Spatial and seasonal dynamics of phytoplankton groups and its relationship with environmental variables in Lake Okeechobee, USA

Chengxue Ma, Ziyu Li, Patteson Chula Mwagona, Abul Rabbany and Jehangir H. Bhadha

ABSTRACT
The concept of phytoplankton functional groups was used to assess phytoplankton community structure in an attempt to better understand their spatial and seasonal variation in Lake Okeechobee, USA. Samples were collected for analyses during summer and winter. 23 phytoplankton functional groups were identified among 102 species, of which 9 groups (H1, M, C, MP, Y, S1, J, X1 and X2) were categorized as dominant. Y represented by Cryptomonas ovata and H1, represented by Anabaena circinalis and Anabaena variabilis, were dominant in some sites in summer corresponding to higher temperatures. In winter, the biomass of the functional groups was dominated by chlorophyta group X2 corresponding to lower temperatures, and relatively high nutrients. Redundancy analysis (RDA) with Monte Carlo test revealed that water temperature (WT), TP, and TN were the most dominant environmental variables which influenced phytoplankton functional group distribution in Lake Okeechobee. Functional group H1 was associated with TN, pH, TP and WT. Similarly, functional group Y was significantly positively correlated with TN, TP and WT but negatively correlated with TN/TP ratios. This study reveals the importance of physical-chemical variables across a spatial and seasonal gradient, in structuring phytoplankton functional groups, and consequently in the assessment of environmental status of the lake.

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Introduction
Phytoplankton encompasses an exceedingly diverse group of organisms, including different taxonomic groups and hundreds of species. For the classification of phytoplankton taxa and their application in understanding aquatic systems, two models have been routinely applied. One model is based on morphological traits (Kruk 2010) and involves the
understanding of purely morphological characteristics of the taxa (Litchman et al. 2010; Salmaso et al. 2015; Borics et al. 2021). While the other is based on the functional traits and requires taxonomic, physiological and ecological knowledge of each particular group (Reynolds et al. 2002; Padisák et al. 2009). Functional groups based on functional characteristics has attracted increasing attention in recent years (Reynolds 2006; Ma et al. 2019). The functional group concept has been used in theoretical studies and in assessing water quality (Padisák et al. 2003; Padisák et al. 2006; Salmaso and Padisák 2007). This concept has provided important information for understanding the dynamics of pelagic communities in tropical (Sarmento et al. 2006), subtropical (Burford and O’Donohue 2006), temperate (Filstrup et al. 2016; Sevindik et al. 2017), and Mediterranean ecosystems (Vila et al. 2005). Although, functional group concept has proved to be more useful for ecological purposes than the previously applied taxonomic groupings (Salmaso and Padisák 2007), this concept have not been sufficiently investigated in large subtropical lakes such as Lake Okeechobee, Florida, USA.

Consideration of temporal and spatial variability of phytoplankton functional groups in aquatic systems is essential for understanding the ecology of aquatic biota (Schindler 2003). Variability in phytoplankton functional groups may be perceived as an impediment to understanding the forces that structure an ecosystem, but it can also be used to assess the relative importance of processes operating within a system (Kratz et al. 1987). Scientists have typically examined space and time separately, either by sampling several aquatic systems in a single year or for many years (Sun et al. 2019; Ma et al. 2021). Investigations have recommended a predominance of spatial over temporal variation (Kratz et al. 1987; Rusak et al. 2002). The variation of phytoplankton from year to year have prompted some to speak of ‘periodicity’ (Yeo 1971), others to speak of ‘succession’ (Ma et al. 2019), while others have related the changes in plankton composition to ‘gradual climate change’, noting the very short generation times of plankton relative to rates of seasonal change (Hebert and Wilson 1994).

