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Spatiotemporal variability of phytoplankton communities in the euphotic layers of a tropical caldera lake (Lake Taal, Batangas, Philippines)

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Abstract. *Inog YUSP, Racoma CJM, Bate J-MB, Benico GA, Tordesillas DT. 2025. Spatiotemporal variability of phytoplankton communities in the euphotic layers of a tropical caldera lake (Lake Taal, Batangas, Philippines). Biodiversitas 26: 3302-3314.* Lake Taal in Batangas, Philippines, is an ecologically and economically significant protected area that supports unique biodiversity. Monsoonal patterns and trophic status play a critical role in shaping the lake, however, their effect on the phytoplankton communities in tropical lakes is poorly understood. To address this gap, a spatiotemporal assessment was conducted to examine the diversity and distribution of phytoplankton communities in the euphotic layers of Lake Taal. Water samples across euphotic layers were collected from north (aquaculture) and south (non-aquaculture) basins during three monsoonal events in 2024 (February (northeast monsoon), August (southeast monsoon), and October (intermonsoon)) at varying depths within the euphotic layer and filtered using a 20-µm plankton net. A total of 40 phytoplankton species, representing five classes, with Cyanophyceae (70.78%) dominating the entire lake in density, indicating eutrophic conditions. Phytoplankton abundance showed significant variation across monsoons and basins, while remaining statistically uniform across the euphotic layers, inferring minimal vertical stratification in density. Aquaculture areas had higher phytoplankton density than non-aquaculture areas. Furthermore, the northeast monsoon had the highest phytoplankton density dominated by *Microcystis aeruginosa,* a harmful algal bloom former, shifting to *Cyanocatena imperfecta* during the southwest to October intermonsoon period. Diversity indices revealed a moderate diversity with high dominance, and ordination methods revealed monsoon-driven events heavily impacted the phytoplankton community structure of the lake. Canonical Correspondence Analysis (CCA) showed that water temperature, turbidity, and dissolved oxygen are key environmental factors shaping phytoplankton community structure, influencing species succession and distribution via light penetration and photosynthesis efficiency. The findings underscore the effects of eutrophication and highlight the need for continuous monitoring and seasonally adaptive environmental management strategies in tropical eutrophic lakes.

Keywords: Eutrophic, freshwater, microalgae, mixed, stratified

INTRODUCTION

Phytoplankton are complex autotrophic microbial communities adapted to diverse aquatic environments, including freshwater, brackish, and marine ecosystems (Olli et al. 2019; Sriwijayanti et al. 2019; Dalu et al. 2022; Naselli-Flores and Padisák 2023; Tambaru et al. 2024). They account for less than a percent of the Earth's total photosynthetic biomass but contribute over half of global net primary production and serve as the base of aquatic food webs (Winder and Sommer 2012; Gal et al. 2016; Henson et al. 2021). Though ecologically important, they can also cause Harmful Algal Blooms (HABs), leading to fish kills and disrupting lake ecosystems (Mowe et al. 2015; Pal et al. 2020; San Diego-McGlone et al. 2024). Thus, they are widely used as water quality, pollution, and productivity indicators (Parmar et al. 2016; Chandel et al. 2024; Hoang et al. 2024). Their distribution is influenced by hydrological factors such as light intensity, nutrients, and temperature, which vary across monsoons (Bellinger and Sigee 2015; Stoyneva-Gärtner et al. 2020; Wang et al. 2024).

Annually, the Philippines and nearby Southeast Asian countries experience interconnected monsoonal events: the Northeast Monsoon (NEM), Southwest Monsoon (SWM), and brief transition phase called Intermonsoon (IM) (PAGASA 2016; de Leon et al. 2024). The NEM brings cold dry winds, and rainfall to the eastern region from November to March while SWM delivers warm, moist winds and rain to the west from May to September. IM is marked by light, variable winds, and warm weather (PAGASA 2016). In tropical countries, monsoons drive seasonal shifts in wind patterns influencing mixing regimes significantly affecting phytoplankton communities (Lewis Jr 1973; Masseran and Razali 2016; Mamun et al. 2020; Matsumoto et al. 2020; Kim and Kim 2021; Aguilar et al. 2023; Mendoza et al. 2023; de Leon et al. 2024).

The establishment of aquaculture in lake systems enhances phytoplankton biomass and diversity due to nutrient enrichment from aquaculture waste (Ji et al. 2016; Ge et al. 2023). Elevated nitrogen and phosphorus favor certain taxa such as cyanobacteria, diatoms, cryptophytes, and dinoflagellates to dominate aquaculture-impacted areas (e.g., lakes and rivers), often exceeding regulatory limits and posing ecological and health risks (Findlay et al. 2009; Li et al. 2012; Ji et al. 2016; Otu et al. 2017; Ge et al. 2023; De Almeida et al. 2025). Aquaculture can accelerate eutrophication and alter phytoplankton composition increasing the risk of HAB events (Ge et al. 2023; De Almeida et al. 2025). In nutrient-prone tropical lakes, intensive aquaculture combined with the naturally warm climate promotes phytoplankton proliferation and HABs (Nazari-Sharabian et al. 2018; Mendoza et al. 2019; Zhao et al. 2022).

The Philippines, with over 400,000 hectares of inland waters, relies on these ecosystems for food security, livelihoods, and economic growth through exportation (Sespeñe et al. 2016; Tahiluddin et al. 2025). One of the leading aquaculture producers in the country is Lake Taal, serving as a primary income source (Mutia et al. 2018; Reyes et al. 2022). It is a Protected Area (PA) known for its unique caldera geomorphology and is categorized as a warm-monomictic lake that experiences monsoonal hydrological changes (Perez et al. 2008; de Leon et al. 2024). Its diverse phytoplankton community plays a key role in food web dynamics especially for endemic species like the freshwater sardine *Sardinella tawilis* (Papa and Mamaril Sr. 2011; Mutia et al. 2018).

Recent studies have classified Lake Taal as eutrophic with recurring cyanobacterial blooms near the aquaculture areas (Rosana et al. 2013; Trinidad 2024). Despite existing regulations, extensive fish farming has negatively impacted the water quality and caused continued deterioration of its biodiversity (Papa and Mamaril Sr 2011; Mendoza et al. 2019; Reyes et al. 2022). The 2020 Taal volcano eruption and its continuous degassing have also affected the lake and its vicinity, potentially altering its water chemistry and ecological balance (Jing et al. 2020; Van Eaton et al. 2022; de Leon et al. 2023; PHIVOLCS 2024). Here, we hypothesize that monsoons shift, eutrophication, and volcanic activity have significantly influenced the phytoplankton community structure in Lake Taal. However, there is currently limited spatiotemporal data on how these communities respond to monsoonal environmental changes, especially from aquaculture and non-aquaculture areas. To address this gap, this study conducted a spatial and temporal assessment of phytoplankton community structure in Lake Taal. Specifically, it aimed to (i) determine the distribution and diversity of phytoplankton in the euphotic layers of aquaculture and non-aquaculture sites, and (ii) evaluate their seasonal variation in relation to physicochemical factors. Findings will offer insights into the lake's current ecological status and support evidence-based management strategies for this protected area.

