

**SPATIAL AND TEMPORAL CHARACTERIZATION OF LIGHT AND NUTRIENT  
LIMITATION IN LAKE DIEFENBAKER: INFLUENCE OF ANTHROPOGENIC  
ACTIVITIES AND UPSTREAM FLOW**

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Requirements for the Degree of Master of Science  
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Saskatoon

By

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## **ABSTRACT**

Management of water quality in lakes and reservoirs often requires an understanding of the factors that control algal biomass. Primary production in freshwater systems may be limited by nutrients such as phosphorus (P) and nitrogen (N), or by physical conditions such as availability of light. Lake Diefenbaker (LD) is a multi-purpose reservoir located on the South Saskatchewan River (SSR). Its uses include, but are not limited to, power generation, flood control, irrigation, and drinking water supply. Prior to beginning this study little was known about the factors that controlled algal populations in this reservoir. To determine if algae and bacteria were nutrient limited or light limited, I measured various biological and environmental conditions and conducted a series of nutrient status assays. Sampling sites were located in the main channel along the length of the reservoir and in a set of embayments. Embayments were of three types, those containing cattle operations, marinas, or no observed anthropogenic activity (reference embayment). Temporal patterns were assessed from monthly samples collected from June to October in 2011 and 2012.

I found that P was the primary limiting nutrient in LD; N deficiency was less prevalent but was associated with high flows and consequent low light. Nutrient and light dynamics in the reservoir followed the expectations of the longitudinal zonation concept (LZC) of Kimmel and Groeger (1984) in most instances. The upstream riverine region was characterized by high flows, high nutrient concentrations and low light penetration. The transition region experienced a reduction in flow (the basin was wider and deeper) that resulted in the settling of particulate matter and an increase in light penetration. Finally, in the lacustrine region, light penetration increased, and P concentrations declined. However, N concentrations either increased or were

consistent along the length of the reservoir and light limitation was widespread due to deep mixing depths, neither expected under the LZC.

Light limitation was more prevalent in 2011 than 2012 due to higher flows and associated turbidity, with higher indications of deficiency in the main channel than the embayments in both years. We did not detect differences in nutrient or light limitation indicators in the embayments exposed to cattle or recreational activities when compared to reference embayments. The lack of an effect may be attributed to greater than normal inflow from the SSR that may have increased flushing of the embayments during the two years of study. The high flows entering Lake Diefenbaker were associated with greater nutrients and turbidity, both of which affected light and nutrient limitation throughout the reservoir.

Overall, the results of this study could suggest that light is the primary limiting factor in LD, with P limitation being secondary. However, long-term constraints on algal biomass will still be controlled by P levels. During these two years of study, light and nutrient limitation was sufficient to limit significant algal blooms. Regardless of whether light or P is considered the ultimate limiting factor, only P can be feasibly controlled. With the anticipated changes to flow and stratification patterns associated with climate change, and the potential for legacy P loading in LD, P reduction strategies need to be considered to protect this important resource for the province of Saskatchewan.

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## LIST OF ABBREVIATIONS

Abbreviation	Explanation
APA	Alkaline Phosphatase Activity
BRPMP	Bow River Phosphorus Management Plan
C (P)	Carbon (Particulate)
chl <i>a</i>	Chlorophyll <i>a</i>
$\bar{E}_{24}$	Mean Water Column Irradiance
ELA	Experimental Lakes Area
$k_d$	Attenuation Coefficient
LD	Lake Diefenbaker
LZC	Longitudinal Zonation Concept
N (T, P, TD, DI)	Nitrogen (Total, Particulate, Total Dissolved, Dissolved Inorganic)
$\text{NH}^{4+}$	Ammonium
$\text{NO}^{3-}$	Nitrate
NRC	National Research Council
NTU	Nephelometric Turbidity Unit
P (T, P, TD)	Phosphorus (Total, Particulate, Total Dissolved)
PAR	Photosynthetically Active Radiation
PDI	Phosphorus Deficiency Index
$\text{PO}_4^{3-}$	Phosphate
QA	Qu'Appelle Arm
SE	Standard Error
SRP	Soluble Reactive Phosphorus
$\text{ssPO}_4^{3-}$	Steady State Phosphate
SSR	South Saskatchewan River
SWSA	Saskatchewan Water Security Agency
TT	Turnover Time
U of S	University of Saskatchewan
US EPA	United States Environmental Protection Agency
WQB	Water Quality Branch
WWF	World Wildlife Fund
$Z_{eu}$	Euphotic Depth
$Z_{mix}$	Mixing Depth

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## **CHAPTER 1 – GENERAL INTRODUCTION**

### **1.1. Introduction to Nutrient and Light Limitation**

Liebig's law of the minimum states that growth is controlled not by the total amount of resources available but by the scarcest resource; the limiting factor. Historically phosphorus (P) has been thought to be the primary limiting factor in freshwater systems (Edmondson, 1970; Schindler, 1974; Vollenweider, 1970), with nitrogen (N) usually considered the secondary limiting nutrient (Dodson, 2005). Phytoplankton energy requirements for uptake and assimilation of nutrients must be met through photosynthesis. Therefore, the algal assemblage can also be limited by light even in nutrient-poor systems (Karlsson et al., 2009). Both light and nutrients are required to sustain growth of aquatic primary producers, and the balance between energy and nutrients affects ecosystem structure and function (Sterner et al., 1997). Determining the factors that control algal growth and primary production in freshwater systems is essential for proper lake management (Cooke et al., 2005).

Whole-lake experiments conducted in the Experimental Lakes Area (ELA) in the 1970s identified P as the primary limiting nutrient in many freshwater systems (Schindler, 1974). Recommendations for widespread P control were then proposed by the International Limnological Congress and the International Ecology Congress (Schindler, 1977). Managing inputs of P resulted in significant reductions in the trophic state of many lakes in North America (National Research Council (NRC), 1992; Schindler et al., 2016). However, broader water quality goals were not fully achieved, specifically in estuaries and coastal marine ecosystems, where N was more limiting (Conley et al., 2009). In freshwater systems, N limitation can be partially relieved by N-fixing cyanobacteria. Schindler et al. (2008) and Scott and McCarthy (2010) both assessed the 37-year record of Lake 227 in the ELA with conflicting results.

Schindler's group found that even when extreme N limitation was detected, algal biomass continued to be produced in proportion to P. These findings further support the P reduction strategy because reductions in N did not result in a decrease in overall algal biomass. In contrast, Scott and McCarthy suggest that chl *a* concentrations decreased with N reductions and therefore compensation by N-fixing bacteria was not sufficient to offset decreases in N inputs. More recently, Schindler's group improved their N fixation estimates and their results suggest that N fixation was able to offset N loading reductions in Lake 227 (Higgins et al., 2017). However, not all problem cyanobacteria are N fixers, and increased N loading has promoted blooms of toxic non-N<sub>2</sub>-fixing cyanobacteria such as *Microcystis* (Paerl et al., 2011a, 2014).

Thus, N has received more attention recently, and reductions of N inputs are being considered as an additional means to reduce eutrophication problems (Conley et al., 2009; Glibert, 2017; Paerl et al., 2011a, 2014; Scott and McCarthy, 2010). In some lakes, P-only reduction strategies are not likely to succeed because P is rapidly recycled between the sediments and water column and N-fixing bacteria are not overly abundant (Havens et al., 2001). As well, if inputs of N are ignored then additional N will travel downstream and eventually arrive at estuaries, where the increased N will exacerbate eutrophication problems (NRC, 2000). Conley argues for dual nutrient strategies in most cases and that the reduction of only one nutrient is short sighted. This issue is highly contentious and has received much attention in recent years (Conley et al., 2009; Dzialowski et al., 2005; Lewis and Wurtsbaugh, 2008; Paerl, 2009; Schindler, 2012; Schindler et al., 2008, 2016; Scott and McCarthy, 2010; Sterner, 2008). Regardless of the debate, there is general agreement that increases in these nutrients are the primary cause of decreasing water quality worldwide (Carpenter et al., 1998). Using a large-scale meta-analysis of nutrient enrichment experiments, Elser et al. (2007) showed that P and N



limitation is strong and widespread across marine, freshwater, and terrestrial ecosystems and co-limitation of both nutrients was common across all systems. Criticism of this meta-analysis include that many of these studies were lab based, bottle experiments that show immediate needs of the planktonic assemblage instead of ultimate limiting factors (Schindler, 2012). More recently, Paerl et al. (2016) found that whole lake experiments more often respond to combined N and P enrichment and therefore advise that dual nutrient management is needed to protect both lakes and downstream ecosystems.

Anthropogenic activities over the last 200 years have amplified the global cycling of N and P by 100% and 400%, respectively (Falkowski et al., 2000). Global increases in biologically available N compounds are largely due to increases in rice cultivation, fossil fuel emissions, and fertilizer production (Falkowski et al., 2000; Galloway et al., 2008). In contrast, increases in P inputs to the biosphere are primarily due to mining of P compounds for fertilizer (Falkowski et al., 2000). Cultural eutrophication, the premature aging of a waterbody due to increases in anthropogenically derived nutrients, is one of the most pervasive threats to water quality on a global basis (Cooke et al., 2005; Schindler, 2012; Smith et al., 1999).

Rapid proliferation of nuisance algae can have serious consequences to ecosystem health as they are a poor nutritive food source to zooplankton (Bernardi and Giussani, 1990), and have the potential to be toxic to animals and humans (Morris, 1999). Algal blooms can produce large amounts of organic material, which upon decomposition, may deplete water of oxygen, potentially resulting in fish kills (Paerl et al., 2001). Furthermore, increases in algal turbidity, due to cultural eutrophication, can lead to the loss of fish biodiversity (Seehausen et al., 1997). However, without adequate light energy, phytoplankton communities may not respond to additions of limiting nutrients (Hecky and Guildford, 1984; Venables and Moore, 2010).

Phytoplankton growth and reproduction can be limited by the availability of light, or more specifically, photosynthetically active radiation (PAR) (Guildford et al., 2000; Thrane et al., 2014; Wozniak et al., 2002). The light-to-nutrient hypothesis (Sterner et al., 1997) states that in a “high” light-to-nutrient environment, autotrophs are more likely to be limited by P, and in a “low” light-to-nutrient environment they are more likely to be limited by light. Chrzanowski and Grover (2001) provided evidence to support this hypothesis in two mesotrophic reservoirs in northern Texas. They found that P limitation was present when the light:TP ratio was above the median value of all samples; conversely, when the light:TP ratio fell below the median, P limitation was less common and light limitation was more evident. In low irradiance situations, simultaneous nutrient (either P or N) and light limitation may occur (Healey, 1985), henceforth this will be referred to as co-limitation. Co-limitation can occur when an increase in either light or nutrients allows the phytoplankton community to partially compensate for the lower availability of the other (Healey, 1985). This partial compensation can be attained through physiological modifications such as the synthesis of light capturing pigments (i.e., chlorophyll *a*) to balance photosynthesis with photo-protection and accumulation of biomass (Falkowski and Raven, 2013; Kirk, 1994). Determining the factors limiting primary productivity is essential to predict and mitigate effects of anthropogenic nutrient loading.

#### *1.1.1. Phosphorus Limitation Parameters*

Many studies have found P to be a limiting nutrient in freshwater systems (Sterner, 2008). Consequently, several techniques have been developed to determine the presence and degree of P limitation in algal and bacterial populations. Common measurements of P limitation include nutrient addition experiments, measurement of nutrient ratios, and bioassays. It is important to differentiate what exactly these indicators are measuring, whether it is the

immediate needs of the planktonic community (proximate deficiency) or long term constraints on algal biomass (ultimate deficiency) (Davies et al., 2004, 2010). Proximate nutrient limitation considers the response of the planktonic community to additions of a nutrient and is therefore specific to the current species composition, their physiological state and the abiotic conditions present at the time of the experiment (Hecky and Kilham, 1988). Generally speaking, particulate nutrient stoichiometry is considered a measurement of ultimate nutrient limitation, as algal biomass is attained in proportion to the nutrient in limited supply. As a result of the differences in P limitation indicators, there are often discrepancies between proximate and ultimate measurements. Here, I employ several types of indicators to obtain a more comprehensive understanding of the P status over both short and long timescales.

The alkaline phosphatase group of enzymes hydrolyze the ester bonds that bind phosphates to dissolved organic molecules rendering the phosphate molecule available for uptake by the planktonic community. Plankton mediated alkaline phosphatase activity (APA) has been widely used as a determinant of P limitation (Pettersson, 1980; Rose and Axler, 1997; Vandergucht et al., 2013). This is a useful indicator of P deficiency because the activity is increased in response to low phosphate ( $\text{PO}_4^{3-}$ ) concentrations (Pettersson, 1980) and repressed when  $\text{PO}_4^{3-}$  concentrations are adequate for growth (Perry, 1972). Increases in APA may take more time to respond to low  $\text{PO}_4^{3-}$  concentrations than more proximate measures of P deficiency (e.g., uptake kinetics) as nutrient uptake and assimilation is the first priority under nutrient limitation (Healey, 1979). Also, APA may linger in the water column after  $\text{PO}_4^{3-}$  requirements are met (Pick, 1987), and therefore, should be carefully interpreted by comparing to other assays.

Measuring the uptake kinetics of radiophosphate is an example of a more direct approach to determining proximate P deficiency in the phytoplankton community. Uptake of  $\text{PO}_4^{3-}$

increases when the planktonic assemblage is P starved (Jansson, 1988), which reduces the turnover time of the dissolved phosphate pool ( $TT_{PO_4}$ ) to levels considered P deficient (Lean and Pick, 1981; Lean et al., 1983).

A steady-state radiobioassay to estimate  $PO_4^{3-}$  concentrations in lakes has also been developed (Hudson and Taylor, 2005; Hudson et al., 2000). This approach assumes that uptake of  $PO_4^{3-}$  is equal to its regeneration by plankton when P is limiting. This technique typically reports  $PO_4^{3-}$  concentrations in the picomolar range in P deficient systems that is 2-3 orders of magnitude lower than soluble reactive phosphorus (SRP) concentrations reported for the same systems (Hudson et al., 2000; Vandergucht et al., 2013). These estimates have been shown to be negatively correlated with PC:PP and PN:PP ratios and with APA, showing that this method is in agreement with other measurements of P deficiency (Vandergucht et al., 2013). In fact, the assay can be considered a more direct test of P deficiency because it directly measures the concentration of the limiting nutrient; the lower the concentration of the  $PO_4^{3-}$  pool, the greater the potential for P limitation.

Particulate nutrient ratios can be used to assess persistent (ultimate) nutrient limitation because these reflect long-term trends in seston nutrient availability (Falkowski et al., 2000; Redfield, 1934). Planktonic stoichiometry can be quite variable and is regulated by the environmental conditions present during growth (Sterner and Elser, 2002). Despite the variability inherent in this measurement, ecological stoichiometry is a useful tool to use in conjunction with other nutrient deficiency indicators to determine the type and severity of nutrient limitation (Guildford et al., 2005; Vandergucht et al., 2013). Redfield (1934) found that the C:N:P molar ratios of algae in the open sea was 106:16:1 and deviations from this ratio would indicate one nutrient, or the other, was limiting growth. Since then, the ratios have been revised for freshwater

systems and the thresholds for P or N limitation set forth by Healey (1975) and Healey and Hendzel (1980) are typically used. Deficiency measurements can be variable and work on different timescales, therefore, the use of several indicators simultaneously allows a more confident assessment of P limitation.

### *1.1.2. Nitrogen Limitation Parameters*

Nitrogen has long been considered the primary limiting nutrient in marine systems. However, evidence for N as a limiting nutrient in freshwater systems has been forthcoming in recent years (Conley et al., 2009; Scott and McCarthy, 2010; Shatwell and Köhler, 2018). Co-deficiency by both N and P has been documented in many freshwater systems (Davies et al., 2004; Harpole et al., 2011). Furthermore, Elser et al. (2007) found that the frequency of N and P deficiency was similar in freshwater systems in an extensive literature review.

Increased uptake of a nutrient, such as nitrogen, can suggest deficiency in that nutrient (Fitzgerald, 1968). Consequently, uptake measurements have been widely applied as nutrient deficiency indicators in both marine and freshwater systems (Healey and Hendzel, 1980). Introduction of ammonium ( $\text{NH}_4^+$ ) to the planktonic assemblage and subsequent measurement of uptake over a 24-hour period can give an indication of the immediate needs of the plankton (proximate deficiency). Measuring short-term uptake of nutrients (N or P) may also identify luxury uptake (storage) during periods of weak to moderate limitation and therefore require careful interpretation (Keenan and Auer, 1974). As with P, nutrient stoichiometry can be used to examine long term trends in nutrient availability. The particulate PC:PN ratio is useful to evaluate ultimate N deficiency despite the variability associated with the measurement. Indicators for N deficiency are not as abundant as deficiency indicators for P, however, it is still

good practice to employ multiple indicators to increase the confidence in the results of these measurements.

### *1.1.3. Light Limitation Parameters*

Photosynthesis is a light-dependent process that converts energy to a usable form for growth, nutrient uptake, and assimilation; consequently, light deficient conditions may limit the growth and reproduction of phytoplankton communities even in the presence of adequate nutrient availability (Hecky and Guildford, 1984; Venables and Moore, 2010).

The light environment in lakes can be assessed by determining the depth of light penetration and the depth at which a freely floating cell will mix (mixing depth,  $Z_{\text{mix}}$ ). The euphotic zone ( $Z_{\text{eu}}$ ) is the maximum depth of the light zone suitable for phytoplankton photosynthesis. This depth is estimated as the depth where the light intensity is 1% of the light at the surface (Khanna et al., 2009). Below this point, light is still available, but is not sufficient for production to exceed respiration and the algal population will decline. If the euphotic depth is greater than the mixing depth ( $Z_{\text{eu}}:Z_{\text{mix}} > 1$ ) then algal population growth will occur throughout the entire mixed layer (Kalf, 2002), provided no other factor is limiting (i.e., nutrients). Conversely, if the euphotic depth is shallower than the mixed layer ( $Z_{\text{eu}}:Z_{\text{mix}} < 1$ ), then a freely-floating algal cell will spend a portion of time without adequate light for photosynthesis.

A more accurate approach to assessing the light environment also takes into account the amount of solar radiation at the water's surface. By combining this information with the vertical attenuation coefficient of PAR ( $k_d$ ) and the mixing depth we can determine the mean water column irradiance ( $\bar{E}_{24}$ ,  $\text{mmol m}^{-2} \text{min}^{-1}$ ), indicates if free floating phytoplankton have sufficient light for growth (Guildford et al., 2000). This parameter can also be examined as a ratio with TP as an additional, albeit, related measurement of light and or P limitation as illustrated by

Chrzanowski and Grover (2001). They found that when the  $\bar{E}_{24}:\text{TP}$  ratio was above the median values for a given lake then bacterial growth was more often limited by P as abundant light and low P availability would shift phytoplankton away from biomass production and promote carbon exudation. When the ratio fell below the median value then bacterioplankton are more likely to be limited by C, as light was more likely to be limiting. As with nutrient limitation indicators, our confidence in the results of these measurements is strengthened with the inclusion of multiple indicators for light limitation. Hence, I will be using  $Z_{\text{eu}}:Z_{\text{mix}}$ ,  $\bar{E}_{24}$ , and  $\bar{E}_{24}:\text{TP}$  to assess the light environment.

## **1.2. Longitudinal Zonation Concept**

The longitudinal zonation concept (LZC) by Kimmel and Groeger (1984) states that reservoirs occupy an intermediate position between rivers and natural lakes on a continuum of aquatic ecosystems. The authors list 3 sections that describe reservoirs. First, a riverine zone characterized by relatively high flow resulting in turbid water with high nutrient concentrations and low light availability. Second, a transitional zone characterized by a broader and deeper basin with reduced flow, resulting in a loss of turbidity and nutrients through sedimentation and a corresponding increase in light availability. And third, a lacustrine zone characterized by a lake-like basin, little flow, low nutrient availability, and relatively high light availability.

Within a given reservoir the boundaries of these regions can be highly variable based on flows. With high flows, the riverine section will extend further into the reservoir than it would with low flows; this in turn can affect the location of the other 2 regions, spatially and temporally. In especially turbid reservoirs, Kimmel and Groeger (1984) suggest that nutrients (P) may not be the primary limiting factor because low light availability has been shown to moderate the effects of nutrient loading. Therefore, a reservoir that experiences a high degree of variability

in flows may experience significant differences in limiting factors from one year to the next. This dynamic feature of reservoirs means that a reservoir such as LD may be limited by nutrients, light, or a combination of factors at different locations in the reservoir and at different times.

