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Long-term Phosphorus Reduction and phytoplankton responses in an urban lake (USA)

Yuan Xiao Grund
Portland State University, ygrund@outlook.com

Yangdong Pan
Portland State University, pany@pdx.edu

Mark Rosenkranz
Portland State University

Eugene Foster
Oregon Department of Environmental Quality

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Yuan Grund [a,*], Yangdong Pan [b], Mark Rosenkranz [c], Eugene Foster [a]

[a] *Oregon Department of Environmental Quality, OR, 97232, USA*
[b] *Department of Environmental Science and Management, Portland State University, Portland, OR, 97207, USA*
[c] *Lake Oswego Corporation, Lake Oswego, OR, 97034, USA*

ABSTRACT

Eutrophication is one of the primary factors causing harmful cyanobacteria blooms in freshwater lakes. This study investigated the long-term changes in water quality and summer phytoplankton assemblages in Oswego Lake, OR, USA, in relation to phosphorus reduction through hypolimnetic aeration and alum applications. Both water quality and phytoplankton assemblages were sampled biweekly during the summers from 2001 to 2013. The concentrations of total phosphorus, soluble reactive phosphorus, and total nitrogen decreased 66%, 93% and 31%, respectively, in response to the hypolimnetic aeration and alum treatments since 2005. Summer phytoplankton assemblages showed a 62% reduction of cyanobacteria biovolume and a shift from cyanobacteria dominance (2001–2005) to diatom and chlorophyte dominance (2006–2013). Cluster analysis identified four statistically different groups of summer phytoplankton assemblages (denoted Groups 1–4). Nonmetric multidimensional scaling analysis indicated that the four groups were associated with different water quality conditions. Group 1 occurred prior to hypolimnetic aeration and was primarily comprised of cyanobacteria, associated with water conditions of high nutrients and high primary production. Group 2, dominated by cyanobacteria and chlorophytes, occurred between hypolimnetic aeration and alum surface application. Group 3 was dominated by diatoms and occurred after alum surface application. Group 4 included R-strategist phytoplankton that quickly respond to environmental changes and occurred in the years following alum injection, drawdown, and inflow alum treatment. Both Group 3 and 4 were associated with reduced nutrients in the lake. We conclude that these lake management practices had strong effects on both production and community compositions of phytoplankton, and advocate for future studies on large-scale climate impacts on lake ecosystems and to identify corresponding best management practices.

1. Introduction

Nutrient pollution is a widespread problem of lakes in the United States (USEPA, 2016). Excess concentrations of nitrogen (N) and phosphorus (P) are among the primary causes of lake eutrophication that results in algal blooms (Huisman and Hulot, 2005; Paerl et al., 2016; Schindler and Vallentyne, 2008). Both N and P are essential elements for the growth of phytoplankton in lakes (Butusov and Jernelöv, 2013; Reynolds, 2006). Enrichment of N and P promotes the growth of phytoplankton in general (McCauley et al., 1989). Particularly, in urban lakes in temperate regions, during the summer growing season, N and P inputs were found to be responsible for the shift in phytoplankton communities towards dominance by cyanobacteria (Downing et al., 2001; Watson et al., 1997) and for the production of cyanobacteria toxins (Davis et al., 2009; Rapala et al., 1997; Rolland et al., 2005).

To control algal blooms resulting from eutrophication, great efforts have been made to reduce nutrients available to phytoplankton production (Ibelings et al., 2016; Paerl et al., 2016). Certain cyanobacteria are able to fix atmospheric N, thus, management strategies for reducing P are more feasible than that of N (Elser et al., 2007; Lewis et al., 2011; Schindler et al., 2008). Urban watershed contributions from diverse sources, such as wastewater treatment plants, fertilized residential lawns, and impervious road surfaces, are the ultimate sources of P input to lakes. Therefore, reduction in the supply of P in watersheds is a sustainable

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approach to prevent algal blooms (Carpenter et al., 1998; Hamilton et al., 2016; Roy et al., 2008). However, a great deal of evidence has shown that P can remain at high concentrations in lake water after significant reduction of P from watershed loading due to continued release of excess legacy P from lake sediments (Søndergaard et al., 2003; Van der Molen and Boers, 1994). Ideally, reduction of nutrients to control algal blooms should focus on P in both the watershed and lake sediments (Cooke et al., 2005).

Control of algal blooms in urban lakes has proven to be a challenge (Birch and McCaskie, 1999; Huser et al., 2016). Reduction of nutrient loading can be achieved in the USA through Clean Water Act required point source effluent limits for nutrients when the nutrient loading is primarily from point sources (ODEQ, 2012). However, when the nutrient loading is primarily from non-point sources (NPS), the management of nutrient loading can be difficult and complex because of limited federal and state regulations (National Research Council, 1992) and the diverse nature of NPS pollution, which can be transported via overland, underground and atmospheric paths that vary with the weather (Carpenter et al., 1998). Effective NPS management is based on best management practices (BMPs), such as development and maintenance of wetlands, retention ponds, and vegetation buffer strips (Paerl et al., 2016). However, in urban lakes, those strategies often face implementation challenges, such as fragmented responsibilities in a single watershed and resistance to change in developed urban areas (Roy et al., 2008). Thus, in-lake management is more practical than watershed nutrient management in some urban lakes because it can deal with watershed nutrient loading and internal cycling from sediment resuspension concurrently (Huser et al., 2016).

In-lake nutrient management mostly targets bioavailable P resuspended from sediments to the water column (Bormans et al., 2016; Søndergaard et al., 2003; Van der Molen and Boers, 1994). Hypolimnetic aeration and aluminum sulfate (alum) treatment are common, traditional approaches to reduce P in urban lakes (Bormans et al., 2016; Huser et al., 2016; Welch and Cooke, 1999). During periods of summer thermal stratification, hypolimnetic anoxia supports sediment P release to the water column (Søndergaard et al., 2003). Hypolimnetic aeration reduces hypolimnetic anoxia by increasing dissolved oxygen content of the hypolimnion without destratifying the lake (Soltero et al., 1994). Alum removes P from the water column by Al–P hydroxide floc coagulation and precipitation. When the Al–P layer settles to the bottom of the hypolimnion, it can block sediment P loading. However, the effectiveness of P inactivation can be reduced by both decreasing adsorption capacity of the aluminum floc and burial of the active Al–P layer by new sedimentation and sediment mixing processes (Lewandowski et al., 2003). Successive alum applications have been developed for the purpose of maintaining aluminum floc for high effectiveness (Cooke et al., 2005; Moore and Christensen, 2009).

Many studies have reviewed the efficacy of bloom control practices (e.g., hypolimnetic aeration and alum treatment), but most evaluations have been based on a single approach and the effects on chlorophyll *a* and/or total phytoplankton abundance (Huser et al., 2016; Suikkanen et al., 2007). Reports involving the integration of multiple practices are only available for a few lakes (Moore and Christensen, 2009; Soltero et al., 1994). Responses of phytoplankton assemblages are often only reported briefly, probably because of the lack of long-term, comparable data of taxonomic identifications for phytoplankton species (Suikkanen et al., 2007). Changes in phytoplankton composition usually indicate shifts in environmental conditions (Reynolds, 2006). Given the goal of nutrient management to control blooms, information on the responses of individual phytoplankton taxa to changes in environmental conditions is more informative.