Lake Okeechobee has a multidecadal legacy of nutrient inflows from agricultural sources, accumulated sediments (internal loads), and phytoplankton community dominance by cyanobacteria. Because of the shallow depth, large fetch and wind regime, periodic sediment resuspension events are common (James et al. 2009). Water column TP concentrations have more than doubled since the mid-1970s (James, Havens, et al. 2011), while TN concentrations have fluctuated around 2.0 mg/L since 1983 (James, Gardner, et al. 2011). Most of the previous studies in Lake Okeechobee have focused on the influence of extreme weather events on the phytoplankton community structure (Beaver et al. 2013), and zooplankton-phytoplankton-nutrients interactions (Havens et al. 1996). In this study, the concept of functional group is used to assess the spatial and seasonal variation of phytoplankton. The main objectives of this study were to: (i) evaluate the spatial and seasonal distributions of phytoplankton functional groups, their composition, and biomass, and (ii) evaluate the ecological status of Lake Okeechobee as revealed by the functional group analyses. Additionally, the study also considered the driving variables that are responsible for variations in phytoplankton functional groups.

Materials and methods

Description of the study area

The study was conducted in Lake Okeechobee, Florida, USA, and its surrounding watershed. Lake Okeechobee is characterized by its large size (1,730 km²), relative shallow depth
(average depth of 2.7 m) and turbid water (Beaver et al. 2013). Temperature in Lake Okeechobee varies from 10.5 °C to 32.2 °C and is rarely below 3.3 °C or above 34.5 °C. Historically, Lake Okeechobee used to experience annual wet and dry seasons, with changes in climatic patterns; in recent years it has also started to experience ‘wet’ and ‘dry’ years, resulting in highly variable water levels (Beaver et al. 2013). Based on the nutrient levels (TP and TN), chlorophyll a concentrations, and Secchi depth (SD), the lake is classified as Eutrophic (Havens et al. 1996). The lake is characterized by three distinct regions: pelagic, littoral, and near-shore, each having distinct physical, chemical, and biological attributes. The lake’s thermal regime is best described as polymictic with stratification occurring approximately five percent of the time (Rodusky et al. 2005). Lake Okeechobee is used for different purposes, recreational, water supply for human consumption, irrigation in farmlands, flood mitigation, ground water recharge, and providing habitat for different endangered species.

**Field sampling methods**

Samples for analyses were collected in summer (July) and winter (December) from the 26 georeferenced sampling sites within Lake Okeechobee and its surrounding watershed (Figure 1). Sites 1 – 7 are located on the northern side of the lake near the Kissimmee River. The main activity on the northern part of the lake is livestock keeping. Sites 8 – 13 are located on the western side of lake. Sites 14 – 21 are located on the southern side of lake near the Everglades Agricultural Area (EAA). Site 22 is located on the eastern side of lake. Sites 23 and 24 are located in the St. Lucie River. Site 25 is located in District Canal located in Belle Glade. Sites 26 is located in the Caloosahatchee River. At each site water temperature (WT) and pH readings were measured using a portable multi-probe (YSI 6600, YSI Inc., Yellow Springs, OH, USA) while water transparency was determined using a 20 cm Secchi disk (SD). Whole water samples from the same site were collected for phytoplankton and physicochemical analyses, sampled using a calibrated 2.5 L van Dorn sampler from 0.5 m depth. Phytoplankton samples were fixed in the field with Lugol’s solution, while samples for nutrients were placed in HCl-rinsed plastic bottles and stored on ice until processing.

![Figure 1. Locations of sampling sites in Lake Okeechobee.](image-url)
Laboratory procedure

Nutrient analyses were conducted at the University of Florida Soil, Water, and Nutrient Management Laboratory at the Everglades Research and Education Center, in Belle Glade, Florida. In the laboratory, total nitrogen (TN) was determined by following ASTM method D8083-16 on Shimadzu TOC-L series instrument equipped with TNM-L module. Total phosphorus (TP) and potassium (TK) was determined by following USEPA method 200.7 on a Inductively Coupled Plasma Optical Emission Spectroscopy (ICP-OES). Total organic carbon (TOC) was determined using the U.S. EPA method 415.3 and analyzed on a Shimadzu Carbon analyzer TOC-L series.

