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Research Article

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Functional Group Responses to Hydrological Disturbance and Environmental Gradients in Eastern Mediterranean Lakes (Türkiye)

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Abstract

This study examines the effects of physicochemical variables on phytoplankton functional groups (FGs) in seven lentic ecosystems, including one natural lake (Akgöl) and six artificial water bodies comprising five reservoirs (Gezende, Alaköprü, Berdan, Bağbaşı, and Ermenek) and one pond (Sarıveliler), in the Eastern Mediterranean River Basin (Türkiye), representing Mediterranean and semi-arid climatic conditions. Phytoplankton and environmental data were collected seasonally (spring and autumn) during 2020–2021 from 18 sampling stations. Strong spatial and temporal heterogeneity was observed among lakes. The shallow, saline-influenced Akgöl Lake showed low functional diversity and dominance of benthic and tychoplanktonic diatoms (codon MP), associated with sediment resuspension and unstable mixing. In contrast, deeper stratified reservoirs (Gezende, Berdan, Ermenek) were dominated by motile dinoflagellates (codon L0), particularly in spring under stable, oxygenated conditions. Seasonal dynamics structured FG composition, with spring assemblages favoring mixing- and oxygen-adapted groups, whereas autumn assemblages shifted toward taxa tolerant of higher turbidity and organic enrichment. Redundancy analysis revealed that salinity, turbidity, suspended solids, and total organic carbon were the main drivers of FG distribution, while nutrients had comparatively weak explanatory power. Together, these variables define a clear mineralization–organic matter–turbidity gradient controlling phytoplankton structure across the basin. Mesotrophic functional groups dominated overall, although their relative contributions varied with local environmental conditions. The results demonstrate that phytoplankton FGs are reliable indicators of ecological status and spatial variability in Eastern Mediterranean lakes. Importantly, the system is structured by a pronounced hydrological degradation gradient driven by coupled salinity, organic matter, and turbidity dynamics, which emerges as the dominant organizing environmental framework. This highlights the need to integrate hydrological regulation, sediment dynamics, and organic matter processes with nutrient management under increasing anthropogenic and climatic pressures.

Keywords Water quality, organic matter, lake ecosystems, functional groups

Introduction

Phytoplankton community dynamics are closely related to the spatio-temporal variability of environmental conditions (Bellinger & Sigee, 2010). Growth and composition are mainly controlled by climatic factors like temperature and precipitation, dissolved gases, nutrient availability, interspecific competition, and herbivory (Reynolds, 2006). These drivers do not impact all species equally but rather preferentially select for particular ecological strategies that result in changes in dominance patterns as well as community structure (Edwards et al., 2015).

Seasonal changes are one of the major forces controlling phytoplankton dynamics by changing physical and chemical conditions in aquatic ecosystems (Edwards et al., 2015). The effects of seasons are most clearly seen in temperate areas,

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Maraşlıoğlu, F. & Topuz, B.

but they also have an important part to play in Mediterranean and subtropical systems (Jeppesen et al., 2014). In these areas, seasonal variations of temperature and precipitation determine the stability of the water column, nutrient availability, and light conditions which are linked to changes in phytoplankton biomass and composition through processes like sediment resuspension, dilution, and hydrological flushing (Fuentes & Petrucio, 2015; Li et al., 2025).

For reservoir ecosystems experiencing seasonal variability in hydrology, water retention time, and nutrient dynamics, sensitivity is generally higher than in natural lakes (Reynolds, 2006). The interplay between phytoplankton communities and environmental drivers—including seasonal, nutrient, and hydrodynamic gradients—is largely shaped by community structure (Padisák et al., 2003; Naselli-Flores & Barone, 2005). Reservoirs are therefore well suited for investigating phytoplankton structure and responses to both local and large-scale environmental changes. Accordingly, changes in phytoplankton community structure are widely used to evaluate water quality and ecological conditions in lake and reservoir ecosystems (Reynolds et al., 2002; Padisák et al., 2009). Ecological niches are defined within this highly multidimensional and interactive system characterized by numerous environmental variables (Hutchinson, 1957). Consequently, the evaluation of phytoplankton communities is complex and requires extensive information as well as advanced taxonomic and structural analytical expertise. Ecological indicators and functional classifications, which simplify complex datasets while maintaining ecological relevance, have therefore become widely applied. Given the structural and functional complexity of phytoplankton communities, classification at different levels of simplification facilitates the interpretation of community responses to environmental gradients (Rangel et al., 2016).

Hydrological degradation is one such ecological gradient that constitutes a key but so far underappreciated factor influencing phytoplankton community structure at least in Mediterranean and semi-arid aquatic ecosystems. In the context of this study, hydrological degradation is defined as the change of natural hydrodynamic conditions through turbidity, sediment resuspension, salinization and organic matter accumulation that shift ecosystem functioning by decreasing water column stability and ecological integrity. These processes, often linked to water level change, climate variability, and anthropogenic pressures are critical for habitat dynamics and ecological responses from phytoplankton functional groups.

In the last decades, functional classifications based on morphological and ecological traits were proposed as good alternatives to purely taxonomic approaches (Lavorel et al., 1997; Follows et al., 2007). Some functional systems depend on physiological traits that come from known relationships between species and environments (Reynolds et al., 2002; Padisák et al., 2009), but these cannot be used regularly because it is hard to get such measurements in monitoring programs (Weithoff, 2003). Morphological traits can be measured easily and are strongly connected with ecological performance; thus, they are the best for studying phytoplankton–environment relationships (Litchman & Klausmeier, 2008). The key ecological processes growth, nutrient uptake, light acquisition, and losses due to sedimentation or grazing are very much linked with cell size and shape attributes plus surface-to-volume ratios (Chindia & Figueredo, 2018).

Most research that apply a phytoplankton functional group lens have a very broad temporal focus, typically only two collection episodes, such as Crossetti et al. (2013) and Abonyi et al. (2018), which are separated by multiple, contrasting seasons. Such seasonal assessments are useful for observing gross functional changes due to dominating environmental gradients, which is common occurrence in phytoplankton studies in very seasonal regions. Seasonal assessments are very useful in studies examining functional group responses due to the fact that phytoplankton are among the fastest-growing organisms in the world (Dubelaar et al., 1999).

Accordingly, this study looks at seasonal changes in the phytoplankton functional group composition and the environmental driving factors in the Eastern Mediterranean River Basin. Based on two contrasting seasonal episodes, this study hopes to achieve the following objectives: i) Determine the main physical and chemical factors that affect the distribution of phytoplankton functional groups, ii) Analyze the seasonal changes in functional group composition and how environmental factors affect these changes, and iii) Determine the ecological health of the reservoirs using a functional group approach on phytoplankton to evaluate the biological quality of the reservoirs.