In this study, we characterized the changes in summer phytoplankton assemblages and their relationships with environmental variables in Oswego Lake, an urban lake in Oregon, USA, over a 13-year period (2001–2013). Specifically, we evaluated the changes in summer phytoplankton assemblages in relation to in-lake P reduction practices. We

therefore hypothesized that in-lake P reduction would drive changes in phytoplankton assemblages. With the purpose of understanding the basic response mechanism of phytoplankton assemblages to lake management, this study may provide important information for future urban lake management to effectively predict, prevent and control harmful cyanobacteria blooms.

2. Materials and methods

2.1. Study site

Oswego Lake (45°24′34″N, 122°41′47″W) is located in northwest Oregon, USA (Fig. 1). The lake is a former channel of the Tualatin River and was formed by the Missoula Floods of the last ice age. It is rich in flood sediments that were deposited in the lakebed (Foster, 2009). The region surrounding the lake was rich in iron ore, and ore mining and smelting was the central industry in the lake town in the mid-1800s. The lake was dammed for power generation and the area surrounding the lake was developed as a residential district in the 1900s. It now consists of one deep basin, two shallow basins and two canals. It has a maximum depth of 16.7 m and a total area of 1.7 km². The lake has one outflow, three inflows, and almost 70 stormwater outfalls in its watershed. The lake has a watershed area of 18.6 km² entirely within the limits of the city of Lake Oswego. The watershed is mostly comprised of urban areas (68%) and forest cover (19%). The climate in the region is directly affected by the Pacific Ocean and is characterized by wet, mild winters and dry, warm summers (Franczyk and Chang, 2009). According to data from the Oswego Lake weather station (Fig. 1), the average monthly temperatures ranged from a low of 4.8 ($\pm$1.3) °C in December to a high of 20.2 ($\pm$1.0) °C in July between 2001 and 2013. The average annual precipitation was 962.1 ($\pm$187.0) mm for the 13 years, which included the wetter years in 2006 and 2012 (>1200 mm) and the dryer years in 2002 and 2013 (~750 mm). On average, more than 70% of the annual precipitation fell between October and March, with less than 10% falling between July and September.

Oswego Lake was previously a hypereutrophic lake and had a long history of cyanobacteria blooms (Johnson, 1985). Since the 1950's, the full water right of 1.6 m³/s was withdrawn from the Tualatin River 24 h a day, year-round to the lake for power generation. Although this practice has been reduced since the mid 1990's, the inflow of nutrient-rich water from the Tualatin River brought large loads of P-rich sediments into the lake (ODQE, 2001). For example, from November 1986 to December 1987, 38.9 million m³ of water were imported from the Tualatin River with a loading of 487,000 kg of sediment and 14,000 kg of P (SRI, 1987). Oswego Lake is also the destination for surface runoff from the local watershed managed by the City of Lake Oswego. Additionally, in 1996, the lake experienced a major flood that contributed a great deal of sediment from the Tualatin River. As a result, there was a large reservoir of P-rich sediment in the lake, which caused significant summer cyanobacteria growth. A *Microcystis* bloom late in the summer of 2004 necessitated restricting lake use to non-contact activities because of the potential for illness from the presence of microcystin toxin.

A number of management practices have been employed in Oswego Lake to reduce and prevent cyanobacteria blooms. Prior to 2001, copper sulfate was used in the lake to reduce the concentration of cyanobacteria. This practice was stopped in 2001 because of possible copper sulfate toxicity to the aquatic biota. Between 2001 and 2013, management efforts focused on reduction of in-lake P to control blooms, which included hypolimnetic aeration, alum surface application, alum injection, inflow water volume reduction and inflow alum treatment. In addition, two drawdowns dropped the water level 3 m in 2006 for 138 days and 7 m in 2010 for 264 days. Although the purpose of these drawdowns was lake and facility maintenance, water level fluctuations can have important consequences on the lake ecosystem (Bakker and Hilt, 2016; Pan et al., 2018). In addition to inflow control of the Tualatin River, the City of Lake Oswego has implemented several stormwater BMPs (e.g., wet retention
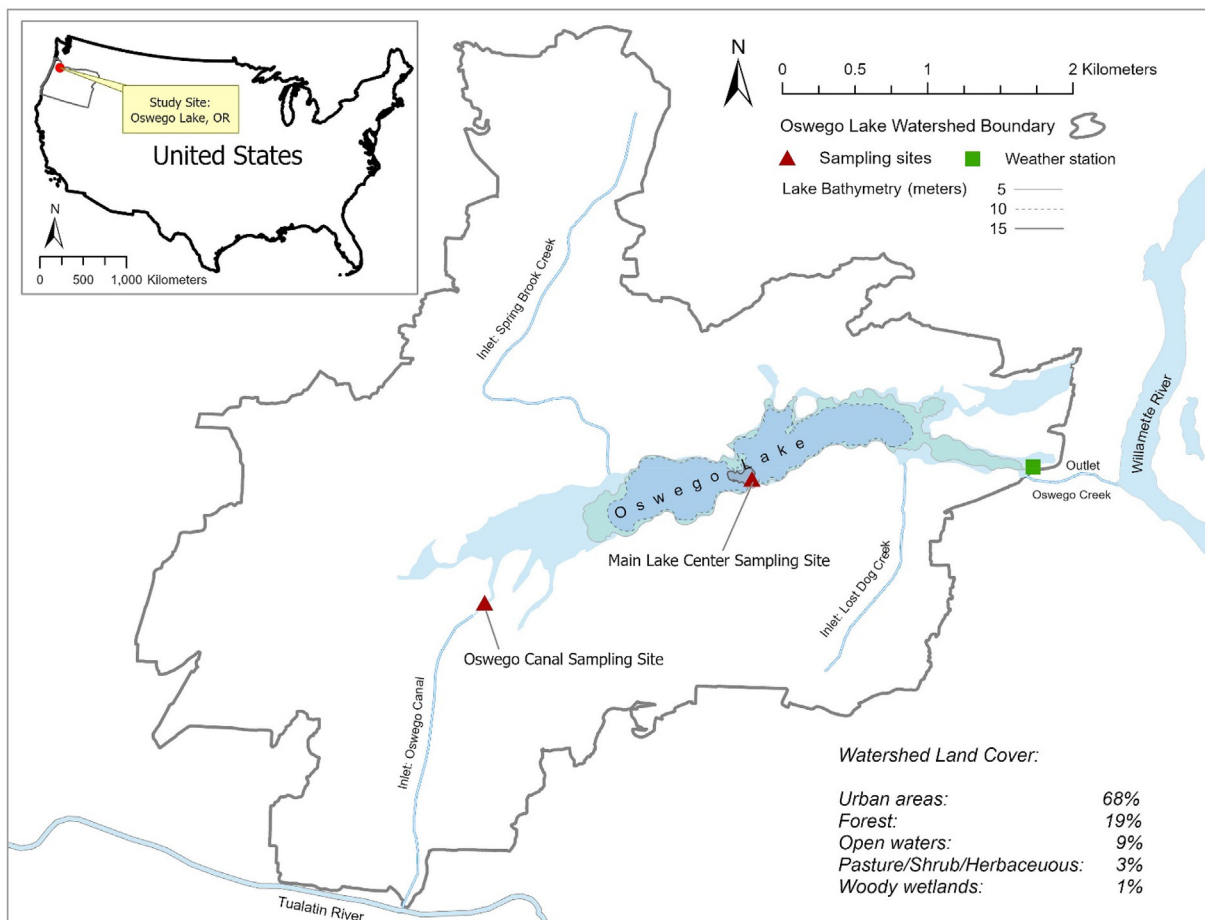
Fig. 1. Watershed map of Oswego Lake, OR, USA. Data source: National Geographic World Map, Oregon Spatial Data Library, and Lake Oswego Corporation.

ponds, dry detention ponds, swales, infiltration rain gardens, underground injection control systems, and lined planter rain gardens), and the Oswego Lake Watershed Council has performed bank stabilization through promotion of native vegetation and removal of invasive species along stream banks.