MATERIALS AND METHODS

Study area

Lake Taal is the third largest lake in the Philippines, surrounding the active Taal Volcano Island, and spans a total surface area of approximately 268 km^2 (Figure 1). It encompasses two cities (Lipa and Tanauan) and nine municipalities (Talisay, Balete, Mataas na Kahoy, Cuenca, Alitagtag, Sta. Teresita, San Nicolas, Agoncillo, and Laurel). The lake lies at a low elevation of 2.5 meters above sea level and has a catchment area of 682.8 km^2 (Perez et al. 2008). Its shoreline extends over 120 km, with a fetch of roughly 10 km. The lake receives inflows from 37 small, partly seasonal rivers and has an average outflow of 15 m^3·s^{-1}. It comprises two prominent basin morphologies: the Northern Basin (NB) and the Southern Basin (SB). A representative site per basin was established (Table 1). The NB (13.95498 N, 121.00195 E), adjacent to the municipality of Talisay, is relatively shallower with a mean depth of 60 meters and supports numerous aquaculture activities. In contrast, the deeper SB (14.06042 N, 120.98702 E), located near Cuenca and San Nicolas, with a maximum depth of 198 meters, has no aquaculture activity in its vicinity (Perez et al. 2008; de Leon et al. 2020, et al. 2023). The lake is classified as Class B waters according to Administrative Order No. 2016-08, suitable for recreational activities involving direct contact with water (Serrano et al. 2023).

Physicochemical measurements

Physicochemical properties were measured *in situ* using a multiparameter water quality sonde (EXO 2, YSI Inc., Yellow Springs, OH, USA) across the euphotic water column to differentiate the water characteristics on each monsoon. This includes the water temperature (°C), dissolved oxygen (mgL^{-1}), pH, conductivity (µScm^{-1}), total dissolved solids (mgL^{-1}), and turbidity (FNU) at each basin.

Phytoplankton sampling and preservation

Sampling was conducted between 08:00 and 14:00 during three monsoonal periods in 2024: February (northeast), August (southwest), and October (intermonsoon). A Secchi disc was utilized to estimate the maximum depth of the euphotic layer patterned following the methods of Poikane (2009). Water samples were collected in triplicate at one-meter intervals from the subsurface to the determined maximum depth using a four liters Niskin Water Sampler (General Oceanics, USA) with a total of 11 L. Subsamples were immediately filtered through a 20-µm plankton net, and a final concentration of 10 mL of composite sample was transferred into 100 mL polyethylene bottles and preserved in a 10% formalin solution. Fresh samples were also collected for the identification of species.

Chlorophyll-a analysis

One liter of lake water per sampling depth was filtered through Whatman® GF/F 0.47-mm glass fiber filters for algal chlorophyll analysis following the protocols of APHA (2017). Extraction was done using 90% acetone and determined using the trichromatic method with a multi-wavelength UV-visible spectrophotometer (Thermo Fisher Scientific, Orion Aquamate 8100, USA). The absorbance of the extract was measured at 630, 647, 663, and 750 nanometer wavelengths. The chlorophyll-*a* concentration was calculated using Jeffrey and Humphrey (1975).

Taxonomic identification and enumeration

Briefly, the filtered water was agitated thoroughly to homogenize the sample, and a 10 µL aliquot subsample was obtained using a micropipette and dispensed on an Improved Neubauer Haematocytometer (Tiefe-Depth Profondeur 0.10 mm; BLAU, Germany) for manual counting of phytoplankton species. Cell density was calculated using the formula of LeGresley and McDermott (2010):

$$\text{cells}\cdot L^{-1} = N \times df \times 10^7$$

Where, *N* is the number of cells counted, *df* is the dilution factor, and 10^7 is the conversion factor from the counting chamber volume (0.0001 mL) to 1 L.

The species were morphologically identified following the published taxonomic keys from Pantastico (1977) and Bellinger and Sigee (2015). In addition, the comprehensive checklist of Rott et al. (2008) in Lake Taal was used to confirm species occurrences. The current taxonomic names were validated from an online database-AlgaeBase (Guiry and Guiry 2025). Phytoplankton species were documented using a compound trinocular microscope (Olympus BX53, Japan) equipped with a camera (Moticam 1080, China) at 400x magnification.

Data analyses

Data analyses were performed using R Statistical Software v.2.6-8. (R Core Team 2021). Sample coverage-based rarefaction and extrapolation curves were utilized to assess sampling completeness using the 'iNEXT' package. Normality was assessed using the Shapiro-Wilk test, and data normalization was achieved through logarithmic and power transformations. As the data followed a normal distribution (p>0.05), a Three-way Analysis of Variance (ANOVA) with Tukey's HSD test was used to determine the difference among the environmental parameters, phytoplankton abundance, and diversity between depths, basins, and monsoonal events.

Table 1. Geographic information and description of research sites

Location	Geographical coordinates	Brief description
North Basin	13.95498 N, 121.00195 E	Extensive aquaculture operations
South Basin	14.06042 N, 120.98702 E	No nearby aquaculture activities

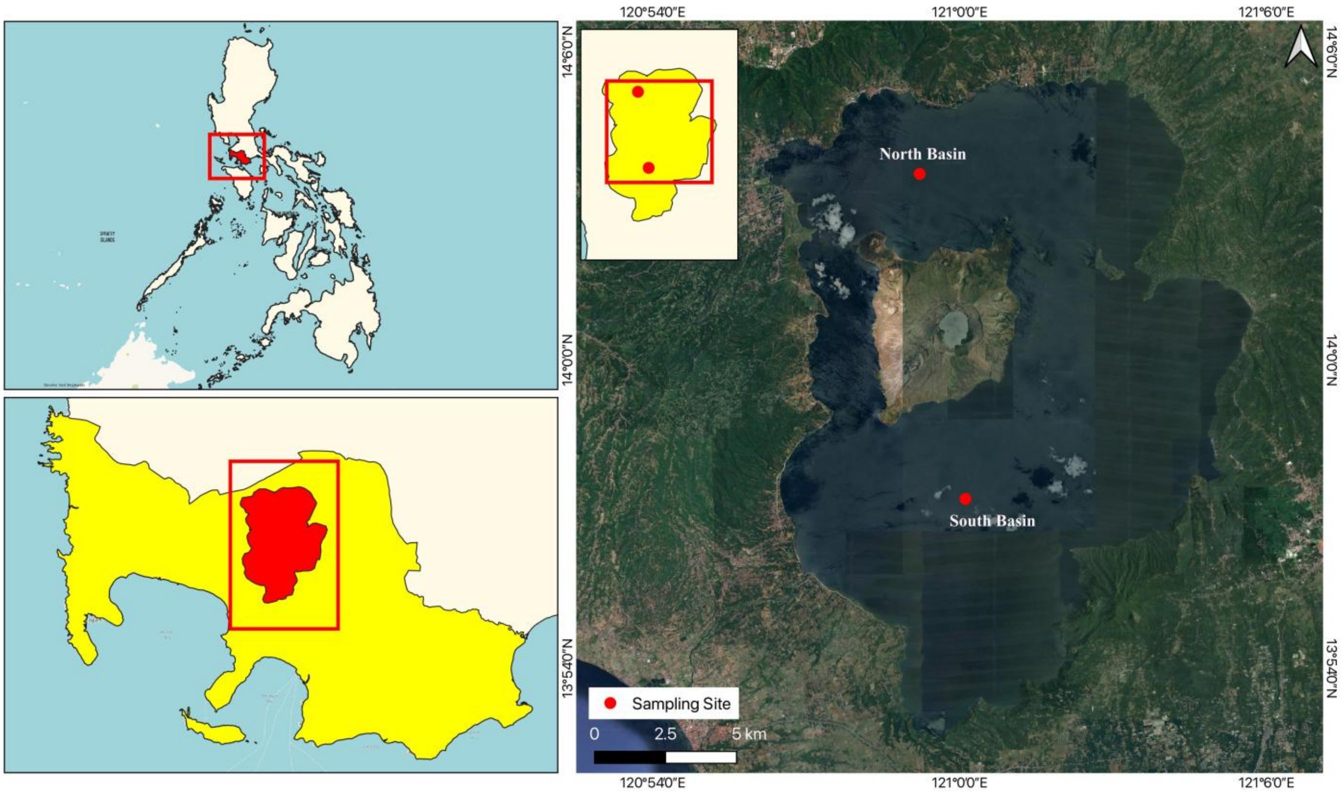

Figure 1. Study site map of Lake Taal showing the two basins and their surrounding municipalities, Batangas, Philippines

Diversity indices were calculated using the 'vegan' package (Oksanen et al. 2018), specifically Shannon-Wiener (H'), Simpson's Diversity (D), and Pielou's Evenness (J). The formulas are as follows:

Shannon-Wiener Index (H') = $\sum_{i=1}^{s} p_i \log(p_i)$

Where, S is the total number of taxa, p_i is the proportion of individuals in taxa i.