### 1.3. Research Introduction

#### 1.3.1. Study System

Lake Diefenbaker (LD) is a multi-purpose reservoir located on the South Saskatchewan River (SSR, Fig. 1.1). Human uses of the reservoir include, power generation, flood control, irrigation, aquaculture, industrial water supply, and recreation. The reservoir also provides source drinking water to >45% of Saskatchewan residents (Saskatchewan Water Security Agency (SWSA), 2012a), therefore proper management of the system is crucial. The SSR has been identified as Canada's most threatened river in terms of flow (World Wildlife Fund (WWF), 2009). Due to the aridness of the region, numerous impoundments, dependence on mountain snow melt, and large withdrawals, it is especially susceptible to climate change.



**Figure 1.1.** Map of the Saskatchewan River Basin showing the location of Lake Diefenbaker. Adapted from North et al. (2015a).



Lake Diefenbaker was completed after the construction of the Gardiner and Qu'Appelle River Dams in 1967. Its watershed originates in the Rocky Mountains and extends across the prairie ecozone, and is fed primarily by the Old Man, Bow, and Red Deer rivers in southern Alberta. The majority (98%) of the water that flows into LD originates in Alberta (SWSA, 2012b) as local inflows from surface runoff or ephemeral creeks are negligible (Centre for Hydrology, University of Saskatchewan, 2012). The reservoir measures 182 km from the Highway 4 bridge to the Gardiner Dam. It covers an area of 394 km<sup>2</sup> and has a storage capacity of 9 km<sup>3</sup> at full supply level (Sadeghian et al., 2015; SWSA, 2012b). LD is dimictic (Hudson and Vandergucht, 2015; Water Quality Branch (WQB), 1988), with an average water residence time of 1.5 years (Hudson and Vandergucht, 2015), flushing rate of 0.77 year<sup>-1</sup>, a mean depth of 22 m, and a maximum depth of 60 m near the Gardiner Dam (Sadeghian et al., 2015; SWSA, 2012b). Historically, LD was classified as oligotrophic to mesotrophic (WQB, 1988). More recently, LD was classified as mesotrophic (Abirhire et al., 2015).

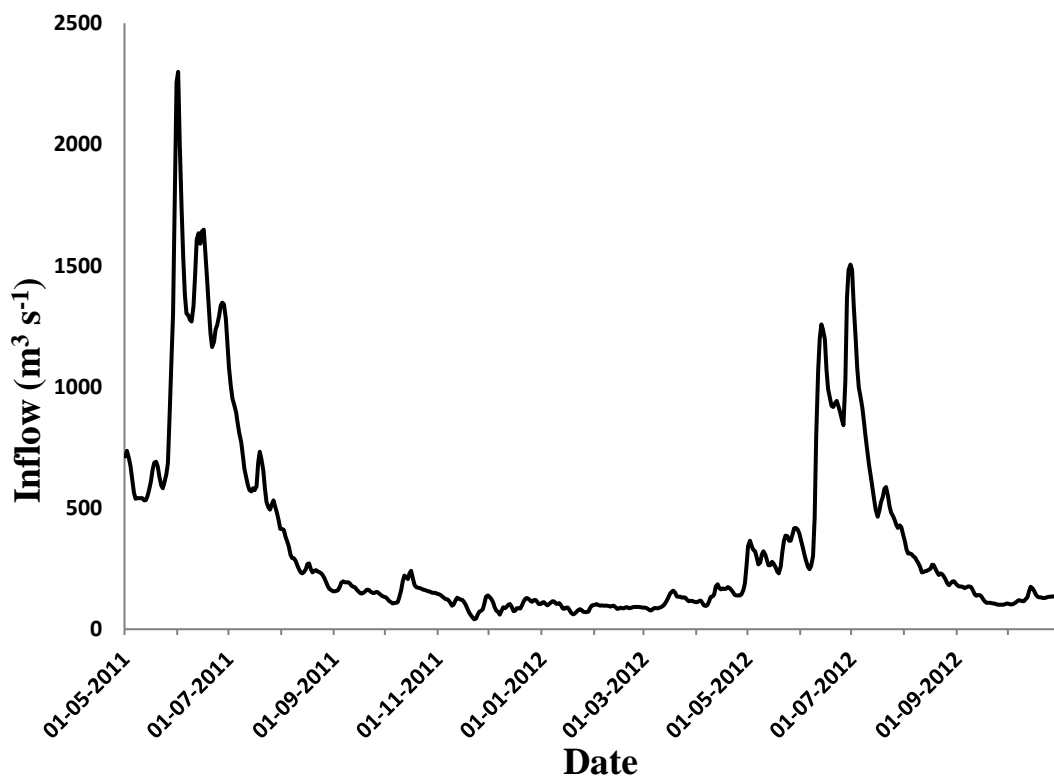
Residents along the shoreline have suggested an increasing frequency of algal blooms in the late summer and fall and an overall decline in water quality in LD (e.g., see Soggie, 2011). In light of recent problems with significant algal blooms in Lake Winnipeg, eutrophication is a major concern on the prairies. Out of the 28 lakes and reservoirs in the Lake Winnipeg basin, LD is 5<sup>th</sup> largest by volume, but has the highest P and N loadings of all systems other than Lake Winnipeg itself (Donald et al., 2015). Although LD is the largest single supplier of freshwater for agricultural, industrial, and municipal use in the province of Saskatchewan, as of the onset of this study, a comprehensive study of LD had not been completed since 1984-85. The knowledge gap, public concerns, and uncertainty associated with climate change prompted the Limnology Laboratory (U of S, Biology Department) to conduct a comprehensive study, of which this thesis

is one part, to examine the susceptibility of LD to ongoing nutrient loads and anthropogenic stressors, including climate change. The assessment of nutrient and light limitation within LD is an integral part of this study because it allows us to determine the factors controlling biomass and physiology of the phytoplankton communities in LD on a seasonal and spatial basis. Although previous studies have been conducted on this system (Hall et al., 1999; Hecker et al., 2012; WQB, 1988), LD is under-studied relative to its importance to the province and in comparison to reservoirs in other regions.

The majority of water flowing into LD enters at the Highway 4 bridge from the SSR, a small portion (<1%) of total water input enters through Swift Current Creek. Average inflow to LD from the SSR is between 200 and 300 m<sup>3</sup> s<sup>-1</sup> and the average annual volume received is 7.8 km<sup>3</sup>. This puts the historical water residence time at ~1.5 years. During this study, LD received higher than average inflows (11.5 km<sup>3</sup> and 8.0 km<sup>3</sup> in 2011 and 2012 respectively; Hudson and Vandergucht, 2015) with higher than average peak flows (Fig. 1.2). In a typical year, flow leaving the Qu'Appelle Dam accounts for ~1.8% of water leaving the reservoir (SWSA, 2012b), with the majority of outflow through the Gardiner Dam.

Lake Diefenbaker is subject to multiple stressors, including shoreline erosion, sedimentation, nutrient loading from upstream sources, climate change, and cultural eutrophication (from aquaculture, shoreline development, and agriculture). There are numerous embayments along the length of the reservoir. Embayments in large water bodies may have different nutrient concentrations than the central area of a lake (Mbonde et al., 2015). The shelter these embayments offer favours human activities, such as human settlements, golf courses, marinas, and cattle operations. LD is home to several marinas and boat launches and is a popular recreational destination in the summer months. Associated increases in impermeable land cover

may increase runoff into nearby water bodies. Boat traffic can increase shoreline erosion (Nanson et al., 1994), impact water clarity, and increase nutrient concentrations (Yousef et al., 1980). Livestock manure production, and associated N and P loads to the SSR watershed, have intensified in recent years (SWSA, 2010). Furthermore, many farmers allow their cattle direct access to LD. Increasing global temperatures are expected to intensify drought and water scarcity worldwide (Prudhomme et al., 2014; Schewe et al., 2014). Climate change is also expected to increase extreme weather conditions (i.e., floods) (Fischer and Knutti, 2015), which bring large amounts of turbidity into the system (Hudson and Vandergucht, 2015; Yip et al., 2015). As the largest source of moderate water quality to the province of Saskatchewan, LD is due for a reassessment of its limnology since the last comprehensive study of 1984-85.



**Figure 1.2.** Inflow into Lake Diefenbaker from May 2011 to October 2012 from the South Saskatchewan River (SSR). Peak flows from the SSR took place in mid-June in 2011 and early July in 2012. Date is in day/month/year format. Adapted from Hudson and Vandergucht (2015).

Median inflows in May, June, and July are 236, 573, and 286 m<sup>3</sup> s<sup>-1</sup>, respectively (SWSA, 2012b).

### 1.3.2. Objectives

Understanding the factors controlling the phytoplankton biomass on spatial (e.g., embayments vs. main channel) and temporal (e.g., seasonal and annual) scales is vital to identifying potential water quality issues. The objectives of the study were to 1) examine the spatial and temporal trends in nutrient and light limitation in the main channel of LD; 2) determine the type and degree of planktonic nutrient (P and N) and light limitation in areas that are potentially affected by cattle watering and marinas; and 3) determine the importance of light as a limiting factor of the phytoplankton community. I anticipate that an examination of light dynamics and nutrient concentrations, combined with a set of nutrient assays will help characterize the light-nutrient environment in LD, and in turn, this information will assist with future water quality management decisions, e.g., which nutrient, if any, should be carefully managed, especially with the potential changes in nutrient loading and flow patterns anticipated with climate change.

## **CHAPTER 2 – SPATIAL AND TEMPORAL TRENDS IN NUTRIENT AND LIGHT LIMITATION WITHIN THE MAIN CHANNEL OF LAKE DIEFENBAKER**

### **2.1. Introduction**

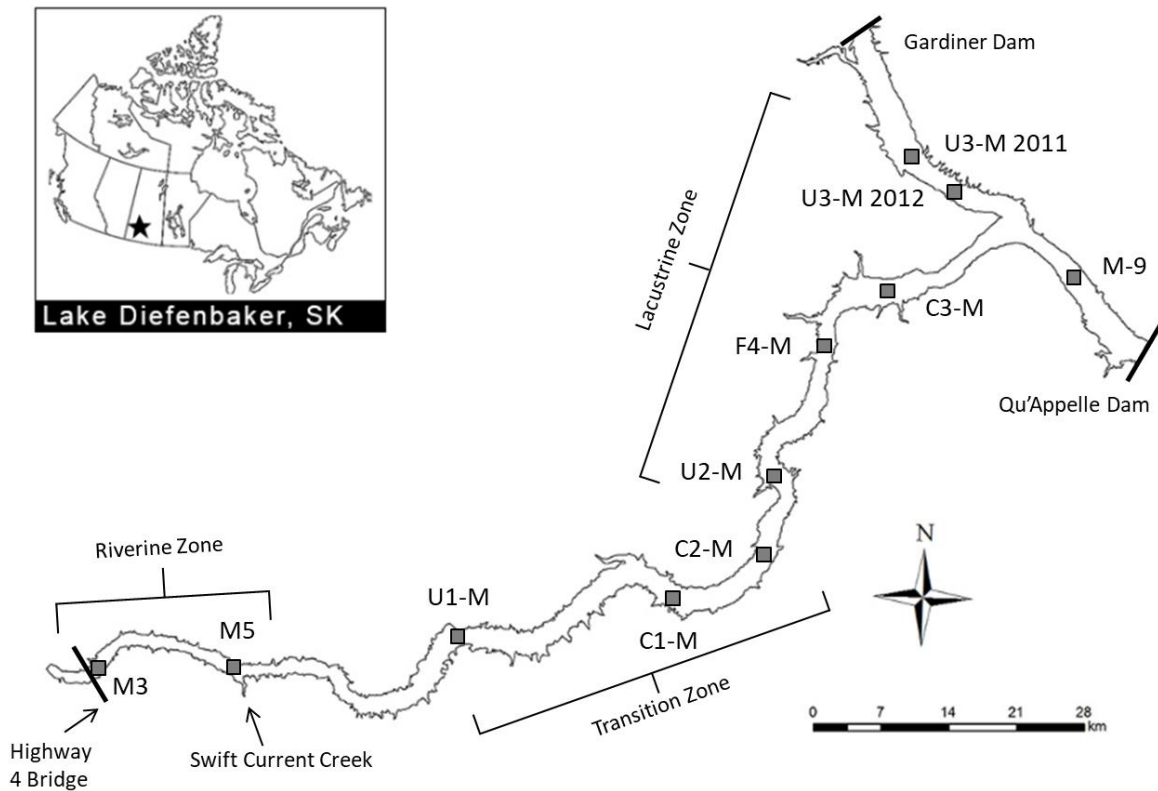
#### *2.1.1. Factors Affecting Nutrient and Light Status*

The debate over the relative importance of P, N or both as limiting nutrients in freshwater systems, and strategies to deal with eutrophication is ongoing (Conley et al., 2009; Higgins et al., 2017, 2017; Schindler, 2012; Schindler et al., 2008, 2016; Scott and McCarthy, 2010).

Photosynthetically active radiation (PAR) is also a key factor in regulating growth and primary production of phytoplankton in freshwater ecosystems. Adequate amounts of light energy are required for primary producers to uptake and assimilate nutrients (Beardall et al., 2001). The balance between these growth limiting resources (light and nutrients) is termed nutrient use efficiency by Sterner (Sterner et al., 1997), such that, in extreme light deficient environments phytoplankton may not respond to nutrients that may be typically considered limiting (Hecky and Guildford, 1984; Venables and Moore, 2010). The interaction between light and nutrients can be further complicated in run-of-the-river reservoirs by incoming turbidity, which can increase nutrient concentrations and decrease the light environment simultaneously (Zohary et al., 2010).

The longitudinal gradient present in reservoirs results in a high degree of spatial heterogeneity. The LZC describes 3 zones within a typical reservoir; the riverine, transition, and lacustrine regions (Kimmel and Groeger, 1984). Patterns in turbidity and the resulting light environment followed the expectations of the LZC in Lake Diefenbaker (Dubourg et al., 2015; Hudson and Vandergucht, 2015). Although the boundaries of the regions within the LZC can be highly variable depending on multiple overlapping gradients (Kimmel et al., 1990), for our purpose, LD can be separated into these three regions. Based on stratification patterns, Hudson

and Vandergucht (2015) described the two most upstream sites (M3 and M5) as the riverine zone, the next three sites (U1-M, C1-M, and C2-M) as the transition zone, and the remaining sites down to the Gardiner Dam as the lacustrine zone (Fig 2.1). They described the Qu’Appelle Arm as a large embayment because the majority of flow bypasses the Qu’Appelle Arm and flows into the Gardiner Arm.



**Figure 2.1.** Map of Lake Diefenbaker showing main channel sites. Note that site U3-M in the Gardiner Arm was moved between 2011 and 2012.

This study is a part of a larger study on LD and the SSR. Many aspects of the reservoir have been characterized in a recent special issue of the *Journal of Great Lakes Research* (Volume 41, Supplement 2, 2015). These studies include a temperature model (Sadeghian et al., 2015), and an assessment of spatial and temporal trends in stratification, turbidity, and dissolved oxygen

(Hudson and Vandergucht, 2015), as well as a look at environmental factors influencing phytoplankton communities (Abirhire et al., 2015; Dubourg et al., 2015). Long term trends in chlorophyll were assessed by satellite imagery (Yip et al., 2015) and historical trends in algal pigments (Tse et al., 2015), and diatom and chironomid assemblages (Lucas et al., 2015) were assessed by depositional sediments. These papers have provided insight into the existing and past characteristics of this reservoir. We have learned that despite residents' concerns, evidence supporting an increase in algal blooms was not found in the reservoir over the last 29 years (Yip et al., 2015). However, North et al. (2015b) found evidence of internal year-round P loading (~24% of external P loads) from the sediments. With the potential for anoxic hypolimnia, especially in years of low flow (Hudson and Vandergucht, 2015), the internal P loading could increase considerably as legacy P would be more readily released from the sediments in a reducing environment. From 2011 to 2013 LD retained over 90% of the TP load from the SSR (North et al., 2015b). In a similar study over a one year period (2013), Dubourg et al (2015) determined that LD was co-limited by light and P. Although the light and nutrient dynamics in LD, and their effects on phytoplankton communities have been looked at in 2013, my study provides 2 additional years of detailed light and nutrient data and a more comprehensive look at spatial trends. Unlike Dubourg et al. (2015), I kept all 10 main channel sites separate during my analyses as opposed to pooling them based on regions. The main channel sites were placed strategically throughout the reservoir to capture the spatial heterogeneity found in LD (Fig. 2.1).

The number of reservoirs worldwide are expected to more than double in the next 25 years (Zarfl et al., 2014). Therefore, it is important to understand the factors that influence the growth and reproduction of algae in such systems for effective water quality management. As a typical run-of-the-river reservoir, LD will serve well as a model to investigate light and nutrient

dynamics along the length of a reservoir and may provide important information for proper management of LD and similar systems. I anticipate the trends in light and nutrient limitation will follow the expectations of the LZC. I expect to see both light and nutrient limitation within the reservoir, with light limitation being most prevalent in the riverine zone (sites M3 and M5) and light availability increasing through the transition zone (sites U1-M, C1-M, and C2-M) and into the lacustrine zone (remaining sites). In contrast, I expect that nutrient concentrations will be high in the riverine zone and decrease along the length of the reservoir, such that nutrient limitation, primarily P limitation, will be most prevalent in the lacustrine zone.

## **2.2. Methods**

In order to assess nutrient and light limitation within the main channel of LD, I used 5 indicators of phytoplankton community P status ( $TT_{PO_4}$ , steady-state (ss)  $PO_4^{3-}$ , APA, PC:PP, PN:PP), 2 indicators of N status (N-debt, PC:PN), 2 indicators of light status ( $\bar{E}_{24}$ ,  $Z_{eu}:Z_{mix}$ ) and 1 indicator of light and P status ( $\bar{E}_{24}:TP$ ). I also recorded total and dissolved PN:PP ratios (Guildford and Hecky, 2000). Limitation thresholds were used, when available, to determine nutrient and light limitation (Table 2.1). I will examine these indicators spatially and temporally in LD to determine the type and degree of limitation on both proximate and ultimate timescales (i.e., as described in Davies et al. 2004 and 2010).

### *2.2.1. Field Sampling*

Samples were collected monthly during the open water season (June-October of 2011 and 2012) throughout the length of LD. Main channel sites (10) extended from Highway 4 to the Gardiner Dam and Qu'Appelle Dams (Fig. 2.1). Epilimnetic water (~20 L, discrete samples) was collected 2 m below the surface with a Van Dorn sampler. Water was gently decanted into



**Table 2.1.** Nutrient and light limitation indicators used in this study. Associated thresholds used to ascribe the degree of limitation are also presented (i.e., extreme, moderate, or no limitation). APA = alkaline phosphatase activity; TT = turnover time; PC = particulate carbon; PN = particulate nitrogen; PP = particulate phosphorus; TN = total N; TP = total P;  $\bar{E}_{24}$  = mean water column irradiance over 24 hours.

Indicator	Units	Limiting Factor Examined	Degree of Limitation		
			No Limitation	Moderate Limitation	Extreme Limitation
APA	nmol P $\mu$ g Chl $a^{-1}$ min $^{-1}$	P	Lower rates		Higher rates
TT (PO <sub>4</sub> ) <sup>a</sup>	min	P	> 60	< 60	<10
PC:PP <sup>b</sup>	atomic ratio	P	<129	129 – 258	>258
PN:PP <sup>b</sup>	atomic ratio	P	< 22	> 22	
PC:PN <sup>b</sup>	atomic ratio	N	< 8.3	8.3 – 14.6	>14.6
N debt <sup>b</sup>	$\mu$ mol N $\mu$ g Chl $a^{-1}$ day $^{-1}$	N	< 0.15	> 0.15	
TN:TP <sup>c</sup>	atomic ratio	P		> 50	
TN:TP <sup>c</sup>	atomic ratio	N		< 20	
$\bar{E}_{24}$ <sup>d</sup>	mmol m $^{-2}$ min $^{-1}$	Light	> 2.5	< 2.5	
$\bar{E}_{24}$ :TP <sup>e</sup>	mmol m $^{-2}$ min $^{-1}$ : $\mu$ g L $^{-1}$ TP	Light or P		< Median (Light) >Median (P)	

<sup>a</sup> Lean et al. (1983), <sup>b</sup> Healey and Hendzel (1979), <sup>c</sup> Guildford and Hecky (2000), <sup>d</sup> Hecky and Guildford (1984), and <sup>e</sup> Chrzanowski and Grover (2001)

collapsible polyethylene bags, transported to the laboratory in a cooler and stored at ambient lake temperature on a 6:18 hr dark:light cycle before processing the following day. All glass and plastic ware was washed in advance with LiquiNox® (P-free detergent), rinsed with methanol, leached in a 10% HCl solution, rinsed with deionized water, and finally rinsed with lake water or filtrate where applicable.