MATERIALS AND METHODS

Study Area

This study focuses on seven lentic ecosystems within the Eastern Mediterranean River Basin, one of Turkey's 25 river basins, comprising one natural lake (Akgöl Lake; L2) and six artificial water bodies, including five reservoirs (Gezende, Alaköprü, Berdan, Bağbaşı, and Ermenek) and one pond (Sarıveliler; L6), covering an area of approximately 2.18×10^4 km². The basin extends between 36° 00′–37° 28′ North latitude

and 32° 06′–35° 09′ East longitudes (DGWM, 2016) and includes the river basins extending from the Sedir River in the west to the Tarsus River in the south and the Göksu River basin (Bayer-Altin & Altin, 2021). Phytoplankton sampling was conducted seasonally (spring and autumn) over a two-year period (2020–2021). Samples were taken from surface waters and selected depths within the photic zone to capture vertical variability. A total of eighteen stations distributed across the seven study water bodies were selected for monitoring studies. The geographical distribution of the study sites is shown in Figure 1, and the detailed characteristics of the water bodies are presented in Table 1.

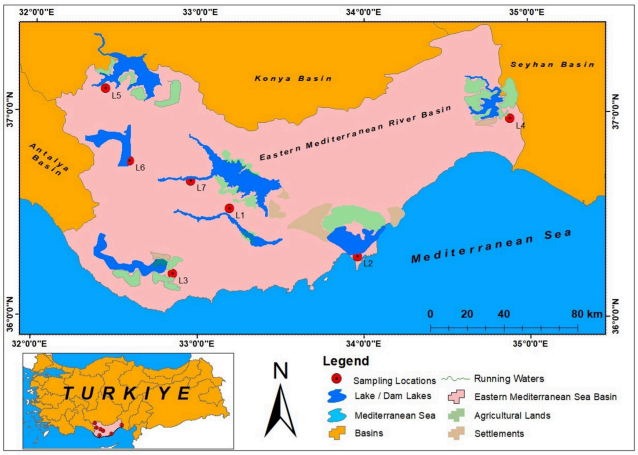

Figure 1. Sampling station details for lakes in the Eastern Mediterranean River Basin: L1, Gezende Reservoir; L2, Akgöl Lake; L3, Alaköprü Reservoir; L4, Berdan Reservoir; L5, Bağbaşı Reservoir; L6, Sarıveliler Pond; and L7, Ermenek Reservoir

Table 1. Morphometric characteristics and hydromorphological classification of the studied water bodies in the Eastern Mediterranean River basin

Site code	Sampling locations	Surface area (ha)	Mean / Max depth (m)	Monitoring station (n)	Euphotic depth (m)	Sampling strategy
L1	Gezende Reservoir	397	23 / 25	3	10,1	composite
L2	Akgöl Lake	820	0,6 / 0.7	3	0,3	surface
L3	Alaköprü Reservoir	140	35 / 39	2	14,6	composite
L4	Berdan Reservoir	670	18 / 20	3	5,4	composite
L5	Bağbaşı Reservoir	180	46 / 50	2	8,4	composite
L6	Sarıveliler Pond	80	0,5 / 0.5	2	0,3	surface
L7	Ermenek Reservoir	5874	77 / 81	3	14,9	composite

Sampling and analysis

Phytoplankton samples were collected from sampling locations where the number of monitoring stations was determined according to lake surface area (>50 ha: 1 station; 50–500 ha: 2 stations; >500 ha: 3 stations). A total of 18 sampling stations were distributed across seven lakes (Table 1). At shallow sites (L2, L6), samples were collected from the surface, whereas at sites deeper than 5 m (L3, L4, L5, L7), depth-integrated composite samples representing the euphotic zone in the pelagic region were obtained by collecting water from the surface down to the euphotic depth at equal vertical intervals within the euphotic zone. Sampling was carried out using a Hydrobios water sampler to obtain quantitative samples, while additional qualitative samples were collected using a plankton net (50 µm mesh size) to ensure better representation of taxonomic diversity. Sampling was conducted seasonally during spring and autumn.

In situ measurements of water temperature (Temp), dissolved oxygen (DO), pH, electrical conductivity (EC) and salinity (Sal) were obtained using a portable multiparameter probe (YSI Pro Plus, Yellow Springs Instruments, USA). Calibration followed guidance from the manufacturer before each field campaign. Water samples in the field were collected, stored in insulated containers and delivered to a laboratory where analyses were conducted within 24 h according to Standard Methods (APHA, 2012). Measured concentrations included turbidity (Turb), suspended solids (SS), biochemical oxygen demand (BOD_5), chemical oxygen demand (COD), total organic carbon (TOC), chlorophyll-a (Chl-a) and dissolved nutrients such as total nitrogen (TN), total phosphorus (TP) nitrate (NO_3^-,), nitrite (NO_2^-) ammonium (NH_4^+) and sulfate (SO_4^{2-}). Detailed descriptive statistics of these physicochemical variables are presented in Maraşlıoğlu et al. (2026), and the same dataset was used here for further ecological and multivariate analyses.

Main physicochemical metrics reflecting chemical enrichment and the degree of disturbance within the water-column were used to define hydrological degradation. Turbidity (Turb) and suspended solids (SS) were indicative of sediment resuspension and physical disturbance, while electrical conductivity (EC) and salinity (Sal), which reflects mineralisation and water balance). Total organic carbon (TOC), and both BOD_5, COD reflected the accumulation of dissolved organic matter as well as internal loading processes. Hydrological degradation gradients across the lakes were defined based on the joint variable levels of these variables.

Phytoplankton Analysis

Phytoplankton samples were collected from the pelagic zones of seven lakes within the Eastern Mediterranean River Basin and subsequently preserved with acidified Lugol's solution (4% final concentration). Diatom samples were treated with hydrochloric acid and heated hydrogen peroxide to remove organic matter, and permanent preparations were made using Naphrax (EC, 2014). While the plankton net was primarily used for qualitative assessment, quantitative analyses were based on water samples collected with a water sampling device. Quantitative analyses were performed on 10 mL subsamples after a 24-hour settling period in Utermöhl chambers. Phytoplankton counts were performed according to the Utermöhl method by scanning the entire settling chamber at appropriate magnifications under an inverted microscope (Utermöhl, 1958).