Simpsons Diversity Index (D) = $\sum_{i=1}^{s} \left(\frac{n_i}{N}\right)^2$

Where, S is the total number of taxa, n_i is the total individual taxa i, N is the total individuals in the sample.

Pielou's Evenness Index (J') = $\frac{H'}{\log(S)}$

Where, H' is Shannon-Wiener Index, S is the total number of taxa.

Differences in phytoplankton communities between basins, monsoons, and depths in the euphotic layer were assessed through a Non-Metric Dimensional Scaling (NMDS) ordination method, utilizing the Bray-Curtis dissimilarity index of the 'vegdist' function, defined as,

$$BC_{ij} = \frac{\sum_{k=1}^{S} |x_{ik} - x_{jk}|}{\sum_{k=1}^{S} (x_{ik} + x_{jk})}$$

Where, BC_{ij} is the Bray-Curtis dissimilarity between sample i and j, x_{ik} and x_{jk} are the abundances of taxon k in samples i and j, respectively, S is the total number of taxa.

The numerator represents the sum of absolute differences in abundances across all taxa. The denominator is the sum of abundances in both samples. This index ranges from 0 (identical composition) to 1 (completely dissimilar).

Analysis of Similarities (ANOSIM) was used to evaluate statistical differences in phytoplankton community structure among basins, monsoons, and depths in the euphotic layers. The resulting pairwise R values from ANOSIM were used to assess absolute partition among groups, with R values >0.25, indicating the separation of phytoplankton groups. Similarity Percentage (SIMPER) was used to determine the overall contribution of each species to the dissimilarity between monsoon, basin, and depth. Detrended Correspondence Analysis (DCA) indicated a unimodal species-environment relationship. Canonical Correspondence Analysis (CCA) was then performed using the 'cca' package to examine the influence of physicochemical parameters on phytoplankton communities. Environmental variables were normalized and screened using Variance Inflation Factor (VIF) and forward selection to identify spatial and environmental variables with significant contributions. The significance of the model was evaluated using Monte Carlo permutation test.

RESULTS AND DISCUSSION

Physicochemical parameters

The lake's physicochemical characteristics in the euphotic zone across different monsoons and basins were presented in Table 2. The euphotic zone extended to a mean depth of five meters across all monsoon events. The lowest (26.55°C) and highest (30.41°C) mean temperatures were both recorded in the NB, during the NEM and October Intermonsoon (OIM), respectively. Both basins exhibited a consistent increase in mean pH from NEM (6.74) to OIM (8.78). The NB showed a decline in DO levels from 7.46±0.12 mgL^{-1} during NEM to 6.17±0.27 mgL^{-1} in OIM, whereas the SB exhibited a more stable range across monsoons (7.35-7.44 mgL^{-1}). Dissolved solids and conductivity remained relatively consistent in the NB and SB, with 3.04-3.06×10^3 µS/cm and 3.25-3.29×10^3 mgL^{-1}, respectively. Elevated turbidity was observed in the SB from NEM (3.17±0.70 FNU) to OIM (18.68±4.37 FNU), while a decrease was seen in the NB from NEM (1.28±0.15 FNU) to OIM (0.59±0.05 FNU). The highest chlorophyll-*a* values were recorded in the NB during SWM (21.43±0.79 µgL^{-1}) and lowest during OIM in the SB (10.09±4.77 µgL^{-1}). Three-way ANOVA revealed significant interactions between basin and monsoon for temperature, pH, DO, and turbidity ($p<0.05$), whereas no significant depth interaction across layers of the euphotic zone was observed ($p>0.05$).

Table 2. Water characteristics of the representative sites in the north and south basins of Lake Taal, Batangas, Philippines, throughout different monsoon events. Lowercase indicates significant differences on each basin across monsoon events ($p<0.05$)

Water parameter	North Basin			South Basin		
	NEM	SWM	OIM	NEM	SWM	OIM
Temp (ºC)	26.19±0.12^{a}	30.5±0.09^{b}	30.61±0.23^{c}	26.91±0.01^{a}	29.87±0.01^{b}	30.21±0.03^{c}
pH	6.71±0.01^{a}	8.97±0.01^{b}	9.02±0.08^{c}	6.78^{a}	8.6±0.14^{b}	8.81±0.14^{c}
DO (mgL^{-1})	7.46±0.12^{a}	7.33±0.03^{a}	6.17±0.27^{b}	7.35±0.14^{a}	7.51±0.05^{a}	7.44±0.20^{a}
Turbidity (FNU)	1.28±0.15^{a}	0.78±0.09^{b}	0.59±0.05^{b}	3.17±0.70^{a}	8.71±1.27^{b}	18.68±4.37^{c}
Cond (×10^3 µScm^{-1})	3.25	3.27	3.29	3.27	3.28	3.28
TDS (×10^3 mgL^{-1})	3.06	3.04	3.06	3.06	3.05	3.05
Transparency (cm)	190±3	210±1	260±1	200±2	210±2	260±2
Chl-*a* (µgL^{-1})	12.92± 2.37^{a}	21.43±0.79^{b}	12.83± 1.27^{a}	15.45± 2.42^{a}	14.65±2.49^{a}	10.09± 4.77^{b}

Note: NEM: Northeast Monsoon, SWM: Southwest Monsoon, OIM: October Intermonsoon

Phytoplankton composition

A total of 40 phytoplankton species under 36 genera, belonging to five classes, were recorded across basins and monsoon events in Lake Taal (Table 3). Chlorophyceae (green algae) had 22 species, followed by Cyanophyceae (Cyanobacteria) with eight, Bacillariophyceae (diatoms) with seven, Dinophyceae (dinoflagellates) with two, and Euglenophyceae (euglenoids) with one species (Figure 2). Cyanophyceae dominated the euphotic zone of the lake with an overall mean relative density of 70.78% across monsoons, followed by Chlorophyceae (25.64%). In comparison, Bacillariophyceae (1.79%), Dinophyceae (1.72%), and Euglenophyceae (0.06%) only accounted for less than three percent of the total phytoplankton density. *Cyanocatena imperfecta* was the most abundant species, comprising 27.56%, followed by *Merismopedia tranquilla* (15.56%) and *Microcystis aeruginosa* (14.06%). The sample coverage-based rarefaction and extrapolation curves for most groups approached 1.0, with several curves demonstrating asymptotic behavior (Figure 3). This indicates that the sampling effort was exhaustive, capturing most of the species' diversity across the monsoonal events and basins.

