ORIGINAL ARTICLE

Phytoplankton functional group dynamics and environmental drivers in a tropical monomictic lake (Lake Yambo, Philippines)

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ABSTRACT

Tropical monomictic lakes, characterized by a single annual mixing event and prolonged stratification, are particularly sensitive to climatic and anthropogenic pressures. Lake Yambo, a tropical monomictic lake in the Philippines, exemplifies such systems, with stratification prevailing during the southwest monsoon and full lake mixing occurring during the northeast monsoon. This study examined vertical and seasonal variations in environmental conditions and phytoplankton functional group composition in Lake Yambo to assess how seasonal stratification and mixing affect functional groups' vertical structure. Monthly sampling from March 2024 to February 2025 was conducted from the subsurface to 30 meters at 5-meter intervals. *In situ* measurements of water temperature, dissolved oxygen, pH, and nitrate (NO_3^-) were obtained using multiparameter probes, while chlorophyll-a, ammonia, and total phosphorus were analyzed in the laboratory. Phytoplankton samples were collected, identified, and counted, with species comprising at least 5% of the total phytoplankton biomass per period classified into their respective functional groups. Lake Yambo exhibited meso-eutrophic conditions characterized by high total phosphorus concentrations but comparatively low chlorophyll-a levels, suggesting that phytoplankton growth is likely limited by nitrogen availability. Seasonal patterns governed thermal stratification and mixing, which, in turn, regulated vertical nutrient gradients. Stratified conditions during the southwest monsoon led to nutrient trapping and hypolimnetic anoxia, while northeast monsoon mixing redistributed nutrients, particularly NO_3^-. These transitions strongly influenced the functional group composition. Seven dominant functional groups (B, F, G, H1, J, L_O, and P) comprised 81% to 97% of the total phytoplankton biomass. Most functional groups declined with depth, but seasonal and vertical variations were distinct: Group G and H1 thrived in warmer surface waters with low nitrate concentrations. Groups J and L_O were associated with cooler, nitrate-enriched surface layers during peak mixing, while Groups B, F, and P were more abundant at deeper layers under the same conditions. These findings support the hypothesis that seasonally driven stratification and mixing in tropical monomictic lakes structure vertical nutrient availability and shape phytoplankton functional group dynamics. Notably, the bloom of Group H1 during post-peak mixing under extreme nitrogen limitation and elevated temperatures poses a health risk, as this group's descriptor taxon, *Dolichospermum*, can produce cyanotoxins. Thus, tropical monomictic lakes experiencing greater eutrophication may face increased risks of these toxic blooms. As a representative tropical monomictic system, Lake Yambo offers valuable insights into how similar systems respond to seasonal mixing and nutrient limitations, providing a framework for understanding and managing ecological risks in these environments.

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Key words: lake monitoring; mixing regime; nutrient dynamics; phytoplankton; tropical lakes.

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INTRODUCTION

Phytoplankton is widely recognized as a biological indicator of water quality due to its distinct and rapid response to environmental changes (Bellinger and Sigee, 2015). Understanding the dynamics of phytoplankton communities and their environmental drivers at various spatial and temporal scales is critical for informed management of eutrophication and recurrent algal blooms (Wang *et al*., 2011). Traditional species-level approaches have provided foundational insights into phytoplankton ecology; however, their application is often limited by the high diversity and taxonomic complexity of phytoplankton communities (Huisman and Weissing, 2001). An increasingly adopted strategy is the use of trait-based approaches such as the phytoplankton functional group model proposed by Reynolds *et al*. (2002), which groups phytoplankton species based on shared ecological traits and environmental preferences (Padisák *et al.*, 2009; Borics *et al.*, 2015). Since environmental factors tend to affect functional traits more than species identity, Reynold's model provides advantages in identifying key ecological processes, summarizing community patterns, and predicting how phytoplankton respond to environmental changes (Longhi and Beisner, 2010; Kruk *et al*., 2021).

While Reynold's functional grouping has been successfully applied in tropical freshwater systems, most functional group-based studies have focused on shallow, polymictic lakes that mix frequently and exhibit rapid environmental variability (Rangel *et al*., 2009; Gebrehiwot *et al*., 2017; da Silva *et al*., 2018). In contrast, tropical monomictic lakes, which stratify for long periods and mix only once a year, have received relatively less scholarly attention. This represents a significant gap in current research, particularly because many tropical lakes fall into this category and are highly vulnerable to nutrient loading and climate-induced changes (Lewis, 2000). In the Philippines, several lakes are classified as warm monomictic, including Lake Lanao (Lewis, 1973), Lake Taal (De Leon *et al*., 2024), and Lakes Sampaloc, Mohicap, Bunot, and Yambo (Aguilar *et al.,* 2023).

Lake Yambo, a representative example of a tropical monomictic lake in the Philippines, stratifies during the southwest monsoon and mixes during the northeast monsoon, with full mixing typically occurring in February (Aguilar *et al*., 2023). Recent studies have highlighted the sensitivity of tropical monomictic lakes to anthropogenic and climatic pressures. For instance, Bannister *et al.* (2019) reported that intensive aquaculture in combination with climate warming can increase the frequency of harmful algal blooms, expand anoxic zones, and trigger periodic fish kills. Likewise, Briddon *et al.* (2023) found that elevated phosphorus loading and reduced light availability can worsen nitrogen limitation, favoring the growth of nitrogen-fixing cyanobacteria.

Despite growing awareness of these pressures, limited research has addressed how phytoplankton functional groups respond to environmental variability in tropical monomictic systems. To address this gap, this study investigated the seasonal and vertical variations in environmental variables and phytoplankton functional group composition in Lake Yambo, emphasizing how the interactions of key environmental drivers shape their dynamics. We hypothesize that in tropical monomictic lakes, seasonally driven thermal stratification and mixing events act as key regulators of nutrient redistribution, thereby influencing the vertical and temporal distribution of phytoplankton functional groups.

METHODS

Study area

Lake Yambo (14.1160° N, 121.3670° E) is one of the seven maar lakes located in San Pablo, Laguna, Philippines (Fig. 1), be-