Taxon-specific biovolume calculations based on geometric shape approximations were used to estimate phytoplankton biomass (Hillebrand et al., 1999; Sun & Liu, 2003). Functional group classification was performed in accordance with Reynolds et al. (2002) and Padisák et al. (2009). To compare the phytoplankton composition among reservoirs with different trophic conditions, functional groups constituting more than 5% of the total phytoplankton biomass were considered dominant. Salmaso et al. (2015) was used to determine the trophic status of these codons.

The taxonomic identification of phytoplankton taxa was carried out using standard references (Huber-Pestalozzi, 1962, 1969, 1974, 1976, 1982, 1983; Komárek & Fott, 1983; Popovski & Pfiester, 1990; Krammer & Lange-Bertalot, 1991a, 1991b, 1999a, 1999b; Cox, 1996; Komárek et al., 1998; Komárek & Anagnostidis, 1999; John et al., 2003; Krammer, 2003). AlgaeBase was used to verify taxon names and author citations (Guiry & Guiry, 2025).

Statistical Analysis

Multivariate analysis of the association between phytoplankton species distribution and physico-chemical parameters was examined using CANOCO version 5.0 (Ter Braak & Šmilauer, 2012). To determine the appropriate ordination method, Detrended Correspondence Analysis (DCA) of the RFGs and environmental data was first conducted. The gradient lengths were short (<3.0) indicating that the RFGs and environmental variables had linear relationship. Therefore, redundancy analysis (RDA) with manual forward selection was chosen (Lepš & Šmilauer, 2003). The significance of the relationships between environmental variables and phytoplankton biovolume was tested using Monte Carlo permutation tests with 499 unrestricted permutations.

Water temperature (Temp), salinity (Sal), turbidity (Turb), electrical conductivity (EC), dissolved oxygen (DO), suspended solids (SS), chemical oxygen demand (COD), biochemical oxygen demand (BOD_5), total organic carbon (TOC), total phosphorus (TP), total nitrogen (TN), nitrate (NO_3^-), nitrite (NO_2^-), ammonium (NH_4^+), sulfate (SO_4^{2-}), pH, and other spatiotemporal variations were investigated using Redundancy Analysis (RDA). Except for pH, environmental variables were subjected to logarithmic transformation [log (X + 1)] to reduce skewness. Phytoplankton functional groups constituting greater than 5% of the total biomass and present in at least three samples were included in the analysis.

RESULTS AND DISCUSSION

Spatial and temporal patterns in the environmental factors

The seven lakes of the Eastern Mediterranean River Basin showed significant differences in physicochemical conditions both in space and time, reflecting differences in morphometry, hydrological regulation, and anthropogenic influence. Akgöl Lake (L2) showed the highest values for many parameters like, water temperature, pH, electrical conductivity (EC), turbidity, suspended solids (SS), chemical oxygen demand (COD), biochemical oxygen demand (BOD5), total nitrogen and total phosphorus among the systems. L6, Sarıveliler Reservoir had consistently lower values of temperature, EC, SS and TN. pH ranged from 7.3 in Gezende Reservoir (L1) to 8.6 in Akgöl Lake (L2), thus all lakes were weakly basic. Groundwater having generally low total organic carbon (TOC) concentrations with values ranging from 3.7 to 3.9 mg L^{-1} in only Bağbaşı Reservoir yielded a mean TOC of 16.5 mg L^{-1}, respectively. The spatial differences suggest a high internal environmental heterogeneity of lakes to local hydromorphological conditions.

At the local scale, salinity and physical disturbance were found to be the main controls over benthic assemblages, especially in the shallow coastal system (L2). Electrical conductivity (EC) was as high as 8920 µS cm^{-1} in autumn, and more importantly remained above freshwater thresholds set by SWQMR (2021), with salinity equivalent of 5.15 ppt, at 7930 µS cm^{-1} in spring (4.46 ppt). The brackish condition definitely is a by-product of the selective processes of evaporative concentration or marine intrusion, both processes routinely observed in coastal Mediterranean lakes (Alvarez-Cobelas et al., 2005). Another feature of Akgöl was detected ultra-high turbidity measurement (151.3 NTU) and suspended solids concentration (78.0 mg L^{-1}). These very turbid conditions restrict light penetration, favoring the selection of phytoplankton communities adapted to turbid and well-

mixed environments (Padisák et al., 2009). These traits make Akgöl a mock-up of a separate hydrochemical system, with salinity and physical stress acting as local drivers.

The nutrient parameters showed very significant seasonal changes (Fig. 2a). Even though nutrient levels were mostly low throughout the basin in spring, autumn TN increased dramatically in some lakes up to values of 4.5-4.9 mg L^{-1} for L3, L4, L5, L6, and L7 compared to spring values that fell as low as 0.09 mg L^{-1} (L6) and 0.2 mg L^{-1} (L4). According to SWQMR (2021), this autumn concentrations would be classified under Class III water quality, indicating basin-wide nutrient fluctuation rather than isolated local enrichment; TP followed similar seasonal increases with a maximum value recorded at 0.14 mg L^{-1} in Akgöl, while Alaköprü (L3), Bağbaşı (L5), and Sarıveliler (L6) shared the minimum concentration at 0.0045 mg L^{-1} each. The highest mean value for NH_4^+ was found in Alaköprü (L3), which recorded a figure of 0.083 mg L^{-1}; this took place particularly during the autumn period.

Organic matter indicators follow the same pattern (Fig. 2b). TOC from Bağbaşı (L5) varied between 7.1 mg L^{-1} in spring to 16.5 mg L^{-1} in autumn; high values of COD and BOD_5 were also recorded at Akgöl (L2) and Bağbaşı (L5) during autumn. Autumn nutrient enrichment is likely associated with agricultural runoff following harvest rains and early autumn rainfall, coupled with sediment-water interactions as thermal stratification breaks down, which may increase organic matter degradation and lead to the possibility of internal phosphorus release.

Seasonal and spatial variations of hydrochemical variables EC, SS, and SO_4^{2-} in seven lakes of the Mediterranean region (Fig. 2c). Higher values of EC and SS were generally reached in autumn at Akgöl (L2) and Bağbaşı (L5), whereas Sarıveliler (L6) remained relatively low during each season. The response of these chemical gradients to nutrient availability and mixing dynamics serves to structure ecosystem functioning at the basin-scale.