Table 3. List of phytoplankton species under five classes and their relative abundance in the north and south basins of Lake Taal, Batangas, Philippines, during different monsoon events

Class/Family	Species	North Basin (%)			South Basin (%)			Mean
		NEM	SWM	OIM	NEM	SWM	OIM	
Cyanophyceae								
Chroococcaceae	*Chroococcus dispersus*	5.76	1.1	2.53	1.24	0.65	3.17	2.23
Leptolyngbyaceae	*Planktolyngbya limnetica*	4.08	5.95	1.72	4.89	15.2	3.98	5.53
Microcystaceae	*Cyanocatena imperfecta*	19	50.75	40.8	11.9	31.28	24.9	27.56
	Merismopedia tranquilla	14	18.36	5.03	19.6	27.07	16.8	15.56
	*Microcystis aeruginosa**	37.1	0.54	8.63	35.2	1.92	13.6	14.06
	Eucapsis parallelepipedon	4.8	5.15	2.42	9.69	1.98	3.6	4.26
Oscillatoriaceae	*Oscillatoria* sp.					0.74		0.69
Chlorophyceae								
Chlorellaceae	*Actinastrum* sp.*		0.42	1.47		0.48		0.73
	Hindakia fallax	1.22	1.87	0.74		2.01	1.73	1.4
Chlorococcaceae	*Chlorococcum* sp.*	0.74	2.55	14.6	1.77	1.01	7.12	4.3
Closteriaceae	*Closterium acutum var. variabile*	0.2	0.06	0.07	0.18	0.07	0.19	0.12
Desmidiaceae	*Staurastrum anatinum*	0.32	0.09	0.31	0.32	0.16	0.47	0.26
	Cosmarium neodepressum	0.12	0.08	0.12	0.22	0.13	0.47	0.18
	Staurastrum gracile	0.07	0.06	0.13		0.14	0.17	0.11
	Staurastrum sp.	0.05	0.06	0.05		0.07	0.12	0.06
Elakatotrichaceae	*Elakatothrix acuta*	0.08	0.1		0.24	0.2		0.14
Golenkiniaceae	*Golenkinia radiata*	0.1					0.09	0.09
Hydrodictyaceae	*Pediastrum duplex*		0.5	0.92		0.7	1.41	0.81
Oocystaceae	*Willea apiculata*					4.44		4.11
	Oocystis marssonii	0.53	0.55	1.38	0.28	1.03	1.08	0.75
	Lagerheimia citriformis	0.45	0.21	0.41	0.31	0.17	0.57	0.32
	Oocystis natans	0.34	0.12	0.39	0.25	0.26	0.59	0.31
Scenedesmaceae	*Coelastrum microporum*	4.4	3.93	9.19	7.93	4.65	7.7	5.83
	Coelastrum indicum	0.93	1.5	1.2	2.38	0.92		1.28
	Scenedesmus sp.	0.82	0.18					0.46
	Tetradesmus lagerheimii	0.33	0.16		0.43			0.29
	Desmodesmus spinosus		0.12	0.18		0.2		0.16
Selenastraceae	*Monoraphidium contortum*	0.22	2.17	4.08	0.4	0.41	2.58	1.53
Volvocaceae	*Pandorina* sp.*	1.97	1.47	1.44	1.03	0.8	2.01	1.34
	Eudorina elegans	1.01	1.44	0.92		1.16	1.25	1.06
Bacillariophyceae								
Aulacoseiraceae	*Aulacoseira* sp.*					0.29		0.27
Bacillariaceae	*Nitzschia* sp.*				0.07	0.1		0.08
Fragilariaceae	*Fragilaria* sp.*					0.59		0.55
	Synedra sp.*	0.05				0.1		0.06
Hemidiscaceae	*Actinocyclus normanii*	0.17	0.07	0.64	0.78	0.25	0.75	0.41
Naviculaceae	*Navicula* sp.*	0.11	0.04		0.18	0.09		0.1
Thalassiosiraceae	*Stephanocyclus meneghinianus*	0.13	0.25	0.27	0.4	0.58	0.41	0.31
Dinophyceae								
Ceratiaceae	*Ceratium furcoides*	1	0.07	0.26	0.23	0.09	5.12	1.68
Peridiniaceae	*Peridinium* sp.*	0.03	0.04		0.04	0.06		0.05
Euglenophyceae								
Euglenaceae	*Trachelomonas* sp.*			0.05			0.09	0.06