2.2. Sampling and measurement

Physical, chemical and/or biological parameters were measured weekly or biweekly at eight sampling sites in Oswego Lake for long-term water quality monitoring. The sampling sites, corresponding with various aspects of lake morphology, included one site at each of two shallow basins, the outlet and two canals, and three sites in the main lake basin. The Main Lake Center and Oswego Canal sites (Fig. 1) and biweekly sampling data from July to September 2001–2013 were used in this study.

The Main Lake Center sampling site has a maximum depth of >15 m (Table S1). During summer thermal stratification, the approximate depths of the epilimnion, thermocline and hypolimnion are 1–5 m, 5–7 m and 7–15 m, respectively. Water temperature, pH, specific conductance, and percent saturation of dissolved oxygen were recorded at every meter from 0.38 m to 15 m below the surface using a YSI 6600 multiparameter water quality sonde. The values of epilimnetic water quality parameters were generated by averaging the YSI sonde measurements at depths between 1 and 5 m. Turbidity, using a grab sample at elbow depth, was measured using a Hatch 2100Q Turbidimeter.

Water samples for total suspended solids (TSS), nutrients, chlorophyll *a*, and phytoplankton were collected using a Kemmerer sampler at specific depths. The epilimnion samples were the equal-volume composite of water samples taken at discrete depths of 1, 2, 3, 4, and 5 m. The hypolimnion samples were the equal-volume composite of water samples taken at discrete depths of 10, 12, and 14 m. The canal samples were collected by placing the Kemmerer sampler in the middle of the water column at a depth of about 1 m. Epilimnetic TSS was measured following the standard method (APHA et al., 1998) (Appendix A1). Nutrients were sampled for total phosphorus (TP), soluble reactive phosphorus (SRP), and total nitrogen (TN). Samples were kept in a dark cooler in the field and were shipped overnight with ice packs to a commercial lab that analyzed the samples using the ascorbic acid method to determine TP and SRP (detection limits of 0.002 mg/L for TP and 0.001 mg/L for SRP) within 48 h, and the persulfate digestion method to determine TN (detection limit of 0.100 mg/L) (APHA et al., 1998; Godomski, 2013). Chlorophyll *a* samples were obtained by filtering 300–500 mL of sampling water with the addition of 1 mL of saturated magnesium carbonate ($MgCO_3$) solution through a 0.45 μm glass fiber filter. Chlorophyll *a* values were determined with a spectrophotometer (APHA et al., 1998) (Appendix A2).

Phytoplankton samples (500 mL each) were preserved with 3 mL Lugol's solution per sample, kept in a dark cooler in the field, and shipped overnight with ice packs to a commercial lab. Phytoplankton cell volume dimensions and identifications were determined by using a 0.1 mL Palmer-Maloney nanoplankton chamber with a calibrated whipple disc and a Leitz compound microscope at 400X high magnification or at 1000X magnification with oil immersion. Geometric cell dimensions of at least 10 organisms of each phytoplankton taxon were computed to obtain average cell volume per taxon and used to calculate cell volumes for the lake sample. Phytoplankton identification was made to the species level when possible. Species identifications were conducted primarily

according to Prescott (1975, 1980), Patrick and Reimer (1966, 1975), Smith (1950), Wehr and Sheath (2003), and recent journal articles (Gibbons, 2013) (Appendix A3).

The Oswego Canal connects the major summer inflow from the Tualatin River to the lake (Fig. 1). The Oswego Canal sampling site is shallow with a depth of approximately 1 m. The grab samples of TP, SRP and TN were collected at this site to reflect nutrient levels in Tualatin River inflows. Sample storage and measurement followed the same protocol as the samples collected in the Main Lake Center sampling site.

2.3. Data analysis

To characterize phytoplankton assemblages, the phytoplankton taxon biovolumes were converted to the percentage of total biovolume of each sample. Rare species (i.e., <3 samples among all samples) were removed from this dataset to reduce noise for further multivariate analysis (Poos and Jackson, 2012). To describe the long-term changes in phytoplankton assemblages, a combination of hierarchical agglomerative cluster method with Ward's minimum variance method (Ward Jr., 1963) was used to identify relatively homogeneous groups of phytoplankton assemblages using the Bray-Curtis dissimilarity index (Bray and Curtis, 1957). Analysis of Similarity (ANOSIM) was used to test for statistically significant differences among the cluster groups (Clarke, 1993). Dominant taxa and indicator taxa were further used to characterize the cluster groups of similar phytoplankton assemblages. Dominant taxa were defined as any taxa accounting for more than 50% of total phytoplankton biovolume within each group. Indicator taxa included taxa of cyanobacteria, diatoms, and chlorophytes that had an indicator species index >0.5 ($p < 0.05$) based on Dufrene-Legendre indicator species analysis (Dufrene and Legendre, 1997). P values of indicator species for all taxa were determined using Monte Carlo permutation tests (1000 times).

Further, nonmetric multidimensional scaling (NMDS) based on a Bray-Curtis dissimilarity matrix was used to visualize changes among the groups of phytoplankton assemblages over time. NMDS is a multivariate ordination technique commonly used in ecological community analysis (Clarke, 1993). NMDS projects each sample into a species-defined ordination space with two or more dimensions based on their ranked dissimilarity. The goodness-of-fit for the NMDS projections was measured as a stress value which quantifies the deviation from a monotonic relationship between the distance among samples in the original Bray-Curtis dissimilarity matrix and the distance among samples in the ordination plot. The NMDS was run 20 times, each with a random starting configuration. The final NMDS dimension was selected based on the lowest stress value among the best solutions.

Changes in phytoplankton assemblages were expected to associate with environmental factors (Table S1). To assess these relationships, environmental variables were related to the NMDS ordination space defined by the species data using the "envfit" function in R (Oksanen et al., 2020). The importance of each environmental variable was assessed using a squared correlation coefficient (r^2). Furthermore, lake management practices were related to the cluster groups of phytoplankton assemblages in a timeline manner to assess the effects of management on the dynamics of phytoplankton communities.

Data analysis was performed using R (R Core Team, 2021). Specifically, the packages 'vegan' (Oksanen et al., 2020) and 'MASS' (Venables and Ripley, 2002) were used for the cluster and NMDS analyses, the package 'labdsv' (Roberts, 2019) for the indicator species analysis, and the package 'timevis' (Attali and Almende, 2020) for the temporal relationship between lake management practices and the cluster groups of phytoplankton assemblages.