The fixed samples for phytoplankton analysis were sedimented for 48 h and concentrated to 30 mL. Identification and counting of phytoplankton species was conducted with an inverted microscope at 400× magnification using several keys, illustrations and techniques from different literature (Prescott 1954; Utermöhl 1958; Komárek and Fott 1983). Biovolume (mm³/L) was estimated based on the solid geometric shape (Hillebrand et al. 1999). Cell volumes of at least 40 algal units were estimated by approximation to the nearest solid geometric solid. Conversion of biovolume into biomass was done as 1mm³/L = 41mg/L (Wetzel and Likens 2000). The species were grouped into functional group as described by (Reynolds et al. 2002; Padisák et al. 2009).

Statistical analyses

Statistical analysis was carried out using the SPSS 19.0 software and data were transformed to manage variance heterogeneity. Variation of environmental parameters and biomass of functional groups were analyzed using One-way ANOVA. Relationships between functional groups and physicochemical parameters were analyzed using the detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA) in CANOCO 4.5 software (Microcomputer Power). Monte Carlo simulations with 499 permutations were used to test the significance of the physicochemical variables in explaining the biomass of phytoplankton FG’s data in the CCA.

Results

Environmental conditions

The mean seasonal values of physical–chemical variables recorded among the sampling sites within the study period are presented in Table 1. Most environmental conditions in Lake Okeechobee varied over space and time. Seasonally, mean WT was highest (27.15 ± 0.97 °C) in summer and lowest (22.72 ± 2.21 °C) in winter. The highest TN (1.45 ± 0.37 mg/L) and TP (0.65 ± 0.46 mg/L) were observed in summer. Secchi disk depth

| Physical–chemical variables | Winter (December) | Summer (July) |
|-----------------------------|-------------------|---------------|
| WT (°C)                     | 22.72 ± 2.21      | 27.15 ± 0.97  |
| SD (cm)                     | 43.42 ± 14.55     | 62.17 ± 27.85 |
| TN (mg/L)                   | 1.05 ± 0.68       | 1.45 ± 0.48   |
| TP (mg/L)                   | 0.02 ± 0.06       | 0.65 ± 0.46   |
| TN/TP                       | 52.5 ± 11.3       | 2.23 ± 1.0    |
| K (mg/L)                    | 4.97 ± 1.11       | 4.98 ± 1.6    |
| pH                          | 8.65 ± 0.3        | 8.14 ± 0.74   |
| TOC (mg/L)                  | 29.81 ± 6.74      | 39.65 ± 13.8  |
(SD) measured in summer of 62.17 ± 12.11 cm was the highest. Interestingly, SD was relatively lower at the sampling sites within or near the central pelagic region of the lake. Mean pH value in winter was 8.65 ± 0.3 which was relatively higher than in summer (8.14 ± 1.57). WT gradually decreased in summer from site 1 to site. Site 19 had the highest WT value measured during summer (Figure 2(a)). In winter, WT was almost constant in sites 1 to 5, followed by sharp decrease in site 6 and 7 and the fluctuation patterns in the remaining sites (Figure 2(a)). No significant differences were observed among the site for pH values both in summer and winter. Site 12 recorded the lowest pH values both in summer and winter (Figure 2(b)). The spatial trend of TN depicted a very interesting pattern both in summer and winter (Figure 2(d)). The mean values of the TN in summer were almost similar in sites 1, 2, 3, 4, 5, 6 and 7. This was followed by an increase and then fluctuating trend in the other sites. Almost similar pattern of the TN recorded in summer was observed in winter, though relative low values in winter (Figure 2(d)). For the TP, the mean values in winter were almost constant with an exception of site 20 where there was a slight increase (Figure 2(e)). However, in summer a fluctuating trend was observed with higher values measure in site 12 and 22 (Figure 2(e)).

Phytoplankton community structure

A total of 102 phytoplankton species belonging to seven taxonomic classes: Chlorophyceae (49 species), Cyanophyceae (14 species), Bacillariophyceae (24 species), Euglenophyceae (3 species), Chrysophyceae (9 species), Cryptophyceae (2 species), and Dinophyceae (1 species) were observed in Lake Okeechobee. The 102 species were grouped into 23 functional groups (Table 2) as described by (Reynolds et al., 2002; Padisák et al. 2009).

