and zooplankton (Nz)

These clustering patterns support the interpretation that PC1 represents a eutrophic-oligotrophic continuum, where higher values reflect greater nutrient availability and environmental support for primary productivity. Meanwhile, PC2 likely corresponds to a grazing or disturbance gradient, where zooplankton-phytoplankton interactions shape community structure independently of physicochemical conditions. This interpretation aligns with ecological theory proposed by Rodríguez-Gálvez et al. (2023), which highlights the dual role of bottom-up and top-down forces in aquatic ecosystems.

Overall, the PCA provides deeper multivariate insight into the dynamic interplay between environmental parameters and plankton communities in Beje Pond. The findings underscore the importance of physicochemical conditions, particularly DO and temperature, in supporting plankton growth, while also highlighting the role of biological regulation in shaping distribution and abundance. These results emphasize that effective ecosystem monitoring should account for both abiotic and biotic drivers, as their interactions collectively influence the structure and functioning of aquatic communities. Understanding these gradients is essential for predicting ecological responses to environmental change, such as eutrophication or climate driven hydrological shifts.

The PCA results demonstrated that temperature was positively and strongly associated with the abundance of both phytoplankton and zooplankton in Beje Pond, with a loading value of 0.543. Temperature influenced zooplankton abundance when it remained within their physiological tolerance range. This finding is consistent with Garcia-Corral et al. (2017), who reported that temperature beyond the tolerance limit can affect the solubility of oxygen required for zooplankton metabolism. In addition, phytoplankton abundance showed a strong positive correlation with pH, indicated by a loading value of 0.539. DO also exhibited a positive relationship with phytoplankton abundance (loading value = 0.579), which can be categorized as moderately strong. This supports the findings of Weinstock et al. (2022), who stated that DO availability in aquatic environments enhances phytoplankton growth by facilitating photosynthesis. On the other hand, zooplankton abundance tended to decrease with increasing temperature and DO levels, potentially due to the acceleration of biological oxidation processes that increase oxygen demand and may create physiological stress. Weinstock et al. (2022) also highlighted the influence of DO on zooplankton populations.

The PCA analysis further revealed a weak correlation between phytoplankton and zooplankton abundance, with correlation values of 0.236 and 0.154, respectively. This suggests that zooplankton abundance in Beje Pond may not be directly dependent on phytoplankton density, but is more likely regulated by physicochemical factors such as temperature, pH, and DO. These findings indicate that environmental conditions play a more critical role in shaping plankton community structures than trophic interactions alone.

The Spearman correlation analysis between environmental parameters (pH, temperature, and DO) and the abundance of phytoplankton (Nf) and zooplankton (Nz) is presented in Figure 14 and summarized in the correlation matrix (Table 5). This analysis provides insights into the strength and significance of ecological interactions among the measured variables. A strong and statistically significant positive correlation was found between pH and temperature ($r = 0.62$, $p < 0.001$), as well as between pH and DO ($r = 0.67$, $p < 0.001$). Similarly, a strong correlation was also observed between temperature and DO ($r = 0.72$, $p < 0.001$), suggesting that these physicochemical parameters are closely interrelated within the pond ecosystem.

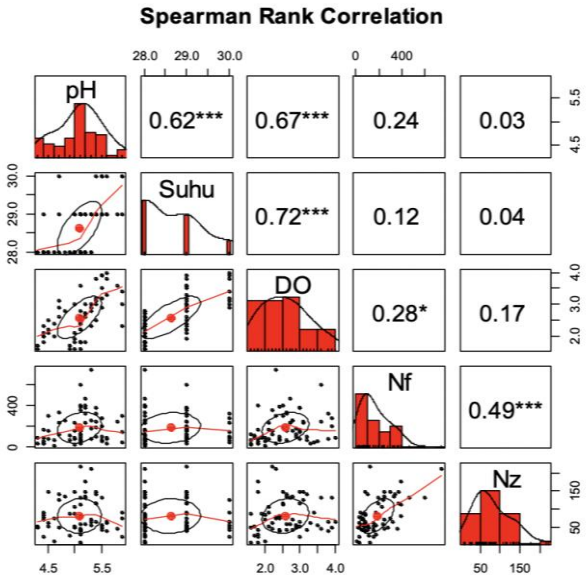

Figure 14. Scatter plots and Spearman significance correlation graphs of physicochemical parameters (pH, temperature, and DO) and abundance of phytoplankton (Nf) and zooplankton (Nz)