3. Results

3.1. Changes in environmental conditions over 13 years

Concentrations of nutrients changed over 13 years. The greatest changes occurred in epilimnetic TP and SRP in 2005 when the alum surface treatment was applied (Fig. 2a). Mean epilimnetic TP declined from 72 μg/L (2001–2004) to 25 μg/L (2005–2013), a 66% reduction, while mean epilimnetic SRP declined from 8 μg/L to 0.6 μg/L, a 93% reduction. Mean epilimnetic TN gradually declined from 585 μg/L to 403 μg/L, a 31% reduction. Mean epilimnetic TN:TP ratio increased from 9 to 18. Meanwhile, the most visible changes in hypolimnetic nutrients occurred in 2001 when hypolimnetic aeration began. Mean hypolimnetic TP declined from 292 μg/L (2001) to 69 μg/L (2002–2013), a 77% reduction, with mean hypolimnetic SRP decreasing from 62 μg/L to 14 μg/L (77%) and mean hypolimnetic TN decreasing from 2083 μg/L to 880 μg/L (58%). In addition, concentrations of nutrients in inflow water from the Tualatin River were high during the study period. Over 13 years, mean inflow TP was 112 μg/L; mean inflow SRP was 45 μg/L; and mean inflow TN was 3667 μg/L. Both the lowest inflow of TP (mean = 50 μg/L) and SRP (mean = 9 μg/L) occurred in 2012, the first year that inflow was treated with alum.

Several other epilimnetic water quality variables, such as pH, turbidity, and total suspended solids (TSS), varied in a similar pattern, showing an increasing trend in higher values between 2001 and 2004 and then decreasing to relatively lower values between 2005 and 2013 (Fig. 2b). Mean pH ranged from 9.4 (2001–2004) to 8.1 (2005–2013), with mean turbidity ranging from 10 NTU to 3 NTU and mean TSS ranging from 10 mg/L to 4 mg/L. Mean chlorophyll *a* was higher between 2001 and 2006 (except in 2002) and lower between 2007 and 2013 (2001 and 2003–2006: 25 μg/L; 2002: 12 μg/L; 2007–2013: 11 μg/L). Specific conductivity, pH, turbidity, TSS, TP, SRP, and TN strongly correlated with chlorophyll *a* (Pearson correlation coefficient $r = 0.60$, 0.54, 0.57, 0.44, 0.67, 0.41, and 0.57 respectively, $p < 0.05$, $n = 38$). Epilimnetic dissolved oxygen was super-saturated (mean = 117%). Epilimnetic water temperature varied between 18.1 °C and 24.3 °C with an average of 22.0 °C.

3.2. Changes in phytoplankton assemblages in relation to environmental conditions

Between July and September from 2001 to 2013, a total of 129 phytoplankton taxa belonging to eight divisions were identified, including 45 chlorophytes, 31 cyanobacteria, 25 diatoms, and 28 taxa belonging to the other five divisions (Table S2). Phytoplankton assemblages were numerically dominated by cyanobacteria (mean relative abundance = 45%), followed by diatoms (23%) and chlorophytes (15%) (Fig. S1).

The relative abundance of cyanobacteria biovolume decreased ($R^2 = 0.5$, $p < 0.001$), which was mainly associated with the decrease of non-N fixers ($R^2 = 0.8$, $p < 0.001$), while that of diatom biovolume increased ($R^2 = 0.5$, $p < 0.001$) over 13 years (Fig. 3a). Two noticeable changes occurred in 2002 and 2006, the second years of operation of the 2001 hypolimnetic aeration and 2005 alum surface application, respectively. Relative abundance of cyanobacteria dropped 40% in both 2002 and 2006 compared to the previous years. Chlorophytes (41%) were high in 2002, while diatoms (35%) were high in 2006.

The cluster analysis identified 4 groups based on phytoplankton assemblages of 50 taxa during the study period (Table 1, Table S2, Fig. 3b, and Fig. S2). The groups were significantly different from one another based on ANOSIM ($R = 0.86$, $p = 0.001$). Group 1 (G1) was dominated by cyanobacteria that accounted for, on average, 81% of the total phytoplankton biovolume, which was mainly comprised of non-N fixers (67%). *Limnoraphis* sp., a filamentous non-N fixing cyanobacteria, was both the dominant species and the indicator species of G1. Group 2 (G2) was dominated by cyanobacteria (60%) and chlorophytes (24%). The dominant species and indicator species in this group were *Microcystis* sp. and *Closteriopsis longissimi* that were both common species found in eutrophic freshwaters. Group 3 (G3) had the highest relative abundance of diatoms (35%) that were more abundant than cyanobacteria (30%). G3 was comprised of common summer eutrophic assemblages, including non-
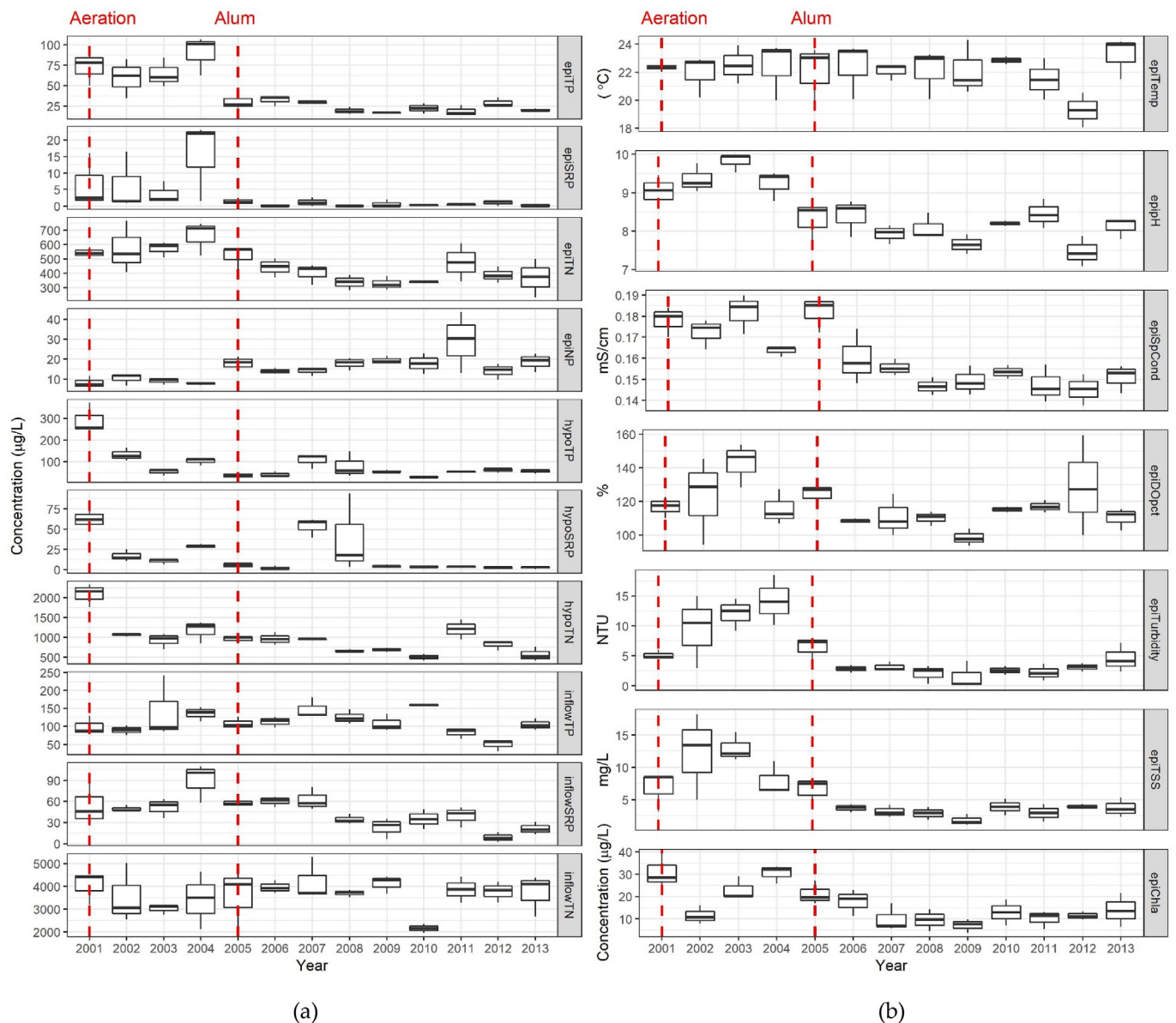
Fig. 2. Boxplots showing year-to-year variations of (a) nutrient variables and (b) other epilimnetic water quality variables between July and September from 2001 to 2013 in the deep basin of Oswego Lake. The box includes the data between first and third quantiles and the median (black bar). The upper whisker extends to the largest value no further than 1.5 IQR (the interquartile range), while the lower whisker extends to the smallest value up to 1.5 IQR. Abbreviations: epi – epilimnion; hypo – hypolimnion; TP – total phosphorus; SRP – soluble reactive phosphorus; TN – total nitrogen; NP – nitrogen to phosphorus ratio; Temp – temperature; SpCond – specific conductance; DOpct – percent saturation of dissolved oxygen; TSS – total suspended solids; Chla – chlorophyll *a*.