Aside from variability in the oxygen regime, also seasonal variations were seen with other parameters (e.g., carbon, nitrogen) (Fig. 2d). Spring maximum dissolved oxygen concentration value was measured as 9.2 mg L^{-1} in Berdan Dam (L4), and autumn minimum value was record-ed as 5.97 mg L^{-1} in Akgöl (L2). Other reservoirs, including Bağbaşı (6.3 mg L^{-1}) and Alaköprü (6.6 mg L^{-1}), recorded notable autumn decreases in DO concentration versus spring results as well. Results indicate these reservoirs expressed a significant decline of water quality class from Class I-II to Class II (SWQMR, 2021). That decline occurred during autumn with warm temperatures (up to 25.6 °C in Akgöl) and high organic matter decomposition rates; this process ensures a higher microbial oxygen consumption. The local maxima in dissolved oxygen observed during autumn could be the result of short-lived seasonal declines also reported in Mediterranean reservoirs when thermal stratification weakens, and organic matter becomes more recyclable (Jeppesen et al., 2015). The largest oxygen reductions recorded in this study were at Akgöl (decline from 8.1 mg L^{-1} in spring to 5.97 mg L^{-1} in autumn) and Bağbaşı (from 8.4 mg L^{-1} to 6.3 mg L^{-1}) implemented during phases of significant poular concentration levels of turbidity and organic matter concentrations coincided with reduced dissolved oxygen values.

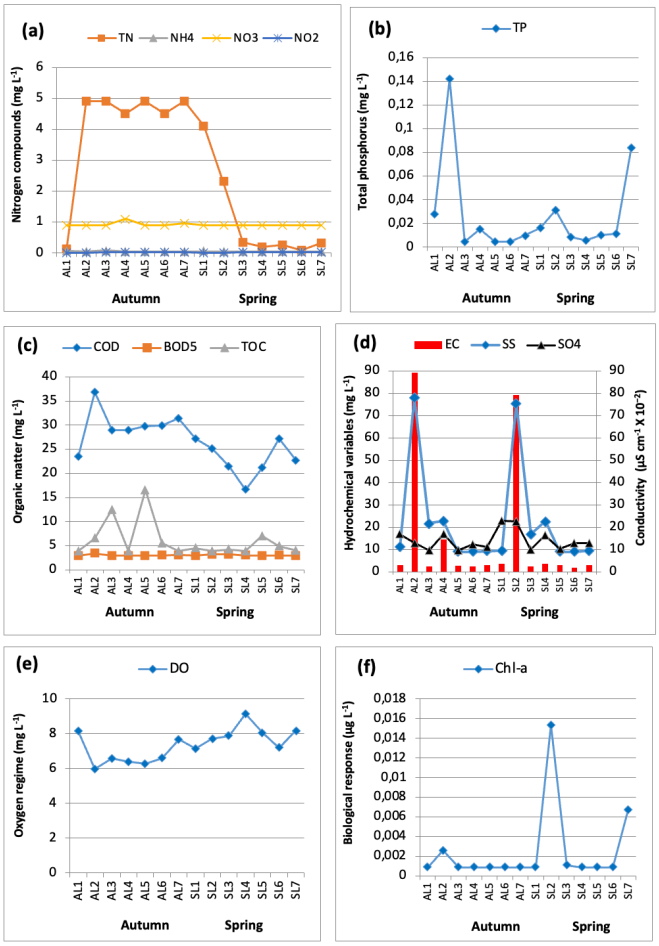

Figure 2. Seasonal patterns of nitrogen compounds (a), total phosphorus (b), organic matter (c), hydrochemical variables (d), oxygen regime (e), and chlorophyll-a (f) in seven lakes of the Eastern Mediterranean River Basin

The chlorophyll-a concentrations exhibited similar seasonal variations (Fig. 2e), with higher autumn values in nutrient-enriched systems, especially Akgöl, and lower concentrations during spring in Sarıveliler and Gezende sites, indicating close relationships between nutrient content, oxygen levels, and phytoplankton abundance.

Overall, the combined results indicate a clear scale-dependent structuring of environmental drivers. Salinity, EC, turbidity, and suspended solids act mostly as local drivers

in shallow coastal systems like Akgöl while dissolved oxygen, total phosphorus, and COD reflect basin-wide nutrient and organic matter dynamics across seasons. The coupling of these three elements seems to be very important for the functioning of ecosystems in these Mediterranean and semi-arid lakes under conditions of combined climatic variability and anthropogenic pressure. From a management perspective, the fact that Akgöl has always been brackish means that it needs specific strategies for the lake; further, since there is regular autumnal degradation in nutrient and oxygen conditions across reservoirs, this indicates an urgent need for basin-scale monitoring with seasonal focus to keep up ecological integrity as per national water quality standards.These combined spatial and temporal physicochemical shifts collectively define a basin-wide hydrological degradation gradient, expressed through increasing salinity, turbidity, suspended solids, and organic matter accumulation, which constitutes the primary environmental framework structuring ecosystem variability across the studied lakes.

Statistical Results

Redundancy Analysis (RDA) was used to explore the relationship between phytoplankton FGs and environmental gradients among seven lakes in the Eastern Mediterranean River Basin. A total of 7 dominant functional groups, each contributing more than 5% to the total biomass, along with 17 physicochemical variables, were included in the RDA ordination. The first four RDA axes accounted for 75.2% of cumulative variation in FGs composition with eigenvalues of 0.26 and 0.22 on axis 1 and axis 2, respectively. The first two axes together explained 48.0% of total variance, meaning that the primary structure for relationships between FGs and environmental variables was well represented in two-dimensional ordination space.

Permutation tests identified salinity, turbidity, suspended solids (SS), electrical conductivity (EC), and total organic carbon (TOC) as the most important environmental factors ($p < 0.05$). Each factor explained about fifteen percent of the variation in FG composition. Effects conditional on terms further emphasized salinity as the main independent driver, followed by TOC, pH, SS, and turbidity ($p < 0.05$). In combination these variables defined a major environmental gradient characterized by increasing mineralization, organic matter accumulation and water-column turbidity. Total phosphorus (TP) and dissolved oxygen (DO) were of marginal significance ($p < 0.10$), while nutrient species (NO_2, NO_3, TN), temperature, sulfate and pH had relatively less independent explanatory power after accounting for the main drivers.

The ordination diagram (Fig. 3) showed that the positive side of axis 1 was strongly associated with salinity, EC, turbidity, SS, BOD_5, and COD; it was generally linked to functional groups such as W2 and MP. Those groups were mostly related to lakes characterized by higher ionic content and organic load in autumn. The negative side of axis 1 related to higher dissolved oxygen and sulfate concentrations was connected with W1 group. Along axis 2, TP and NO_2 defined a secondary gradient separating nutrient-enriched condition-adapted groups from relatively lower nutrient availability L0 and Y group members. For the most part axis one reflected a salinity–organic matter–disturbance gradient while axis two represented a nutrient-related gradient influencing functional group distribution.