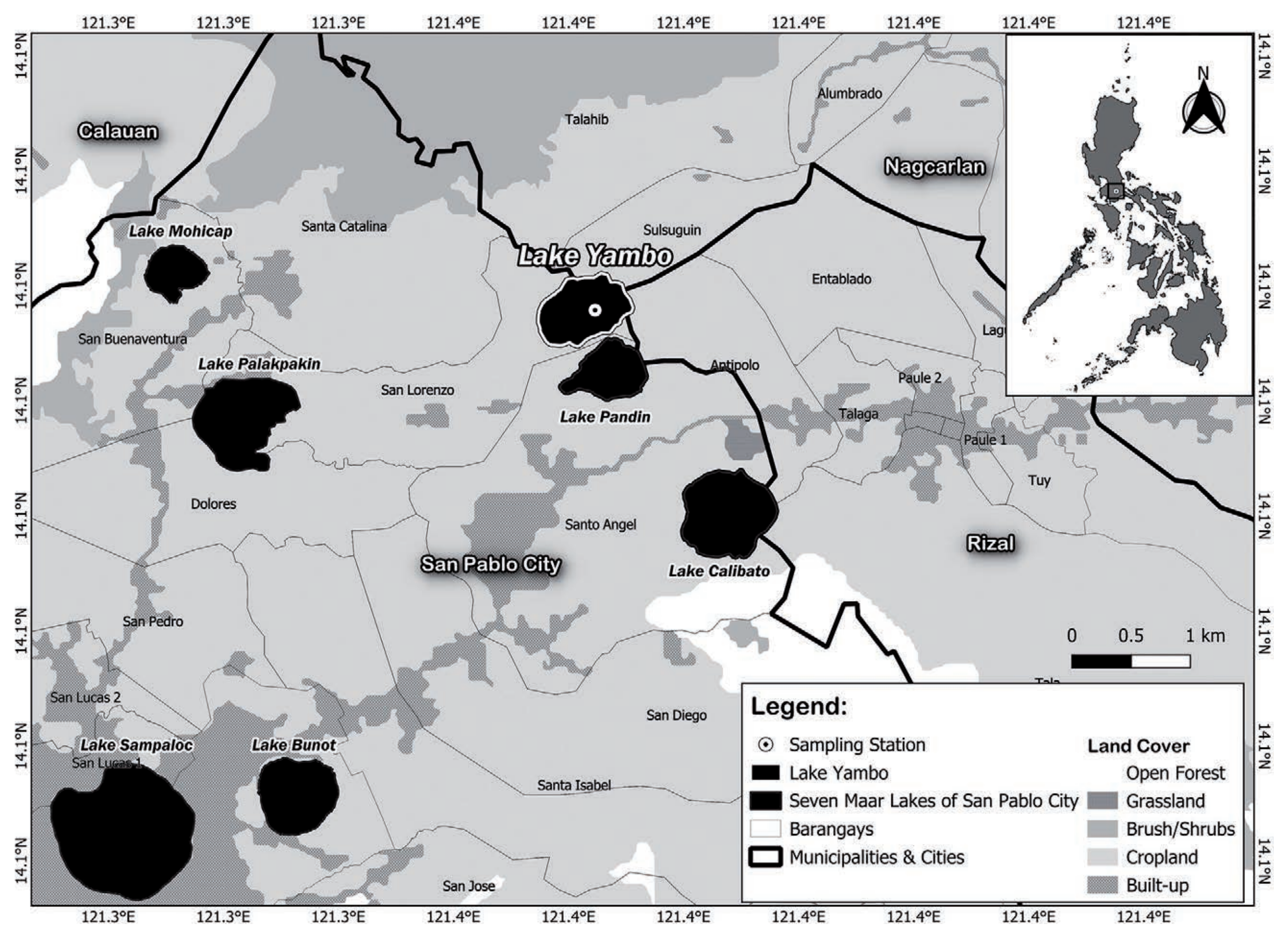

Fig. 1. Map of the sampling station in Lake Yambo, Laguna, Philippines.

lieved to have formed through a phreatic eruption of Mount Banahaw-San Cristobal (Zapanta *et al*., 2008). It is situated at an elevation of 160 m asl, with a maximum depth of 38 m and a surface area of 30.5 ha. The lake receives water primarily from rainfall, surface runoff, and inflow from a local creek known as "Kali-e," which originates from Mt. Mabilog (Brillo, 2016). Lake Yambo is distinct among the seven maar lakes due to its endorheic nature, resulting in water loss only through seepage and evaporation. As a result, the lake's surface area fluctuates significantly, shrinking during the dry season and expanding during the rainy season. Its remote location, farther from major roads and the city center, also makes it less vulnerable to urban expansion (Bannister *et al*., 2019). Furthermore, it had the smallest lakeshore population among the seven maar lakes in 2015, with only around 2,000 residents (Mendoza-Pascual *et al.*, 2021).

The climate of the Philippines is primarily influenced by two prevailing monsoon seasons: the southwest monsoon and the northeast monsoon. The southwest monsoon typically produces a pronounced wet season from May to October, while the northeast monsoon brings a dry season from November to April (Aguilar *et al.*, 2023). The seven maar lakes, including Lake Yambo, fall under a Type 1 climate, characterized by a short dry season annually (Mendoza-Pascual *et al.*, 2021). Lake Yambo exhibits a warm monomictic mixing regime, with one mixing period occurring annually during the northeast monsoon, peaking in February (Bannister *et al*., 2019; Bicaldo *et al*., 2024).

Environmental data collection and analysis

Monthly fieldwork was conducted from March 2024 to February 2025. However, sampling for July and October could not be conducted due to unforeseen circumstances and weather disturbances. Sampling was conducted as early as possible in August to compensate for the missing July data. No alternative sampling was possible for October, resulting in a gap in the dataset.

In situ measurements of water temperature [C°], dissolved oxygen (DO) [mg L^{-1}], pH, conductivity [µS cm^{-1}], total dissolved solids (TDS) [ppm], salinity [ppt], and turbidity (FNU) were recorded throughout the water column using a YSI multiparameter sonde (EXO2, YSI Inc., USA). Nitrate (NO_3^-) [mg L^{-1}] concentration was measured using a Hach IntelliCAL™ Nitrate Electrode, calibrated with nitrate-nitrogen standards. For ammonia (NH_3) [mg L^{-1}] and total phosphorus (TP) [mg L^{-1}] analysis, 100 mL triplicate samples of unfiltered water were collected at seven depths (surface to 30 m) in 5 m increments using a 5 L Niskin sampler. Triplicate 1 L water samples for chlorophyll-a (Chl-a) [µg L^{-1}] analysis were collected in opaque high-density polyethylene bottles. NH_3 was analyzed using the phenate method, while TP was measured using persulfate digestion followed by the ascorbic acid method. Standard protocols for sample collection, preservation, and analysis were followed (Baird *et al*., 2017). Chl-a values were calculated using the trichromatic method, accounting for absorbance at 750 nm to correct for turbidity (Jeffrey and Humphrey, 1975). The trophic status of Lake Yambo was evaluated using the Trophic State Index (TSI) models of Lamparelli (2004) and Cunha *et al.* (2013), which were designed for tropical waters.

Phytoplankton collection and analysis

Phytoplankton samples were also collected at seven depths (surface to 30 m) in 5 m increments using a 5 L Niskin sampler. 1 L of water was collected at each depth and preserved with 40 mL of buffered formalin, prepared by dissolving 20 g of sodium borate in 1 L of 37% formaldehyde (Baird *et al*., 2017). Samples were concentrated using the sedimentation method by leaving sampling bottles undisturbed for 24 hours (Edler and Elbrächter, 2010). After settling, 750 mL of the supernatant was siphoned off with a 2 mm hose. The remaining 250 mL was transferred to a smaller container, left to settle for another 24 hours, then reduced to 50 mL by siphoning off 200 mL. Counting was performed in triplicate by extracting a 1 mL aliquot from the 50 mL concentrated sample. Each aliquot was placed in a Sedgewick-Rafter counting chamber and allowed to settle for 15-20 min. Phytoplankton micrographs were captured using an Olympus BX53 microscope (Olympus Corporation, Tokyo, Japan) equipped with a Moticam camera (Motic, Hong Kong) to aid in morphological identification using taxonomic guides (van Vuuren *et al*., 2006; Tamayo-Zafaralla, 2014; Bellinger and Sigee, 2015). Identification and counting were performed at 400× magnification, and cell density per taxon was calculated following Mitrovic and Croome (2009). Phytoplankton biovolume was calculated based on the geometric configuration of each taxon using the formulas from Hillebrand *et al*. (1999). A calibrated Moticam microscope camera software was used to measure 20-30 individuals per taxon to determine the average biovolume. Algal biovolume per taxon per month was calculated by multiplying the mean cell density of each taxon by its corresponding biovolume. Biovolume was converted to fresh-weight biomass, assuming a specific gravity of 1.0, where 1 mm^3 L^{-1} = 1 mg L^{-1} (Xiao *et al*., 2011). Species contributing at least 5% of the total biomass per month were considered dominant and classified into their respective functional groups based on the classification proposed by Reynolds *et al*. (2002) and revised by Padisák *et al*. (2009).