motile diatoms (*Aulacoseira* sp. and *Fragilaria* sp.), motile dinoflagellates (*Ceratium hirundinella*), N fixing cyanobacteria (*Aphanizomenon flos-aquae* and *Dolichospermum* sp.), and chlorophytes (*Pandorina* sp.). Group 4 (G4) was dominated by chlorophytes (38%) and diatoms (30%), while cyanobacteria were the least abundant in this group. The dominant species and the indicator species of G4 belonged to cosmopolitan taxa found in various water trophic conditions, including oligotrophic to mesotrophic *Oocystis* sp. and eutrophic *Coelastrum* sp.. With respect to taxa richness and diversity, G3 was most diverse (42 taxa; Shannon's diversity index (DI) = 2.9), followed by G4 (34 taxa; DI = 2.4), G2 (38 taxa; DI = 2.1) and G1 (43 taxa; DI = 1.9).

The NMDS plots revealed that phytoplankton assemblages shifted from cyanobacteria dominance to diatom and chlorophyte dominance over 13 years along NMDS axis I (Fig. 4a–c). The NMDS axis I primarily reflected the gradients of nutrients (e.g., epilimnetic and hypolimnetic TP and TN, and inflow SRP) (Fig. 4d–f and Table 2). This change corresponded to the four groups identified by the cluster analysis. The NMDS

axis I separated the cyanobacteria-dominated G1 and G2 with nutrient-rich conditions from the diatom and chlorophyte-dominated G3 and G4 with lower nutrient concentrations. Specifically, hypolimnetic nutrients were associated with G1, although only hypolimnetic TP and TN were significant vectors, while inflow SRP was significantly associated with G2. Other environmental variables that were significantly correlated with the NMDS space defined by phytoplankton assemblages included pH, dissolved oxygen, and chlorophyll *a*, indicating high primary production (G1), as well as specific conductivity, turbidity and TSS, indicating turbid water conditions (G2), and NP ratio (G4).

3.3. Changes in phytoplankton assemblages in relation to lake management practices

The changes in phytoplankton assemblage cluster groups were closely associated with lake management practices in temporal terms (Fig. S3). G1 dominated by cyanobacteria was associated with the period before
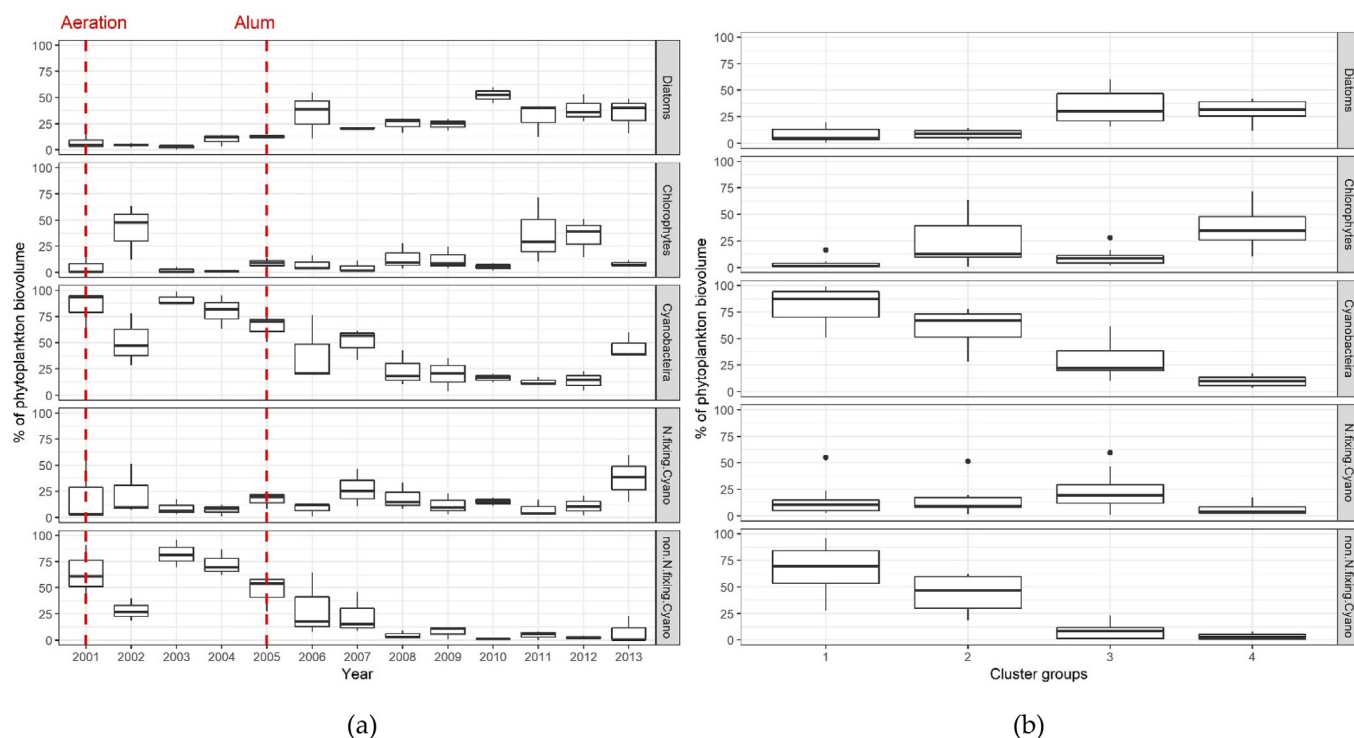
(a)