Vertical temperature profiles were taken with a sonde (YSI 6600 V2). The thermocline was defined as the point where there was a  $0.5^{\circ}\text{C m}^{-1}$  change in water temperatures. The mixing depth ( $Z_{\text{mix}}$ , m) was reported as the depth from the top of the water column to the top of the thermocline, or the full water column depth when stratification was not present. The maximum depth ( $Z_{\text{max}}$ , m) at each station was determined using bathymetric maps and confirmed with a fish finder at time of sampling and during each sonde cast. Daily reservoir levels were obtained from the Water Survey of Canada website. Sites were also characterized by the shortest linear distance down the length of the main channel from the Highway 4 Bridge. This measurement was used to control for the upstream to downstream gradient present in the reservoir. Rates of inflow into the reservoir were obtained from Hudson and Vandergucht (2015).

### *2.2.2. Biological and Chemical Parameters*

Total N (TN), total dissolved N (TDN,  $<0.2 \mu\text{m}$ ) and nitrate ( $\text{NO}_3^-$ ) concentrations were determined by second derivative spectroscopy (Bachmann and Canfield, 1996; Crumpton et al., 1992). Ammonium ( $\text{NH}_4^+$ ) was determined colorimetrically using the phenol-hypochlorite technique according to Stainton et al. (1974). Total P (TP), and total dissolved P (TDP,  $<0.2\mu\text{m}$ ) underwent persulfate oxidation (Menzel and Corwin, 1965), then all P fractions (TP, TDP and soluble reactive P (SRP)) were determined colorimetrically according to Parsons et al. (1984). Particulate C and N samples were collected by vacuum filtration on pre-combusted glass fiber filters (Advantec GF75, nominal pore size  $0.7 \mu\text{m}$ ). Filters were dried for 3 hours at  $60^{\circ}\text{C}$  and stored at room temperature until analysis. Mass of C and N samples were determined using an ANCA-GSL sample preparation unit coupled to a Tracer 20 mass spectrometer (Europa Scientific). Particulate P was calculated as the difference between TP and TDP. Chlorophyll *a* (chl *a*) was analyzed according to Bergmann and Peters (1980) with the following changes;

absorbance was read at 665 nm rather than 655 nm, and chl *a* samples were left in 95% ethanol for 24 h in the dark at room temperature rather than refrigerated (Arvola, 1981; Dessouki et al., 2005).

### 2.2.3. Nutrient Bioassays

Radiophosphate uptake bioassays were started the day after water collection. Carrier-free radiophosphate ( $^{33}\text{PO}_4$ , final activity  $\sim 50,000$  cpm  $\text{mL}^{-1}$ ) was added to 1 L of lake water in clean collapsible polyethylene containers. I determined planktonic uptake of radiophosphate by subsampling the dissolved pool (syringe filtration, 25 mm diameter polysulphone,  $<0.2$   $\mu\text{m}$  pore size) at 1, 2, 5, 8, 12, and 30 minutes after radiophosphate injection, and then continued subsampling at less frequent intervals until a full 24-hour period had elapsed. Radioactivity was measured by liquid scintillation counting and corrected for background activity. Quenching of samples was not detected. Radioactivity remaining in the dissolved fraction over time was fitted to a polynomial function of best fit (Bentzen and Taylor, 1991; Currie and Kalff, 1984; Vandergucht et al., 2013). The uptake constant ( $k$ ) was determined by finding the derivative of the polynomial at time zero and dividing it by the total radioactivity. The reciprocal of the uptake constant,  $k$ , is the phosphate turnover time ( $\text{TT}_{\text{PO}_4}$ ,  $\text{min}^{-1}$ ). The incubation was terminated at approximately 24 hours with the addition of unlabeled  $^{31}\text{PO}_4^{3-}$  as a competitive inhibitor (final concentrations  $\sim 1\text{mg L}^{-1}$ ) to prevent further uptake of radiophosphate (Hudson and Taylor, 1996). I measured the return of radiophosphate from the particulate to the dissolved pool approximately 1 hour after the addition of the competitive inhibitor and again after 8 hours and 24 hours. The resulting slope provided an estimate of the release rate of dissolved P that was used to calculate the regeneration rate ( $R$ ,  $\text{ng L}^{-1} \text{hr}^{-1}$ ) of the planktonic assemblage (Hudson and Taylor, 1996). Finally, regeneration rates were used to calculate the steady state phosphate

concentration ( $\text{ssPO}_4^{3-}$ ,  $\text{ng L}^{-1}$ ) as in Hudson et al. (2000):  $\text{ssPO}_4^{3-} = R/k$ . Lower estimates of  $\text{ssPO}_4^{3-}$  were indicative of greater P limitation (i.e., concentrations of  $\text{ssPO}_4^{3-}$  in the picomolar range were indicative of greater P limitation than those in the nanomolar range). Incubation containers were kept in an environmental chamber at ambient light and temperature.

Alkaline phosphatases are produced by bacteria and algae to hydrolyze ester bonds between  $\text{PO}_4^{3-}$  and dissolved organic molecules. Increased alkaline phosphatase activity (APA) is indicative of greater P limitation in the water column. APA was determined fluorometrically (Pettersson, 1980) in whole lake water and lake filtrate ( $<0.2 \mu\text{m}$ ) with a Varioskan<sup>®</sup> Flash spectral scanning multimode reader (Thermo Electron Corporation). Particulate APA was determined by subtracting dissolved activity from total activity and normalized to chl *a* concentrations. Healey and Hendzel's (1980) APA threshold was developed using o-methyl-fluorescein-phosphate as a substrate. This threshold was not directly applicable to my APA measurements, as I used an alternate substrate, 4-methylumbelliferyl phosphate (Vandergucht et al., 2013). Regardless of the substrate used, the APA rates show relative changes in P limitation, as P becomes more limiting, APA rates increase, and conversely, as P limitation relaxes, APA rates will decrease.

Planktonic N deficiency was determined using the N-debt method (Healey, 1975; Healey and Hendzel, 1979, 1980). Briefly, a spike of  $\text{NH}_4\text{Cl}$  ( $\sim 5 \mu\text{M}$ ) was added to lake water and incubated in the dark at ambient lake temperature for 24 hours. Autoclaved lake water was used as a control. Samples from each bag were taken in triplicate at time zero and 24 hours. All samples were processed using the phenol-hypochlorite technique for ammonium concentrations (Stainton et al., 1974).

#### 2.2.4. Light Measurements

Vertical profiles of photosynthetically active radiation (PAR) were taken with a Biospherical BIC compact four-channel radiometer (Biospherical Instruments, San Diego CA). The vertical attenuation coefficient of PAR ( $k_d$ ) was determined using the linear regression of the natural logarithm versus depth. The euphotic depth ( $Z_{eu}$ ) was determined as the depth where the light intensity was 1% of the light at the surface. Mean water column irradiance ( $\bar{E}_{24}$ ,  $\text{mmol m}^{-2} \text{min}^{-1}$ ), or the amount of PAR that a free floating cell would receive over a 24 hour period, was calculated using the following equation from Guildford et al. (2000).

$$\bar{E}_{24} = \bar{E}_0 \times (1 - \exp(-1 \times k_d \times Z_{mix})) \times (k_d \times Z_{mix})^{-1}$$

Where  $\bar{E}_0$  (mean daily incident irradiance) was estimated from global radiation measurements from the meteorological station at the University of Saskatchewan (<http://www.usask.ca/weather/kfarm/>).

### 2.3. Results

#### 2.3.1. General Limnological Characteristics

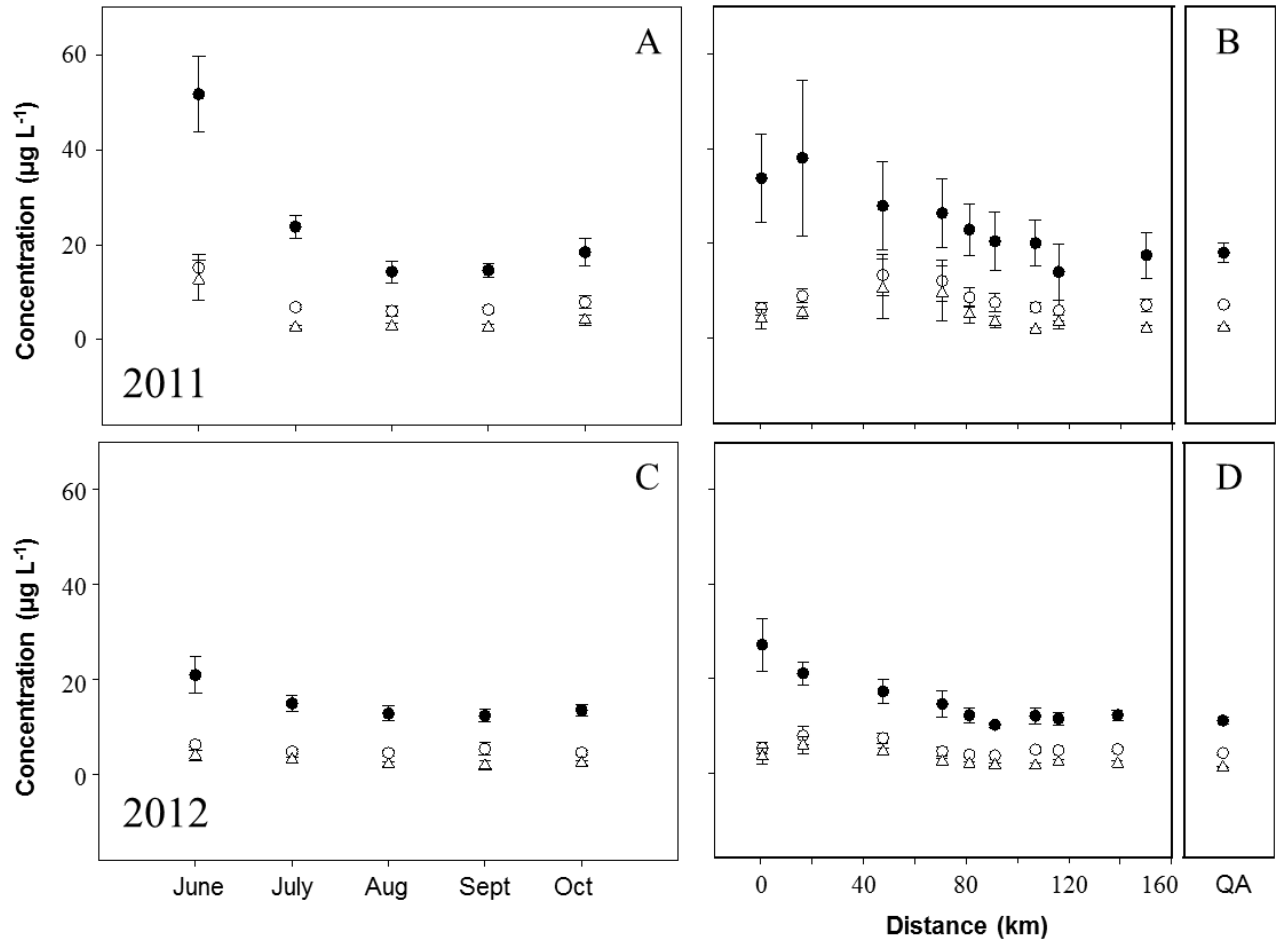
Lake Diefenbaker exhibited a wide range in nutrient concentrations over the two sampling seasons (Table 2.2). Although I saw a wide range in all nutrients in both years, overall nutrient concentrations were statistically greater in 2011 than in 2012 ( $P < 0.05$ , except  $\text{NH}_4^+$ ; See Table 2.2, Figs. 2.2 and 2.3). The average pH in LD was 8.4 with very little spatial or temporal variation. The average summer water temperature at 2 m below the surface in LD was  $17.4^\circ\text{C}$  with 2011 being slightly warmer than 2012. July and August were the warmest months in both years.

**Table 2.2.** Nutrient concentrations ( $\mu\text{g L}^{-1}$ ) in Lake Diefenbaker. Values represent all main channel epilimnetic water samples from 2011, 2012, and both years combined.

	2011		2012		Both Years	
	<u>Average</u>	<u>Range</u>	<u>Average</u>	<u>Range</u>	<u>Average</u>	<u>Range</u>
<b>TP</b>	24.5	10.4 – 103.7	14.9	7.9 – 48.7	19.6	7.9 – 103.7
<b>TDP</b>	8.5	4.0 – 30.5	5.1	2.9 – 15.2	6.8	2.9 – 30.5
<b>SRP</b>	4.7	0.5 – 35.8	2.7	0.05 – 10.7	3.7	0.05 – 35.8
<b>TN</b>	615	304 – 1076	446	226 – 628	530	226 – 1076
<b>TDN</b>	549	192 – 932	383	129 – 627	465	129 – 932
<b>NO<sub>3</sub></b>	340	34 – 717	221	49 – 405	282	34 – 717
<b>NH<sub>4</sub><sup>+</sup></b>	15.3	0.5 – 79.7	11.9	1.2 – 98.4	13.6	0.5 – 98.4
<b>Chl <i>a</i></b>	4.59	0.50 – 16.2	3.71	0.61 – 14.3	4.15	0.50 – 16.2

### 2.3.2. Spatial and Temporal Trends

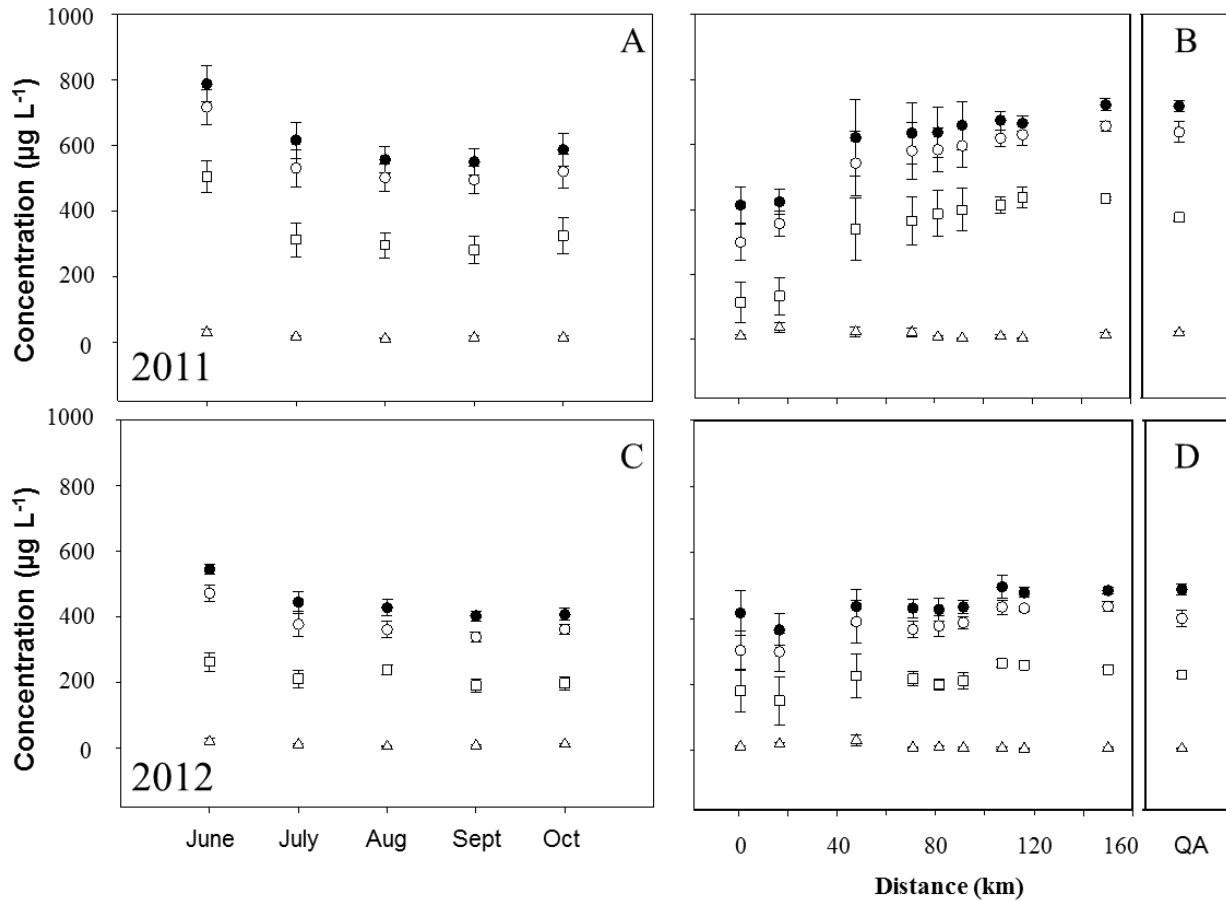
Total phosphorous (TP) concentrations were highest in June of both years and declined to a minimum in August and September followed by small increases in October after fall turnover had occurred; TDP and SRP followed similar trends (Fig. 2.2). The majority of the P-load entering the reservoir was in particulate form, especially during the high flows and turbid conditions of June and July of both years. Total N concentrations were also highest in June of both years and declined somewhat in July and August with small increases in concentrations in September or October or in both months. TDN and NO<sub>3</sub> followed similar trends (Fig. 2.3), whereas NH<sub>4</sub><sup>+</sup> stayed low and constant throughout the season.



**Figure 2.2.** Phosphorus concentrations in the main channel of Lake Diefenbaker. Average TP (●), TDP (○), and SRP (△) and standard error (SE) by month (A and C; all main channel sites within the month) and along the length of the reservoir (B and D; 5 sampling dates at each site, QA = main channel site in Qu'Appelle Arm).

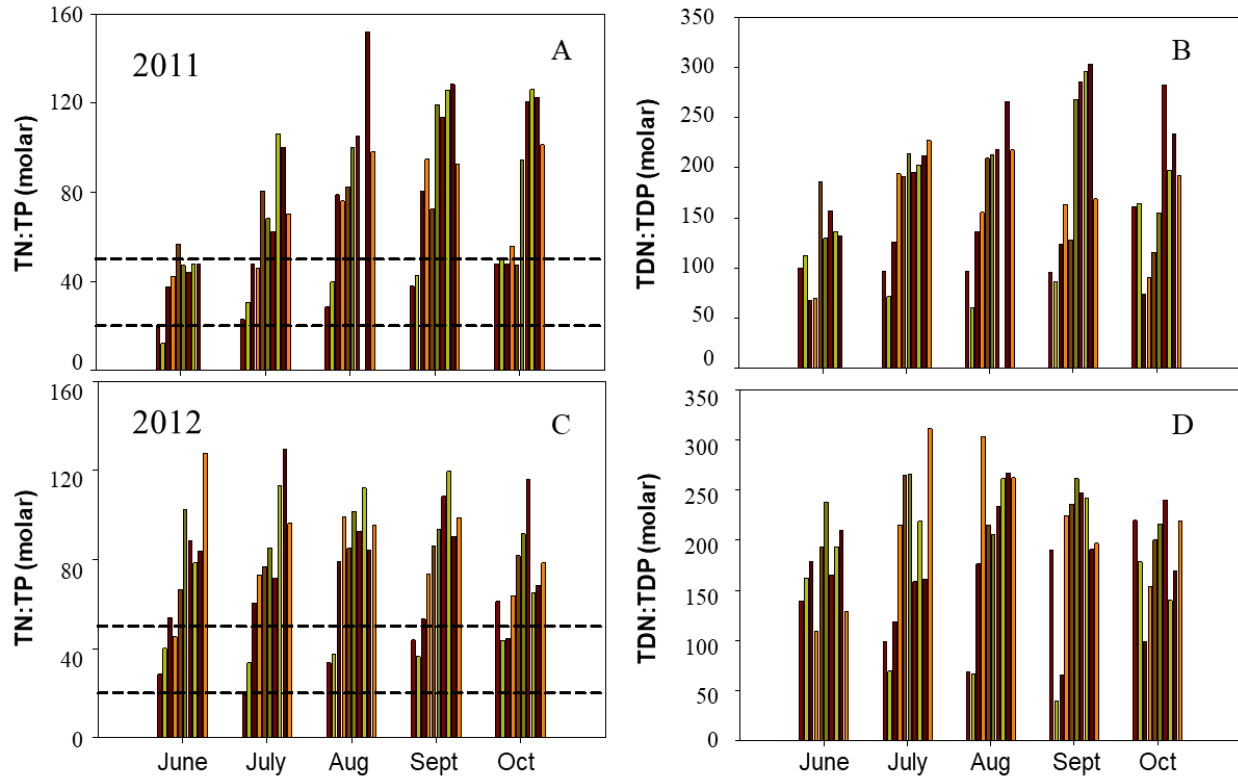
Phosphorus and nitrogen dynamics differed along the length of the reservoir. As TP concentrations declined along the length of the reservoir, TN concentrations increased. This occurred in both years but was more pronounced in 2011 (Figs. 2.2 and 2.3). Dissolved P (TDP and SRP) increased from the upstream sites to midstream sites (distance from Highway 4 ~50 to 65 km) and then declined towards the arms in 2011. In 2012, dissolved P forms showed a slight increase from Hwy 4 to ~50 km downstream at which point they declined slightly and then remained fairly similar throughout the remainder of the reservoir (Fig. 2.2). TDN and  $\text{NO}_3$

followed the trends in TN very closely in both years. Ammonium increased slightly to midstream sites and then declined and remained low into the arms (Fig. 2.3). The difference in P and N dynamics within the reservoir resulted in increasing PN:PP ratios (total and dissolved) along the length of the reservoir (Fig. 2.4).