Data visualization and statistical analysis

Environmental parameters were analyzed using linear mixed-effects models (LMMs) or generalized linear mixed-effects models (GLMMs) with a Gamma distribution, depending on the data distribution. Variables approximating normality were modeled with LMMs, while positively skewed variables without zeros were analyzed using Gamma GLMMs with a log link function. Both model types included fixed effects of depth, season, and their interaction to assess seasonal differences in vertical patterns. Month was included as a random intercept to account for repeated temporal measurements. Season-specific slope estimates were calculated, and 95% confidence intervals were visualized as shaded ribbons on the response scale to represent model uncertainty. To capture monthly vertical variations in key environmental variables that could not be fully revealed by the regression, especially during peak mixing events that cause full lake turnover, contour maps were employed.

Tweedie GLMMs were employed to accommodate the zero-inflated and continuous nature of the data to assess depth- and season-related patterns in the biomass of each functional group. Depth, season, and their interaction were treated as fixed effects, with month as a random effect. Season-specific slopes and 95% confidence intervals were similarly visualized with shaded ribbons. Monthly vertical biomass distributions of each functional group were illustrated using contour maps to highlight both temporal and depth-related trends, particularly during periods of peak mixing. In addition, stacked bar charts were used to depict monthly changes in the relative biomass composition of each functional group.

Detrended Correspondence Analysis (DCA) indicated an Axis 1 gradient length of 3.12, supporting Canonical Correspondence Analysis (CCA) over Redundancy Analysis (RDA) due to higher adjusted R^2 (0.161 *vs* 0.026). Log (x + 1) transformation was applied to positively skewed variables, and variables with a Variance Inflation Factor >20 were removed to reduce multicollinearity. Forward selection with a Monte Carlo Permutation Test (999 permutations) identified significant depth-related environmental drivers ($p<0.05$) retained in the final CCA plot. Contour maps were visualized in SigmaPlot version 15.0, and the rest of the data visualization and analyses were done in RStudio version 3.6.

RESULTS

Trophic status

Lake Yambo exhibited meso-eutrophic conditions based on Trophic State Index (TSI) values calculated using two established models. The annual mean TSI was 58.0 ± 1.2 using Lamparelli (2004) and 56.0 ± 0.9 following Cunha *et al*. (2013), corresponding to mesotrophic and eutrophic classifications, respectively. Monthly assessments showed that both models identified eutrophic conditions in November and December, coinciding with elevated nutrient levels (Tab. 1). Using Cunha's criteria, the lake was classified as eutrophic in 6 out of 12 months, while Lamparelli's model indicated eutrophic conditions in only 2 months. These differences reflect variation in threshold criteria, but both models point to a transitional trophic state.

Vertical and seasonal dynamics of environmental factors

Seasonal changes in tropical, warm monomictic lakes like Lake Yambo strongly influence vertical structure, yet not all environmental parameters respond to these monsoon-driven shifts. Turbidity, conductivity, total phosphorus (TP), and pH exhibited strong vertical patterns that remained consistent across seasons. Turbidity ($p<0.001$), conductivity ($p<0.0001$), and TP ($p<0.05$) increased significantly with depth, while pH values dropped ($p<0.0001$), indicating that these parameters are primarily regulated by depth-driven processes rather than seasonal shifts (Fig. 2).

In contrast, water temperature, dissolved oxygen (DO), ammonia (NH_3), nitrate (NO_3^-), and chlorophyll-a (Chl-a) were closely tied to seasonal dynamics. Water temperature ($p<0.0001$) and DO ($p<0.001$) consistently decrease with depth but showed steeper declines during the southwest monsoon ($p<0.0001$). Surface waters were about 2.55°C colder during the northeast monsoon, indicating stronger thermal stratification during the southwest monsoon. This pronounced stratification restricted oxygen penetration, contributing to hypoxic conditions (<1 mg L^{-1}) in the hypolimnion.

Ammonia (NH_3) concentrations increased with depth ($p<0.0001$), with a sharper gradient during the southwest monsoon ($p<0.001$), reflecting enhanced trapping of NH_3 in the deeper, isolated layers. On the other hand, nitrate (NO_3^-) levels declined significantly with depth ($p<0.001$) only during the southwest monsoon, while remaining relatively stable throughout the water column during the northeast monsoon. This pattern suggests that stratification during the southwest monsoon restricts vertical mixing, leading to nutrient segregation.

Chlorophyll-a (Chl-a) concentrations demonstrated subtle but important differences between seasons. During the southwest monsoon, Chl-a showed a slight but non-significant increase at depth (β = +0.00406, p=0.1675), possibly indicating some phytoplankton adaptation to deeper light zones. However, during the northeast monsoon, Chl-a concentrations significantly decreased with depth (β = -0.00990, $p<0.01$), suggesting surface accumulation during active mixing when nutrients are more available in the photic zone.

The monthly vertical profiles highlighted critical changes during peak mixing in January and February (Fig. 3). NH_3 concentrations dropped across the water column, while NO_3^- levels increased, indicating active nutrient redistribution. The vertical profile of TP revealed notable increases during early mixing, followed by reductions in deeper layers as mixing intensified. Chl-a also displayed clear vertical shifts, peaking just below the thermocline (20

Tab. 1. Monthly Trophic State Index (TSI) values and classifications in Lake Yambo (March 2024-February 2025) based on two calculation methods.

Month	TSI_{LA}				TSI_{CU}			
	Chl-a	TP	Average	Classification	Chl-a	TP	Average	Classification
Mar. 2024	52.34	61.14	56.74	Mesotrophic	52.00	58.37	55.18	Mesotrophic
Apr. 2024	52.21	61.78	56.99	Mesotrophic	51.90	58.79	55.34	Mesotrophic
May 2024	51.76	60.40	56.08	Mesotrophic	51.57	57.88	54.72	Mesotrophic
June 2024	53.21	62.95	58.08	Mesotrophic	52.64	59.56	56.10	Eutrophic
Aug. 03, 2024	53.80	64.99	59.40	Mesotrophic	53.08	60.90	56.99	Eutrophic
Aug. 30, 2024	53.50	62.71	58.11	Mesotrophic	52.85	59.40	56.13	Eutrophic
Sept. 2024	52.44	62.45	57.44	Mesotrophic	52.07	59.23	55.65	Mesotrophic
Nov. 2024	54.66	64.69	59.68	Eutrophic	53.71	60.71	57.21	Eutrophic
Dec. 2024	55.06	63.99	59.53	Eutrophic	54.01	60.25	57.13	Eutrophic
Jan. 2025	54.58	61.52	58.05	Mesotrophic	53.65	58.62	56.13	Eutrophic
Feb. 2025	51.41	62.22	56.81	Mesotrophic	51.31	59.08	55.19	Mesotrophic

Chl-a, chlorophyll a; TP, total phosphorus; TSI_{LA}, Lamparelli (2004); TSI_{CU}, Cunha *et al.* (2013).

m) during the southwest monsoon, at 25 m during early mixing, and concentrating at the surface during peak mixing.