(b)

Fig. 3. Boxplots showing (a) year-to-year variations of the phytoplankton assemblages among the major taxonomic groups between July and September from 2001 to 2013 in the deep basin of Oswego Lake; and (b) comparisons of relative abundance of the phytoplankton taxonomic groups among 4 cluster groups based on cluster analysis.

the major management practices were implemented (hypolimnetic aeration in August 2001 and alum injection in March 2008). G2 dominated by cyanobacteria and chlorophytes occurred from one year after

Table 1
Dominant taxa and indicator taxa of four phytoplankton groups based on cluster analysis. Presented here are the assemblages of the taxa comprising >50% of total phytoplankton biovolume and the taxa (belonging to cyanobacteria, diatoms, and chlorophytes) with an indicator species index >0.5 ($p < 0.05$) based on Dufrene-Legendre indicator species analysis.

Assemblage	Taxonomic Group	Relative Abundance	Indicator Species Index
Group 1			
Limnoraphis sp.	non-N fixing Cyanobacteria	52%	0.8
Unicellular Cyanobacteria	Cyanobacteria		0.5
Group 2			
Microcystis sp.	non-N fixing Cyanobacteria	31%	0.7
Closteriopsis longissimi	Chlorophyte	23%	0.9
Group 3			
Aulacoseira sp.	Diatom	25%	0.7
Ceratium hirundinella	Dinoflagellate	10%	
Aphanizomenon flos-aquae	N-fixing Cyanobacteria	9%	
Fragilaria sp.	Diatom	6%	
Dolichospermum sp.	N-fixing Cyanobacteria		0.5
Pandorina sp.	Chlorophyte		0.5
Group 4			
Coelastrum sp.	Chlorophyte	26%	0.6
Fragilaria sp.	Diatom	21%	0.6
Ceratium hirundinella	Dinoflagellate	9%	
Oocystis sp.	Chlorophyte		0.7
Asterionella formosa	Diatom		0.5

hypolimnetic aeration to one year before inflow reduction (June 2005) and alum surface application (August 2005). G3 dominated by diatoms and cyanobacteria occurred after alum surface application in August 2005. G4 dominated by chlorophytes and diatoms occurred in 2009 (the year after alum injection), 2011 (the year after a long period of drawdown) and 2013 (the year after inflow alum treatment).

4. Discussion

4.1. Responses of phytoplankton assemblages to P reduction

The phytoplankton assemblages of Oswego Lake have experienced profound changes in the 13-year study period. The summer phytoplankton assemblages have shifted from cyanobacteria dominance to diatom and chlorophyte dominance (Figs. 3 and 4). As in-lake nutrient concentrations were substantially reduced after the alum application and hypolimnetic aeration, a shift from the phytoplankton communities dominated by cyanobacteria to diatoms and chlorophytes also occurred. There is no single factor that drives phytoplankton assemblage dynamics; it is a complex combination of physical, chemical, and biological phenomena including light, temperature, nutrients, and food-web structures (Kosten et al., 2012). However, it has been widely accepted that P is typically the limiting nutrient in lakes and has a strong correlation with phytoplankton production (Carpenter, 2008; McCauley et al., 1989; Prairie et al., 1989; Schindler, 2012; Schindler et al., 2008); therefore, P is commonly used as a primary trophic indicator (Carlson, 1977). Eutrophic lakes with internal P loading during vertical thermal stratification are particularly favorable for the massive development of cyanobacteria because cyanobacteria can migrate upward to the epilimnion through production of gas vesicles and downward to the nutrient-rich hypolimnion through the collapse of these vesicles (Carey et al., 2012; Oliver and Walshy, 1984).

Changes in summer phytoplankton assemblages were significantly correlated with changes in physical and chemical water conditions (Fig. 4) and strongly associated with lake management practices
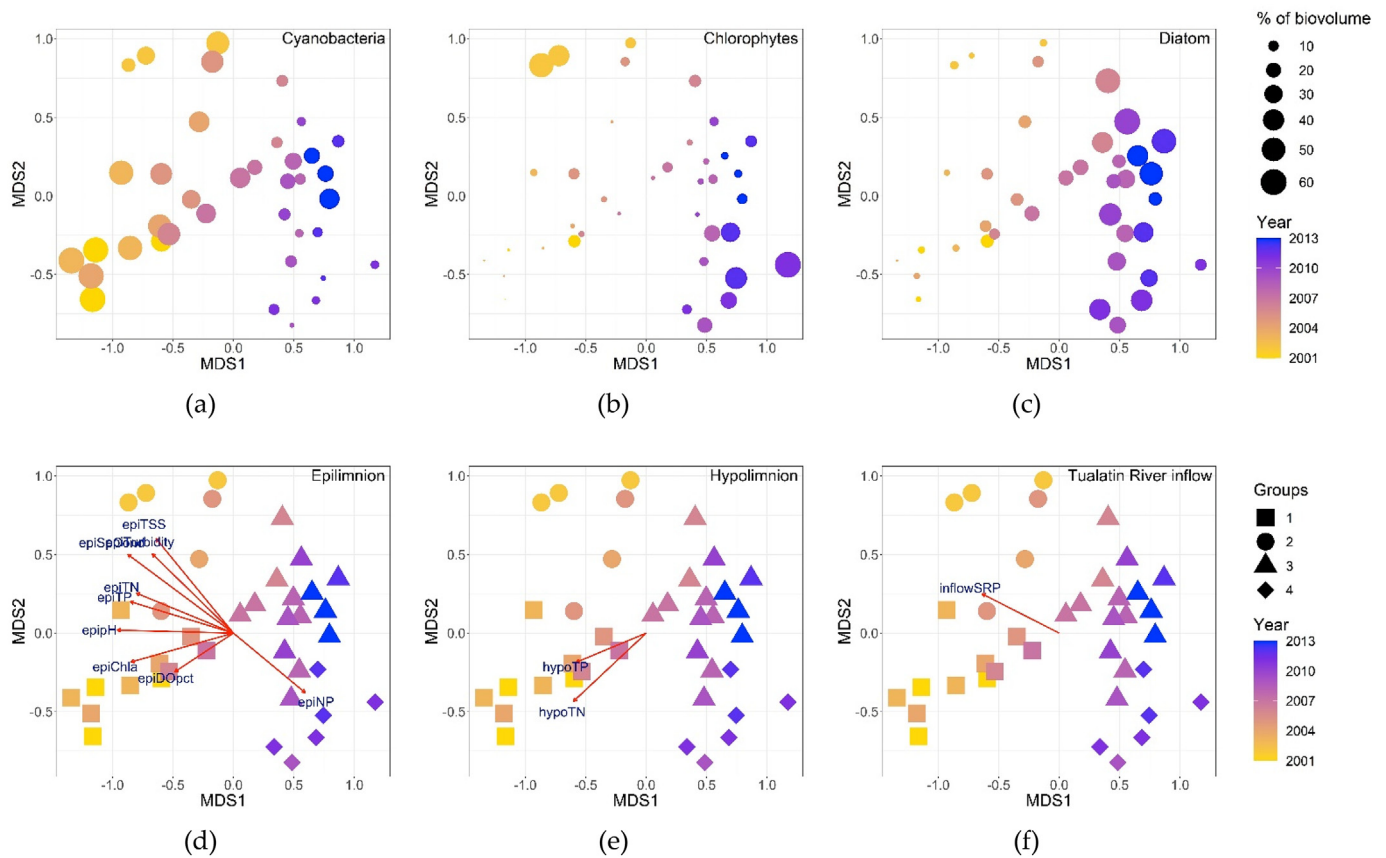
Fig. 4. Plots of non-metric multidimensional scaling (NMDS) analysis showing temporal variation of the phytoplankton assemblages between July and September from 2001 to 2013 in the deep basin of Oswego Lake, superimposed with % of (a) cyanobacteria, (b) chlorophytes and (c) diatoms in each sample (bubble size is proportional to the relative abundance of total phytoplankton biovolume), and superimposed with the cluster groups and the major environmental variables of (d) epilimnion, (e) hypolimnion and (f) Tualatin River inflow which are significantly associated with the NMDS ordination.