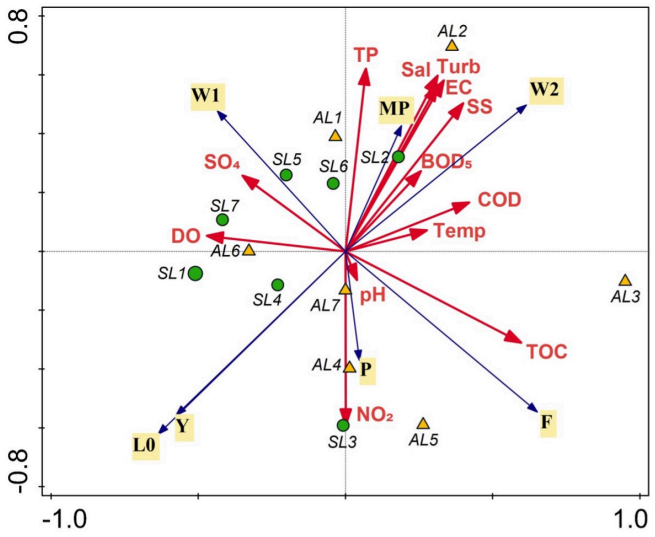

Figure 3. Redundancy analysis (RDA) ordination showing relationships between sampling sites, phytoplankton functional groups (FGs), and environmental variables. Arrows indicate environmental variables, and letters on yellow backgrounds represent FGs. Seasons are denoted as S (spring) and A (autumn). The full names of the lakes are given in Figure 1

There was clear separation according to seasons in the ordination space (Fig. 3). Samples from autumn (2020), represented by orange triangular symbols, were mostly found on the positive side of axes 1 and 2, which are closely aligned with salinity, EC, turbidity, SS, BOD_5, COD, and TOC. More specifically AL2 and AL3 were very much in line with these variables meaning that high ionic content and organic matter accumulation occurred during the autumn period. The spring samples indicated by green circles were mostly found on the negative side of axis 1. This means that they are associated with higher dissolved oxygen and sulfate concentrations at relatively lower mineralization levels. SL1, SL4, and SL7 are close to the DO and SO_4 vectors with W1 functional group.

Temporal variability in lakes such as L1, L4, and L7 was as important as spatial differences in structuring the FG composition. Assemblages in autumn were always linked

to increased mineralization, organic loading, and turbidity. This suggested that instability in hydrology with dynamics of internal organic matter intensified during this period. Conditions of spring then acted like a transitional phase characterized by better mixing oxygenation.

Collectively these multivariate associations suggest that the first RDA axis reflects a basin-wide environmental gradient underlain by coupled physicochemical stressors that can be interpreted as a continuum of hydrological conditions across the lakes studied, statistically well-supported by strong biotic–abiotic correlations of axis 1 with salinity, turbidity, suspended solids, electrical conductivity BOD_5 and COD. Within this gradient, Akgöl Lake (L2) was at the highly positive end, representing highest hydrological degradation, while Gezende Reservoir (L1) and Sarıveliler Pond (L6), with low disturbance and stable hydrological conditions, were found at the negative end. Bağbaşı Reservoir (L5) and the remaining lakes (L3, L4, and L7) occupied intermediate positions along this along this environmental gradient. Using standardised values of salinity, turbidity, total suspended solids, electrical conductivity (EC), and total organic carbon (TOC), lakes were rank ordered objectively along the RDA axis 1-derived measure of hydrological degradation gradients from least impacted systems at the low end of the RDA axis 1 originally derived gradient (Gezende, Sarıveliler) to most impacted system at the high end of this gradient (Akgöl).

RDA results suggest that variation in the presence of functional groups throughout the studied lakes is largely determined by prevailing physicochemical gradients rather than nutrient availability. Our results identify salinity, organic matter build-up and turbidity as the most influential controls at the basin-scale. The MP group dominated systems located on the right half of RDA axis 1, while opposite sites at left-hand side were represented by the L0 group from Gezende (L1) and Sarıveliler in the case of Lakes. This split provides a direct illustration of the discriminating influence of salinity and turbidity on functional group composition. TP and inorganic nitrogen forms contributed to RDA axis 2 but were largely weak independent effects, confirming that nutrients are best regarded as a secondary (rather than primary) gradient. Our results are in the line with findings that physical and hydrological controls were major factors determining concentrations of nutrients (e.g., Güzel et al., 2023), but differ from those describing systems where nutrients exert a primary control on phytoplankton composition (Yuan et al., 2025).

Using an RDA-based interpretation, the distribution of phytoplankton functional groups in the Eastern Mediterranean River Basin mainly reflected basin-scale gradients of salinity, organic matter accumulation and turbidity. Seasonal variability is a second filter that changes the influence of certain drivers in individual lakes. The firm associations of MP and W2 groups with mineralization and turbidity gradients—and the reverse relationships of L0 and Y groups with conditions more strongly associated with oxygenation and stability—provide a basis for asserting that this ordination pattern reflects at least some ecological processes rather than pure correlation. In other words, these gradients derived from statistically based synthesis provide a mechanistic basis for understanding patterns in seasonal dominance as well as transitions between lake-specific functional groups described in the following section.

Phytoplankton Functional Group Dynamics

Functional groups of phytoplankton are considered as effective ecological indicators since they combine the species-specific traits with the environmental constraints such as nutrient status, hydrodynamic regime, and climatic variability (Padisák et al., 2009). In our study, functional composition followed seasonal and spatial environmental variations closely, supporting the predictability of FG responses to prevailing ecological conditions in the Eastern Mediterranean River Basin.

Ninety phytoplankton taxa pertaining to eight major taxonomic divisions were recorded from the seven lakes. Seventeen functional groups were described based on 48 descriptor taxa, and their representative species and taxonomic affiliations are given in Table 2. Despite this taxonomic diversity, phytoplankton biomass was structured by a few dominant functional groups; coda L0 and MP were the most influential across the entire basin. The dominance of L0 and MP in mesotrophic lentic systems has been similarly reported in other aquatic ecosystems (Gong et al., 2022; Ma et al., 2022; Yuan et al., 2025). The spatial percentage distribution of dominant FGs among lakes is summarized in Table 3.