Vertical and seasonal distribution of phytoplankton functional groups

A total of 38 phytoplankton genera from five phyla were identified in Lake Yambo. Chlorophyta and Charophyta (green algae) were the most species-rich (43.59%), followed by Bacillariophyta (diatoms) at 35.90%, Cyanophyta (cyanobacteria) at 15.38%, and Dinophyta (dinoflagellates) at 5.13%. Seven dominant phytoplankton functional groups (B, F, G, H1, J, L_O, and P) accounted for 81% to 97% of total biomass monthly (Tab. 2). All functional groups showed a clear decline in biomass with increasing depth, although the patterns varied by season (Fig. 4). Interestingly, Groups F (southwest monsoon: β = –0.118, p<0.0001; northeast monsoon: β = –0.118, p<0.0001) and G (southwest monsoon: β = –0.116, p<0.05; northeast monsoon: β = –0.170, p<0.05) maintained significant declines at depth across both monsoon seasons, with no observable seasonal differences. In contrast, Groups B and L_O exhibited higher biomass during the northeast monsoon (p<0.05 and p<0.01, respectively) and declined significantly with depth only during this season (β = –0.0285, p<0.05; β = –0.233, p<0.001). The biomass of Group J declined sharply with depth during the southwest monsoon (β = –0.1089, p<0.0001), while in the northeast monsoon, the decline was more gradual (β = –0.0446, p<0.001). Similarly, Group P showed a sharper decline with depth during the southwest monsoon, although this trend was not statistically significant (p=0.205).

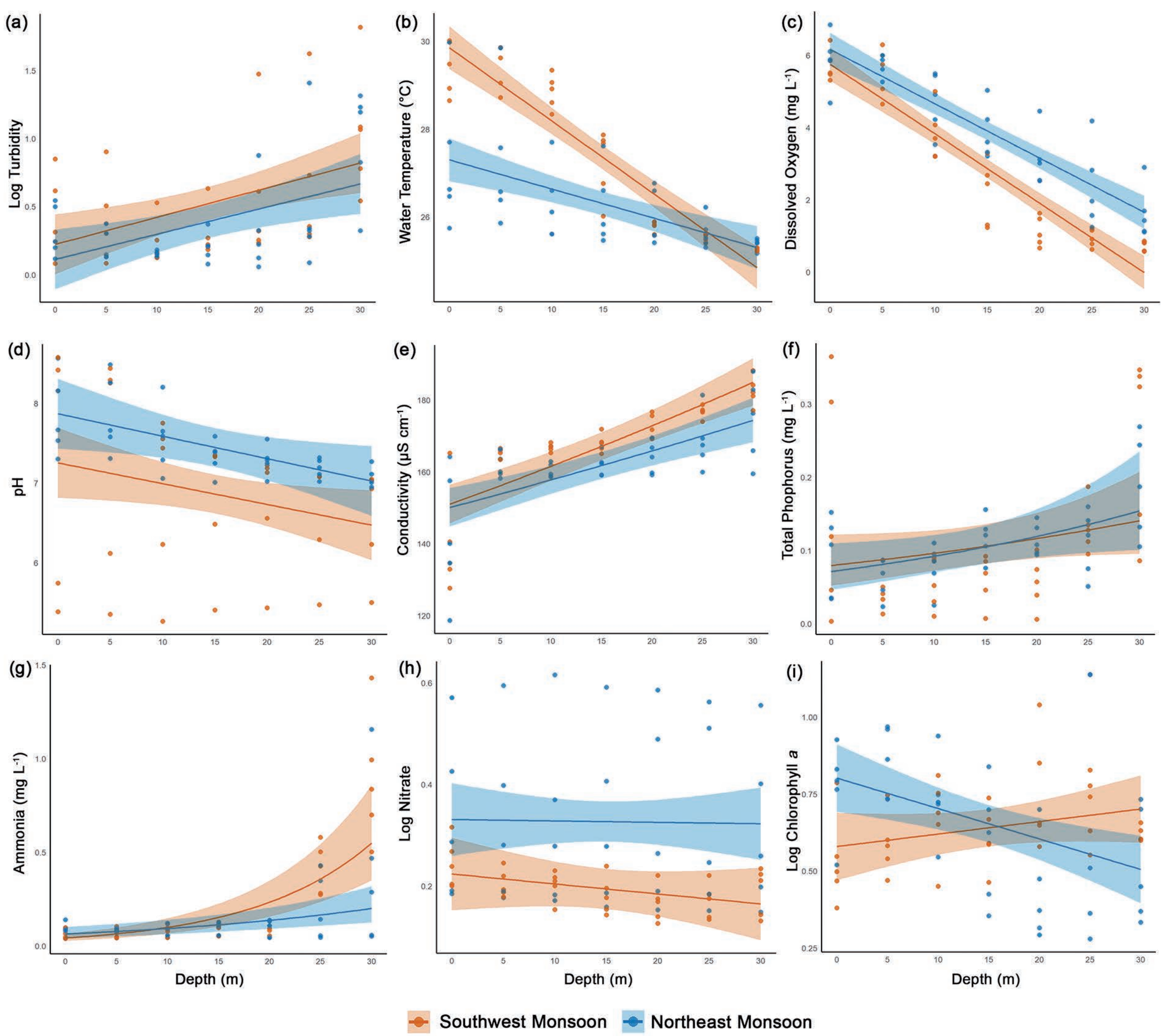

Fig. 2. Seasonal variation in environmental variables across depths modeled using mixed-effects analyses. a) Log turbidity; b) temperature; c) dissolved oxygen; d) pH; e) conductivity; f) total phosphorus; g) ammonia; h) log nitrate; i) log chlorophyll-a. Shaded areas show 95% confidence intervals.