Table 2
Results from the environmental vectors fitting in the ordination space of the NMDS plot with variable scores along the two ordination axes (NMDS1-2), goodness-of-fit statistic r^2 and its significance (*p*-value). Results were sorted by r^2.

Variables	Abbreviation	Unit	r^2	*p*-Value	
Epilimnetic specific conductance	epiSpCond	mS/cm	0.60	0.001	***
Epilimnetic pH	epipH		0.55	0.001	***
Epilimnetic total suspended solids	epiTSS	mg/L	0.46	0.001	***
Epilimnetic total phosphorus	epiTP	µg/L	0.45	0.001	***
Epilimnetic chlorophyll *a*	epiChla	µg/L	0.44	0.001	***
Epilimnetic total nitrogen	epiTN	µg/L	0.42	0.001	***
Epilimnetic turbidity	epiTurbidity	NTU	0.42	0.001	***
Hypolimnetic total nitrogen	hypoTN	µg/L	0.33	0.002	**
Epilimnetic nitrogen to phosphorus ratio	epiNP		0.29	0.005	**
Inflow soluble reactive phosphorus	inflowSRP	µg/L	0.28	0.008	**
Hypolimnetic total phosphorus	hypoTP	µg/L	0.22	0.006	**
Epilimnetic percent saturation of dissolved oxygen	epiDOpct	%	0.18	0.034	*
Epilimnetic water temperature	epiTemp	°C	0.14	0.087	.
Hypolimnetic soluble reactive phosphorus	hypoSRP	µg/L	0.12	0.107	
Epilimnetic soluble reactive phosphorus	epiSRP	µg/L	0.11	0.141	
Inflow total phosphorus	inflowTP	µg/L	0.03	0.599	
Inflow total nitrogen	inflowTN	µg/L	0.03	0.577	

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1; *p*-values based on 1000 permutations.

(hypolimnetic aeration and alum application) (Fig. 3 and Fig. S3). The results were comparable to the other cases of alum applications to lakes where alum resulted in reduction of in-lake TP and chlorophyll *a* concentrations and improvements in water clarity (Huser et al., 2016; Welch and Cooke, 1999). For example, Mirror and Shadow lakes, WI, both within residential watersheds, were eutrophic due to storm sewer loading and internal loading. Alum additions successfully reduced mean TP from 93 to 20 µg/L (78% reduction) in Mirror Lake and from 55 to 23 µg/L (58% reduction) in Shadow Lake (Welch and Cooke, 1999). Similarly, in Dollar Lake, OH, a small urban lake, alum lowered surface TP by 65% from the pretreatment concentration of 82 µg/L and chlorophyll *a* by 61% from 41 µg/L (Welch and Cooke, 1999). Huser et al. (2016) studied the short-term effects of alum on 83 urban lakes of varying size, morphology, and hydrology and found that alum reduced epilimnetic TP from 101 to 36 µg/L (64% reduction) and chlorophyll *a* from 43 to 16 µg/L (63% reduction), and increased Secchi depth from 1.6 to 2.4 m (50% increase).

4.2. P reduction and lake restoration

Many lake restoration programs focused on reduction of P have proved to be effective in reducing cyanobacteria blooms (Huser et al., 2016; Moore and Christensen, 2009; Zamparas and Zacharias, 2014). For example, in Newman Lake, WA, alum addition coupled with hypolimnetic aeration were implemented for control of in-lake P and cyanobacteria blooms. Newman Lake is a dimictic lake and has stable thermal stratification between May and September. Cyanobacteria blooms in Newman Lake occurred annually in the 1970s and 1980s primarily due to summer hypolimnetic oxygen depletion and internal P loading (Moore

et al., 2009). Cyanobacteria peaked in 1989, accounting for >90% of total phytoplankton biovolume (Moore and Christensen, 2009). The restoration efforts in Newman Lake have included whole-lake alum surface treatment in 1989, hypolimnetic oxygenation from spring to fall since 1992, and microfloc alum hypolimnetic injection during spring and fall turnovers and summer stratified periods since 1997. During 1997, 2007, cumulative management efforts have successfully reduced average summer TP from pre-restoration 55 μg/L to an average of 21 μg/L. Cyanobacteria blooms were no longer evident after the first whole-lake alum treatment, and cyanobacteria comprised <8% of total phytoplankton biomass, while diatoms comprised between 50% and 75% and chlorophytes comprised <15% of total phytoplankton biomass (Moore et al., 2009, 2012). Species shifts also occurred, as almost exclusive *Microcystis* sp. decreased after the first alum treatment while *Dolichospermum flos-aquae* increased in the cyanobacteria assemblage (Moore et al., 2009). Later, *Aulacoseira* sp. became the most abundant phytoplankton during aeration (Thomas et al., 1994). This shift in phytoplankton assemblages from cyanobacteria dominance to diatom and chlorophyte dominance was most likely a response to lower P availability (Moore and Christensen, 2009).