Note: *: Indicates new locality record in Lake Taal, Batangas, Philippines

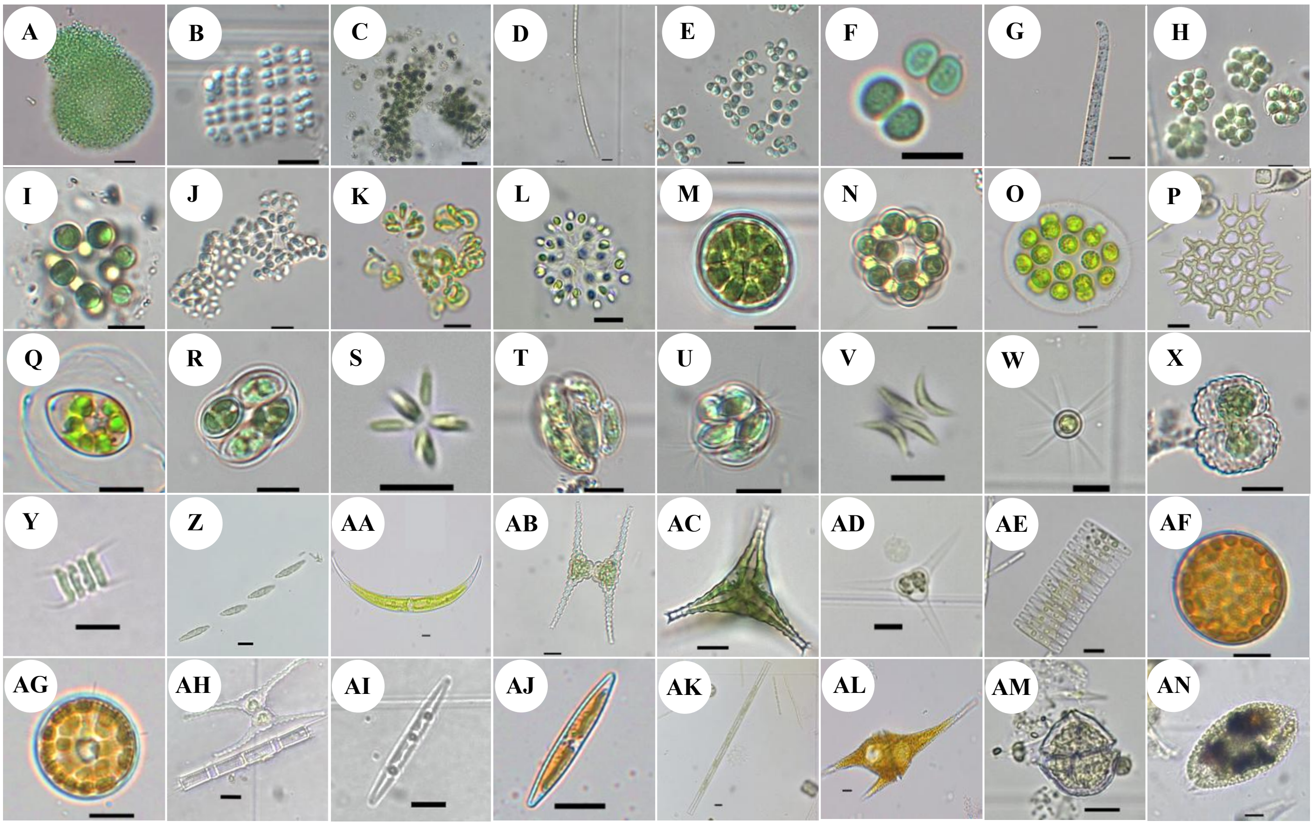

Figure 2. Phytoplankton species recorded in Lake Taal, Batangas, Philippines. Cyanophyceae (A-G), Chlorophyceae (H-AD), Bacillariophyceae (AE-AK), Dinophyceae (AL-AM), and Euglenophyceae (AN). A. *Cyanocatena imperfecta*, B. *Merismopedia tranquilla*, C. *Microcystis aeruginosa*, D. *Planktolyngbya limnetica*, E. *Eucapsis parallelepipedon*, F. *Chroococcus dispersus*, G. *Oscillatoria* sp., H. *Coelastrum microporum*, I. *Chlorococcum* sp., J. *Willea apiculata*, K. *Monoraphidium contortum*, L. *Hindakia fallax*, M. *Pandorina* sp., N. *Coelastrum indicum*, O. *Eudorina elegans*, P. *Pediastrum duplex*, Q. *Oocystis marssonii*, R. *Oocystis natans*, S. *Actinastrum* sp., T. *Scenedesmus* sp., U. *Lagerheimia citriformis*, V. *Tetradesmus lagerheimii*, W. *Golenkinia radiata*, X. *Cosmarium neodepressum*, Y. *Desmodesmus spinosus*, Z. *Elakatothrix acuta*, AA. *Closterium acutum* var. *variabile*, AB. *Staurastrum gracile*, AC. *Staurastrum anatinum*, AD. *Staurastrum* sp., AE. *Fragilaria* sp., AF. *Actinocyclus normanii*, AG. *Stephanocyclus meneghinianus*, AH. *Aulacoseira* sp., AI. *Navicula* sp., AJ. *Nitzschia* sp., AK. *Synedra* sp., AL. *Ceratium furcoides*, AM. *Peridinium* sp., AN. *Trachelomonas* sp. Scale bar: 10µm

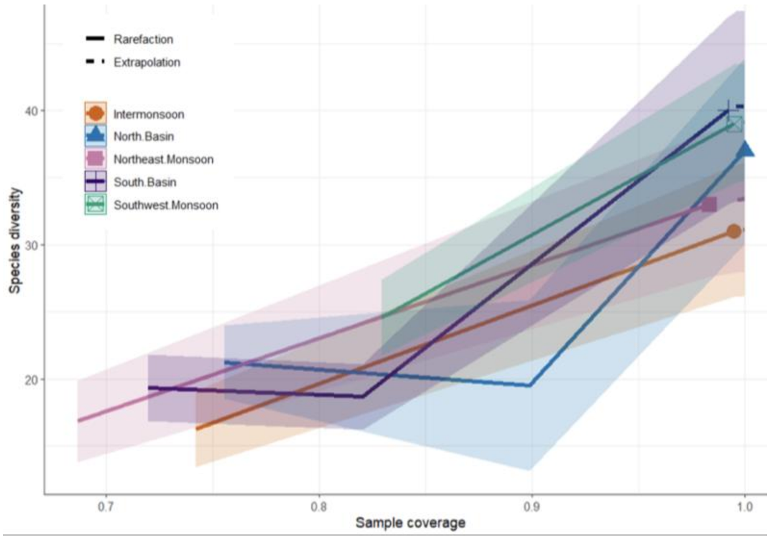

Figure 3. Sample coverage-based rarefaction and extrapolation curves showing species diversity across different monsoonal events and basins. Solid lines represent rarefaction estimates, while dashed lines indicate extrapolated values. Shaded areas refer to confidence intervals (0.95)

Basin and depth

Cyanobacteria dominated the euphotic layers during NEM and SWM with more than 50% relative density at each depth on both basins (Figures 4.A and 4.B). During the SWM, diatom abundance was lower in the SB, and dinoflagellates were negligible in both basins. In the OIM, green algae increased in both basins, along with a rise in diatoms in the NB (Figure 4.C). Although the relative proportions of dominant groups were similar in both basins, the SB exhibited higher species richness (s: 39) but lower mean density (1.92×10^7 cellsL^{-1}) compared to the NB (s: 36, 2.87×10^7 cellsL^{-1}). *Cyanocatena imperfecta* and *M. aeruginosa* dominated the NB, whereas *M. tranquilla, C. imperfecta*, and *M. aeruginosa* were abundant in the SB. Additionally, *Aulacoseira* sp., *Fragilaria* sp., *Nitzschia* sp., *Willea apiculata*, and *Oscillatoria* sp. were exclusive in the NB, while *Scenedesmus* sp. was absent in the SB. Three-way ANOVA revealed a significant difference in phytoplankton density across monsoons and basins in Lake Taal ($p<0.05$), while no significant variations across depths were observed in the euphotic layers ($p>0.05$).

Monsoon

Generally, the abundance of phytoplankton decreased from NEM to OIM. Mean phytoplankton density peaked during the NEM at 3.07×10^7 cellsL^{-1} and was at the lowest during the OIM at 1.51×10^7 cellsL^{-1}. This was largely driven by a decline in cyanobacteria density during NEM from 2.55×10^4 cellsL^{-1} (82.21%) to 9.24×10^3 cellsL^{-1} (61.62%) during OIM, lowering the overall mean phytoplankton density. Consequently, there was an observable rise in the relative density of green algae from NEM (15.23%) to OIM (32.82%). Dominant species shifted across monsoons, from *M. aeruginosa* (37.06%) during the NEM to *C. imperfecta* during the SWM (41.01%) and OIM (32.86%). *Chlorococcum* sp. and *Ceratium furcoides* increased from NEM to OIM, whereas *M. tranquilla* decreased. Moreover, a subtle increase in density was also observed in *Monoraphidium contortum*, *Oocystis marssonii, Pediastrum duplex, Desmodesmus spinosus, Staurastrum gracile,* and *Staurastrum* sp. Tukey's post-hoc analysis revealed OIM varied significantly from both SWM and NEM ($p<0.05$).

Diversity

Alpha diversity

Observed species richness peaked during the SWM in both basins, and at the lowest during NEM and OIM (Figure 5.A). The mean phytoplankton community structure in the euphotic zone of Lake Taal had a moderate diversity (H') across monsoons, ranging from 1.34 to 2.40 (Figure 5.B). However, Three-way ANOVA revealed no significant difference in diversity (H') across basins, monsoons, or euphotic layer depths ($p>0.05$), indicating consistent species diversity across space and time.

The dominance of some species was supported by Simpson's diversity index and Pielou's evenness mean values (Figures 5.C and 5.D). The SB during the OIM exhibited the most diverse (H': 2.4) yet highly uneven (J: 0.25) phytoplankton communities in Lake Taal. Evenness differed significantly between basins and monsoons ($p<0.05$), particularly during the SWM and OIM.

Beta diversity

NMDS ordination revealed seasonal clustering of phytoplankton communities within the euphotic layers across monsoon and basins, with a stress value of 0.149, indicating a fair representation of the data (Figure 6). A distinct separation between basins was also observed during SWM. However, clusters with 95% CI exhibited overlap among monsoons. Analysis of Similarities (ANOSIM) of phytoplankton abundance revealed a significant difference between monsoons implying a moderately strong temporal variation (R-value: 0.56, $p<0.05$), whereas a statistically significant, yet ecologically weak spatial variation of phytoplankton abundance between the north and south basins (R-value: 0.18, $p<0.05$). Consistent with ANOVA results, similarity between depths in the euphotic layer of the lake was observed ($p>0.05$). Similarity Percentage (SIMPER) revealed that species that contributed the most variation across each monsoon event were *P. limnetica, Chlorococcum* sp., and *M. tranquilla*. The cumulative contribution of *Chlorococcum* sp. (74.56%), *P. limnetica* (69.43%), *M. tranquilla* (63.67%), and *M. aeruginosa* (49.87%) has the most influence on dissimilarity between the north and south basins.