The seasonal and spatial variation of the nine most dominant phytoplankton functional groups is shown in Figure 3. The mean phytoplankton functional groups biomass range from 0.10 to 14.09 mg/L in summer (Figure 3(a)), with high biomass value recorded in site S3 and the least in site S23. The biomass of the phytoplankton functional groups measured in sites S1 to S5 was statistically significant different from those measured in the other sites. Functional group Y dominated by Cryptomonas ovata and group X2 dominated by Chlamydomonas globosa and Chlamydomonas ovalis shared the dominance in sites S1 to S5. In winter, the phytoplankton functional group biomass was dominated by chlorophyta group X2 and J corresponding to low temperature and relatively high nutrients (Figure 3(b)).

Similar to other studies (Gillet et al. 2015; Ma et al. 2019), phytoplankton functional groups biomass was dominated by chlorophyta group X2 and J in winter corresponding to low temperatures and relatively high nutrients (Figure 3(b)). Group J which was mainly dominated by Scenedesmus quadricauda is prominent in shallow, highly enriched systems (including many low-gradient rivers) (Reynolds et al. 1993; Padisák et al. 2009). In summer, group H1 mainly represented by Anabaena circinalis and Anabaena variabilis and group Y represented by Cryptomonas ovata were the dominant species corresponding to high temperature values. Moreover, some species of chlorophyta belonging to functional group X2 accounted for a big proportion of the total biomass in summer.

Relationship between environmental and the biomass of phytoplankton functional groups

Detrended correspondence analysis (DCA) showed that the gradient length of the longest axis was shorter than 3. Thus, redundancy analysis (RDA) was subsequently selected (Figure 4). Water temperature, TP, TN, pH, SD, TOC, TN/TP, and TK were adopted as
Figure 2. Spatial distributions of environmental variables in Lake Okeechobee (a) WT, (b) pH, (c) SD, (d) TN and (d) TP.
environmental variables. In the data matrix of species, only those dominant functional groups were incorporated into the RDA analyses. As shown in Figure 4, WT, TP, and TN contributed the most to phytoplankton functional group distribution in Lake Okeechobee (Figure 4). Functional group Y was significantly positively correlated with TN, TP and WT but negatively correlated with TN/TP ratios. Group X1 mainly dominated by *Ankistrodesmus angustus* and *Ankistrodesmus acicularis* was positively associated with WT and TP.

**Discussion**

**Water quality**

A good ecological condition is critical for aquatic organism production (Ma et al. 2013). Thus, monitoring and assessing the water quality of the lakes can help to forecast critical
Table 2. List of phytoplankton species with their taxonomic, functional groups, and percentage contribution to their total biomass for Lake Okeechobee.