Changes in nutrients and phytoplankton assemblages observed after alum addition and hypolimnetic aeration in Oswego Lake are very similar to the findings in Newman Lake. Previous analysis on Oswego Lake identified that internal loading was one of the most significant sources of P in the lake (Gibbons and Welch, 2004). Therefore, hypolimnetic aeration since 2001 and alum application since 2005 have been implemented in Oswego Lake to reduce internal P loading and control cyanobacteria blooms. Since 2005, after alum treatment in Oswego Lake and hypolimnetic aeration, summer phytoplankton assemblages showed a 62% reduction of cyanobacteria biovolume (Fig. 3a), and cyanobacteria-dominated phytoplankton communities gradually shifted to diatom and chlorophyte dominance (Fig. 3b and Fig. S3). Based on concepts of community ecology, the succession of dominant species is partly a consequence of changes to environmental conditions (Reynolds, 2006). Compared to the "pre-shift" years of 2001–2004, the most remarkable changes to nutrient levels have occurred since 2005, which may be the most probable explanation for the presence of the diatom dominant phytoplankton communities (Group 3). Furthermore, in Oswego Lake, the dominance of *Aulacoseira* occurred in summer stratification periods, which is very likely a direct result of hypolimnetic aeration. *Aulacoseira* is not capable of independently staying within the photic zone, due to its heavy silicon body, without upwelling water currents during summer stratification. It is apparent that the hypolimnetic aeration in Oswego Lake circulated lake water and generated vertical mixing of the water to sufficiently resuspend *Aulacoseira* in the photic zone for facilitating its growth. Lund (1971) observed a significant increase in summer *Aulacoseira* populations during the artificial destratification of a small lake in the English Lake District. Similarly, Thomas et al. (1994) reported that *Aulacoseira* particularly adapted to hypolimnetic aeration induced a turbulent environment and became the most abundant phytoplankton during summer aeration in Newman Lake. Therefore, the hypolimnetic aeration in Oswego Lake apparently played an important role in establishing dominance of *Aulacoseira* in summer phytoplankton communities.

However, hypolimnetic aeration reducing internal P loading from anoxic lake sediments may not be effective in reduction of P in the lake if watershed nutrient loading is high as well (Beutel and Horne, 1999; Liboriussen et al., 2009). Results from this study and a recent survey on the effects of management on water quality in Oswego Lake by Costadone et al. (2021) have shown that hypolimnetic aeration alone prior to alum treatment did not significantly lower nutrient concentrations in the epilimnion, and that the major shift of dominant species from cyanobacteria to diatoms and chlorophytes occurred after the alum treatment, which suggests that hypolimnetic aeration alone was not sufficient, but the synergistic effect of hypolimnetic aeration and alum treatment is most impactful. Oswego Lake, within an urban watershed, has a high

watershed/drainage area to lake area ratio (>10:1), indicating a strong influence of the watershed on the lake (Schueler and Simpson, 2001). The drainage pipe network contains 70 stormwater outfalls surrounding the lake, and 40% of stormwater from the city of Lake Oswego drains into the lake directly through these pipes (Rubenson, 2016). In addition, three stream inflows contribute significant P to the lake (ODEQ, 2001; Johnson, 2009). A significant correlation was found between inflow SRP and in-lake SRP (Pearson correlation coefficient $r = 0.52$, $p < 0.001$, $n = 38$) in Oswego Lake; thus, inflow alum treatment is necessary to nutrient management (Heinzmann and Chorus, 1994; Pilgrim and Brezonik, 2005).

Alum treatment coupled with aeration in Oswego Lake, as well as in other lake restoration projects, has been effective in reduction of in-lake phosphorus concentrations and in control of cyanobacteria blooms (Cooke et al., 2005). Current annual ongoing costs for alum treatment and aeration in Oswego Lake are approximately $150,000 and $50,000, respectively. These costs include maintenance, labor, and consumables. USEPA (2015) reported that the costs associated with alum application could be more than $28 million in capital and $1.4 million in annual operation and maintenance in Lake Lawrence (1.3 km^2), Washington. Alum treatment and aeration can be very costly (USEPA, 2015); however, where watershed restoration is complicated by administrative and logistical challenges in urban settings, alum treatment and aeration can be more cost-effective approaches to eliminate in-lake phosphorus loading from both internal and external sources (Huser et al., 2016).

4.3. P reduction as a management tool: Confounding factors and challenges

Climate change, characterized by conditions such as rising temperatures and changing precipitation patterns, causing extreme weather conditions like storms and droughts, modifies physical, chemical, and biological processes of nutrient cycles (Huntington, 2006; Reichwaldt and Ghadouani, 2012). At the watershed level, warming stimulates rock weathering and soil erosion, and intensified precipitation due to warming increases runoff of sediments and nutrients to the receiving lakes (Carey et al., 2012; Paerl and Huisman, 2008). Soil erosion is a major source of P in the watersheds of northwestern Oregon that is between an uplifted subduction complex of the Coast Range and active andesitic volcanoes of the Cascade Range (Abrams and Jarrell, 1995; Retallack and Burns, 2016). Many of the watersheds in northwestern Oregon are underlain by P-rich volcaniclastic marine sandstones and siltstones and large areas of the basin floor are covered by nutrient-rich silts from the Missoula Floods dating back to the last ice age (Foster, 2009; Retallack and Burns, 2016). These watershed geological characteristics dictate that the Oswego Lake watershed is a native P source to the lake. Future study on large-scale climate impacts on lake and watershed ecosystems should afford a deeper understanding of phytoplankton assemblage dynamics and improve lake management strategies.

In addition, lake water level drawdown can have important impacts on the lake ecosystem. For example, nutrients and plankton in lakes can be partly removed when the water body is flushed out (Bakker and Hilt, 2016; Pan et al., 2018). Drawdown, to some extent, can be a "reset" and an important disturbance of the lake ecosystem. In Oswego Lake, no significant changes in the phytoplankton assemblages were observed after the first drawdown; however, in the two years following the second drawdown, chlorophytes reached one of three high relative abundance values and a more diversified assemblage of chlorophytes and diatoms occurred, which indicated that duration and strength of drawdown may affect lake ecosystems. Group 4 probably was a result of the second drawdown because the phytoplankton species in Group 4 are regarded as R-strategists that can respond quickly to environmental changes (Reynolds, 2006).

Water quality management in urban lakes, such as Oswego Lake, has unique challenges, including dynamic nature of lake systems, costly alum treatment and aeration, significant nutrient input from surrounding

watersheds, strong influence of human modifications on water levels, and uncertain impacts of the climate on lake ecosystems. Given that the watershed is the ultimate source of nutrient input to lakes, reduction in supply of nutrients from lake watersheds is a sustainable approach to protect long-term water quality. In the United States, the watershed approach is gaining recognition and community involvement in the watershed is encouraged (USEPA, 1996). Managing watersheds holistically for nutrient control and implementing integrated watershed management bring together collaborative efforts of watershed stakeholders, including federal, state, and local government agencies and private landowners, which couple with TMDL processes to address point and non-point sources of nutrient pollution to protect and improve water resources (Haith, 2003).

5. Conclusions

This study investigated a long-term change in phytoplankton assemblages in an urban lake to better understand which factors most likely influenced such a change. From 2001 to 2013, the summer phytoplankton communities of Oswego Lake shifted in dominance from cyanobacteria to diatoms and chlorophytes. Our results suggest that lake management practices had strong effects on both the production and community compositions of phytoplankton. We suggest that there is a need for future studies on large-scale climate impacts on lake ecosystems and to identify corresponding best management practices.

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Author contributions

Yuan Grund: Conceptualization, Methodology, Data curation, Formal analysis, Writing- Original draft preparation. Yangdong Pan: Conceptualization, Methodology, Formal analysis, Supervision, Writing - Review and Editing. Mark Rosenkranz: Conceptualization, Methodology, Supervision, Writing - Review and Editing. Eugene Foster: Conceptualization, Supervision, Writing - Review and Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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