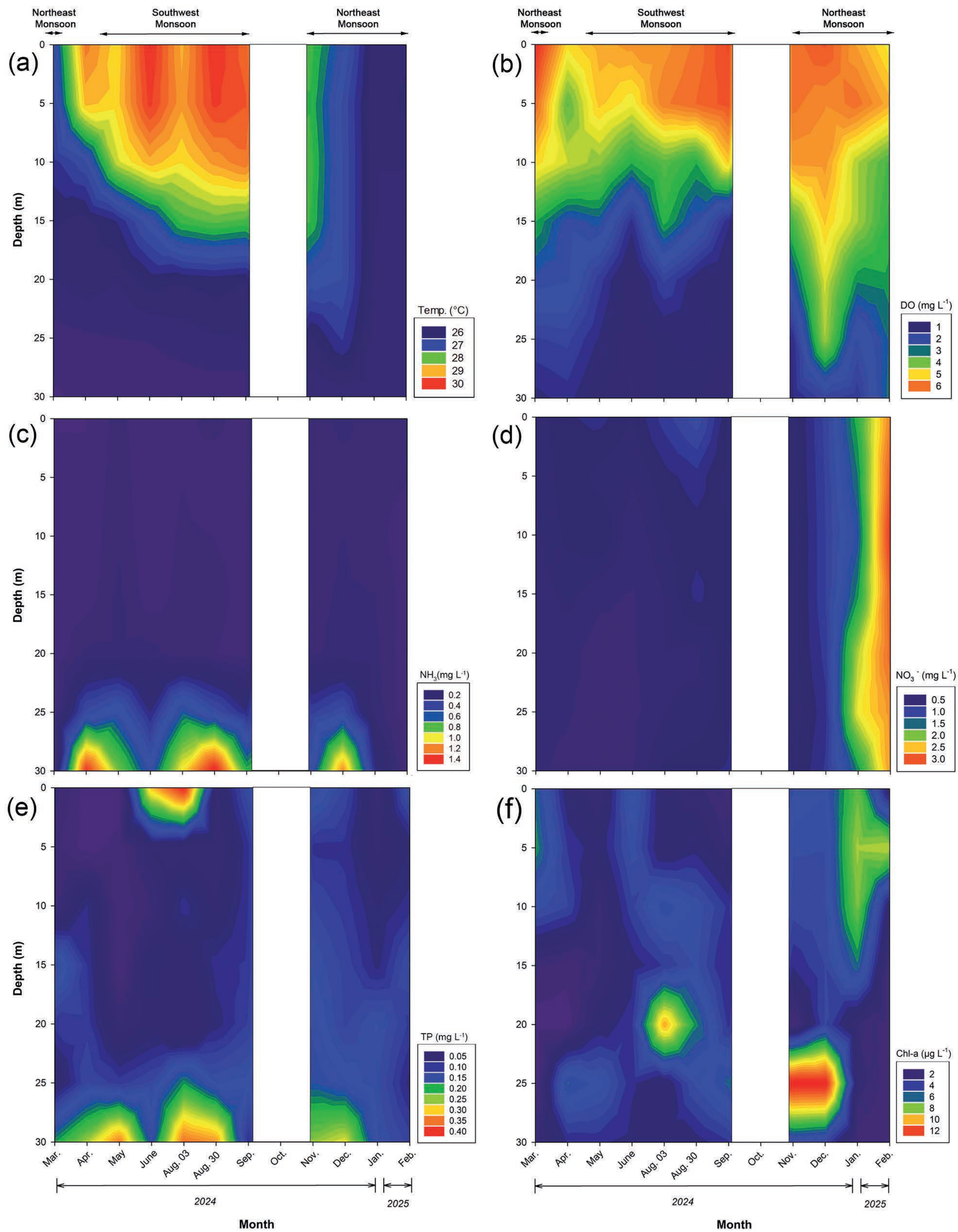

Fig. 3. Monthly vertical profiles of temperature (a), dissolved oxygen (DO) (b), ammonia (NH_3) (c), nitrate (NO_3^-) (d), total phosphorus (TP) (e), chlorophyll-a (Chl-a) (f) from March 2024 to February 2025.

Monthly vertical profiles further illustrated these dynamics, capturing peak mixing trends (Fig. 5). For instance, although both Groups B and L_O declined at depth during the northeast monsoon, Group B was detected as deep as 20 m, while Group L_O was mostly confined to the upper 10 m during peak mixing. Group H1 emerged only after peak mixing and was absent throughout the rest of the year. Despite the depth-driven declines of Groups J and P in the regression analysis, vertical profiles revealed that both still maintained substantial biomass at deeper depths during peak mixing, reaching as far as 30 m.

The relative biomass composition of the seven dominant functional groups showed clear seasonal shifts (Fig. 6). Group P dominated throughout the year, except in June and November when Group G sharply increased to 84.39% and 64.06%, respectively. Group F was most abundant during transitional months (April: 20.96%; September: 47.32%), while Groups L_O (24.09%) and H1 (20.82%) peaked at the end of the northeast monsoon, reflecting their preference for mixing-driven conditions. Group J reached its highest relative biomass during the northeast to southwest monsoon transition (April: 10.83%). Total biomass was significantly higher during the southwest monsoon (p=0.004), underscoring the influence of stratification on surface productivity.

Environmental drivers of phytoplankton functional group dynamics

The Canonical Correspondence Analysis (CCA) revealed that the distribution of the biomass of the phytoplankton functional groups in Lake Yambo is strongly influenced by four key environmental drivers: NO_3^-, water temperature, pH, and conductivity (Fig. 7). The first two CCA axes accounted for 90.13% of the total constrained variance, with CCA1 explaining 61.03% and CCA2 explaining 29.11%. CCA1 was positively related to NO_3^- (r = 0.913) and negatively associated with water temperature (r = -0.970), while CCA2 was positively associated with pH (r = 0.722) and conductivity (r = 0.856). pH and conductivity may indicate vertical position, since the regression analysis showed that pH is higher near the surface and conductivity is greater at depth, regardless of monsoon seasons. Groups B, F, and P were positively associated with NO_3^- and conductivity but negatively with water temperature and pH, suggesting these groups thrive in nutrient-rich, cooler conditions and extend deeper to access nutrients. Groups J and L_O showed higher biomass in cooler, alkaline waters with elevated NO_3^- and lower conductivity, indicating a preference for nutrient-rich surface layers typical of mixed conditions. In contrast, Groups G and H1 increased in biomass with higher water temperature and pH, but declined with rising NO_3^- and conductivity. This pattern suggests adaptation to NO_3^--limited, warmer surface waters during stratification.

DISCUSSION

Trophic status and nutrient limitation

The trophic status of Lake Yambo has been characterized differently over time, with earlier assessments relying on single parameters rather than a combined Trophic State Index (TSI). Between 2006 and 2008, the lake was classified as oligotrophic, characterized by low nutrients and high dissolved oxygen levels (Zapanta *et al*., 2008). In 2016–2017, it was considered mesotrophic based on elevated chlorophyll-a (Chl-a) concentrations (Mendoza *et al*., 2019). More recent evaluations indicated eutrophic to hypereutrophic conditions driven by high total phosphorus (TP) levels (Mendoza-Pascual *et al*., 2021). In this study, Lake Yambo is categorized as mesotrophic to eutrophic using an integrated TSI that incorporates both TP and Chl-a. Although TP concentrations reached hypereutrophic thresholds, relatively low Chl-a concentrations moderated the overall TSI score.

The total nitrogen (TN) to TP ratio is commonly used to assess the limiting nutrient for phytoplankton growth. However, the relatively low Chl-a despite high TP is consistent with patterns observed in other deep tropical lakes, likely indicating nitrogen (N) limitation (Quinlan *et al*., 2020). Two factors likely explain this decoupling: phosphorus (P) retention below the euphotic zone due to thermal stratification and N limitation. Stratification traps P-rich particles in the hypolimnion, reducing P availability in surface waters (Riley and Prepas, 1985; Qin *et al*., 2020). Additionally, Lewis (1974) suggested that N limitation is likely in tropical lakes, including Lake Lanao, Philippines, due to high N loss from denitrification in warm conditions, which can limit phytoplankton growth.

In Lake Yambo, seasonal shifts in nitrate (NO_3^-) availability influence which phytoplankton functional groups dominate, shaping ecological responses and informing water quality management. Identifying this possible primary limiting nutrient in Lake Yambo is therefore essential for the formation of effective eutrophication mitigation strategies (Ansari and Gill, 2014).

Tab. 2. Descriptor phytoplankton species (≥5% of the total biomass), their functional group, and monthly total biomass from 0 m to 30 m in Lake Yambo.