**Figure 2.3.** Nitrogen concentrations in the main channel of Lake Diefenbaker. Average TN (●), TDN (○), NO<sub>3</sub> (□), and NH<sub>4</sub> (Δ) and SE by month (A and C; all main channel sites within the month) and along the length of the reservoir (B and D; 5 sampling dates at each site, QA = main channel site in Qu'Appelle Arm).





**Figure 2.4.** Total and dissolved PN:PP ratios along the main channel in 2011 (A and B) and 2012 (C and D). Each month is organized from the most upstream site (M3, left) to the most downstream site (Gardiner arm, 2<sup>nd</sup> from the right) with the site in the Qu'Appelle arm (M9) the furthest right. Values above the top dashed line (TN:TP = 50) indicate P limitation, values below the bottom dashed line (TN:TP = 20) indicate N limitation, values between dashed lines indicate neither P nor N limitation (according to Guildford and Hecky 2000).

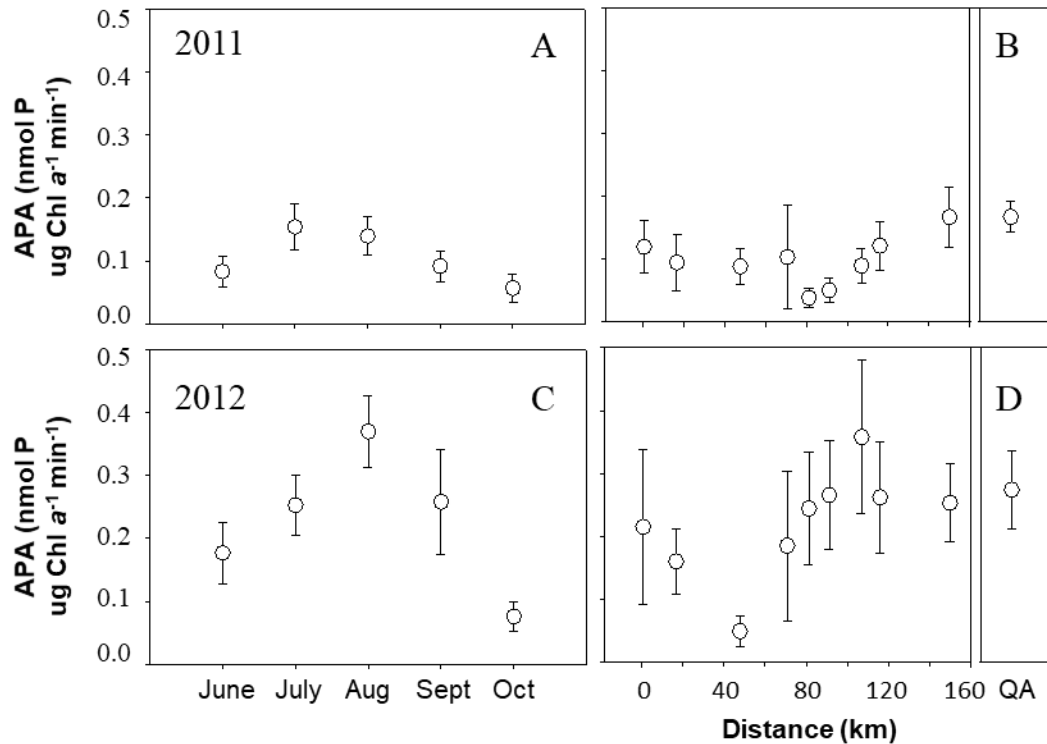
### 2.3.2.1. Phosphorus Limitation

Alkaline phosphatase activity (APA) ranged from 0.0043 to 0.7195 nmol P  $\mu\text{g chl } a^{-1} \text{ min}^{-1}$  (Table 2.3, Fig. 2.5 A-D). Overall, APA values were higher in 2012 than 2011 (Table 2.3). In both years APA levels were lowest in June and October with the highest levels present during the warmer months when stratification was present (Fig. 2.5 A and C). In 2011, APA rates were constant throughout the year and throughout the length of the reservoir (Fig 2.5 A and B). In comparison, APA rates in 2012 were more variable, with rates increasing to a maximum in

August and then declining for the rest of the season. Spatially, APA rates declined from the riverine zone to the beginning of the transition zone where the lowest rates were seen. APA rates then increased throughout the transition zone and then remained high and consistent throughout the remainder of the reservoir (Fig. 2.5D). Overall, the spatial and temporal trends in APA rates were similar in both years, however the range was smaller in 2011 (Table 2.3).

**Table 2.3.** Nutrient limitation indicators in Lake Diefenbaker. Values represent all main channel epilimnetic water samples from 2011 and 2012.

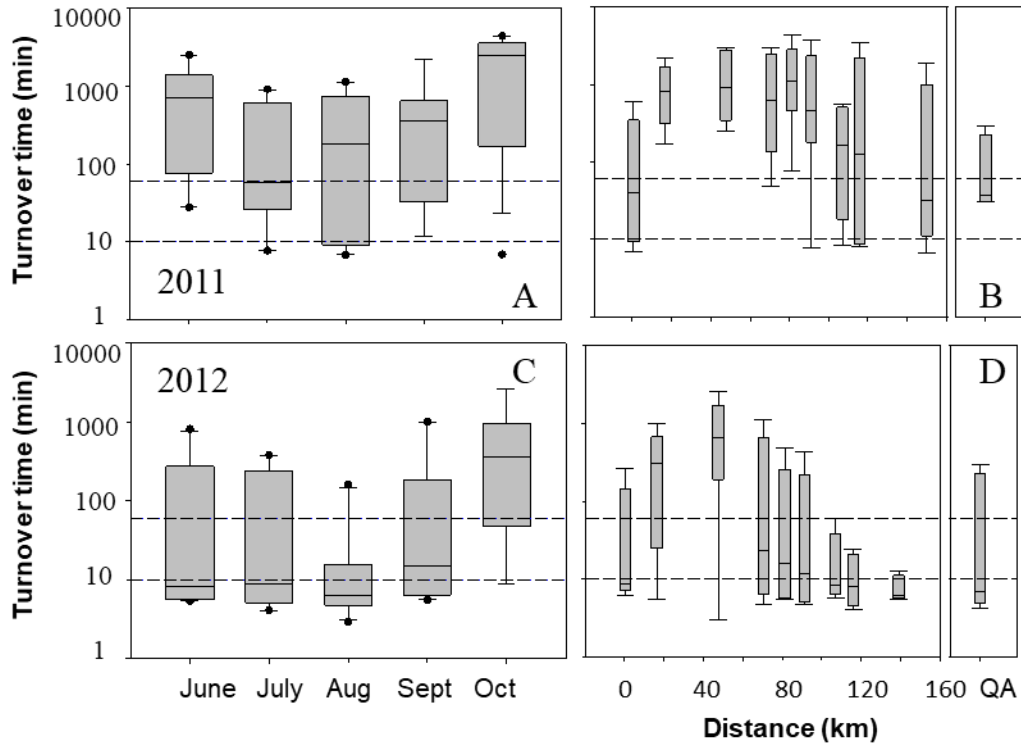
	2011		2012	
	<u>Average</u>	<u>Range</u>	<u>Average</u>	<u>Range</u>
<b>APA (nmol P <math>\mu\text{g Chl a}^{-1} \text{min}^{-1}</math>)</b>	0.10	0.01 – 0.35	0.23	0.004 – 0.72
<b>TT<sub>P04</sub> (min)</b>	816	6.67 – 4457	417	2.94 – 6110
<b>ssPO<sub>4</sub><sup>3-</sup> (ng L<sup>-1</sup>)</b>	1200	9.45 – 4732	280	5.17 – 1971
<b>PC:PP (molar)</b>	110	30.5 – 278	113	42.6 – 289
<b>PN:PP (molar)</b>	15.01	3.11 – 30.4	16.5	6.31 – 41.9
<b>PC:PN (molar)</b>	7.32	5.43 – 10.1	6.76	4.74 – 11.33
<b>N-debt (<math>\mu\text{mol N } \mu\text{g Chl a}^{-1} \text{day}^{-1}</math>)</b>	0.22	0.0 – 1.26	0.12	0.0 – 0.96
<b>TN:TP (molar)</b>	70.6	12.1 – 152	73.7	19.0 – 130
<b><math>\bar{E}_{24}</math> (mmol m<sup>-2</sup> min<sup>-1</sup>)</b>	1.22	0.23 – 2.33	2.47	0.60 – 9.61
<b><math>\bar{E}_{24}</math>:TP (mmol m<sup>-2</sup> min<sup>-1</sup>: <math>\mu\text{g L}^{-1}</math>)</b>	0.06	0.003 – 0.16	0.21	0.04 – 0.82



**Figure 2.5.** APA rates in the main channel of Lake Diefenbaker by month (A and C; mean and standard error (SE) of all main channel sites within the month) and along the length of the reservoir (B and D; mean and SE of 5 sampling dates at each site; QA = main channel site in Qu'Appelle Arm).

In 2011 turnover times ( $TT_{PO_4}$ ) in the main channel of the reservoir indicated P limitation ( $TT_{PO_4} < 60$  min) 15 out of 49 times, with 6 of the 15 indicating extreme P limitation ( $TT_{PO_4} < 10$  min, Table 2.4 and Fig. 2.6 A and B). P limitation was most often found in mid to downstream sites in July, August and September in 2011. In 2012,  $TT_{PO_4}$  indicated main channel sites were P limited 34 out of 48 times, with 22 being extremely P limited (Table 2.4 and Fig. 2.6 C and D). In August of 2012, most main channel sites were extremely P limited, with P limitation relaxing in September and October. Spatially, P deficiency followed a similar pattern in both years, decreasing from upstream to Prairie Lake (site U1-M, ~45km downstream, fewest instances of P limitation in both years), then increasing throughout the transition region and

further increasing in the arms. In general, the sites that were stratified typically exhibited short  $TT_{PO_4}$ . It should be noted that sites C3-M (~120 km) and U3-M (~140 km) had insufficient uptake in October of 2012 to adequately calculate  $TT_{PO_4}$ : hence the October  $TT_{PO_4}$  data from these sites has not been included in the calculation of mean rates.



**Figure 2.6.** Turnover time of the phosphate pool in the main channel of Lake Diefenbaker by month (A and C; all main channel sites within the month) and along the length of the reservoir (B and D; 5 sampling dates at each site; QA = main channel site in Qu’Appelle Arm). Values below dashed lines (< 10 min) indicate extreme P limitation, values in between dashed lines (10 – 60 min) indicate moderate P limitation (Lean et al., 1983; see Table 2.1). Boxes show median and 25<sup>th</sup> and 75<sup>th</sup> percentiles, whiskers show 90<sup>th</sup> percentiles, and dots show outliers.

**Table 2.4.** Nutrient deficiency as assessed by N-debt and  $TT_{PO_4}$ . N = nitrogen deficient, Mod P = moderate P limitation, P = extreme limitation, P + N and Mod P + N = co-limitation, -- = neither P nor N limitation, nd = no data. The order of sites extends from the most upstream site (M3) to the most downstream site (U3-M); site M9 is in the Qu'Appelle Arm.

2011	June	July	Aug	Sept	Oct
M3	N	Mod P + N	--	Mod P	P
M5	N	N	N	N	--
U1-M	N	N	N	--	N
C1-M	N	--	N	Mod P	N
C2-M	N	--	--	--	--
U2-M	N	P	N	--	--
F4-M	Mod P	--	P	--	--
C3-M	N	P	P	--	--
U3-M 2011	--	Mod P	P	Mod P	--
M9	--	Mod P	Mod P	Mod P	--

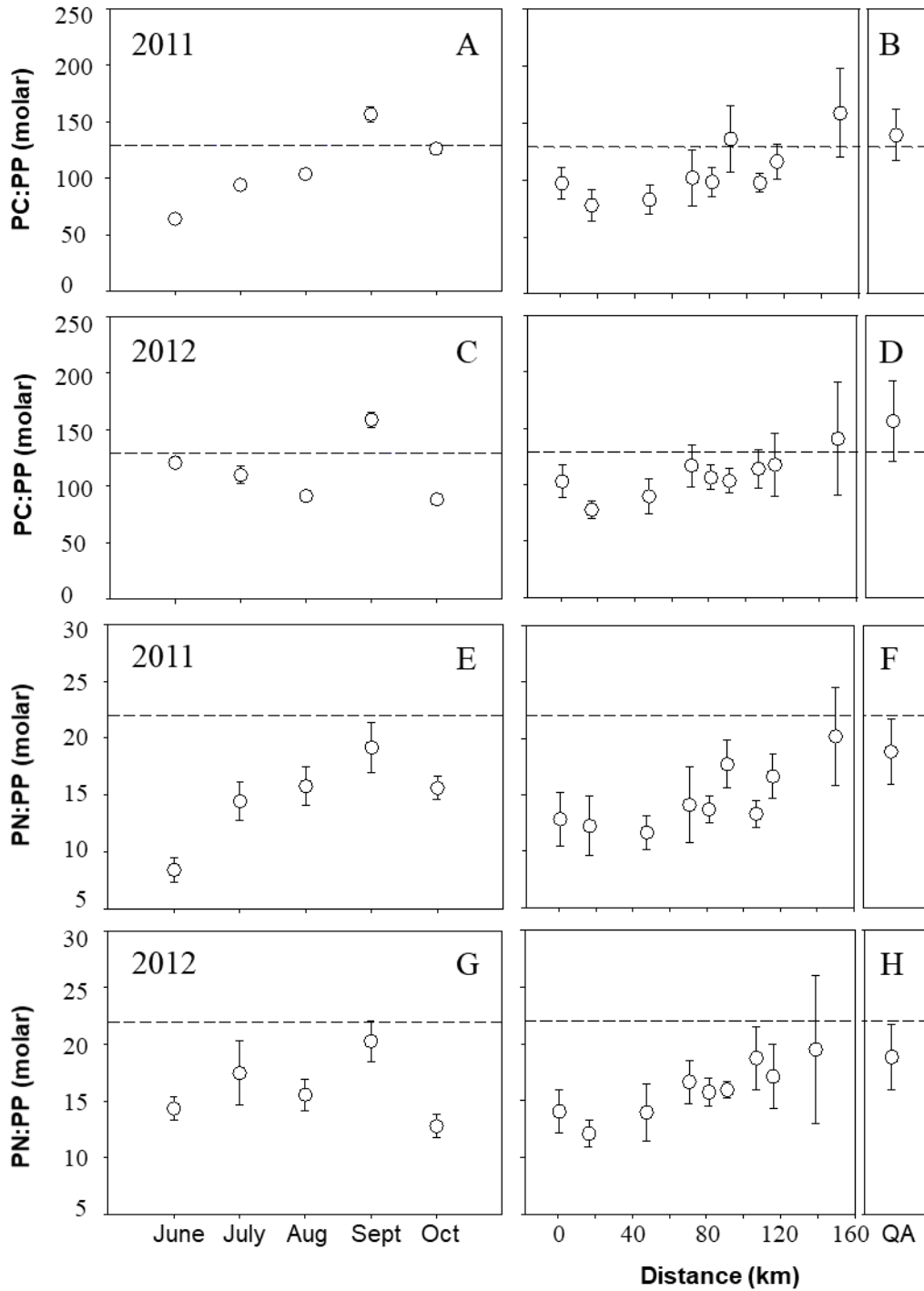
2012	June	July	Aug	Sept	Oct
M3	N	Mod P	P	P	P
M5	N	--	P	--	Mod P
U1-M	N	N	P	--	--
C1-M	P	--	P + N	Mod P	--
C2-M	Mod P	P	P + N	Mod P	--
U2-M	P + N	Mod P	P	Mod P	--
F4-M	P	P	P	Mod P + N	Mod P + N
C3-M	P	P	Mod P	Mod P	nd
U3-M 2012	P + N	P	Mod P	P	nd
M9	P	P	--	P	--

Steady-state phosphate ( $ssPO_4^{3-}$ ) concentrations (not shown) are closely related to, and therefore, follow similar trends as the turnover times of the dissolved phosphate pool. Average  $ssPO_4^{3-}$  concentrations in 2011 were  $\sim 1200$  ng L<sup>-1</sup> (Table 2.3) with the lowest concentrations in the lacustrine regions during times of stratification. In 2012 the average  $ssPO_4^{3-}$  concentrations were lower overall ( $\sim 280$  ng L<sup>-1</sup>, Table 2.3), concentrations decreased from June to August, and

then increased in September and October. Spatially, the greatest  $\text{ssPO}_4^{3-}$  concentrations were found to be at the beginning of the transition zone and then decreased steadily to F4-M. Both the Gardiner and Qu'Appelle Arms exhibited consistently low concentrations ( $< 20 \text{ ng L}^{-1}$ ) from July to late September.

In 2011 PC:PP ratios indicated moderate P limitation (i.e. mole C:mole P  $>129$ ) 12 out of 48 times and extreme P limitation ( $>258$ ) once, at the site closest to the Gardiner Dam in late August. These ratios increased from June to September in 2011 and decreased somewhat in October (Fig. 2.7A). Ratios tended to be higher in the mid to downstream portions of the reservoir with the lowest ratios seen in the riverine zone in both years (Fig. 2.7 B and D). In 2012, PC:PP ratios indicated P limitation 13 out of 48 times sampled, again the site closest to the Gardiner Dam (U3-M) showed extreme P limitation at the end of July, and again in late September. Average PC:PP ratios were greater in June of 2012 than in 2011 and then declined from June to August. Again, PC:PP ratios were highest in September and declined in October. Spatially PC:PP ratios were similar to 2011 with the highest ratios present in the arms.

In 2011, particulate PN:PP ratios indicated P limitation ( $>22$ ) 6 out of 48 times, all of which occurred in late August and September in the lacustrine portion of the reservoir. Average molar PN:PP ratios were slightly higher in 2012 (16.5) than in 2011 (15.0) but they followed similar trends both spatially and temporally (Fig. 2.7). In 2012, particulate PN:PP ratios indicated P limitation 7 out of 48 times, these agreed well with PC:PP ratios. This occurred from July to late September, and in all but one instance, was in the lacustrine portion of the reservoir. The site at Prairie Lake (U1-M) showed P limitation in mid-August while it was still stratified (the epilimnion deepened and reached bottom by September).