Canonical correspondence analysis

Environmental variables explained 80.25% of the variation of the phytoplankton community in the CCA biplot (Figure 7). Monte Carlo simulations showed that the environmental variables significantly accounted the variation in species composition ($p<0.01$). Water Temperature (WT), Dissolved Oxygen (DO), and turbidity are key environmental drivers for most phytoplankton species ($p<0.01$), whereas dissolved solids weakly influence other species. CCA1 had a significant correlation ($p<0.01$) with WT and turbidity, representing the primary ecological gradient shaping species distribution. Green algal species including *P. duplex* (Ped) and *Actinastrum* sp. (Acta), and a dominant cyanobacteria, *M. tranquilla* (Mer), in the upper right quadrant (quadrant I) were positively correlated with WT and inversely with DO, suggesting a preference for warmer, low-oxygen waters. *Chlorococcum* (Chlo) and *M. contortum* (Mon) were linked to waters with high-light penetration, whereas *C. furcoides* (Cer), *Chroococcus dispersus* (Chro), and *Lagerheimia citriformis* (Lag) were associated with areas of high DO. *Navicula* sp. and *M. aeruginosa* (Mic) were found to be associated with highly turbid and colder water, suggesting blooms of this species may occur in lowlight and cold environments, whereas *C. imperfecta* (Cya) was found to be clustered near the center and is weakly influenced by WT.

Discussion

The results revealed that the lake undergoes distinct environmental changes driven by monsoonal shifts. Similar patterns have been documented in Lake Taal by de Leon et al. (2024), highlighting the strong influence of seasonal climatic transitions on limnological conditions. One of the significant changes observed was in temperature and pH, which is closely linked to the lake's mixing regimes occurring in conjunction with monsoon changes. The lake undergoes complete mixing during the NEM, driven by strong trade winds that promote vertical mixing between the surface and bottom temperatures, resulting in colder temperatures and lower pH levels in the euphotic layer (Perez et al. 2008; de Leon et al. 2024). In contrast, the warmer temperatures during the SWM reflect the peak of thermal stratification, driven by reduced wind mixing and increased surface heating (Aguilar et al. 2023; de Leon et al. 2024).

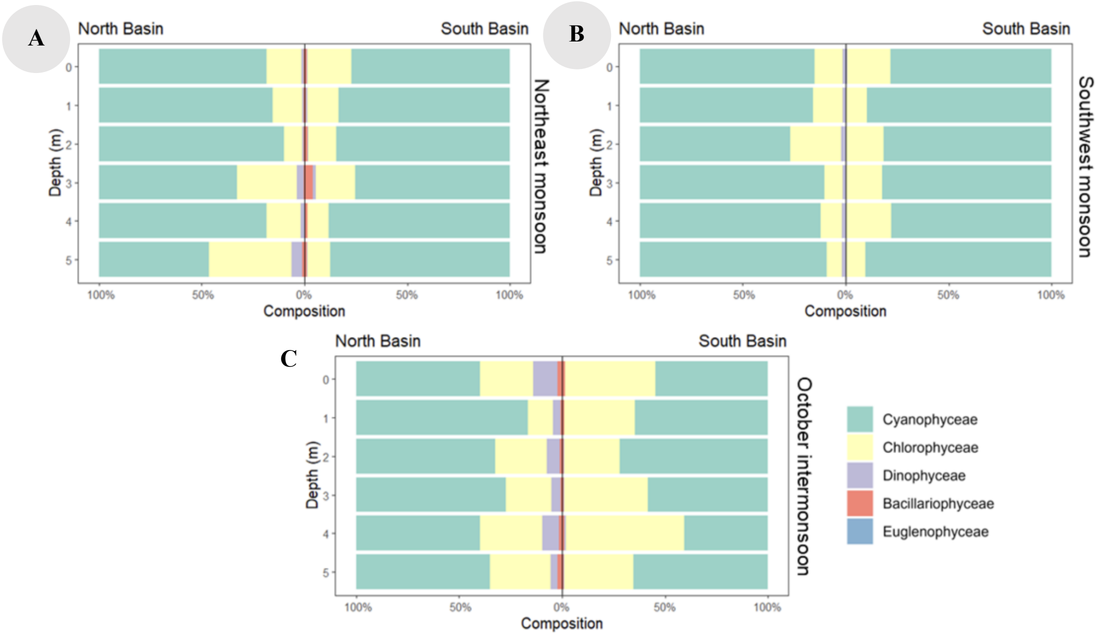

Figure 4. Composition of phytoplankton classes along the euphotic layers (0-5 meters) from the northern and southern basins of Lake Taal, Batangas, Philippines, on varying monsoon events. A. Northeast Monsoon, B. Southwest Monsoon, C. October Intermonsoon

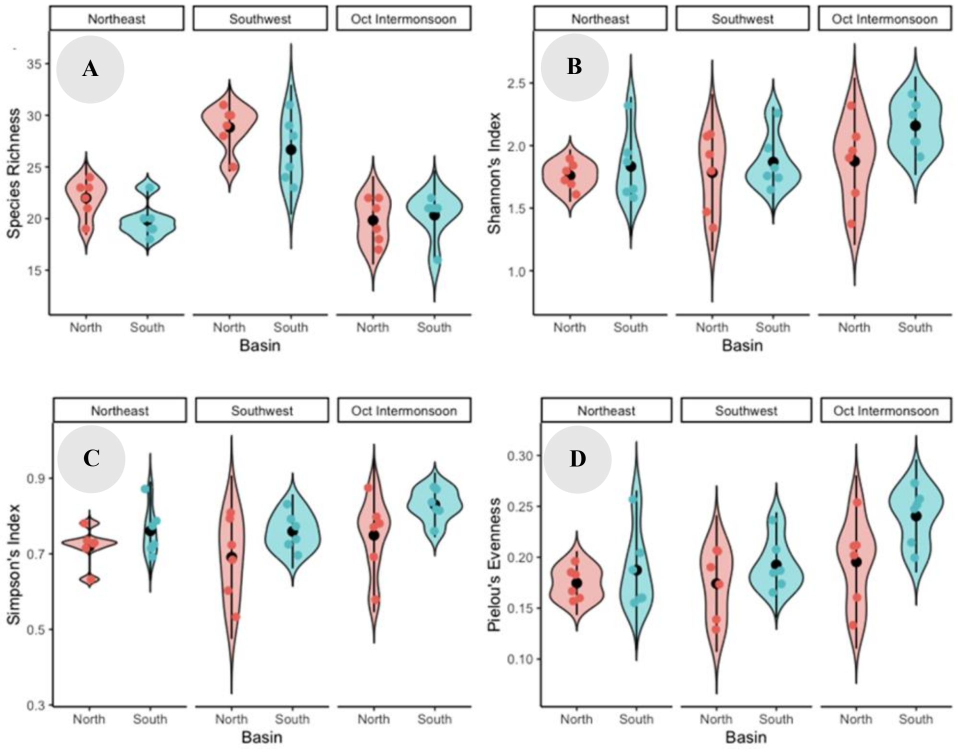

Figure 5. Violin plot of the phytoplankton diversity indices in the north and south basins across monsoon events. A. Species richness, B. Shannon Diversity Index, C. Simpson's Index, D. Pielou's Evenness. Red: North basin, Blue: South basin