Descriptor species	Functional group	Monthly total biomass (mg L^{-1}) Mar.	Apr.	May	June	Aug. 03	Aug. 30	Sep.	Nov.	Dec.	Jan.	Feb.
Discostella sp.	B	0.055	0.020	0.005	0.001	0.024	0.007	0.796	0.149	0.221	0.112	0.355
Oocystis spp.	F	0.277	0.241	0.042	0.106	0.020	0.132	1.268	0.042	0.127	0.008	0.225
Volvox sp.	G	0.507	0.000	0.000	3.978	0.833	2.952	0.000	4.045	0.000	0.000	0.000
Dolichospermum sp.	H1	0.397	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
Pediastrum sp., *Tetraedron* sp.	J	0.064	0.125	0.192	0.188	0.049	0.068	0.059	0.053	0.041	0.005	0.106
Ceratium sp.	L_O	0.018	0.011	0.000	0.000	0.000	0.007	0.013	0.042	0.016	0.116	1.031
Staurastrum sp., *Aulacoseira granulata*, *Aulacoseira* sp.	P	0.418	0.540	3.113	0.146	4.799	5.095	0.425	1.676	1.499	3.686	2.168

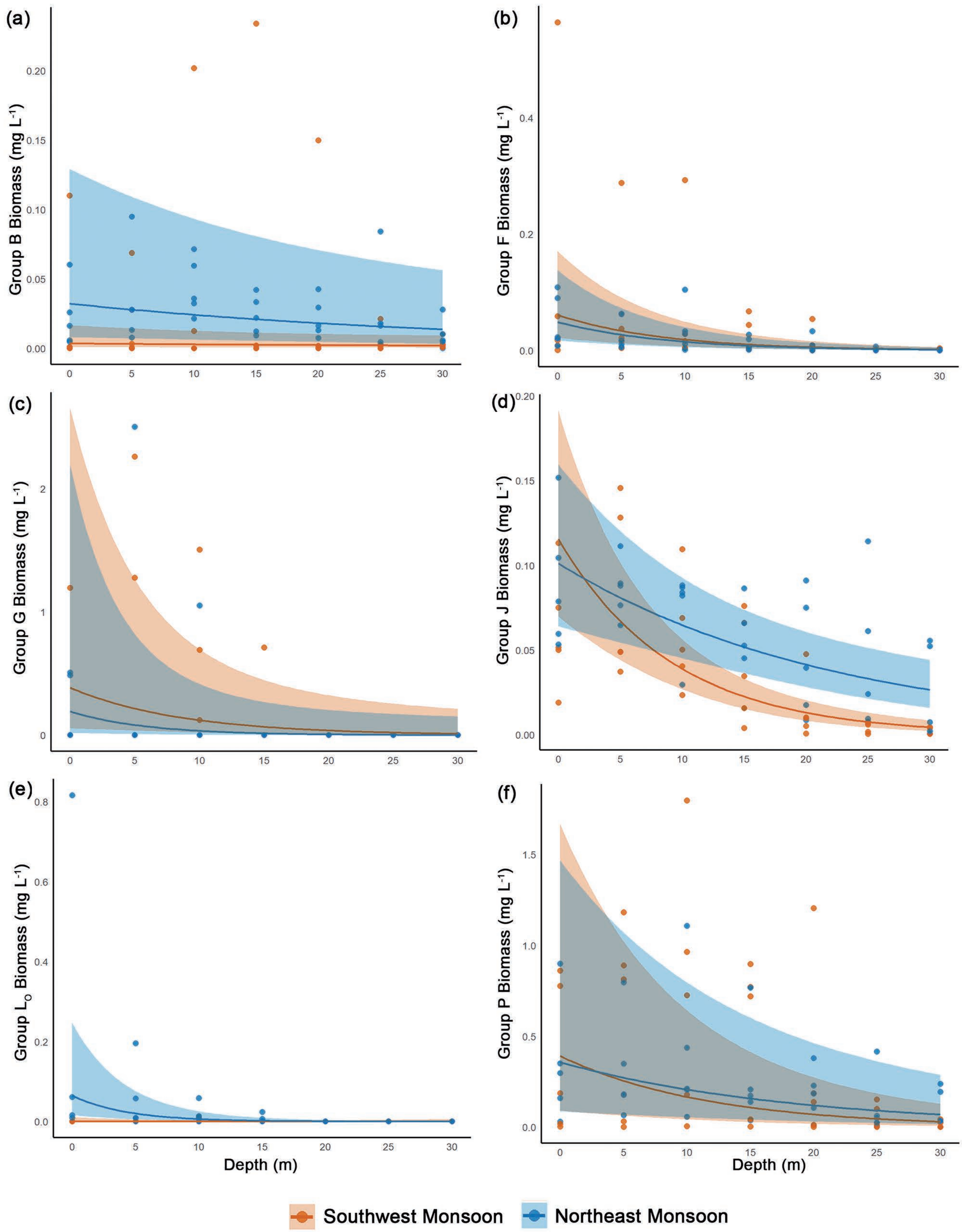

Fig. 4. Seasonal variation in biomass of the dominant phytoplankton functional groups with depth modeled using Tweedie generalized mixed-effect models. a) Group B; b) Group F; c) Group G; d) Group J; e) Group Lo; f) Group P. Shaded areas show 95% confidence intervals.

Seasonal stratification and mixing as drivers of environmental conditions and phytoplankton functional group dynamics

Monsoon-driven stratification and mixing in Lake Yambo structured the vertical patterns in temperature, oxygen, and nutrient profiles. During the southwest monsoon, surface heating and weak winds led to strong thermal stratification and hypolimnetic anoxia (Mendoza-Pascual *et al*., 2021). In contrast, stronger winds during the northeast monsoon triggered mixing, gradually breaking down stratification and reoxygenating the hypolimnion (Aguilar *et al*., 2023).

Nutrient profiles followed a similar seasonal pattern. Ammonia (NH_3) accumulated in the hypolimnion under stratified, low-