Table 2. Phytoplankton functional groups, representative species, and trophic states in seven lentic ecosystems (* Indicates the dominant functional group)

Codon	Habitat Characteristics	Representative species	Tolerance	Susceptibility
B	Mesotrophic trophic, small-to-medium, or large shallow water bodies	*Pantocsekiella ocellata*	Low light	Elevated pH, water stratification
C	Eutrophic, small and medium-sized lakes/reservoirs	*Asterionella formosa*	Low light	Water stratification

Codon	Habitat Characteristics	Representative species	Tolerance	Susceptibility
D	Shallow, turbid waters including rivers; high turbulence	*Encyonema silesiacum* *Nitzschia acicularis* *Nitzschia* spp.	Scouring	Reduced turbulence, increased light
E	Oligotrophic or heterotrophic type, small water bodies, shallow water	*Dinobryon* spp.	Low nutrients	CO_2 deficiency
F*	Mesotrophic-to-eutrophic in nutrients, clean, and strong water mixing	*Elakatothrix* sp. *Oocystis borgei* *Oocystis lacustris* *Nephrocytium* sp.	Low nutrients, mixing	CO_2 deficiency
G	Eutrophic, stagnant water bodies	*Eudorina* sp. *Pandorina* sp.	High light	Nutrient deficiency
J	High nutrient, mixed, shallow water	*Pediastrum* spp. *Scenedesmus* sp. *Tetraedron* sp. *Crucigenia* sp.	High nutrients	Low light / sinking
L0*	Mesotrophic-to-eutrophic, medium-to-large water bodies, can be deep or shallow	*Ceratium hirundinella* *Peridinium* spp. *Peridinium cinctum* *Peridinium gatunense*	Nutrient stratification	Prolonged deep mixing
MP*	Frequently mixed, turbid, shallow waters	*Cocconeis* sp. *Cymbella* spp. *Navicula* spp. *Epithemia* spp. *Gomphonema angustatum* *Gomphonema* spp. *Surirella* sp. *Ulnaria ulna* *Oscillatoria* sp.	Mixing, low light, turbidity	Water stratification
N	Continuously or semi-continuously mixed water bodies	*Cosmarium* sp.	Low nutrients	Water stratification, elevated pH
P*	Similar to N but in more eutrophic conditions	*Aulacoseira granulata* *Fragilaria* spp. *Nitzschia sigmoidea* *Staurastrum gracile*	Low light, low carbon content	Water stratification, silicon deficiency
S1	The mixture is cloudy and has low transparency	*Leptolyngbya fragilis* *Leptolyngbya tenuis* *Limnothrix redekei* *Planktothrix agardhii* *Phormidium* spp.	Extremely low light	Scouring
S2	Warm, highly alkaline, shallow water	*Spirulina* sp.	Low light	Scouring
W1*	Organic pollution, shallow water	*Ankistrodesmus* sp. *Euglena* spp. *Lepocinclis* spp. *Phacus* sp.	High organic load (BOD)	Grazing pressure
W2*	Mesotrophic, shallow waters with moderate organic enrichment	*Trachelomonas* spp.	Organic/ benthic conditions	Strong mixing, flushing
X1	Highly eutrophic, shallow water bodies	*Monoraphidium griffithii* *Monoraphidium* spp.	Water stratification	Nutrient deficiency, filter feeding
Y*	Still-water environment	*Cryptomonas* sp.	Low light	Grazing pressure

Table 3. Percentage contribution of phytoplankton functional groups to total biomass in the seven lakes of the Eastern Mediterranean River Basin.

		Sampling Sites						
		L1	**L2**	**L3**	**L4**	**L5**	**L6**	**L7**
Functional groups	**B**	5.6	0.1	–	0.6	4.3	0.1	2.7
	C	–	–	–	–	0.4	–	–
	D	0.2	0.1	0.4	0.2	0.5	0.5	0.2
	E	2.6	–	0.1	0.5	0.8	0.4	1.0
	F	–	–	18.2	0.1	3.2	0.0	–
	G	–	–	0.3	0.1	–	–	–
	J	–	0.3	0.6	4.0	3.4	–	–
	L0	49.8	–	27.4	79.0	64.5	44.6	63.3
	MP	26.2	76.9	1.6	4.7	3.9	21.3	25.9
	N	–	–	0.6	–	–	–	–
	P	3.4	0.5	1.7	3.6	8.4	1.0	1.1
	S1	0.5	2.2	4.6	2.5	–	0.1	1.2

	Sampling Sites						
S2	0,02	–	–	–	–	–	–
W1	6.0	14.1	–	4.3	5.2	29.1	4.8
W2	0.1	5.6	18.7	–	–	–	–
X1	–	0,2	–	–	–	–	–
Y	5.2	–	22.5	0.2	2.5	2.6	0.8

Note: "-" indicates not detected in the sampling sites.

Functional groups exhibited clear seasonal and trophic patterns across seven Eastern Mediterranean lentic systems (Figure 4). According to the functional classification of phytoplankton proposed by Salmaso et al. (2015), codons B, F, L0, and MP are associated with mesotrophic conditions, whereas E and N indicate oligotrophic environments. In contrast, codons C, G, J, P, W2, X1, and Y are related to eutrophic conditions, while D, S1, S2, and W1 are characteristic of hypertrophic states. The growth of mesotrophic functional groups defined autumn in our study, accounting for 76.8% of the total biomass (20.0 mg L^{-1}), with especially strong contributions from L0 (8.3 mg L^{-1}) and MP (10.5 mg L^{-1}). The eutrophic (2.8 mg L^{-1}; 10.9%) and hypertrophic groups (3.1 mg L^{-1}; 11.8%) only comprised a very small portion while the oligotrophic groups were minimal (0.5%). Although mesotrophic groups (72.6%; 9.1 mg L^{-1}; dominant) were still the most abundant spring, their relative contribution was slightly lower than in autumn, but there was a significant increase in eutrophic groups (16.5%; 2.1 mg L^{-1}). This change was facilitated by a higher amount of Y (1.54 mg L^{-1}) and P (0.27 mg L^{-1}), indicating possible seasonal release of limiting factors, giving rise to nutrient availability in the wetlands. Functional groups categorized as oligotrophic (1%) and mesotroph (75%) combined on average made up~76% of the total biomass across both seasons compared to 5% for eutrophics (2.5%) and hypertrophs (2.1%). The strong dominance of mesotrophic conditions in our study agrees with other studies asserting that under the mesotrophic condition, L0 and MP dominated communities in many aquatic ecosystems (e.g., Gong et al., 2022; Yuan et al., 2025).Among lakes, spatial variability was high (Table 3). This was due primarily to a higher contribution of codon L0 (2.4 mg L^{-1} for Gezende (L1) and 2.6 mg L^{-1} L^{-1} for Berdan (L4) in spring, which are both indicative of mesotrophic conditions). Conversely, the mesotrophic codon MP was increased in autumn at Akgöl Lake (7.2 mg L^{-1}) and Gezende Reservoir (1.4 mg L^{-1}), reflecting higher biomass accumulation but may also reflect localized improvements in environmental heterogeneity under mesotrophic conditions. Codons grouped as eutrophic (C, G, J, P, W2, X1, and Y) and hypertrophic (D, S1, S2, and W1) showcased spatially heterogeneous distributions across the system. High contributions from eutrophic and hypertrophic areas also characterized Alaköprü Reservoir (Y= 1.2 mg L^{-1} in spring) and Berdan Reservoir (J = 0.3 mg L^{-1} in autumn), possibly indicating short-term nutrient enrichments creating localized productivity hotspots. In contrast, Bağbaşı and Sarıveriler Pond were characterized by low biomass on all trophic levels, indicating prevailing low productive conditions in those ecosystems. Functional structure of Ermenek Dam (L7) was relatively even, including low inputs from mesotrophic codons (L0 and MP) along with less diversified contributions from eutrophic and hypertrophic codons that were consistent albeit lower in representation (e.g., Y, P, S1). Our results indicate that mesotrophy-associated taxa dominate in the seasonally stable regime from autumn (MP) to spring (L0). Increased water column stability and reduced turbulence attributed this seasonal shift from MP to L0 (Ma et al., 2022).