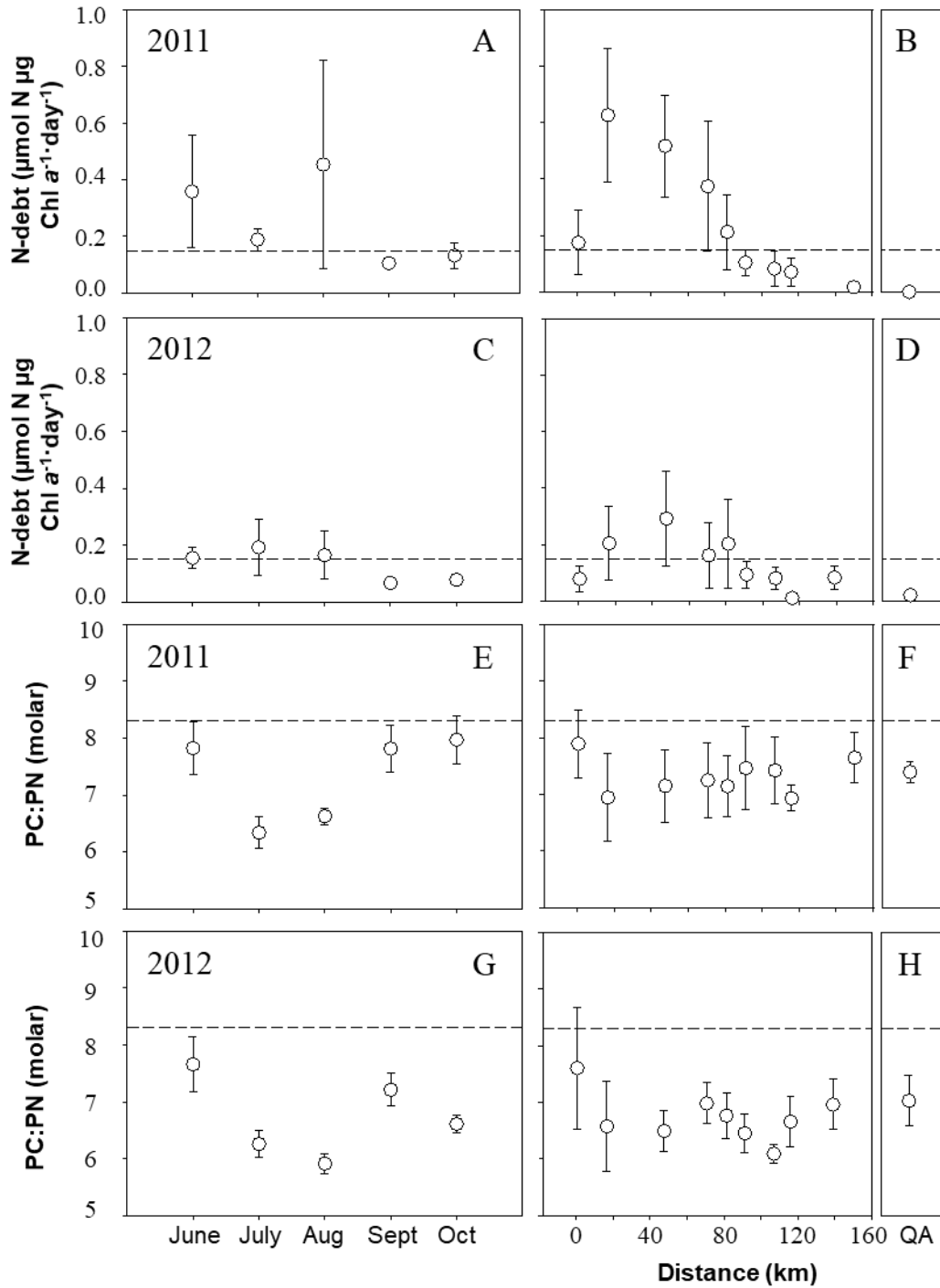
**Figure 2.7** Particulate nutrient ratios in the main channel of Lake Diefenbaker by month (A, C, E, and G; mean and SE of all main channel sites within the month) and along the length of the reservoir (B, D, F, and H; mean and SE of 5 sampling dates at each site; QA = main channel site in Qu'Appelle Arm). Values above dashed lines indicate P limitation (Healey and Hendzel, 1979)).

### 2.3.2.2. Nitrogen Limitation

Overall, N trophic status indicators showed more N deficiency in 2011 than 2012 (higher average N-debt and PC:PN values, Table 2.3). N-debt values were highest in June and August of 2011. In June of 2011, 7 out of 10 of the main channel sites indicated N deficiency (Table 2.4). The large error bars in August are due to site M5 and the sites in the transition zone exhibiting very high values while the lacustrine section showed little to no ammonium uptake with the N-debt method (Fig. 2.8 A and B). In 2012, I saw similar trends with N-debt values suggesting N deficiency in June, July, and August, specifically at sites M5 and the sites in the transition zone (Table 2.4 and Fig. 2.8 C and D). In both years I observed little deficiency in the lacustrine section. For example, I did not detect ammonium uptake in the Qu'Appelle arm during the two years.

In 2011, PC:PN ratios were highest in June, September, and October with several measurements indicating moderate N deficiency ( $>8.3$ , 10 out of 49 times sampled). The upstream sites (M3 and M5) were moderately N deficient in June and almost all other sites were moderately N deficient in either late September or October. Similar trends were seen in 2012; upstream sites M3 and M5 were moderately N deficient in June and conversely, the three sites closest to the dams (C3-M, U3-M and M9) were moderately N deficient in late September. Overall, PC:PN ratios were higher in 2011 than 2012. In 2012, PC:PN ratios only suggested moderate N deficiency in 5 out of 48 times sampled.

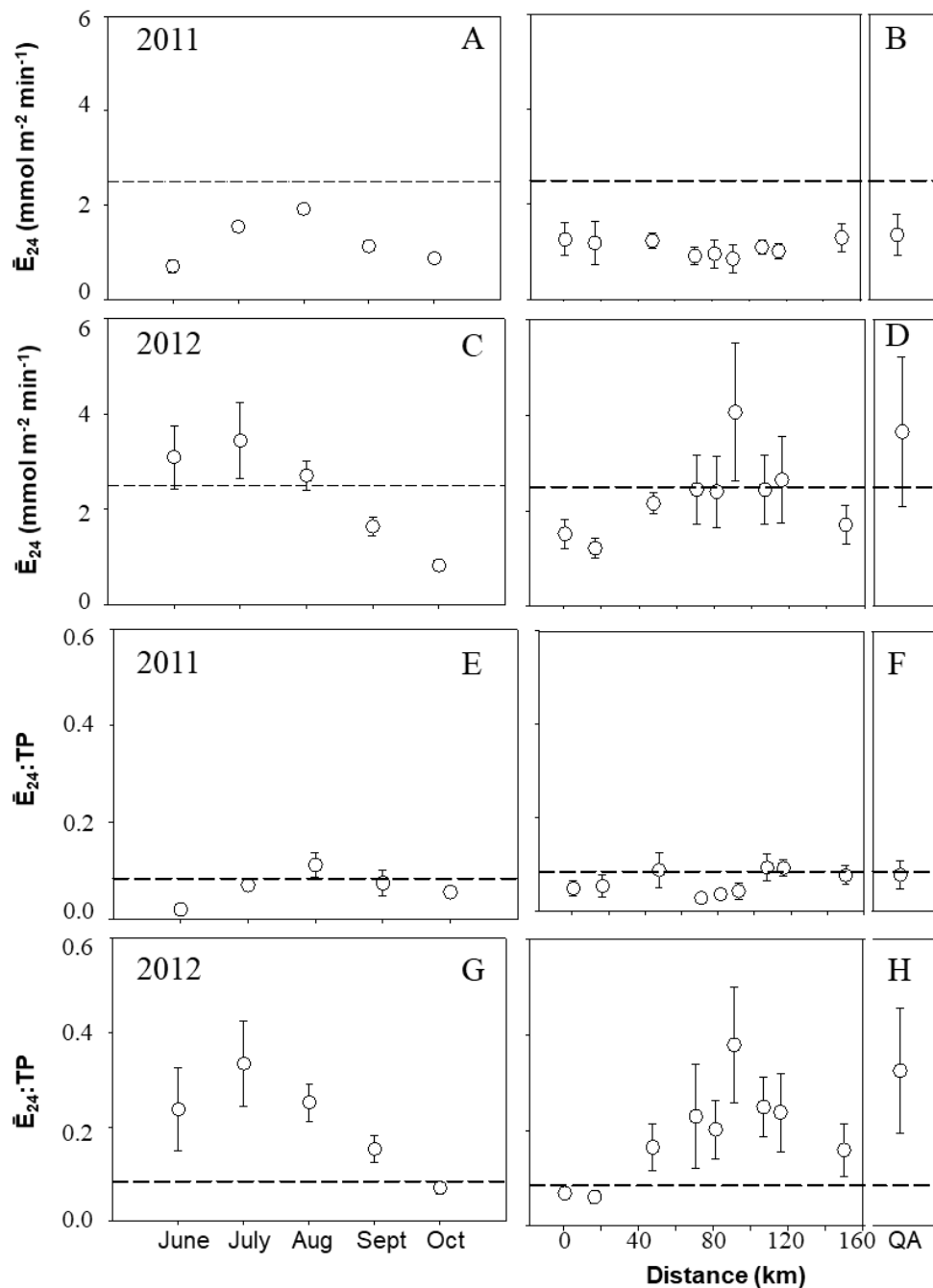




**Figure 2.8** Average N-debt and particulate PC:PN in the main channel of Lake Diefenbaker by month (A, C, E, and G; mean and SE of all main channel sites within the month) and along the length of the reservoir (B, D, F, and H; mean and SE of 5 sampling dates at each site; QA = main channel site in Qu'Appelle Arm). Values above dashed lines indicate N deficiency (Healey and Hendzel (1979)).

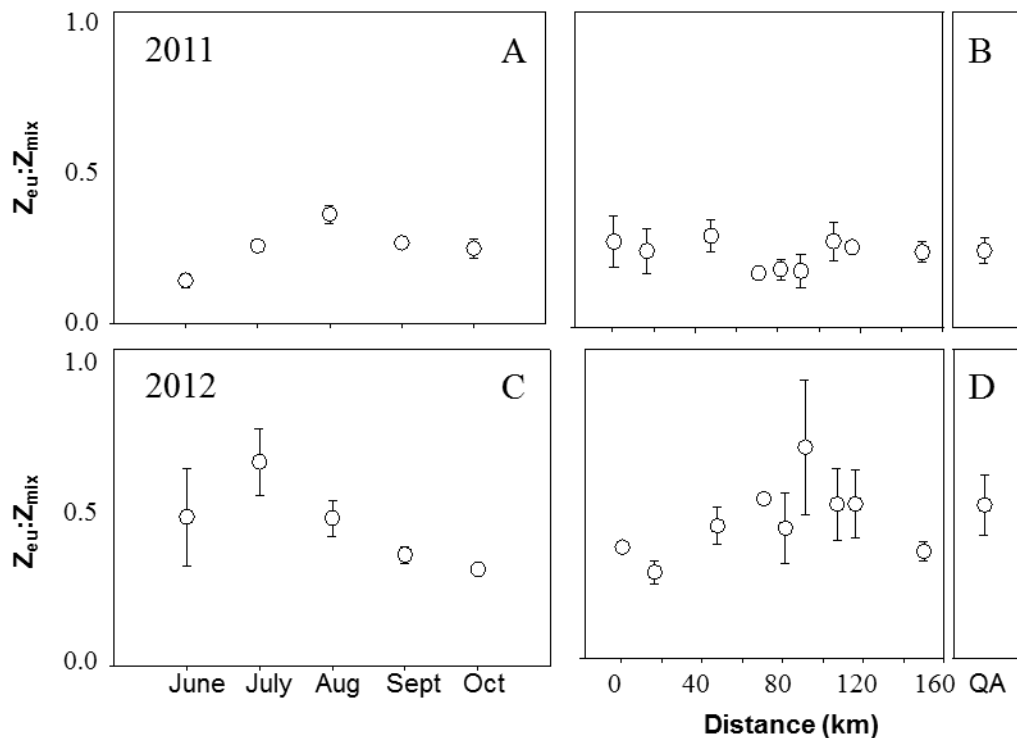
### 2.3.2.3. Light Limitation

Mean irradiance in the mixed layer ( $\bar{E}_{24}$ ) indicated light limitation ( $< 2.5 \text{ mmol m}^{-2} \text{ min}^{-1}$ ) on every sampling date in 2011 ( $n = 31$ ) and 26 out of 40 times in 2012. In 2011,  $\bar{E}_{24}$  values were low, indicating strong light limitation in June, they increased until August (still light-limited) and then decreased again in September and October (Fig. 2.9A). Spatially,  $\bar{E}_{24}$  values were low and consistent throughout the reservoir in 2011 suggesting strong light limitation throughout (Fig. 2.9B). In contrast, in 2012,  $\bar{E}_{24}$  values were relatively high with the average values above the threshold indicating light limitation in June, July, and August (Fig. 2.9C). There was considerably more variability in  $\bar{E}_{24}$  values in 2012 than in 2011 (Fig. 2.9 A-D and Table 2.3). The riverine zone had relatively low  $\bar{E}_{24}$  values in 2012, indicating stronger light limitation, which relaxed in the transition and lacustrine zones. The greatest average  $\bar{E}_{24}$  values were present at sites U2-M and M9 (see large error bars in Fig. 2.9D), due to favourable light conditions in June, July, and August of 2012. Because the  $\bar{E}_{24}$ :TP ratios are compared against median ratio from the reservoir over both years, and the ratios overall were higher in 2012, these results are not surprising. All measurements in 2011 fell below the median value and almost all measurements in 2012 fell above the median. Therefore, the water column was more limited by light in 2011 than 2012.



**Figure 2.9** Light status indicators ( $\bar{E}_{24}$ , and  $\bar{E}_{24}:TP$ ) in the main channel of Lake Diefenbaker by month (A, C, E, and G; mean and SE of all main channel sites within the month) and along the length of the reservoir (B, D, F, and H; mean and SE of 5 sampling dates at each site; QA = main channel site in Qu'Appelle Arm).  $\bar{E}_{24}$  (A-D) values below dashed line are considered light limited according to Hecky and Guildford (1984). Dashed lines in E-H represent the median (0.085 mmol m<sup>-2</sup> min<sup>-1</sup>:  $\mu\text{g L}^{-1}$  TP) from both years combined, values below the line may be light limited, values above line may be P limited, according to Chrzanowski and Grover (2001).

Almost all  $Z_{eu}:Z_{mix}$  values were below 1 indicating that the euphotic depth was shallower than the mixing depth on most sampling dates (Fig. 2.10). The one exception to this was at U2-M on July 23, 2012 where  $Z_{eu} = 9.2$  m and  $Z_{mix}$  was determined to be 6.6 m based on our definition of the thermocline as the point at which there was  $\geq 0.5^{\circ}\text{C m}^{-1}$  change in water temperatures. Here, full stratification had not yet developed; however, by the following month the euphotic depth was unchanged, but the mixing depth was  $>20$  m. Hence this situation at U2-M was short-lived. Trends in  $Z_{eu}:Z_{mix}$  followed the trends seen in  $\bar{E}_{24}$  very closely. The average  $Z_{eu}:Z_{mix}$  value for both years combined was 0.35, with the yearly averages being 0.26 and 0.45 for 2011 and 2012, respectively. This agrees with  $\bar{E}_{24}$  and  $\bar{E}_{24}:\text{TP}$  results showing that light availability increased in 2012 compared to 2011.



**Figure 2.10** Light status indicator ( $Z_{eu}:Z_{mix}$ ) in the main channel of Lake Diefenbaker by month (A and C; mean and SE of all main channel sites within the month) and along the length of the reservoir (B and D; mean and SE of 5 sampling dates at each site, QA = main channel site in Qu'Appelle Arm). All values are below 1 suggesting that freely floating algal cells are spending a portion of time without adequate light for photosynthesis.

### 2.3.3. Comparisons Between Years

A greater volume of water entered LD in 2011 than 2012 (11.5 and 8.0 km<sup>3</sup> respectively; Hudson and Vandergucht, 2015). This resulted in greater loads and concentrations of nutrients in LD in 2011 from the SSR (Figs. 2.2, 2.3 and Table 2.2). Nutrient limitation indicators also differed between the two sampling seasons with N deficiency being more prevalent in 2011, and P limitation being more prevalent in 2012 (Tables 2.3 and 2.4). Light limitation was ubiquitous in 2011 but less frequent in 2012.

## 2.4. Discussion

### 2.4.1. General Limnological Characteristics

Although a previous study had described LD as polymictic (Hall et al., 1999), I found that the reservoir was dimictic. Stratification began in June and July and persisted in the deeper sites along the main channel (U1-M to M-8) until fall overturn in October. The shallow, upstream sites remained fully mixed with the exception of M5 in July of 2012 when weak stratification was present (Hudson and Vandergucht, 2015). The relatively shallow site in the Qu'Appelle arm (M-9) remained fully mixed except in July of 2011 and July and August of 2012, after which the epilimnion extended to the bottom and was therefore fully mixed again (Hudson and Vandergucht, 2015).

The average TP (24.5 µg L<sup>-1</sup>) and chlorophyll *a* (4.59 µg L<sup>-1</sup>) concentrations characterize LD as a mesotrophic system based on Carlson and Simpson's 1996 classification. However, due to the heterogeneous nature of the system the higher TP (maximum = 104 µg P L<sup>-1</sup>) concentrations would fall into the eutrophic or even hypereutrophic category and the lower concentrations would be considered almost oligotrophic (minimum = 10.4 µg P L<sup>-1</sup>). The lowest chl *a* concentrations (minimum = 0.50 µg L<sup>-1</sup>) would also be considered oligotrophic. The

highest concentrations of TP and chl *a* were present in the riverine zone and the lowest concentrations were in the lacustrine zone. These patterns in TP and chl *a* follow the expectations of the LZC (Kimmel and Groeger, 1984).

Lake Diefenbaker received above normal peak flows from the SSR in both years (Fig. 1.2). Nutrient (P and N) concentrations were greatest during high flow events (Fig. 2.2 and 2.3). However, they differed in their relative composition and behaviour within the reservoir. A greater proportion of the P entering the system was in particulate form relative to N (see Figs. 2.2 and 2.3, particulate portion is the difference between totals and total dissolved fractions). Regardless of flow, N was mostly in dissolved forms. Once in the reservoir the particulate P settled out of the water column quickly as the reservoir widened and the water slowed in the transition zone (Dubourg et al., 2015). Beyond this point I saw a further decline in TP in the reservoir mostly due to a decline in PP. In contrast, N concentrations increased throughout the reservoir in 2011 and remained relatively constant in 2012. This resulted in a rapid change in the TN:TP molar ratios from the riverine to the lacustrine sections (Fig. 2.4). At the most upstream sites, I observed relatively low TN:TP ratios. Ratios that suggested N limitation (TN:TP < 20, Guildford et al., 2000) were observed in both years in the riverine section (M3 and M5) early in the season. However, if a portion of P was sediment-bound or apatite then this ratio may not accurately reflect available P. In June of 2011, the average TN:TP ratio was lower throughout the reservoir than in June of 2012 (39.3 and 71.5 respectively,  $P < 0.01$ ). For example, P limitation was only indicated at one main channel location (C2-M) in 2011 but P limitation was present at all but 3 main channel sites in 2012 (M3, M5, and C1-M). In both years the TN:TP ratios increased from upstream to downstream locations and over the sampling season (June – October), these changes are mostly due to the decrease of PP along the length of the reservoir

and throughout the season. The trends in TN:TP were similar between the years (Fig. 2.4) as were the overall averages and ranges (Table 2.3). Average yearly TN:TP ratios (70.6 and 73.7 in 2011 and 2012, respectively) suggest LD is P limited, however there is considerable variability, such that we see the potential for both N and P deficiency within the reservoir (Table 2.4 and Fig. 2.4). Dissolved ratios (TDN:TDP) followed similar trends as TN:TP, with lower ratios present in the upstream region early in the season and increasing along the length of the reservoir, this is primarily due to the increase in N throughout the reservoir (Fig. 2.4 C and D). Overall, the spatial and temporal trends seen in the total and dissolved ratios are consistent with the results of the N-debt and  $TT_{PO_4}$  assays (Table 2.4), which lends confidence to my results.

#### *2.4.2. Limiting Factors in Lake Diefenbaker*

##### *2.4.2.1. Phosphorus*

Overall, the limitation indices for P were consistent with each other. The second sampling season saw higher APA rates, lower  $TT_{PO_4}$ , lower  $ssPO_4^{3-}$  concentrations and higher PC:PP, PN:PP and  $\bar{E}_{24}$ :TP ratios than 2011, all suggesting relatively more P limitation in 2012 than in 2011.

Spatial and temporal (within a season) trends in APA rates and  $TT_{PO_4}$  were also consistent, showing strong P deficiency in August of 2012. Increases in APA, and therefore P limitation, from the riverine section to the lacustrine portion has been seen in other systems (Elser and Kimmel, 1985; Healey and Hendzel, 1980). In LD, APA rates and  $TT_{PO_4}$  suggested increasing P deficiency from the transition region to the lacustrine region (Figs. 2.5 and 2.6). However, the riverine region showed relatively greater P deficiency than the transition region. P limitation increased in the riverine section throughout the season and persisted into the fall. In contrast, all other sites saw a decrease in P limitation by October. It should be noted that the

other sites had experienced overturn and became isothermal by October (Hudson and Vandergucht, 2015). The drop in temperature and increase in dissolved P after turnover resulted in very long  $TT_{PO_4}$  that introduced considerable variation about the seasonal mean as seen in Figure 2.6 B and D. In 2012, P limitation was prevalent (as determined by  $TT_{PO_4}$ ), with the exception of the most upstream sites in June. P limitation relaxed by October at most sites when the water column had become isothermal and well mixed (Table 2.4). Although not shown graphically,  $ssPO_4^{3-}$  concentrations followed the same pattern seen in  $TT_{PO_4}$  and APA rates. Average yearly  $ssPO_4^{3-}$  concentrations (1200 and 280  $ng\ L^{-1}$  in 2011 and 2012 respectively) overlapped with the large set of lakes in Hudson et al. 2000 and Vandergucht et al. 2013 (0.36 – 2004  $ng\ L^{-1}$ ).