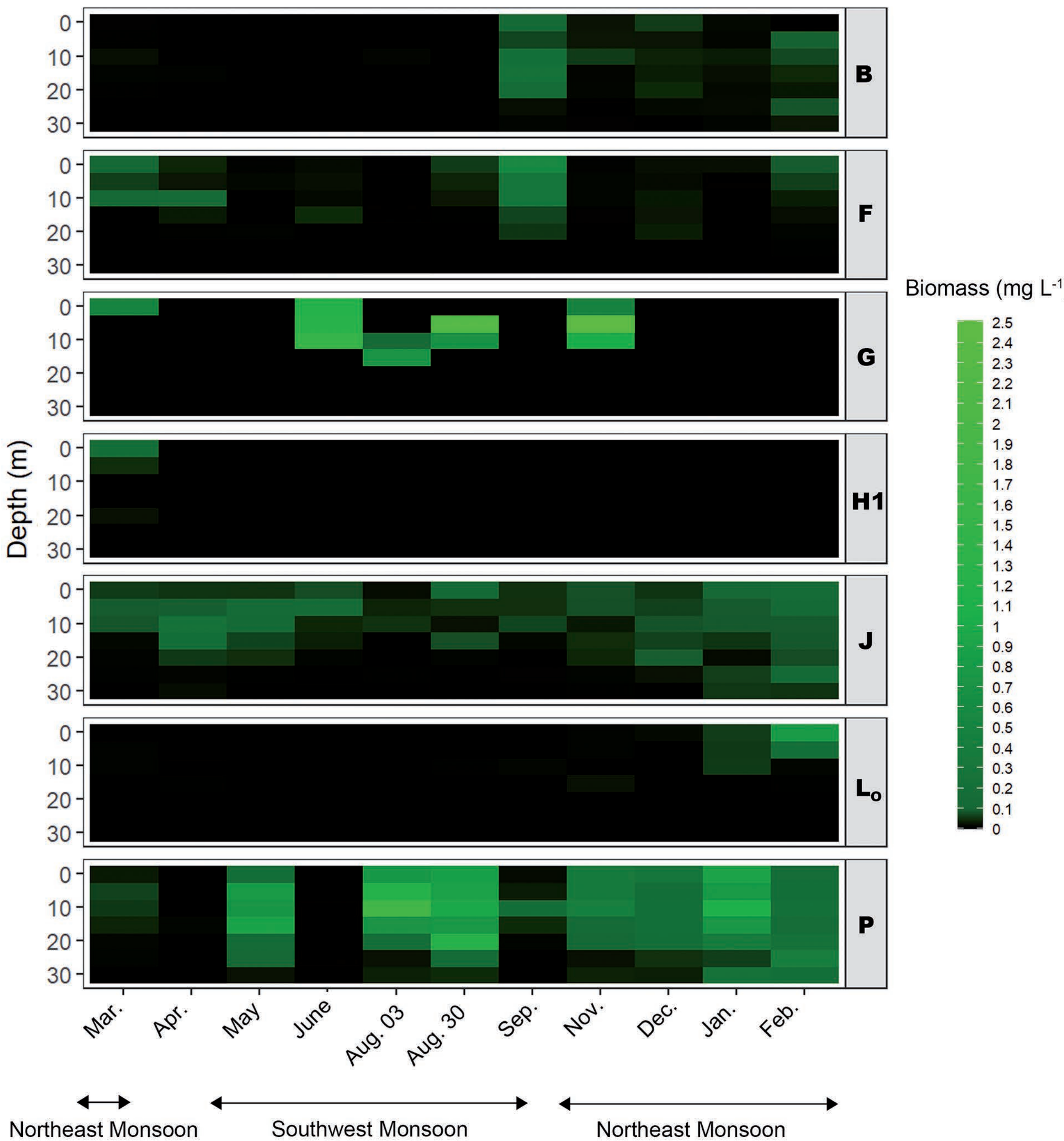

Fig. 5. Monthly vertical biomass distribution of the dominant phytoplankton functional groups in Lake Yambo from March 2024 to February 2025.

oxygen conditions due to sediment ammonification and suppressed nitrification (Beutel, 2006). Partial mixing during the early northeast monsoon (November–December) left NH_3 concentrated at depth. However, full turnover in January–February redistributed NH_3 upward and enriched NO_3^- throughout the water column, indicating enhanced nitrification as oxygen penetrated deeper layers. Diao *et al*. (2023) reported that full turnover stimulates nitrifying bacterial activity, supporting this mechanism. These dynamics confirm Lake Yambo's classification as a tropical monomictic lake, with January–February as a critical transitional

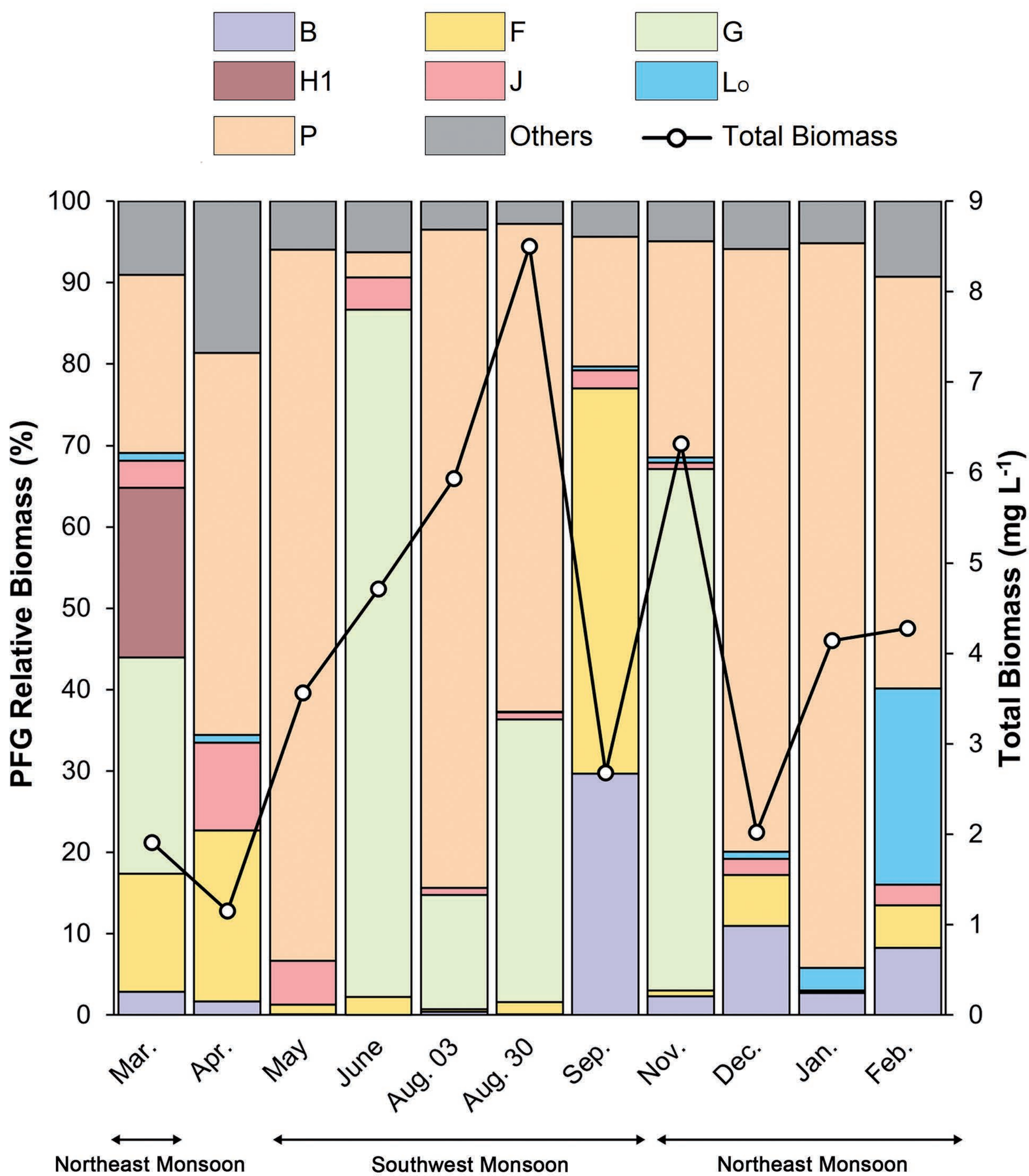

Fig. 6. Monthly variation in the relative biomass percentage of dominant phytoplankton functional groups and total biomass from 0 m to 30 m in Lake Yambo from March 2024 to February 2025.

phase when vertical gradients collapse and nitrogen (N) cycling intensifies.

The functional group composition responded to these shifts. Groups F and G consistently declined with depth regardless of season, limited by light and surface nutrient availability (Reynolds *et al*., 2002; Padisák *et al*., 2009; Becker *et al*., 2010). In contrast, Groups B, L_O, J, and P showed greater seasonal and vertical variation. Group B extended deeper during mixing, L_O remained surface-oriented, and Group J shifted downward with nutrient redistribution. Group P, which includes *Aulacoseira granulata*, also extended to 30 m during mixing, reflecting its tolerance to lake mixing and reduced light availability (Becker *et al*., 2009; Varol, 2019). Group H1 appeared after turnover, coinciding with declining NO_3^- levels, likely exploiting N-limited conditions via N fixation (Dong *et al*., 2019).