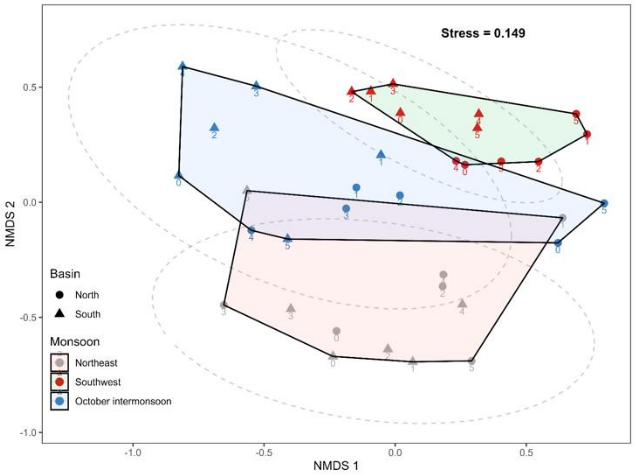

Figure 6. Non-Metric Multidimensional Scaling (NMDS) ordination based on Bray-Curtis dissimilarity showing the compositional differences in phytoplankton communities across sampling depths between monsoons and basins of Lake Taal, Batangas, Philippines. Convex hulls (solid line) represent group boundaries, while ellipses (dashed line) indicate 95% confidence intervals around group centroids

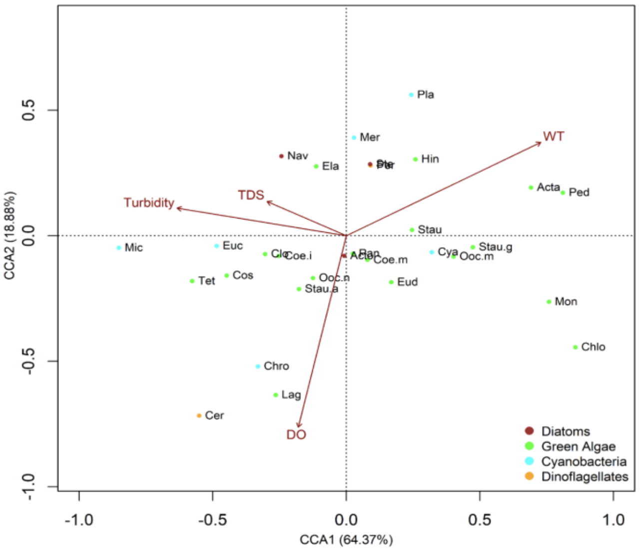

Figure 7. Canonical Correspondence Analysis (CCA) biplot of phytoplankton species abundance against environmental variables in the euphotic zones of Lake Taal, Batangas, Philippines. Full line arrows represent environmental variables, and colored circles represent different phytoplankton groups. Axis 1 accounts for 64.37% of the variance with an eigenvalue of 0.22, while Axis 2 accounts for 18.88% with an eigenvalue of 0.06. Acto: *A. normanii*, Ste: *S. meneghinianus*, Nav: *Navicula* sp., Chlo: *Chlorrococcum* sp., Clo: *C. acutum* var *variabile*, Acta: *Actinastrum* sp., Coe.i: *C. indicum*, Coe.m: *C. microporum*, Eud: *E. elegans*, Hin: *H. fallax*, Lag: *L. citriformis*, Mon: *M. contortum*, Ooc.m: *O. marssonii*, Ooc.n: *O. natans*, Pan: *Pandorina* sp., Ped: *P. duplex*, Tet: *T. lagerheimii* , Des: *D. spinosus*, Sce: *Scenedesmus* sp., Stau.a: *S. anatinum*, Stau.g: *S. gracile*, Stau: *Staurastrum* sp., Chro: *C. dispersus*, Cya: *C. imperfecta*, Euc: *E. parallelepipedon*, Mer: *M. tranquilla*, Mic: *M. aeruginosa*, Osc: *Oscillatoria* sp., Pla: *P. limnetica*, Cer: *C. furcoides*, Per: *Peridinium* sp.

These environmental shifts influence the lake's biological communities. Temperature and pH were highly collinear and are important drivers for the type of phytoplankton species to dominate in the euphotic layers. Lake Taal was dominated by cyanobacteria across basins and monsoon events as the warmer and alkaline conditions favor their proliferation (Guedes et al. 2018). Chlorophyll-a concentrations supported previous studies indicating the lake is eutrophic (Rosana et al. 2013; de Leon et al. 2020). This is consistent with most studies in lakes dominated by cyanobacteria, as they are generally associated with eutrophic freshwater environments and may persist year-round (Vanderley et al. 2021). Similar maar lakes, including Lake Palakpakin, Sampaloc, and Bunot of San Pablo, Laguna, have also been assessed as eutrophic and dominated by cyanobacteria as indicated by cell counts and canthaxanthin pigments (Mendoza et al. 2019; Navarrete et al. 2019; Briddon et al. 2023). Rising temperatures due to global warming and excessive nutrient loading can lead to increased cyanobacterial dominance in surface waters (Lürling et al. 2018; Giani et al. 2020).

The current study also revealed that species-level abundance and dominance varied with environmental heterogeneity across monsoons and basins. Rott et al. (2008) studied Lake Taal in 1999, when it was still classified as oligotrophic, and recorded a shift from diatoms as the dominant group during the mixing period (NEM) to dinoflagellates during thermal stratification (SWM). Although their annotated checklist recorded 45 phytoplankton species, only 29 were observed in the current study, with 11 new locality records added to the updated checklist (Rott et al. 2008; Papa and Mamaril 2011). This may indicate changes in environmental conditions that have occurred over time, such as the change in trophic classification from oligotrophic to eutrophic, potentially driven by the extensive aquaculture and prolonged lake warming due to climate change (Mutia et al. 2018; Nazari-Sharabian et al. 2018; de Leon et al. 2020; Gomes et al. 2020; Xu et al. 2022). These changes may have favored the proliferation of cyanobacteria and eutrophication-associated species, contributing to the local displacement of several other taxa, including the endemic diatom *Thalassiosira visurgis* (Rott et al. 2008, Bellinger and Sigee 2015; Cantrell and Lam 2021).

During NEM, physical mixing across the water column redistributes hypolimnetic nutrients upward, promoting phytoplankton growth while altering its vertical distribution (Radbourne et al. 2019; Ahmed et al. 2021; de Leon et al. 2024). In contrast, the presence of a thermocline during SWM restricts nutrient exchange as well as the elevated surface water temperature, can lead to a reduced abundance and altered community composition as observed in this study (Mesman et al. 2021; Wang et al. 2024). Despite this, a significantly higher chlorophyll-a concentration, and phytoplankton abundance, but with a lower diversity, in the aquaculture area during SWM were observed. Similar to the studies of De Almeida et al. (2025) on the effects of aquaculture in a natural lake in Brazil, cyanobacterial growth can be caused by the stable water column with higher light penetration (less turbid), warmer alkaline waters, and external nutrient loading, which may have originated from aquaculture (Mowe et al. 2015; Vanderley et al. 2021). The impacts of aquaculture on the phytoplankton communities are well established, often promoting the dominance of fast-growing cyanobacterial species like *M. aeruginosa* and *C. imperfecta,* while limiting niche availability for other species (Gomes et al. 2020; Xu et al. 2022; Ge et al. 2023; Alpecho et al. 2024). This condition may have led to competitive exclusion, where dominant species outcompete others, resulting in decreased community diversity (Masuda et al. 2020; Cantrell and Lam 2021; Mutia et al. 2022).