| Class          | Genus                | Species                   | Functional groups | Percent of total biomass (%) |
|----------------|----------------------|---------------------------|-------------------|------------------------------|
| Cyanophyceae   | Merismopedia         | Merismopedia minima       | L0                | 1.44%                        |
|                |                      | Merismopedia marssonii    | L0                | 0.32%                        |
| Synechocystis  | Synechocystis        | Synechocystis minuscula   | L0                | 0.00%                        |
|                |                      | Chroococcus               | Chroococcus minutus | 0.39%                      |
| Phormidium     | Phormidium           | Phormidium allorgei       | S1                | 0.09%                        |
| Raphidiopsis   | Raphidiopsis         | Raphidiopsis curvata      | S2                | 1.87%                        |
| Anabaena       | Anabaena             | Anabaena cirinalis        | H1                | 2.77%                        |
|                |                      | Anabaena variabilis       | H1                | 0.32%                        |
| Aphanizomenon  | Aphanizomenon flos-aque | Coelosphaerium          | MP                | 1.33%                        |
| Coelosphaerium |                      |                           |                   |                              |
| Bacillariophyceae | Fragilaria          | Fragilaria brevistriata   | P                 | 0.17%                        |
|                |                      | Fragilaria virensens      | P                 | 0.01%                        |
| Melosira       | Melosira             | Melosira varians          | TB                | 0.01%                        |
|                |                      | Melosira granulate        | P                 | 0.05%                        |
|                |                      | Melosira granulata var. angustissima | P | 0.64% |
| Synedra        | Synedra              | Synedra acus              | D                 | 3.47%                        |
|                |                      | Synedra tabulate          | D                 | 0.01%                        |
| Cyclotella     | Cyclotella           | Cyclotella meneghiniana   | C                 | 6.26%                        |
| Navicula       | Navicula             | Navicula exigua           | MP                | 1.05%                        |
|                |                      | Navicula anglica          | MP                | 0.08%                        |
|                |                      | Navicula radiosa          | MP                | 0.05%                        |
|                |                      | Navicula dicerphala       | MP                | 0.03%                        |
| Meridion       | Meridion             | Meridion circulare        | MP                | 0.00%                        |
| Cocconeis      | Cocconeis            | Cocconeis placenta        | MP                | 0.25%                        |
| Cymbella       | Cymbella             | Cymbella ventricose       | MP                | 0.00%                        |
| Gyrosigma      | Gyrosigma            | Gyrosigma acuminatum     | L0                | 0.11%                        |
| Surirella      | Surirella            | Surirella angustata       | MP                | 0.85%                        |
| Cymatopleura   | Cymatopleura         | Cymatopleura solea        | MP                | 0.02%                        |
| Amphora        | Amphora              | Amphora ovalis            | L0                | 0.03%                        |
| Pinnularia     | Pinnularia           | Pinnularia major          | MP                | 0.31%                        |
| Diatoma        | Diatoma              | Diatoma vulgare           | MP                | 0.02%                        |
| Chrysophyceae  | Hantzschia           | Hantzschia Grunow         | D                 | 0.04%                        |
| Ceratoneis     | Ceratoneis           | Ceratoneis arcus          | MP                | 0.01%                        |
| Chromulina     | Chromulina           | Chromulina elegans        | X3                | 1.08%                        |
| Synura         | Synura Ehrenberg     | Chromulina globosa        | X3                | 0.01%                        |
| Bitrichia      | Bitrichia            | Bitrichia Phaseolus       | X3                | 0.19%                        |
| Dinobryon      | Dinobryon            | Dinobryon divergens       | E                 | 0.00%                        |
| Mallomonas     | Mallomonas           | Mallomonas Perty          | Ws                | 0.09%                        |
| Ochromonas     | Ochromonas           | Ochromonas                | X3                | 0.03%                        |
| Cryptophyceae  | Cryptomonas           | Cryptomonas ovate         | Y                 | 14.42%                       |
|                |                      | Chroomonas acuta          | X2                | 0.16%                        |
| Euglenophyceae | Euglena              | Euglena oxyuris           | W1                | 3.94%                        |
| Lepocinclis    | Lepocinclis          | Lepocinclis steinii       | W1                | 0.04%                        |
| Trachelomonas  | Trachelomonas        | Trachelomonas granulosa   | W2                | 0.01%                        |
| Dinophyceae    | Glenodinium          | Glenodinium pulvisculus   | Y                 | 2.15%                        |
| Chlorophyceae  | Chlamydomonas        | Chlamydomonas ovalis      | X2                | 7.26%                        |
|                |                      | Chlamydomonas globosa     | X2                | 16.83%                       |
| Ankistrodesmus | Ankistrodesmus       | Ankistrodesmus angustus   | X1                | 1.43%                        |
|                |                      | Ankistrodesmus acicularis | X1                | 2.32%                        |

(continued)
crisis of environmental impairment (USEPA 2011). In this study, most of the water quality variables measured varied over space and time. The highest values of TN and TP were observed in summer potentially due to runoff from the agricultural farms. Previous studies conducted in Lake Okeechobee by (Havens et al. 1994) also revealed that nutrients loads and water inflow volumes were maximal during summer. Sampling sites located within or near the central pelagic region of the lake had relative lower SD values probable because of the overlying mud sediments (James et al. 2009). Spatially, there were changes from site 1 to site 26 for almost all measured environmental variables.