Most functional groups (Groups B, F, J, L_O, and P) were associated with cooler, nitrate-rich conditions characteristic of peak mixing, which is consistent with the evidence that NO_3^- availability promotes phytoplankton growth in N-limited systems (Huszar and Caraco, 1998). In contrast, Groups G and H1 were linked to warmer, nitrogen-depleted surface layers during stratified periods.

Insights from Lake Yambo in the context of tropical monomictic lakes

One of the few studies on tropical monomictic lakes is by Barbosa *et al*. (2011), who investigated Lake Carioca in southeastern Brazil. They reported Group L_O (*Ceratium*) favoring the mixing period, similar to Lake Yambo, where Group L_O co-dominated with Groups B, F, and P in February, coinciding with peak NO_3^- concentrations. This contradicts the typical pattern where Group

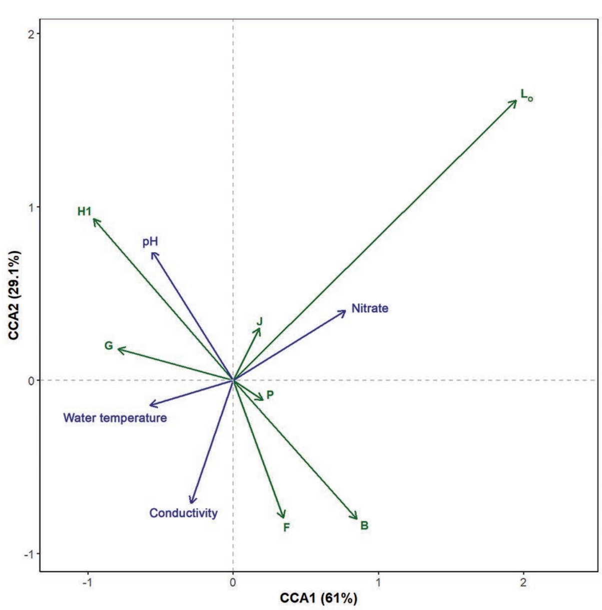

Fig. 7. Canonical correspondence analysis (CCA) biplot of the monthly depth biomass of dominant phytoplankton functional groups and significant environmental variables (p<0.05) in Lake Yambo.

L_O prefers stratified systems and is sensitive to lake mixing (Reynolds *et al*., 2002; Wang *et al*., 2011; Xiao *et al*., 2011). Matsumura-Tundisi *et al.* (2010) offered a possible explanation, showing that *Ceratium* blooms in a tropical reservoir were triggered by mixing events that transported cysts from sediments to the surface, along with elevated P and N levels.

Perhaps the most compelling insight from Lake Yambo is the surface layer dominance of Groups G and H1 under high water temperatures and low NO_3^- concentrations, conditions typical of stratified periods. Climate warming is expected to prolong these stratification periods in lakes globally (Sahoo and Schladow, 2008), suggesting that tropical monomictic lakes may increasingly favor phytoplankton tolerant to warm N-limited waters. The descriptor taxon of Group G, which is *Volvox*, thrives in stratified, eutrophic environments by efficiently storing phosphate, even under NO_3^- limitation (Kirk, 2003; Wang *et al*., 2011; Varol, 2019). Group H1 adapts to N-poor conditions by fixing atmospheric N via specialized heterocysts (Dong *et al*., 2019). It also regulates buoyancy through gas vesicles, allowing vertical positioning to maximize light capture, which is especially important under low euphotic depth during mixing or turbid conditions (Liu *et al*., 2019). This physiological flexibility gives both groups a competitive edge during N limitation under extended stratification.

Similar trends have been observed in warm monomictic systems in other climatic regions. In Brazil's subtropical meso-eutrophic Faxinal Reservoir, Becker *et al*. (2009) observed Group H1 preference towards high temperatures, stable stratification, and low NO_3^- levels. This dominance was linked to poor ecological conditions and harmful blooms. In the Mediterranean Batman Dam Reservoir in Turkey, Varol (2019) also reported the preference of Groups G and H1 to high temperatures and N-limited conditions. This recurring dominance of N-fixing or N-efficient groups in warm monomictic lakes across other climatic regions may highlight a global pattern. However, this trend may be amplified in tropical systems where elevated temperatures and baseline N limitation are more pronounced (Lewis, 2000).

What makes this trend particularly concerning is that Lake Yambo is only mesoeutrophic. In more eutrophic or hypereutrophic tropical monomictic lakes, where anthropogenic and aquaculture pressures are higher, N limitation may be even more pronounced. This could increase the frequency and severity of blooms by Groups G and H1. Notably, Group H1 includes N-fixing Nostocales known for producing cyanotoxins, which pose ecological threats and significant health risks (Cirés and Ballot, 2016; Li *et al*., 2016).

Implications for management and monitoring

The results of this study point to a clear demand for more targeted monitoring and management in Lake Yambo, particularly during key transitions following full mixing. The late March to early April 2024 bloom was dominated by N-fixing *Dolichospermum* and emerged under severe N depletion and rising water temperatures. This highlights a high-risk period that remains under-monitored. Quarterly monitoring by the Laguna Lake Development Authority (LLDA) is a good baseline, but our study shows that more frequent sampling during transitional periods is critical. Cyanotoxin testing during bloom events is also essential for risk assessment and recreational safety. The LLDA's existing policy framework (Memorandum Circular No. 2021-04) is a solid foundation, but enforcement and periodic review are necessary. Should future monitoring confirm toxic blooms, the policy should be updated to include specific response strategies.

Nutrient management in N-limited tropical lakes requires a different approach than in temperate systems (Lewis, 2000). Simply reducing N may promote N-fixing cyanobacteria if phosphorus remains high (Schindler *et al*., 2008). Schindler (2012) emphasized that small-scale experiments often miss key lake-wide feedback, highlighting the importance of whole-lake, long-term studies. Drawing lessons from other tropical lakes that have implemented nutrient controls can help design more context-appropriate strategies. At present, key information is still missing for Lake Yambo, including actual nutrient limitation ratios, pollution sources, and clear management goals. Addressing these gaps through sustained monitoring and collaborative efforts from relevant agencies would not only improve Lake Yambo's management but also provide critical insight for developing effective whole-lake nutrient strategies in other tropical monomictic systems.

CONCLUSIONS

This study examined how seasonal stratification and mixing shape the vertical and temporal dynamics of environmental conditions and, in turn, influence phytoplankton functional group composition in Lake Yambo, a tropical monomictic lake in the Philippines. Findings indicate that the lake is meso-eutrophic and likely nitrogen-limited, with most functional groups responding to increases in nitrate availability, particularly during peak mixing in the northeast monsoon. During this period, cool, nitrate-rich conditions favored Groups J and L_O in surface layers, while Groups B, F, and P thrived at the deeper layers due to their tolerance of low-light, well-mixed conditions. Following full turnover, however, declining concentrations of ammonia and nitrate coincided with reduced overall phytoplankton biomass and the dominance of nitrogen-efficient Groups G and H1 in surface waters. The emergence of Group H1 during nitrogen-depleted conditions following peak mixing is especially concerning, as it includes toxin-producing cyanobacteria such as *Dolichospermum* and *Aphanizomenon*. These results underscore the importance of high-frequency monitoring during transitional periods and support the need for adaptive, nutrient-specific management strategies tailored to tropical monomictic lakes. Ultimately, insights from Lake Yambo provide a valuable reference for understanding the ecological consequences of stratification, mixing, and nutrient cycling in similar systems, and for anticipating and mitigating the risk of harmful algal blooms under future climate warming and persistent nitrogen limitation.

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