The shifts in abundance and diversity of phytoplankton across the different monsoon events highlight the importance of the ecological and physicochemical characteristics of the water, such as turbidity and dissolved oxygen, as drivers for light penetration and indicators of efficient photosynthesis, as shown in the CCA biplot (Cui et al. 2023). Cyanobacteria preferred to thrive in warmer waters, which decreased the abundance of other species. Studies have also shown effects on cell size, colony, and growth rates of phytoplankton at both species and community levels in relation to temperature and light availability (Edwards et al. 2016; Zohary et al. 2021). Despite exhibiting moderate diversity in both basins, dominant species shifted across monsoon events. The proliferation of *M. aeruginosa* during the NEM was evident due to the lower water temperature, creating optimal conditions for its growth, ranging 20-25ºC, with a rapid accumulation of cell density occurring between 26 and 35ºC (Wei et al. 2022a; Guo et al. 2023). However, the increased SO_2 degassing of the Taal volcano during the NEM may have reacted with the atmospheric water vapor to form sulfuric acid (H_2SO_4), leading to acid rain that can enter the lake system. Additionally, sulfur upwelling, a common phenomenon in lakes of volcanic origin, may have lowered the lake's pH (<7) which should create unfavorable conditions for *M. aeruginosa* (Liotta et al. 2021; Wei et al. 2022b; de Leon et al. 2024; PHIVOLCS 2024). CCA biplot revealed this species to favor high turbidity and colder areas. Given this, their high density may be influenced by other factors, such as nutrient availability, as their dominance has been associated with higher nitrogen concentrations (Mowe et al. 2015). The abundance of this species should be carefully monitored as it has the potential to form HABs and produce cyanotoxins such as microcystins (hepatotoxic peptides), posing significant health risks to plants, animals, and humans through contaminated water or bioaccumulation (Wei et al. 2022b). Moreover, this species has the ability to increase its microcystin concentrations during mixed periods with high turbulence, negatively affecting the overall lake biodiversity (Onyango et al. 2020). Many studies have reported the health hazards from oral exposure to microcystins, ranging from hepatocellular damage to primary liver cancer (Melaram et al. 2022).

During SWM, cyanobacterial blooms were reported amidst the presence of a strong stratification (Trinidad 2024). The cyanobacterial blooms observed were *C. imperfecta* dominating the surface layers (50.75%) and can be attributed to the warm, calm waters and external nutrients, as the bloom was reported near aquaculture areas. The presence of aquaculture and effluents from households in the northern region of the lake may have contributed to the excess inorganic nutrient input, promoting algal growth (Medallon and Garcia 2021; Ge et al. 2023). Furthermore, the high temperature and pH in the surface layers of the lake during the SWM were within the preferred conditions of the colonial *C. imperfecta,* with the optimal temperature for growth near 30ºC, and were reported to be present in a variety of environments from deep to shallow and oligo to eutrophic waters (Recknagel et al. 2015). Aside from its occurrence in the bodies of water in the Netherlands, blooms of this species in Lake Trummen (Sweden), Kinneret (Israel), and Lajes reservoir (Brazil) were also reported, with nitrate as the main factor for its growth (Recknagel et al. 2015; Joosten 2017). Although *C. imperfecta* has no known cyanotoxin, high cyanobacterial abundance during blooms can be detrimental to the lake's biodiversity, as the algae decomposition can cause hypoxia, resulting in fish kills and ecosystem disruption (San Diego-McGlone et al. 2024). The warmer water temperature and cyanobacterial bloom may also have contributed to the displacement of the mixotrophic dinoflagellate species *C. furcoides* and *Peridinium* sp. from the euphotic zone during SWM, potentially causing them to migrate to the colder, low-light and deeper layers via vertical migration (Macêdo et al. 2021; da Silva et al. 2024). In OIM, the water temperature and pH were similar to the SWM, however, the lower phytoplankton density and higher turbidity in the SB indicated large amounts of suspended particles were present in the upper layers. This reflects the ongoing physical mixing as the lake transitions from stratification to a fully mixed state in NEM (de Leon et al. 2024). Additionally, the low oxygen, turbidity, and phytoplankton density in the NB may indicate low nutrients in the euphotic layers as driven by the recent bloom during SWM. Lake stratification limits nutrient exchange with the thermocline acting as a physical barrier, decreasing the overall phytoplankton density in the euphotic zones (Jung et al. 2016; Mesman et al. 2021; Cui et al. 2023).

The CCA and NMDS ordinations supported that seasonal mixing regime, and environmental homogeneity shaped the phytoplankton distribution within the euphotic layers. Clusters suggest that although community composition differed, the variation was subtle and monsoons shared considerable similarity, reducing the visual distinctness of the separation. These monsoonal events drive seasonal changes in water circulation, nutrient availability, and biological activity, influencing the fluctuations of phytoplankton biomass and diversity (Gal et al. 2016; Jung et al. 2016; Yang et al. 2017; Kim and Kim 2021). Temporal variation can be caused by environmental conditions such as the seasonal changes in temperature, pH, and turbidity, while spatial variation was likely due to subtle spatial factors, including depth, local nutrient concentrations, and other local hydrodynamic conditions in each basin. This also supports an earlier study conducted in the lake linking monsoonal mixing patterns to phytoplankton variability (Rott et al. 2008).

This study gives a snapshot of seasonal variations of phytoplankton communities, which aids in predicting their abundance in similar tropical eutrophic caldera lakes. Other factors, like microclimatic conditions, can vary within monsoons. The study detected differences in phytoplankton abundance between aquaculture and non-aquaculture areas. However, to fully understand the impact of nutrient loading from aquaculture on phytoplankton communities, further research should include specific nutrient parameters in their sampling. An in-depth study of the vertical distribution of phytoplankton is recommended to verify and determine the overall effects of mixing regimes and other environmental factors that contribute to their abundance and distribution in the vertical column. Furthermore, as the country heavily relies on aquaculture for local livelihood and national economic progress, continuous lake monitoring and the carrying capacity of the lake should be strictly monitored to prevent excessive phytoplankton abundance. Ecological restoration and cessation of aquaculture can restore phytoplankton communities to more natural states, but ongoing nutrient control is essential for lasting improvements (Ji et al. 2016; Xu et al. 2022). Continuous monitoring is also imperative to estimate the onset of phytoplankton blooms and prevent adverse effects on the lake and fisheries, as warming and excessive nutrient loading can trigger their presence. Regular phytoplankton and water quality monitoring are necessary to manage risks and guide sustainable aquaculture practices (Ji et al. 2016; Hoang et al. 2024; De Almeida et al. 2025).

In conclusion, monsoon-driven environmental changes, specifically temperature, dissolved oxygen, and turbidity, significantly influenced phytoplankton abundance and dominance in aquaculture and non-aquaculture areas in Lake Taal. Phytoplankton abundance was higher in aquaculture sites due to the difference in turbidity, temperature, and dissolved oxygen. Meanwhile, the observed similarity in abundance and diversity across depths can be attributed to the homogeneity of environmental conditions within the surface waters. Lastly, the recent phreatic eruption altered the physicochemical properties of the lake but had no effect on the phytoplankton composition; hence, other environmental factors may have contributed to the changes observed. The study provides insights into the phytoplankton dynamics crucial for monitoring and regulation in a eutrophic tropical caldera lake. By integrating the study’s findings into conservation and management plans, local governments can develop sustainable aquaculture while addressing the lake’s ecological challenges.

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