| Class         | Genus            | Species                  | Functional groups | Percent of total biomass (%) |
|---------------|------------------|--------------------------|-------------------|-------------------------------|
|               | Chodatella       | Chodatella quadrirseta   | J                 | 0.07%                         |
|               | Chodatella       | Chodatella citiate       | J                 | 0.07%                         |
|               | Chodatella       | Chodatella subsalsa      | J                 | 0.01%                         |
|               | Tetrastrum       | Tetrastrum elegans       | J                 | 0.22%                         |
|               | Tetrastrum       | Tetrastrum               | J                 | 1.37%                         |
|               | Tetraëdron       | Tetraëdron trigonum      | J                 | 0.50%                         |
|               | Tetraëdron       | Tetraëdron caudatum      | J                 | 0.15%                         |
|               | Tetraëdron       | Tetraëdron trilobulatum  | J                 | 0.01%                         |
|               | Tetraëdron       | Tetraëdron pusillum       | J                 | 0.26%                         |
| Westella      | Westella botryoides |                         | F                 | 1.14%                         |
| Westellopsis  | Westellopsis linearis |                     | F                 | 0.10%                         |
| Scenedesmus   | Scenedesmus bijuga |                         | J                 | 0.27%                         |
|               | Scenedesmus      | Scenedesmus dimorphus    | J                 | 0.84%                         |
|               | Scenedesmus      | Scenedesmus quadricula   | J                 | 7.14%                         |
|               | Scenedesmus      | Scenedesmus spinusus     | J                 | 0.13%                         |
|               | Scenedesmus      | Scenedesmus platydiscus  | J                 | 0.83%                         |
|               | Scenedesmus      | Scenedesmus denticulatus | J                 | 0.25%                         |
| Coelastrum    | Coelastrum       | Coelastrum microporum    | J                 | 0.20%                         |
| Eudorina      | Eudorina         | Eudorina elegans         | G                 | 0.09%                         |
| Pandorina     | Pandorina         | Pandorina morum          | G                 | 0.20%                         |
| Schroederia   | Schroederia      | Schroederia setigera     | XI                | 0.02%                         |
|               | Schroederia      | Schroederia ritzschiodes | XI                | 0.02%                         |
| Pediastrum    | Pediastrum       | Pediastrum birtadiatum   | J                 | 0.17%                         |
|               | Pediastrum       | Pediastrum tetras        | J                 | 0.01%                         |
|               | Pediastrum       | Pediastrum tetras        | J                 | 0.04% var.tetraodon           |
| Selenastrum   | Selenastrum      | Selenastrum gracile      | F                 | 0.35%                         |
|               | Selenastrum      | Selenastrum minutum      | F                 | 0.09%                         |
| Kirchneriella | Kirchneriella    | Kirchneriella lunaris    | F                 | 0.09%                         |
| Treubaria     | Treubaria        | Treubaria crassispina    | F                 | 0.03%                         |
| Quadrigula    | Quadrigula       | Quadrigula chodatil      | F                 | 0.00%                         |
| Dictyoaphaerium | Dictyoaphaerium | Dictyoaphaerium pulchellum | F              | 0.88%                         |
| Ulothris      | Ulothris         | Ulothris variabilis      | MP                | 0.12%                         |
| Stichococcus  | Stichococcus     | Stichococcus bacillaris  | F                 | 0.06%                         |
| Crucigenia    | Crucigenia       | Crucigenia quadrata      | J                 | 0.18%                         |
|               | Crucigenia       | Crucigenia tetrata       | J                 | 0.10%                         |
|               | Crucigenia       | Crucigenia apiculate     | J                 | 0.08%                         |
| Actinastrum   | Actinastrum      | Actinastrum fluviatile   | J                 | 0.03%                         |
| Oocystis      | Oocystis         | Oocystis elliptica       | F                 | 0.32%                         |
| Closterium    | Closterium       | Closterium gracile parvulum | P              | 0.06%                         |
| Cosmarium     | Cosmarium obtusatum |                      | N                 | 0.50%                         |
|               | Cosmarium        | Cosmarium depressum      | N                 | 0.08%                         |
| Staurastrum   | Staurastrum      | Staurastrum gracile      | N                 | 0.45%                         |
| Mougeotia     | Mougeotia       | Mougeotia Agardh         | T                 | 0.05%                         |
Phytoplankton distribution

The high number of functional groups that was observed in this study was really surprising. It is known that lakes are frequently dominated by a few species or a certain functional group of algae in the late successional state, being called equilibrium (Reynolds et al. 1993; Sommer et al. 2012) or steady-state assemblages (Naselli-Flores et al. 2003). Nine groups (H1, M, C, MP, Y, S1, J, X1 and X2) were categorized as dominant groups.