Increased flows typically bring higher suspended sediment loads and accompanying nutrients into waterbodies (Graf, 1984; McCarney-Castle et al., 2010), this was the case in LD during the peak inflows of 2011 and 2012. The stoichiometry of the incoming particulate matter dictated the molar nutrient ratios observed in the reservoir, especially in the upstream regions. The low PC:PP and PN:PP ratios observed early in the season in both years was due to the relatively large influx of particulate P. However, a significant fraction of P entering the system during high flows may either be biologically unavailable (Ekholm, 1994; Sonzogni et al., 1982) or rapidly lost to sedimentation (Gloss et al., 1981; Kelly, 2001). Following the abatement of the peak flows, PC:PP and PN:PP ratios increased throughout both seasons to levels suggesting P limitation. The increase observed in both particulate nutrient ratios and total PN:PP ratios along the length of the reservoir suggested decreasing P availability from up to downstream regions, this agrees with the expectations of the LZC.



I employed a large number of P limitation indicators to assess P limitation on different timescales. Proximate (Davies et al., 2004) measures of P limitation (APA and  $TT_{PO_4}$ ) agreed very well with each other, but also agreed with longer term assessments of P limitation (i.e., as indicated by nutrient stoichiometry). Hence, P limitation was confirmed as a common condition in the reservoir.

#### 2.4.2.2. Nitrogen

N-debt values often exceeded the threshold for deficiency in 2011, specifically in the riverine and transition regions in the first half of the season. Some N deficiency was present in 2012 and tended to occur at similar locations and times as was observed in 2011 but was not as widespread or as persistent (Fig. 2.8 and Table 2.4). Nitrogen deficiency was most frequently observed (with the N-debt technique) during high flow events, which carried a relatively larger portion of P than N, but N-debt was not significantly correlated with inflow (Spearman's rho,  $P = 0.184$ ). N-debt values were negatively related to total, dissolved, and particulate PN:PP ratios as well as chl *a* concentrations ( $P = 0.0047$ ,  $P = 0.0003$ ,  $P = 0.0011$ , and  $P = 0.0334$ , respectively). When PN:PP ratios were low, N-debt rates were higher, i.e., N deficiency was present when PN:PP ratios were low. However, chl *a* concentrations, which can be used as a surrogate for algal biomass, were low when N-debt values indicated deficiency. This may indicate that algae were not responsible for the ammonium uptake and instead bacteria may have been dominating uptake.

Bacterioplankton production and biomass has been shown to increase with turbidity or when high concentrations of suspended clays are present (Goosen et al., 1999; Lind and Dávalos-Lind, 1991; Lind et al., 1997). Additionally, it has been shown that under low light conditions, increases in N requirements are relatively greater than those for P (Healey, 1985).

### 2.4.2.3. Light

Overall, the main channel sites in Lake Diefenbaker were found to be limited by light 80% of the time (n=71) based on  $\bar{E}_{24}$  values. However, there was a difference between years. In 2011, the main channel sites were deemed light limited 100% of the time, whereas in 2012 they were found to be limited by light only 65% of the time. Despite fewer measurements of the light environment in 2011, there was still sufficient data to demonstrate that light limitation was more prevalent in 2011 than in 2012. For example, light sufficiency was evident in 2012 in much of June, July, and early August. Spatially, the light limitation indicators were consistent throughout the reservoir in 2011 and showed an increase in light availability along the length of the reservoir in 2012, especially in the transition region. Low light availability is well documented in turbid reservoirs (Hart, 1988; Sobolev et al., 2009; Vanni et al., 2006). During times of peak flows, turbidity rapidly increases in LD (<10 NTU to >200 NTU; Hudson and Vandergucht, 2015), this can explain the poor light environment during and immediately following the peak flows. Subsequent decreases in flow, along with the widening of the reservoir allowed the sediment load to settle and light penetration increased as observed in the transition region in 2012. Interestingly, in 2012, in the lacustrine region, the light limitation indicators decreased slightly. However, instead of being due to lower light penetration (as is the case upstream) this is due to the deeper mixing depth. Trends in all of the light limitation indicators are similar. Most  $\bar{E}_{24}:TP$  values in 2011 fell below the median with values from 2012 largely falling above the median value (Fig. 2.9 E-H). Furthermore, the euphotic depth was almost always shallower than the mixing depth, indicating that a free-floating algal cell would experience periods of insufficient light for photosynthesis. It should, however, be noted that these indicators all contain similar variables. For example, both  $\bar{E}_{24}$  and  $Z_{eu}:Z_{mix}$  calculations include the mixing depth and a

measurement of light penetration. Therefore, some agreement between them may be expected. Nonetheless, good agreement between these different indicators adds confidence that light limitation was common in LD and more prevalent in 2011 than in 2012.

#### *2.4.3. Differences in the Nutrient and Light Environments between 2011 and 2012*

The differences in the light environment and nutrient concentrations between my sampling years are likely associated with differences in the volume of flows from the SSR and the associated non-algal turbidity. The peak flow in 2011 was greater and of longer duration than that in 2012 (Fig. 1.2). Flood peaks are associated with high erosion rates that can deliver suspended sediments and increased turbidity downstream (Grove et al., 2013). Increased suspended particulate matter will, in turn, affect light penetration in the water column (Ji, 2017). The 2011 peak flow was of a longer duration and carried higher concentrations of particulate matter to the reservoir than in 2012 (average PP at M3 in 2011 and 2012 was 27.5 and 21.9  $\mu\text{g L}^{-1}$ , respectively), thus resulting in a larger particulate load entering the reservoir in 2011. Finally, the greater particulate load affects light penetration (average  $k_d$  in the main channel was 1.20 and 0.60  $\text{m}^{-1}$  in 2011 and 2012, respectively).

#### *2.4.4. Support for the Longitudinal Zonation Concept*

Patterns in light and nutrients were consistent with the expectations of the LZC in most instances (Kimmel and Groeger, 1984). The riverine zone was characterized by higher nutrient concentrations and low light availability. As the reservoir widened and flow slowed in the transition zone, P concentrations declined, and light conditions improved with the settling of particulate matter from the water column. The lacustrine zone was characterized by even lower P concentrations and deeper light penetration, which also agrees with the LZC. However, due to the deeper mixing depths, light was more limiting in the lacustrine zone than the transition zone,

an outcome not expected under the LZC. The LZC predicts relatively low nutrients in the lacustrine zone and that nutrient supply is primarily by internal recycling (regeneration). Planktonic P regeneration rates did not increase along the length of the reservoir and instead slightly declined from up- to down-stream sections (unpublished data). Although we did see a decline in P concentrations in the lacustrine zone, the opposite was true for N that either increased (in 2011) or was constant (in 2012) along the length of the reservoir which is not predicted by the LZC.

The relative amounts of N and P that entered the reservoir with the flows, as shown in both the total and dissolved PN:PP ratios (Fig. 2.4), allowed the system to briefly experience N deficiency during the highest flows (Table 2.4). However, the rapid sedimentation of P and the increase of N along the length of the reservoir resulted in LD being primarily limited by P. Overall, light may be the primary limiting factor during these two high flow years and their accompanying turbidity.

## **2.5. Conclusions**

Initial N-debt measurements in 2011 seemed to suggest N deficiency. However, an examination of both years of data and data from more recent years (Dubourg et al., 2015) it is evident that P is likely the primary limiting nutrient in LD. Nitrogen appears to be limiting at times, but this was associated with other factors, i.e., high flow, turbidity and low light. I also saw increases in dissolved N throughout the length of the reservoir, but a decline in available P (TDP, SRP, and  $ssPO_4^{3-}$ ). Reservoir transition zones have been found to be N fixation hotspots (Scott et al., 2009), which may help to explain the increases in  $NO_3$  along the length of the reservoir. However, Donald et al. (2015) found that LD is retaining N (TN and Dissolved Inorganic N (DIN)) so the increases observed here may be due to time between sampling in our

study, i.e., if a pulse of N entered the system we may have missed it in the riverine region but captured it in the transition and lacustrine regions, giving the appearance that N concentrations were increasing along the length of the reservoir. Heterocyst biovolume was found to be higher in 2011 than in 2012 ( $1.85 \text{ mm}^3 \text{ m}^{-3}$  and  $0.93 \text{ mm}^3 \text{ m}^{-3}$ , respectively) that agrees with the results of the N-debt assay (Table 2.4 and Figure 2.8). However, heterocyst biovolumes overall were low and likely played a minor role in N fixation in LD (Personal communication, Y. Ponomarenko, University of Saskatchewan).

The pervasive presence of light limitation could suggest that PAR is the main agent affecting primary productivity in LD. However, long term constraints on algal biomass will still be dictated by P levels. Light deficiency may act as a buffer to limit primary productivity on short timescales, potentially reducing the frequency of bloom activity. However, flows in the SSR are predicted to decline with climate change (Tanzeeba and Gan, 2012; WWF, 2009). This, in turn, may cause a reduction in suspended loads and inorganic turbidity to the reservoir (Vogt et al., 2015). As a result, light may become more available in the riverine and transition zones, thus removing or reducing the buffer against increases in primary productivity. Light will still have the potential to become limiting in the lacustrine region, especially if the mixing depth deepens, such that algal cells spend more time below the photic zone. However, light availability will likely increase as non-algal turbidity declines and nutrient limitation, particularly of P, has the potential to become the primary limiting factor on short and long timescales.

Nutrient and light availability were found to be sufficiently limiting spatially and temporally to prevent significant algal blooms in LD in 2011 and 2012. It is however still important to take into account the degree of limitation and the nature of the limiting factor when considering the reservoir from a management perspective. Nitrogen deficiency was present at

times in the reservoir but was transient and was not significant when assessing longer-term measurements of nutrient limitation (particulate ratios). In contrast, P limitation was widespread in time and space and was seen in both short and long-term measurements of limitation. Light limitation although widespread and persistent, is still somewhat transient in nature, in that it can change based on cloud cover, turbidity, or wind. Light availability is less amenable to human regulation; however, P loading has been reduced sufficiently in many regions with accompanying improvements in water quality (NRC, 1992; Schindler et al., 2016). Hence, a focus on P reduction should be an ongoing watershed management approach in the SSR basin.

Although the reservoir receives large P loads, these loads consist largely of particulate P and are not readily available for uptake. This particulate P also rapidly settles out of the water column. Like many reservoirs, LD acts as a sink for P (Donald et al., 2015; North et al., 2015b), with much of the P load settling to the bottom sediments. A partially anoxic hypolimnion has been observed in LD during summer stratification in 1984 (WQB, 1988). Increasing global temperatures will lead to warmer surface waters, stronger vertical stratification, and lengthening of seasonal stratification (Paerl et al., 2011b), this may promote greater anoxia and internal nutrient loading in reservoirs. Additionally, increasing global temperatures have the potential to increase growth rates, dominance, persistence, and activity of various species of harmful cyanobacteria (Paerl and Huisman, 2009). I did not see significant algal blooms during my study and an assessment of long term chl *a* concentrations showed that algal blooms have not been increasing in frequency over the last 29 years (Yip et al., 2015). Nonetheless, managing P inputs into LD is still a prudent strategy, because if prairie warming results in increased anoxia, then internal P loading may become a significant issue. Given the potential for legacy P loading in LD, in addition to the anticipated changes in light availability, stakeholders and policy makers

should be committing to lower P loadings into the system to protect the future health of this important resource to the province of Saskatchewan.

## **CHAPTER 3 – THE EFFECT OF CATTLE AND MARINAS ON NUTRIENT AND LIGHT LIMITATION IN EMBAYMENTS**

### **3.1. Introduction**

#### *3.1.1. Potential Effects of Cattle Operations*

Watersheds that are dominated by agricultural land use experience an increase in N and P loadings due to fertilizer and animal waste runoff, soil erosion, and a loss of buffering in riparian zones (Hall et al., 1999). Escalation of food production and meat consumption worldwide has increased the amount of land used for agriculture (Hooda et al., 2000; Tilman et al., 2002). The intensification of livestock practices over the last century has increased the amount of nutrients available for transport over land to waterbodies (Milne, 2005). The majority of LD's 760 km shoreline is agricultural land; housing both crops and cattle. Over 55% of the reservoir's catchment area is made up of cropland with an additional 4% of pastureland (International Lake Environment Committee Foundation, 1993). On average, runoff accounts for ~2% of the natural flow into LD's watershed (SWSA, 2012b). Access to water is essential to livestock management and allowing direct access to a water body is an easy and inexpensive way to water cattle. This type of watering practice can impact water quality by introducing direct deposition of animal waste and increased erosion and run-off due to destruction of riparian zones (Government of Alberta, 2002). Multiple studies on the effects of livestock production on surrounding water quality have been conducted (Anzai et al., 2016; Capece et al., 2007; Gu et al., 2008; Sun and Wu, 2012). These studies found that cattle operations resulted in significant amounts of N and P entering nearby water bodies. Although literature on the effects of direct defecation into water bodies is lacking, there is the potential to see an effect in areas exposed to this type of activity in LD. This may present as an increase in total nutrient concentrations or a shift in nutrient limitation (i.e., based on the nutrient composition of manure). Webb and Archer (1994) indicate

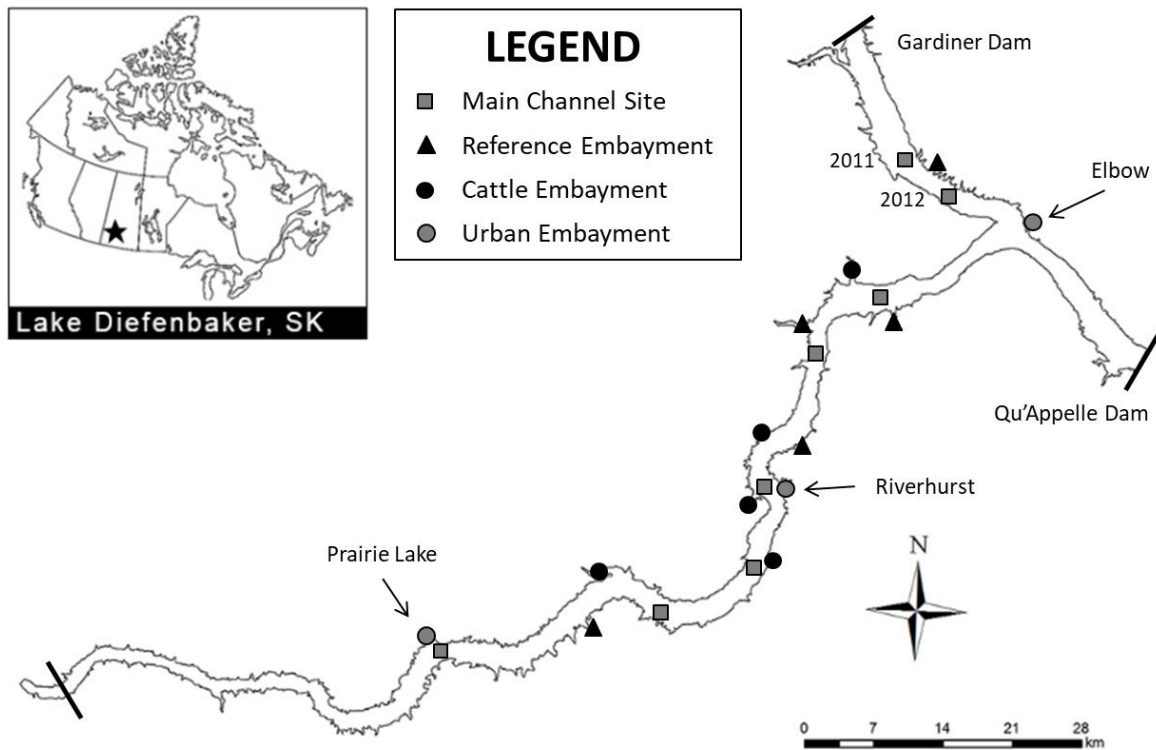


that 6 kg TN and 3.1 kg TP are present in one ton of cattle waste. This represents a 4.3:1 (molar) PN:PP ratio, suggesting that in cattle affected areas N limitation may occur if sufficient quantities enter the water column. Alternatively, if increased soil erosion due to cattle activity at the water's edge were to pose more of a risk, then I may find P limitation. Hewlett et al. (2015) found that the relative contribution of PN:PP would strongly favour P limitation (TN:biologically available P = 84:1 molar ratio). Lake Diefenbaker has many cattle farms that allow herds direct access to the reservoir (personal observation). Such practices can result in loss of water quality from increased inputs of nutrients (e.g., defecation and soil erosion). Prairie lakes are significantly impacted by such land use practices and may result in localized increases in algal biomass (Hall et al., 1999).

### *3.1.2. Potential Effects of Marinas and Recreational Activity*

Urbanization leads to an increase in impermeable land cover (e.g., sidewalks, parking lots, roofs, and roads) and this leads to an increase in surface runoff into waterways. Nonpoint sources include runoff or infiltration of water from roads, industrial areas, and golf courses. This may include contaminants such as metals, pesticides, herbicides, and nutrients. Both Riverhurst and Elbow have golf courses and marinas located alongside Lake Diefenbaker and Prairie Lake Regional Park has cabins, a campground, and a boat launch in its embayment (Fig. 3.1). Nutrient loading from golf courses has been well studied at both the field scale and watershed scale (Easton and Petrovic, 2005; Gaudreau et al., 2002; King et al., 2001; Kunimatsu et al., 1999; Winter and Dillon, 2005). These studies generally conclude that if the turf is well maintained the concentrations of nutrients in runoff are well below cause for concern (King et al., 2007). However, during storm events, the concentrations of phosphates in runoff from a golf course may exceed acceptable levels. King et al. (2007) investigated storm run-off samples from an

Austin TX golf course and found that  $0.51 \text{ kg PO}_4\text{-P ha}^{-1}\text{yr}^{-1}$  was transported to surface waters that did exceed the US EPA recommendations at the time. This was found to be comparable to rates of soluble P run-off from agricultural lands. Concurrent nitrate transport ( $1.2 \text{ kg NO}_3\text{-N ha}^{-1}\text{yr}^{-1}$ ) did not exceed recommendations and therefore was not found to be a substantial environmental risk (King et al., 2007).



**Figure 3.1.** Map of embayment and main channel sampling locations in 2011 and 2012. Note that the main channel site in the Gardiner arm changed locations from 2011 to 2012.

A possible point source of nutrients from marinas may come from fuel for modern combustion engines. It contains both nitrogen and phosphorus compounds as additives. Hallock and Falter (1987) estimated that 300 mg TN and 1.0 mg TP [664:1 (molar)] were added to surrounding water per litre of fuel consumed; these levels were deemed insignificant when

compared to other sources of nutrient loading. If fuel consumption were affecting nutrient limitation I may expect to see P limitation within potentially impacted embayments based on the ratio of PN:PP input from fuel combustion. Boat traffic can also impact water clarity, disturb aquatic plants, and increase shoreline erosion (Asplund, 1996; Asplund and Cook, 1997; Nanson et al., 1994). However, inputs from golf courses, fuel, shoreline erosion and turbulence caused by wakes may be added in proportions that do not favour N or P limitation. Therefore, I may not see differences in nutrient limitation, but instead, see increased nutrient concentrations in the embayments housing marinas or towns. In addition to the potential changes in nutrient concentrations, increased run-off and boating activities may increase turbidity that will affect the light environment in the embayments and therefore light also warrants examination as another limiting factor.

Given the importance of Lake Diefenbaker to the province of Saskatchewan and the lack of research on anthropogenic nutrient inputs to the reservoir I decided to assess whether these activities were affecting localized nutrient and light status within embayments housing them. I hypothesized that I would see increased nutrients within the embayments housing cattle operations and marinas. I expected that I would be able to detect differences in nutrient limitation or concentrations, or the light environment in these embayments when compared to embayments without these activities.

### *3.1.3. Experimental Design*

To investigate the potential effects of cattle and urban activities in LD, I measured nutrient concentrations and assessed nutrient and light limitation in embayments exposed to cattle operations and marinas and compared these against embayments that were not exposed to either cattle or marinas (reference embayments).