In Lake İznik, Oğuz et al. (2020) reported a mesotrophic trophic structure based on habitat characteristics of functional groups detected in their study lakes; however, the main functional groups and dominant species we identified differed from those reported for our lakes. All these results suggest that although changes among lakes are site-specific regarding hydrodynamics, nutrient regimes and ecological filters (mesotrophic groups being the dominant driver of phytoplankton biomass throughout), lake type does significantly affect species composition.

Ecosystem variability was very high among lakes and the relative biomass distribution of functional groups varied widely from lake to lake, but for most other ecosystems, the L0 and MP groups dominated that overall pattern (Table 2). The biomass extremes were dominated by only one FG, often codon L0 with spring assemblages but not during autumn where the FGs had much more evenly distributed contributions to total biomass. Total biomass in spring was lower than autumn except for L1 and L3 suggesting that seasonal restructuring was not purely compositional shift but also involved quantitative contraction in many systems.

Higher biomass peaks (9.3 mg L^{-1}) occurred during the sampling at Akgöl when coincident water temperature (25.6°C) and total phosphorus concentration (0.14 mg L^{-1}). This strengthens the established link between thermophilic organisms such as phytoplankton, hot temperature, and nutrient enrichment (Zanco et al., 2017). Nevertheless, patterns of functional dominance have shown that not only nutrient concentration facilitates community structure but also how hydrological instability and turbidity effects the groups that would dominate.

Functional group dominance by season differed greatly among lakes. Between autumn and spring however, AL1 exhibited a clear codon L0 dominance as Codon MP was dominant in both

AL1 and AL2 during autumn. Codon L0 was the prevalent group for both seasons in SL1, while AL3 was F and W2 autumn mix, but changed to coda L0 and Y in spring. One dominant codon (L0) remained the majority codon in many lakes (AL4, SL4 and AL5) throughout the year but this percentage grew during spring. At the same time, AL6 indicated greater inputs of coda MP and W1 with the return of spring. Table 3 quantifies these spatial and temporal differences and the relative frequency of phytoplankton functional groups in lakes and seasons is depicted in Figure 4.

The species-level contributions helped to better clarify these dynamics. The dominant species in the basin were *Peridinium cinctum*, comprising about 20–43% of total biomass across seven lakes. Codon MP dominance was represented by many diatom species, except in Akgöl where *Gyrosigma balticum* alone contributed 51% of total biomass. The overall dominant representative species with their maximum relative biomass contributions are summarized in Table 4. These findings indicated that codon L0 dominance resulted from very few highly competitive dinoflagellates, whereas codon MP dominance was an assemblage-level response related to sediment interaction and turbidity.

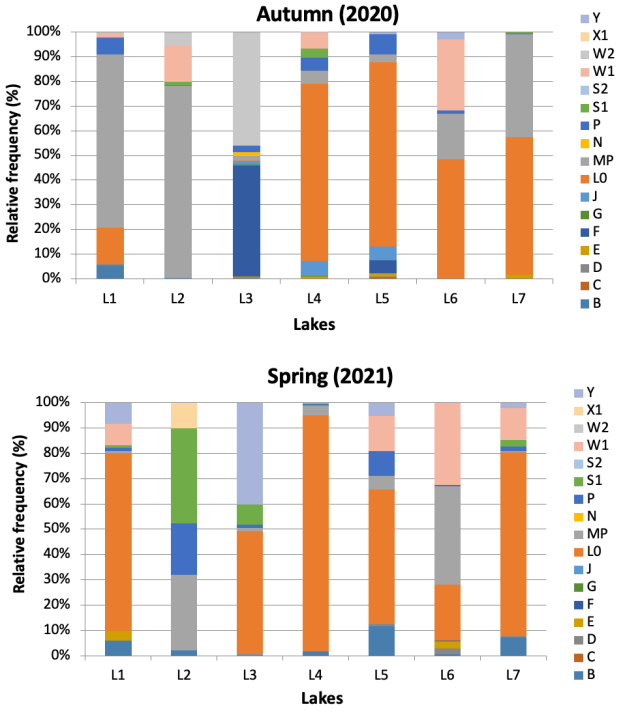

Figure 4. The relative frequency (%) of phytoplankton functional groups during seasons in seven lakes of the Eastern Mediterranean River Basin (The full names of the lakes are given in Figure 1)

Table 4. Overall dominant representative phytoplankton species and their maximum relative biomass contributions across the seven lentic systems of the Eastern Mediterranean River Basin

Dominant Representative species	Functional group	Lentic system	Maximum biomass %
Peridinium cinctum	L0	L1, L3, L4, L5, L6, L7	43% (in L4)
Ceratium hirundinella	L0	L1, L4, L7	27% (in L7)
Gyrosigma balticum	MP	L2	51% (in L2)

Note: Values indicate the maximum relative biomass contribution (%) recorded for each species among the seven lakes.