*Figure 3.* Distribution of phytoplankton functional groups biomass in Lake Okeechobee. (a) Summer and (b) Winter.

**Phytoplankton distribution**

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defined by contributing a minimum of 5% of the total biomass as recommended in literature (Reynolds et al. 2002). The remaining 14 functional groups were grouped together as ‘others’ group. The nine dominant groups accounted for more than 90% of the total phytoplankton biomass hence used to analyze the composition and dynamics of phytoplankton community in the Lake Okeechobee (Table 2). Interestingly, *Anabaena circinalis* and *Anabaena variabilis* of functional group H1 were the dominant species in site S4 corresponding to high pH values. According to (Atici and Obali 2006), *Anabaena circinalis* and *Anabaena variabilis* can outcompete other phytoplankton species in polluted environments because they have the ability to utilize carbon from the polluted environments at high pH levels. This therefore suggests that the river draining into Lake Okeechobee through near site S4 has some degree of pollution.

These seasonal variations of phytoplankton functional groups observed in the current study concur with the Plankton Ecology Group (PEG) model of freshwater aquatic systems (Sommer et al. 2012). As stated in the PEG model, group X2 and J belonging to chlorophytes dominate in winter when nutrients are available and temperatures are low. Moreover, in early summer chlorophytes develops when nutrients are available. In summer, when temperature is high and silica is limiting cyanobacteria (*Anabaena circinalis* and *Anabaena variabilis*) becomes dominate. (Kosten et al. 2012) verified that under warmer water temperatures, cyanobacteria often occur as the dominant phytoplankton community. Group MP and X2 are also sensitive to water mixing; therefore, their dominance in summer could also be explained by the thermal stratification phenomena which prevent water mixing (Reynolds et al. 2002).
**Phytoplankton functional groups driving factors in Lake Okeechobee**

Different studies have established that water temperature, food resources, water transparency, nutrients and hydrology are important drivers that influence structuring of phytoplankton community (Agawin et al. 2000). Similarly, this current study has revealed that the phytoplankton functional groups are influenced by environmental variables that vary with temporal in Lake Okeechobee. From the RDA results, functional group H1 was associated with TN, pH, TP and WT. Similarly, functional group Y was significantly positively correlated with TN, TP and WT but negatively correlated with TN/TP ratios. According to (Reynolds et al. 2002) functional group Y are found in a wide range of habitats, and are tolerant of low light and sensitive to grazing. Moreover, Y group is tolerant of high light attenuation coefficients and are strongly influenced by nutrients which is in agreement with the results of the RDA biplot diagram (Figure 4). Group X1 mainly dominated by *Ankistrodesmus angustus* and *Ankistrodesmus acicularis* was positively associated with WT and TP. In general, species of Cyanobacteria and Chlorophyta are adapted to the higher temperatures that occur in summer, while Bacillariophyta are adapted to lower temperatures of winter (Ma et al. 2019). These characteristics matched well with the results observed in our study. The RDA results also indicated that water temperature was one of the most important factors driving the phytoplankton community.

**Conclusions**

In this current study, we identified a total of 102 phytoplankton species belonging to 23 functional groups. The predominant functional groups were H1, M, C, MP, Y, S1, J, X1 and X2. The biomass of phytoplankton functional groups was relatively higher in summer and lower in winter. Water temperature, TP, and TN were the most important environmental variables which influenced phytoplankton functional group distribution in Lake Okeechobee. Functional group H1 was associated with TN, pH, TP and WT. Similarly, functional group Y was significantly positively correlated with TN, TP and WT but negatively correlated with TN/TP ratios. This study reveals the importance of physical-chemical variables in the spatial and seasonal gradient, in structuring phytoplankton functional groups, and consequently in the assessment of environmental status of the lake.

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**Disclosure statement**

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Data availability statement

The datasets generated during and/or analyzed during the current study are available from the corresponding author on reasonable request.

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