Study embayments (exposed and reference) were selected after a survey of the reservoir in June of 2011. Embayments that contained evidence of cattle at the water's edge (manure, cattle footprints, or actual cattle) were classified as cattle embayments. Urban exposed embayments were set in the embayments housing the marinas at Prairie Lake Regional Park and the towns of Riverhurst and Elbow. These embayments are popular for boating and recreational activities. Reference embayments were chosen based on proximity and similarity in morphometry to the exposed embayments but lacked any evidence of cattle or urban exposure. Because the reference embayments had neither cattle nor urban activity present, they served as a control for both treatments (cattle and urban). Main channel sites were placed strategically throughout the length of the reservoir to capture the spatial variability within the reservoir and to act as a longitudinal reference for the exposed and reference embayments because the reservoir exhibits a strong upstream to downstream environmental gradient (See Abirhire et al., 2015; Dubourg et al., 2015; Hudson and Vandergucht, 2015, and chapter 2 of this thesis). For the purposes of this portion of the study, the main channel sites in the riverine zone (M3 and M5) and the site in the Qu'Appelle arm (M9) have been excluded. The most upstream sites were excluded because they are shallow, nutrient rich locations when compared to the remainder of the main channel sites. In addition, the embayments are far removed from the upstream location (> 30 km). Site M9 was excluded because more than 98% of the water flows out through the Gardiner Dam (SWSA, 2012a), and as such, the Qu'Appelle arm of the reservoir acts more like a large embayment than a continuation of the main channel (Hudson and Vandergucht, 2015). With this statistical design, I had five cattle exposed embayments, 3 urban exposed embayments, five reference embayments, and seven main channel reference sites (Fig. 3.1).

To assess the effects of cattle and marinas on the planktonic community I applied five indicators of P status ( $TT_{PO_4}$ ,  $ssPO_4^{3-}$ , APA, PC:PP, PN:PP), two indicators of N status (N-debt, PC:PN), and three indicators of light status ( $\bar{E}_{24}$ ,  $\bar{E}_{24}:TP$ ,  $Z_{eu}:Z_{mix}$ ) with  $\bar{E}_{24}:TP$  also serving as an additional indicator of P status. I also measured nutrient concentrations (TP, TDP, SRP, TN, TDN,  $NO_3$ , and  $NH_3$ ) and looked for differences between embayment types. Limitation thresholds used to determine nutrient and light limitation are listed in Table 2.1. I will assess whether the results of these indicators differ based on the presence or absence of cattle or marinas and recreational activities.

## **3.2. Methods**

### *3.2.1. Field Sampling*

Field sampling procedures are described in detail in section 2.2.1. Monthly samples were collected at each embayment site and the main channel sites situated between Prairie Lake and Gardiner Dam from June to October of 2011 and 2012 (Fig. 3.1). I used the shortest linear distance down the length of the main channel from the Highway 4 Bridge to each main channel site to account for the upstream to downstream gradient present in the reservoir (Fig. 3.1). The distance of each embayment downstream of the Highway 4 bridge was also determined.

### *3.2.2. Biological and Chemical Parameters*

Analyses of all N and P fractions were performed as described in section 2.2.2.

### *3.2.3. Nutrient Bioassays*

Analyses for APA,  $TT_{PO_4}$ ,  $ssPO_4^{3-}$ , and N-debt were performed as described in section 2.2.3.

### *3.2.4. Light Measurements*

Mean water column irradiance ( $\bar{E}_{24}$ ,  $\text{mmol m}^{-2} \text{min}^{-1}$ ) and  $Z_{\text{eu}}$  were determined as described in section 2.2.4.

### 3.2.5. Statistical Analyses

Prior to analysis, Shapiro-Wilk tests ( $p > 0.05$ ) and Q-Q plots were used to evaluate normality of the data and homogeneity of variance. Box-Cox transformations were performed on variables that failed to meet the assumptions of parametric statistics (Box and Cox, 1964). I assessed changes in nutrient limitation indicators and in nutrient concentrations (TP, TDP, SRP, TN, TDN,  $\text{NO}_3$ , and  $\text{NH}_3$ ) in relation to exposure to cattle and marinas within LD using a linear mixed effect model (*lme*). The use of a mixed effect model accounts for the presence of repeated measures in time (monthly sampling at the same sites) in the experimental design (Pinheiro and Bates, 2000). The two years of sampling were treated separately to remove any bias resulting from sampling only 5 out of 12 months of each year. I used the following model structure to assess whether my variables were affected by cattle or urban activities.

$$Y_i = \beta_0 + \beta_1 \text{Treatment} + \text{Distance} + \varepsilon_i$$

Where  $Y_i$  is the transformed parameter at site  $i$ , Treatment is the fixed effect (variable of interest) representing Cattle, Urban, and Reference embayments and Main Channel sites. Distance downstream (measured from Hwy 4) is set as the random term to remove effects of the environmental gradient present in the reservoir. Random factors that we cannot control experimentally, or the stochastic part of the model, are represented by  $\varepsilon_i$ . If a significant difference was found with the linear mixed effects model, then a *post-hoc* Tukey test was run to confirm significance. All statistics were performed in R version 3.3.1 (R Development Core, Team, 2016).

## 3.3. Results

### 3.3.1. General Limnological Parameters

The average pH in LD was 8.4; and was similar across all embayment types as well as the main channel. The average temperature at 2 m below the surface was also consistent between sites, with 2011 being slightly warmer than 2012. July and August were the warmest months in both years. Sampling locations exhibited a wide range in nutrient concentrations; overall these were significantly greater in 2011 than in 2012 ( $P < 0.001$ , except  $\text{NH}_4^+$ ). Average concentrations were similar between all embayment types and the main channel sites ( $P > 0.05$ , Table 3.1).

### 3.3.2. Nutrient and Light Status in Embayments and the Main Channel

I found no significant differences ( $P > 0.05$ ) in nutrient and light limitation indicators or nutrient concentrations between any of the embayments (cattle, urban, and reference), with the following exceptions. Phosphate turnover times ( $\text{TT}_{\text{PO}_4}$ ) and  $\text{ssPO}_4^{3-}$  concentrations appeared to be significantly greater ( $P < 0.05$ ) in the Cattle (C) exposed sites than the reference (R) and urban (U) sites in 2011 (Figs 3.2 and 3.3). When checked with a *post-hoc* Tukey test the differences in TT were not significant ( $P_{\text{C-R}} = 0.130$  and  $P_{\text{C-U}} = 0.106$ ). However,  $\text{ssPO}_4^{3-}$  concentrations were found to be near significant ( $P_{\text{C-R}} = 0.0831$  and  $P_{\text{C-U}} = 0.0582$ ). Other P deficiency indicators (PC:PP, PN:PP, and APA) and P concentrations (TP, TDP, and SRP) were not significantly different in the cattle embayments in 2011. In 2012 there were no differences between the types of embayments for any of the nutrient or light limitation indicators or nutrient concentrations (Figs 3.2 – 3.5).

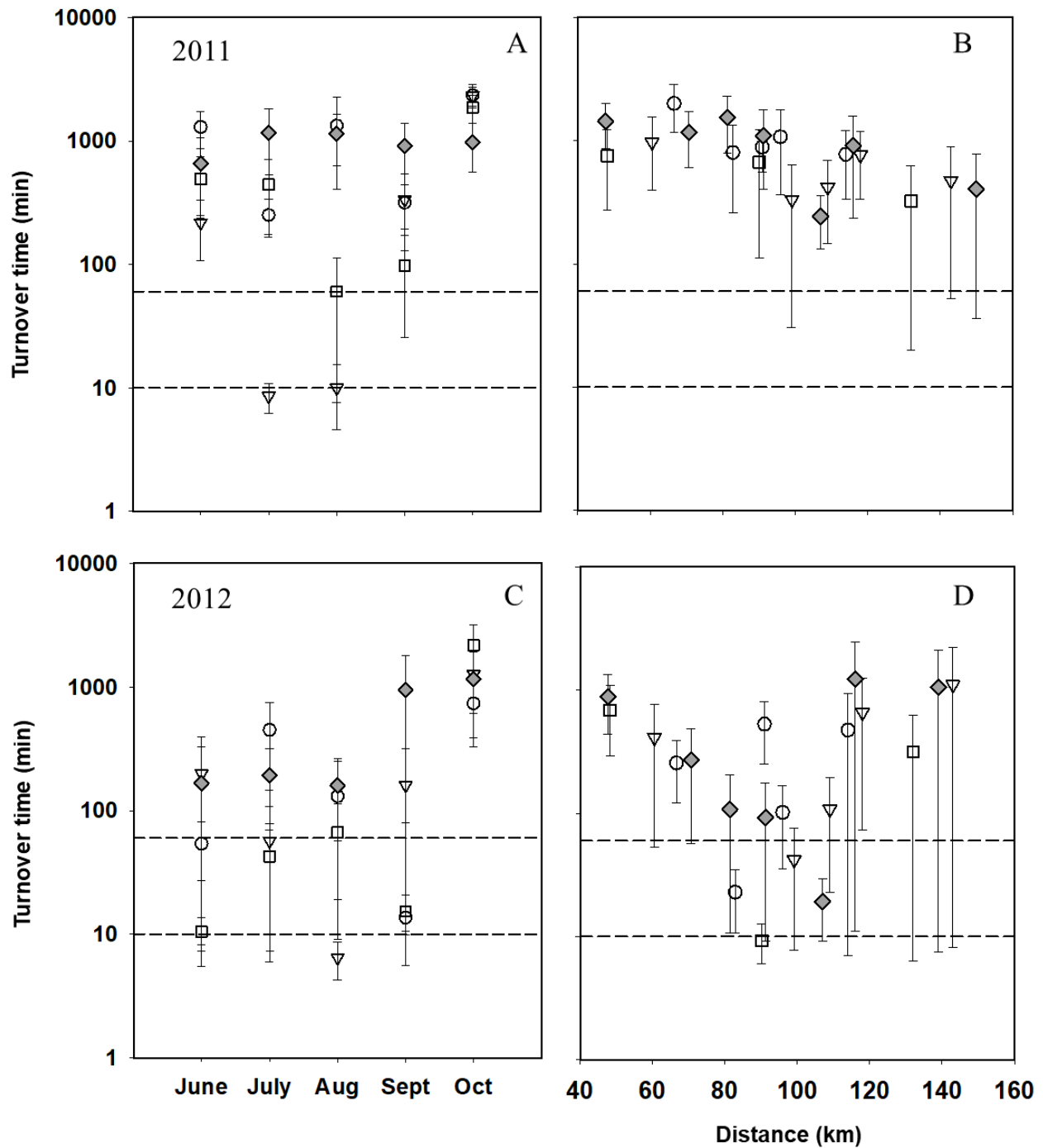
**Table 3.1.** Nutrient concentrations ( $\mu\text{g L}^{-1}$ , average  $\pm$  standard error) in cattle, urban, and reference embayments and the main channel of LD in 2011 and 2012.

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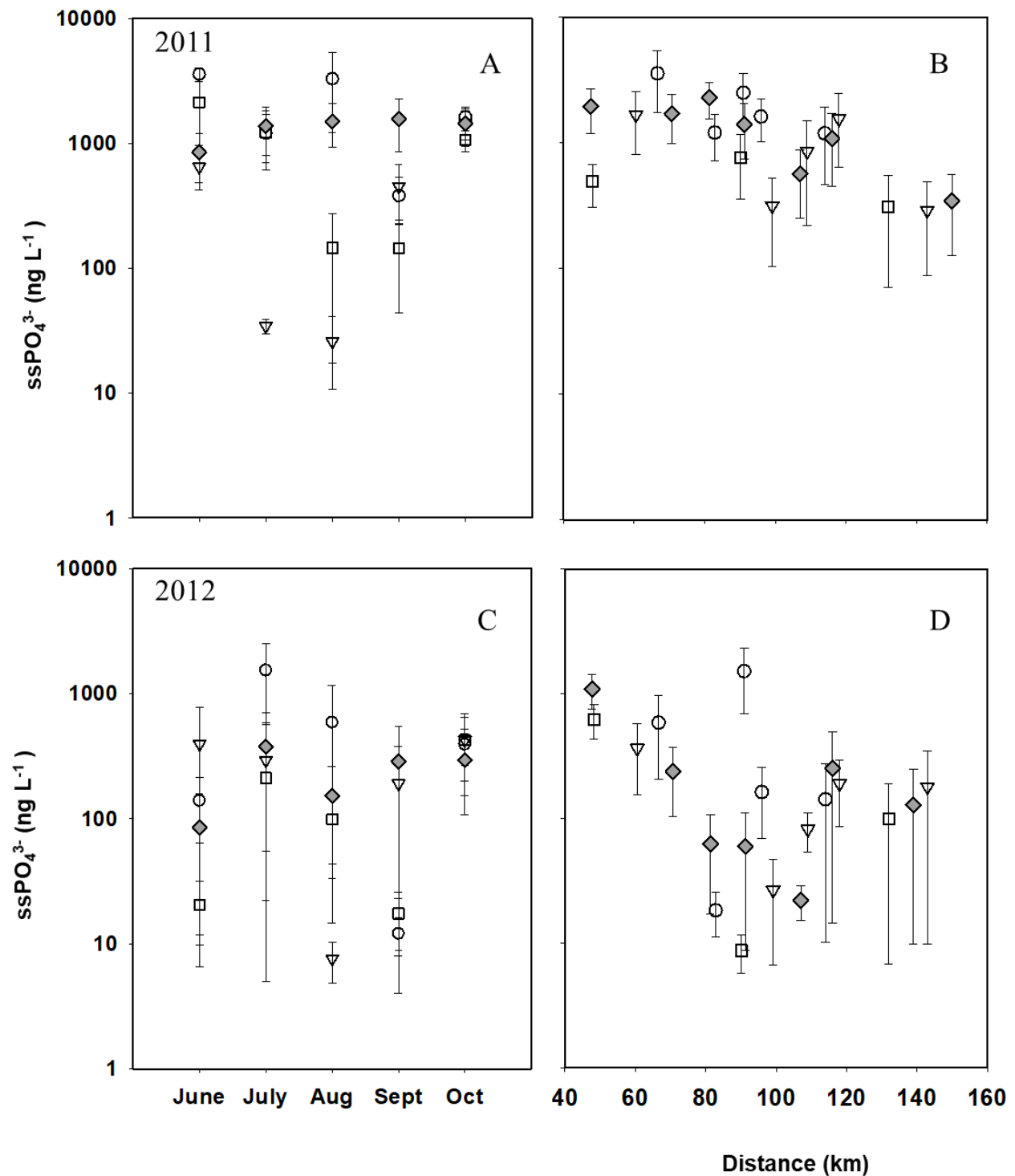
<b><u>Variable</u></b>	<b><u>Year</u></b>	<b><u>Cattle</u></b>	<b><u>Urban</u></b>	<b><u>Reference</u></b>	<b><u>Main</u></b>
<b>TN</b>	2011	681 ± 29	656 ± 48	685 ± 34	659 ± 25
<b>TDN</b>	2011	618 ± 27	588 ± 43	609 ± 27	602 ± 23
<b>NO<sub>3</sub></b>	2011	404 ± 23	378 ± 38	395 ± 23	397 ± 22
<b>NH<sub>3</sub></b>	2011	14.8 ± 3.8	11.6 ± 5.2	11.2 ± 2.8	12.3 ± 3.1
<b>TP</b>	2011	23.5 ± 2.5	22.6 ± 3.7	22.3 ± 3.0	21.9 ± 2.3
<b>TDP</b>	2011	9.00 ± 0.99	8.71 ± 1.27	8.38 ± 1.2	8.91 ± 1.04
<b>SRP</b>	2011	4.87 ± 1.02	3.77 ± 1.09	3.43 ± 0.78	5.05 ± 1.30
<b>Chl <i>a</i></b>	2011	3.94 ± 0.49	4.59 ± 0.63	5.09 ± 0.87	4.34 ± 0.38
<b>TN</b>	2012	458 ± 13	451 ± 29	465 ± 11	455 ± 12
<b>TDN</b>	2012	398 ± 13	393 ± 18	410 ± 11	404 ± 12
<b>NO<sub>3</sub></b>	2012	229 ± 11	221 ± 18	235 ± 11	232 ± 9
<b>NH<sub>3</sub></b>	2012	8.7 ± 2.0	13.3 ± 5.8	10.1 ± 1.7	11.3 ± 2.8
<b>TP</b>	2012	13.4 ± 0.84	12.3 ± 1.36	11.8 ± 0.8	12.8 ± 0.7
<b>TDP</b>	2012	4.89 ± 0.28	5.11 ± 0.39	4.96 ± 0.35	4.84 ± 0.30
<b>SRP</b>	2012	2.46 ± 0.25	2.52 ± 0.41	2.43 ± 0.39	2.31 ± 0.27
<b>Chl <i>a</i></b>	2012	2.56 ± 0.23	2.74 ± 0.31	2.71 ± 0.33	3.15 ± 0.36

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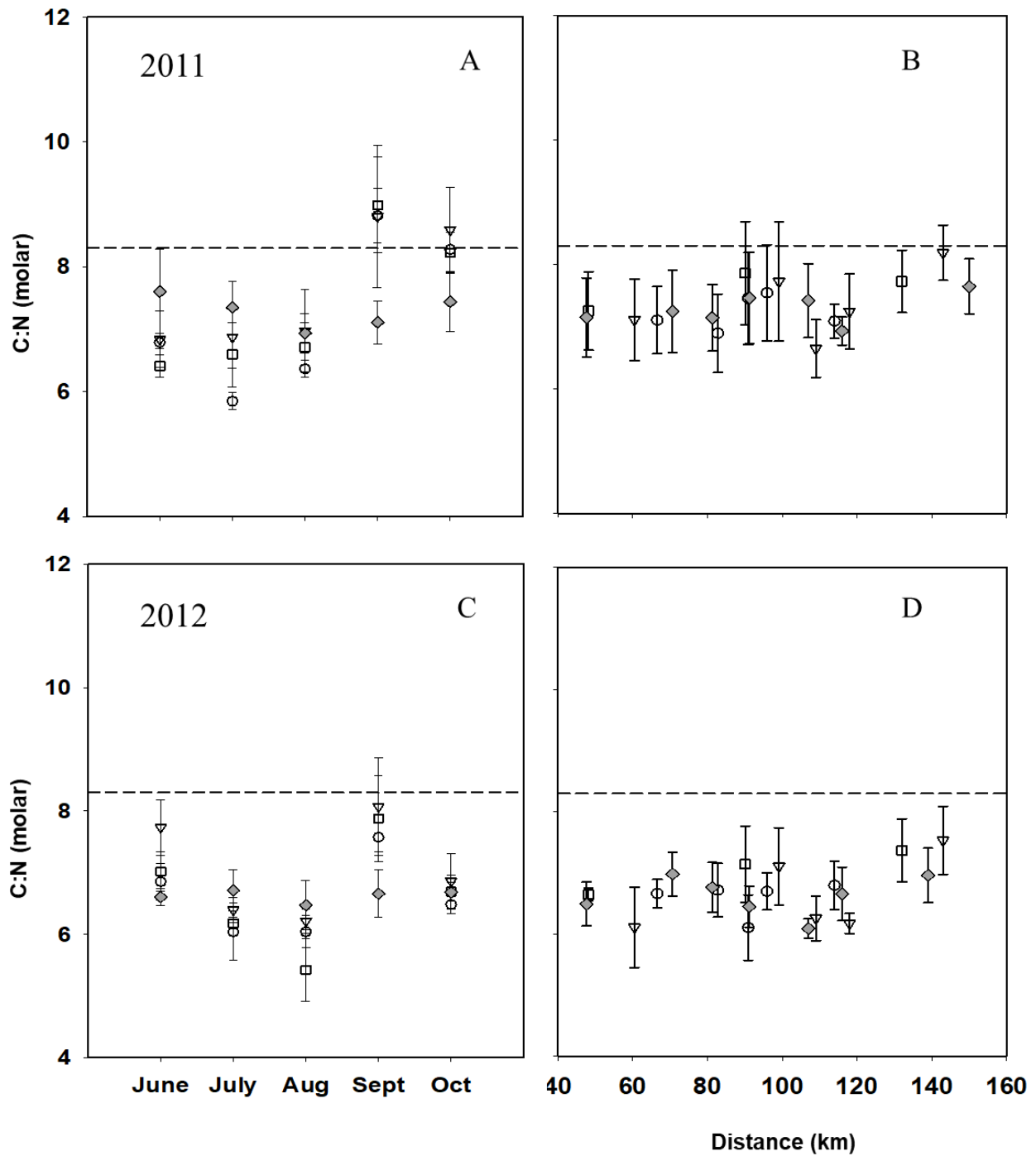