Redundancy analysis (RDA) has shown that coda L0 and MP biomass are significantly related to temperature, turbidity, electrical conductivity, total phosphorus, and BOD_5, confirming that physicochemical gradients regulate the biological structure in our system. Indeed, similar findings from other studies support our results (Søndergaard et al., 2005; Zanco et al., 2017). Although codon MP contained the highest taxonomic richness (34 taxa), it did not contribute as strongly to total biomass as codon L0, which contained only five taxa. This contrast highlights that functional dominance is not proportional to species richness, but rather depends on ecological competitive strength under existing environmental filters.

The codon L0 is primarily represented by the species *Ceratium hirundinella*, *Peridinium cinctum*, and *Peridiniopsis* spp. (see Table 2 for representative taxa). It was the main functional group forming biomass in the basin. It was subdominant in autumn but became dominant in spring, indicating that less disturbance and greater stability of the water column favored its growth. In our study, dinoflagellates of this group have high motility and vertical migration abilities which enable them to take advantage of light and nutrient gradients in stratified systems, consistent with known traits of this functional group (Rangel et al., 2009; Bellinger & Sigee, 2010). Interestingly, codon L0 biomass was higher in spring during this study even though temperature and nutrient concentrations were lower than those of autumn. Our finding suggests that physical stability combined with reduced hydrodynamic stress is more important than absolute nutrient levels for codon L0 success in our study lakes. The absence of codon L0 from shallow, highly turbid L2 and L6 indicates that excessive inorganic turbidity and hydrological disturbance exceed the tolerance threshold even for motile dinoflagellates. Therefore, codon L0 can be seen as an indicator of relatively stable mesotrophic lentic conditions within the basin.

The group MP, typical of shallow lakes with inorganic turbidity, was the second main functional component, as indicated in Table 2. It mainly comprised benthic and tychoplanktonic

diatoms such as *Cocconeis*, *Navicula*, *Gomphonema*, *Surirella*, *Ulnaria ulna*, and some *Oscillatoria*; hence codon MP dominated especially in autumn (see Table 3). Maximum biomass recorded for this group was at 7.2 $mg\,L^{-1}$ at shallow AL2 mostly attributed to *Gyrosigma balticum* as per details provided in Table 4. However, the predominance through a benthic-tychoplanktonic diatom stresses also the impacts by sediment resuspension and inorganic turbidity in structuring of phytoplankton communities in our shallow systems. Significantly fewer codon MP taxonomic richness (28 to 13 taxa) persisted from autumn to spring highlighting the strength of seasonal environmental filtering with only disturbance-tolerant species surviving changes to spring conditions. Most of the autumn dominance was due to species like *Gyrosigma balticum* and *Cocconeis placentula* var. *euglypta* while *Peridinium cinctum* (L0) had more power in spring as can be seen in Table 4. The seasonal turnover from coda MP- to L0-dominated assemblages reflects the transition from turbulence-dominated diatom assemblages to stratification-favoured motile dinoflagellates.

Although the overall composition of the community varied seasonally, several representative taxa, such as *Peridinium cinctum*, *Ceratium hirundinella*, *Gyrosigma balticum*, and *Cryptomonas ovata* were most abundant in both seasonal differences and inter-lake similarity (Table 4). This confirms that the ecosystem functioning in the Eastern Mediterranean lakes is structured by a small number of ecologically strategic taxa acting as representatives of broader functional communities.

In summary, phytoplankton biomass models in the basin are determined by the interaction between nutrient enrichment, temperature, and hydrodynamic regime. The fluctuation between L0 (stable, motile dinoflagellates) and MP (turbidity-tolerant diatoms) groups reflects seasonal and lake-specific changes in environmental conditions. These findings confirm that the functional group approach provides a robust ecological model for interpreting phytoplankton responses to environmental gradients in mesotrophic Mediterranean lake systems. Our findings demonstrate that the functional group approach provides a robust ecological framework for interpreting phytoplankton responses to environmental gradients in mesotrophic Mediterranean lake systems.

CONCLUSION

Integrated assessment of physicochemical conditions and phytoplankton functional group dynamics across the Eastern Mediterranean River Basin offers a clear perspective on how lake typology and seasonal forcing together control phytoplankton organization in Mediterranean and semi-arid systems. Phytoplankton structure was not determined by nutrient availability but mainly by hydrological disturbance, salinity, turbidity, and organic matter dynamics. These drivers acted hierarchically with site-specific physical forcing interacting with basin-scale physicochemical gradients to determine functional composition.

High physical disturbance lakes particularly the shallow saline influenced Akgöl Lake had reduced functional diversity dominated by benthic and tychoplanktonic groups (MP) due to intensified sediment resuspension, high turbidity, and unstable mixing regimes. Reservoirs with greater water column stability supported motile dinoflagellate-dominated assemblages (L0), particularly in spring when increased oxygenation accompanied by reduced disturbance allowed exploitation of resources vertically. The mesotrophy-adapted L0 group consistently dominated stable lakes (~51% of total biomass), while the MP group peaked in turbid disturbance-prone lakes reflecting site-specific environmental conditions; these are contrasting FG configurations that demonstrate how functional group composition integrates the ecological consequences of morphometry, hydrology, and physicochemical variability at the lake scale.

Basin-wide FG succession was further structured by seasonal forcing. Spring conditions favored mixing-adapted oxygenated groups at moderate nutrient concentrations while autumn conditions favored taxa tolerant to increasing turbidity, organic loading, and intensified mineralization processes. In some lakes, seasonal shifts equaled or exceeded spatial differences in shaping functional composition which highlighted the importance of temporal resolution for ecological assessment. Redundancy analysis indicated that salinity-related variables and organic matter indicators exerted stronger and more consistent control over FG distribution than nutrients alone, supporting a basin-scale hydrological degradation gradient characterized by coupled salinity, turbidity, and organic matter dynamics. This indicates functional substitution and trait-based reassembly among groups rather than uniform biomass amplification.

Phytoplankton functional groups were collectively robust indicators of ecological status, spatial heterogeneity, and temporal reorganization of phytoplankton assemblages within heterogeneous lake systems. In addition, phytoplankton FGs provided mechanistic evidence for the role played by physical disturbance, salinity, and organic matter on phytoplankton assemblages in Mediterranean-type lakes. The studies indicated that nutrient management strategies would not be sufficient to ensure ecological integrity but rather that hydrological management, sediment management, and

salinity/organic matter management strategies should be incorporated into basin management strategies. Seasonal and lake type factors should be included in the management strategies together with trophic state approaches to phytoplankton management.

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