Table 5. Spearman correlation matrix (r and p-values) between environmental variables and plankton abundance

Variables	pH	Temperature	DO	Phytoplankton (Nf)	Zooplankton (Nz)
pH	-	r = 0.62, p < 0.001	r = 0.67, p < 0.001	r = 0.24, p > 0.05	r = 0.03, p > 0.05
Temperature	r = 0.62, p < 0.001	-	r = 0.72, p < 0.001	r = 0.12, p > 0.05	r = 0.04, p > 0.05
DO	r = 0.67, p < 0.001	r = 0.72, p < 0.001	-	r = 0.28, p < 0.05	r = 0.17, p > 0.05
Phytoplankton (Nf)	r = 0.24, p > 0.05	r = 0.12, p > 0.05	r = 0.28, p < 0.05	-	r = 0.49, p < 0.01
Zooplankton (Nz)	r = 0.03, p > 0.05	r = 0.04, p > 0.05	r = 0.17, p > 0.05	r = 0.49, p < 0.01	-

In contrast, the correlation between pH and phytoplankton abundance (Nf) was weak and not statistically significant ($r = 0.24$, $p > 0.05$), indicating that pH fluctuations had little direct effect on phytoplankton density. This result aligns with previous findings by Lin et al. (2025), who reported that variations in pH do not significantly influence phytoplankton abundance in freshwater environments. A similarly weak and non-significant correlation was found between pH and zooplankton abundance (Nz) ($r = 0.03$, $p > 0.05$), suggesting limited direct influence of pH on zooplankton dynamics.

The relationship between temperature and plankton abundance was also weak and statistically insignificant for both phytoplankton ($r = 0.12$, $p > 0.05$) and zooplankton ($r = 0.04$, $p > 0.05$). These findings suggest that temperature alone was not a key driver of plankton population changes during the study period. Similar patterns have been observed in other freshwater ecosystems, where temperature exerted only a minor influence compared to nutrient loading or grazing pressure (Klisarova et al. 2023).

A weak but statistically significant correlation was found between DO and phytoplankton abundance ($r = 0.28$, $p < 0.05$). This likely reflects oxygen enrichment in surface waters via photosynthetic activity by phytoplankton. As noted by Kihara et al. (2014), elevated DO concentrations often result from atmospheric diffusion and oxygen production through photosynthesis. However, no significant correlation was observed between DO and zooplankton abundance ($r = 0.17$, $p > 0.05$), indicating that zooplankton were not directly influenced by DO levels under the conditions observed.

A moderate and statistically significant correlation was found between phytoplankton and zooplankton abundance ($r = 0.49$, $p < 0.01$), highlighting a potential trophic link in which phytoplankton serve as a primary food source for zooplankton. This relationship suggests that bottom-up regulation may influence zooplankton populations within this ecosystem. Additionally, a total of 20 phytoplankton species from three major taxonomic classes were identified in the Beje Pond, with Zygnematophyceae being the most dominant. Notably, species such as *C. nivalis*, *C. elongatum*, and *S. costatum* were consistently observed during the sampling period, indicating a high degree of ecological adaptability to changing environmental conditions.

While the PCA analysis revealed a general positive association between pH, temperature, and DO with plankton abundance, Spearman correlation results indicated that not all associations were statistically significant, particularly between pH and phytoplankton abundance. Moreover, environmental drivers such as moonlight intensity, predation pressure, and food availability were observed to influence the vertical distribution and abundance of both phytoplankton and zooplankton. These findings underscore the complex interplay of abiotic and biotic factors that shape plankton community structure in tropical peatland ponds.

These findings highlight how lunar-driven behavioral plasticity interacts with physicochemical gradients to shape plankton dynamics in tropical peatland waters, a topic that remains underexplored in limnological research. Such insights are crucial for understanding ecosystem responses to environmental variability and for informing long-term monitoring and management of sensitive freshwater systems.

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