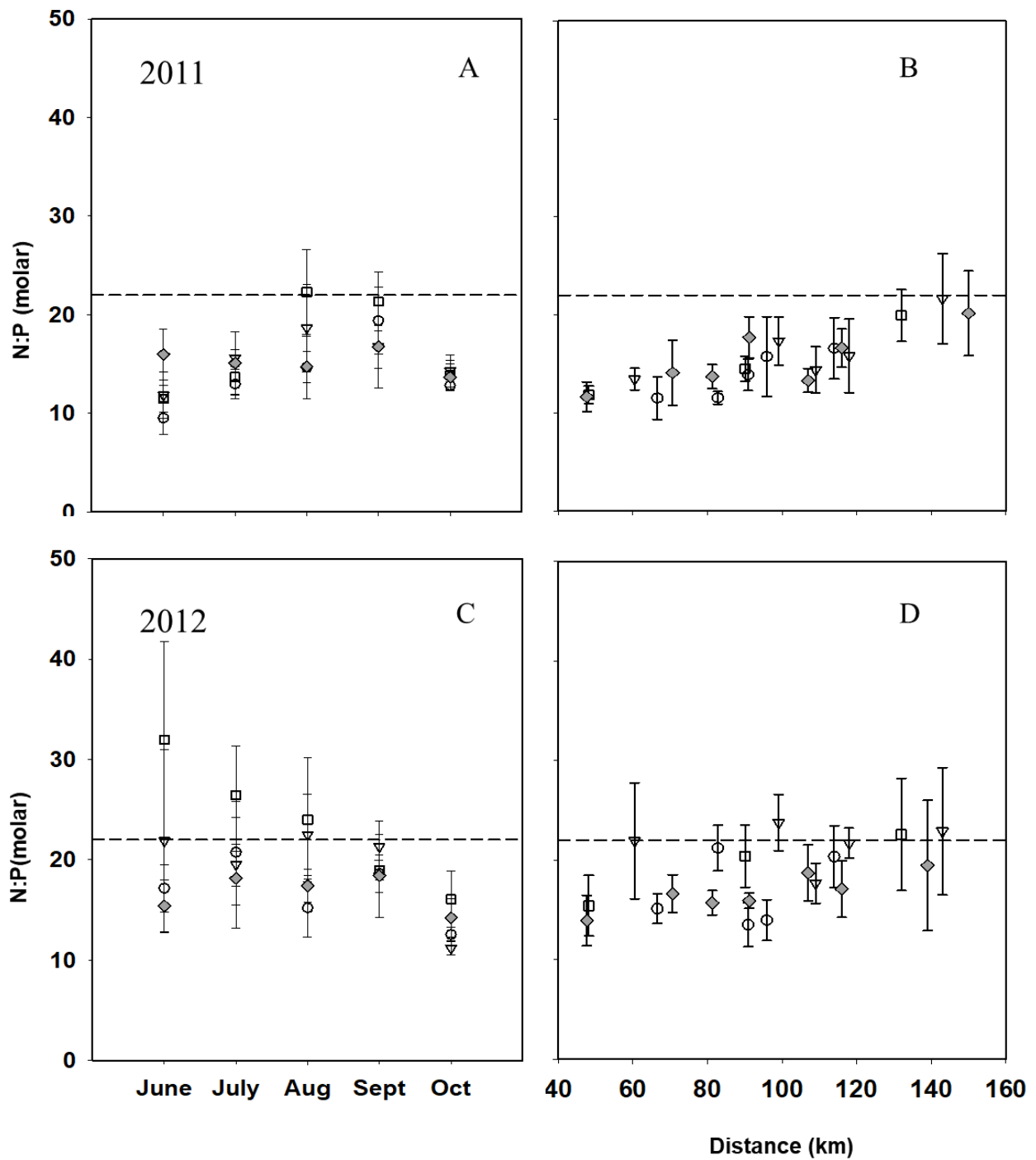
**Figure 3.2.** Comparison of average monthly (A and C) and site specific (B and D) phosphate turnover times (TT) in cattle (○), urban (□), and reference (▽) embayments and the main channel (◆) of Lake Diefenbaker. Values below dashed lines indicate moderate (TT<60 min) and extreme (TT<10 min) P limitation (Lean et al. (1983)). Error bars represent standard error. Example: (|-○-|) in June represents the mean and SE of all cattle embayments from the month of June.



**Figure 3.3.** Comparison of average monthly (A and C) and site specific (B and D) steady state phosphate concentrations ( $ssPO_4^{3-}$ ) in cattle (o), urban (square), and reference (∇) embayments and the main channel (diamond) of Lake Diefenbaker. Error bars represent standard error. Example: (|o-|) in June represents the mean and SE of all cattle embayments from the month of June.



**Figure 3.4.** Comparison of average monthly (A and C) and site specific (B and D) PC:PN ratios in cattle (○), urban (□), and reference (▽) embayments and the main channel (◇) of Lake Diefenbaker. Values above dashed lines indicate N limitation (Healey and Hendzel (1979)). Error bars represent standard error. Example: (|-○-|) in June represents the mean and SE of all cattle embayments from the month of June.



**Figure 3.5.** Comparison of average monthly (A and C) and site specific (B and D) PN:PP ratios in cattle (○), urban (□), and reference (▽) embayments and the main channel (◇) of Lake Diefenbaker. Values above dashed lines indicate P limitation (Healey and Hendzel (1979)). Error bars represent standard error. Example: (|-○-|) in June represents the mean and SE of all cattle embayments from the month of June.

Light limitation measurements were often significantly different ( $P < 0.5$ ) in the main channel when compared to the exposed and reference embayments. I assessed this further. Mean irradiance in the mixed layer ( $\bar{E}_{24}$ ) consistently showed that the main channel was more limited by light than the embayments (Table 3.2 and Figs. 3.6 and 3.7), and significance was confirmed with *post-hoc* Tukey tests in all instances. When normalized by TP concentrations ( $\bar{E}_{24}:TP$ ), only the differences between the main channel and the reference embayments were found to be significant (Table 3.2).

**Table 3.2.** Comparison of light conditions in the water column of reference and exposed embayments and the main channel sites. Results of linear mixed effects model with Treatment as the Fixed effect, Distance as the Random effect, and the Main channel set as the intercept. Significant P-values are in bold ( $P < 0.05$ ).

	Estimate	Std. error	DF	t-value	p-value
<b>2011</b>					
<i>Fixed effect</i>					
$\bar{E}_{24}$					
Intercept	1.1581	0.1529	40	7.5737	0.0000
Urban	0.8475	0.2792	16	3.0355	<b>0.0079</b>
Cattle	0.9600	0.2369	16	4.0526	<b>0.0009</b>
Reference	1.1721	0.2369	16	4.9480	<b>0.0001</b>
<i>Random effect</i>					
	Std. Dev.				
Distance	0.0000				
<i>Fixed effect</i>					
$\bar{E}_{24}:TP$					
Intercept	0.2414	0.0228	40	10.5791	0.0000
Urban	0.0637	0.0417	16	1.5278	0.1461
Cattle	0.0589	0.0354	16	1.6648	0.1154
Reference	0.0981	0.0354	16	2.7746	<b>0.0135</b>
<i>Random effect</i>					
	Std. Dev.				
Distance	0.0000				

**2012**

**Fixed effect**

$\bar{E}_{24}$

Intercept	0.3298	0.0450	53	7.3259	0.0000
Urban	0.2084	0.0801	16	2.6010	<b>0.0193</b>
Cattle	0.2002	0.0716	16	2.7959	<b>0.0130</b>
Reference	0.2172	0.0704	16	3.0865	<b>0.0071</b>

**Random effect**

	Std. Dev.
Distance	0.0000

**Fixed effect**

$\bar{E}_{24:TP}$

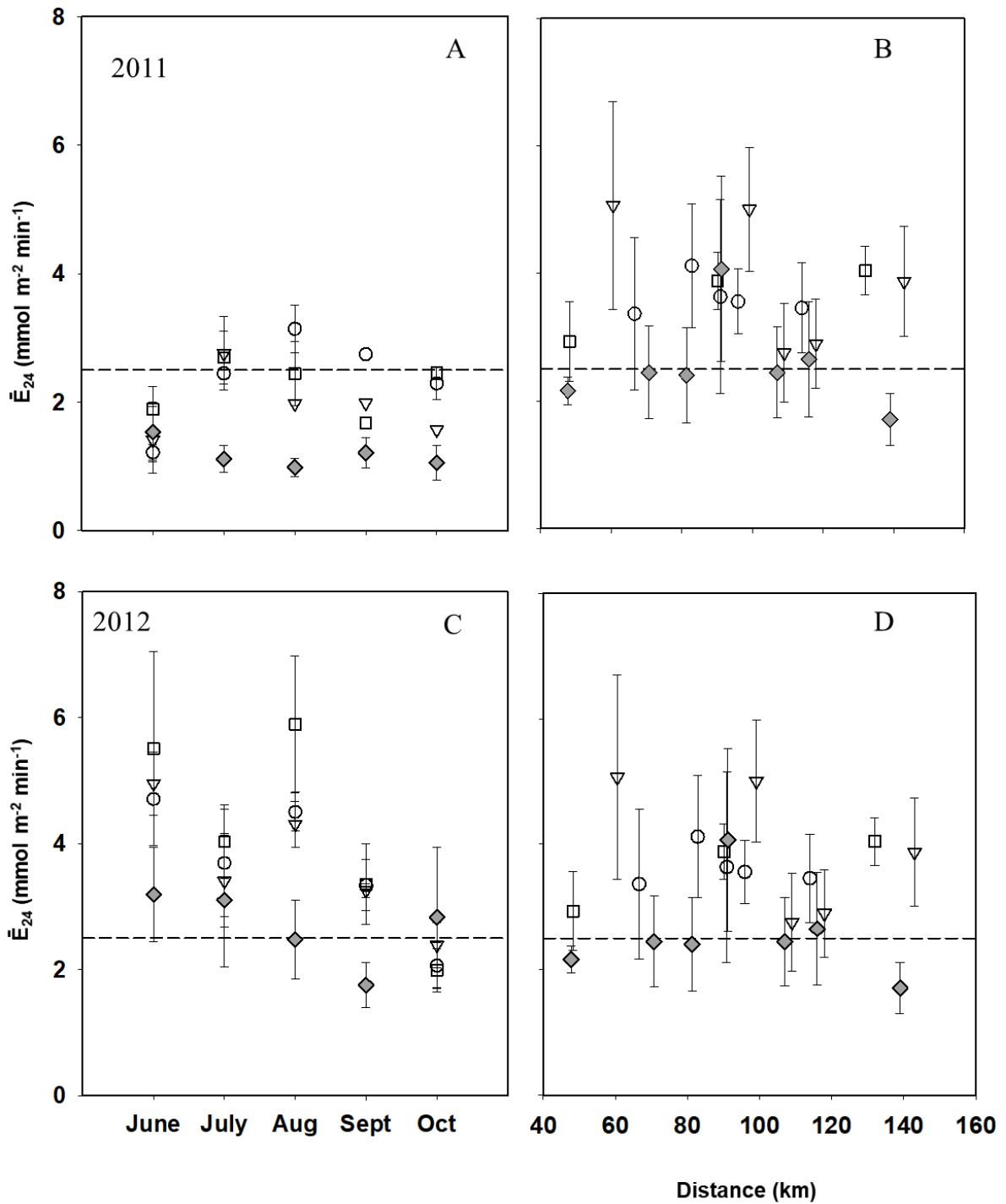
Intercept	-0.7253	0.0572	53	-12.6859	0.0000
Urban	0.2314	0.1018	16	2.2726	0.0372*
Cattle	0.1726	0.0909	16	1.8996	0.0757
Reference	0.2455	0.0893	16	2.7494	<b>0.0143</b>

**Random effect**

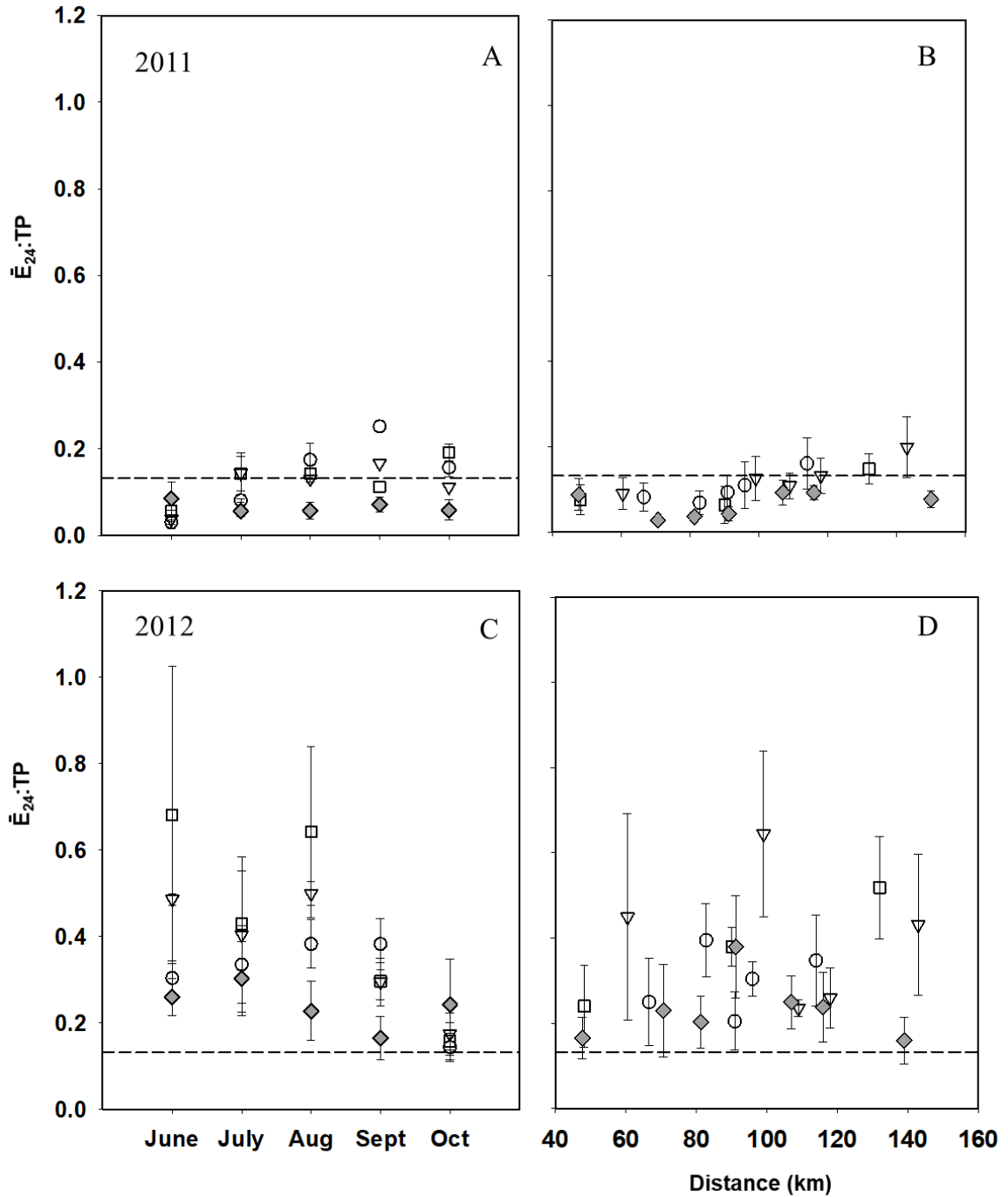
	Std. Dev.
Distance	0.0346

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\* Tukey test did not confirm significance ( $P = 0.1034$ )



**Figure 3.6.** Comparison of average monthly (A and C, all sites of a type within a month) and site specific (B and D, over 5 months) mean water column irradiance ( $\bar{E}_{24}$ ) in cattle (○), urban (□), and reference (▽) embayments and the main channel (◇) of Lake Diefenbaker. Values below dashed lines indicate light limitation (Guildford et al. (2000)). Error bars represent standard error. Example: (|○|) in June represents the mean and SE of all cattle embayments for the month of June.



**Figure 3.7.** Comparison of average monthly (A and C) and site specific (B and D) ratio of light to phosphorus ( $\bar{E}_{24}:TP$ ) in cattle (○), urban (□), and reference (▽) embayments and the main channel (◇) of Lake Diefenbaker. Dashed lines represent the median ( $0.132 \text{ mmol m}^{-2} \text{ min}^{-1} \cdot \mu\text{g L}^{-1}$ ) from both years combined, values below the line may be light limited, values above line may be P limited, according to Chrzanowski and Grover (2001). Error bars represent standard error. Example: (|○|) in June represents the mean and SE of all cattle embayments for the month of June.



### 3.4. Discussion

#### 3.4.1. Does exposure to cattle or marinas affect nutrient status or the light environment?

I did not detect a difference in the nutrient or light status between the exposed and reference embayments. With the exception of  $\text{ssPO}_4^{3-}$  concentrations in 2011, a difference was not found in nutrient concentrations, nutrient status, or the light environment between the embayments exposed to cattle or urban activities and the reference embayments. Both 2011 and 2012 experienced higher than average flows from the SSR, and as such, the water residence time in the reservoir was greatly reduced. If this caused the embayments to flush more rapidly, there may not have been sufficient time for nutrient inputs from these anthropogenic activities to affect the nutrient status within the embayments. Spatial patterns within reservoirs and their embayments can change based on flows, with more defined differences often present when flows are low (Nogueira et al., 1999). The results of this study may have been different, if it had been conducted during years when discharge into the reservoir from the SSR was average or below average.

In 2011, the  $\text{ssPO}_4^{3-}$  concentrations were found to be nearly significantly higher ( $P < 0.1$ ) in the cattle embayments when compared to the reference embayments. Based on typical composition of cattle waste (PN:PP 4.3:1; Webb and Archer, 1994), I might expect to see N limitation in areas exposed to direct defecation by cattle. If N were limiting, the concentration of bioavailable forms of P (i.e.,  $\text{ssPO}_4^{3-}$ ) may be elevated, therefore, this may suggest that an effect of cattle operations in the embayments was present. However, none of the other P limitation indicators or N deficiency indicators showed differences in the cattle embayments at the same time. These results may also suggest that the  $\text{ssPO}_4^{3-}$  assay is more sensitive to differences,

nevertheless, without agreement between more indicators it is difficult to draw conclusions or suggest an effect.

### *3.4.2. Difference in the Light Environment between the Main Channel and the Embayments*

A nutrient effect was not observed between the main channel and embayment sites (cattle, urban, reference), however, mean irradiance in the mixed layer ( $\bar{E}_{24}$ ) was significantly different in the main channel sites than in the embayment sites in both years (Table 3.2). The main channel was consistently more light-deficient than the embayments. There is an obvious explanation for this if we examine the components of the equation for calculating  $\bar{E}_{24}$ . The equation consists of the 24-hour PAR measurement, the mixing depth ( $Z_{\text{mix}}$ ), and the extinction coefficient ( $k_d$ ). Average 24-hour PAR measurements are almost identical as the value is the same for any measurements taken on a given day ( $P = 0.73$ , z-test, 23.38 and 23.44  $\text{mmol m}^{-2} \text{min}^{-1}$  in the main channel and embayments respectively). The light attenuation measurements are also similar ( $P = 0.61$ , z-Test),  $0.73 \pm 0.08$  and  $0.77 \pm 0.04$  (average  $\pm$  standard error) in the main channel and embayments, respectively. Based on the mean light attenuation results, the overall average euphotic depth (the region where almost all photosynthesis occurs) is near 6.3 m. The mixing depth is the major difference between the main channel and the embayments. The average mixing depth in the main channel was  $25.1 \pm 1.1$  m, whereas the average mixing depth in the embayments was  $12.7 \pm 0.4$  m. Hence, a freely floating algal cell would have sufficient light approximately half of the time in the embayments and only a quarter of the time in the main channel. The reason for the difference in the mixing depths is the maximum depth of the embayment sites. The average maximum depth in the embayments is  $13.4 \pm 0.6$  m, whereas the average maximum depth in the main channel is  $38.4 \pm 1.0$  m. In other words, the mixing depth in the embayments is determined by the depth of the embayments, whereas the mixing depth in the

main channel is not limited by depth, and therefore can extend much deeper resulting in freely floating algal cells having access to less light. As a result, the  $\bar{E}_{24}$  was always significantly different between the embayments and the main channel, a difference resulting from the depth of the embayments and main channel and not an anthropogenic effect.

### **3.5. Summary**

Direct cattle watering in the reservoir will result in additional nutrients entering the water column; the animals are defecating near the shore if not directly in the water and their access to the water's edge will increase bank and shore erosion. This activity will also disrupt the sediments, potentially stirring up settled nutrients and increasing the sediment load to the water column, which will ultimately affect the local light environment. Similarly, marinas and boating will add nutrients and sediment load to the water column through increased run off from impervious surfaces at the marinas and towns, increased soil erosion from boat induced waves and turbulence and human activities (e.g., accidental or intentional dumping of waste). However, I did not detect a localized anthropogenic effect on nutrient limitation, light limitation, or nutrient concentrations within the embayments exposed to either cattle or urban activities in LD. This is not to say that nutrient loading or sediment load increases from these activities is not occurring, only that I was not able to detect any consistent or persistent differences, during 2 high flow years, with this study design. The nearly significantly higher  $ssPO_4^{3-}$  concentrations in the cattle embayments when compared to the reference embayments may suggest nutrient loading within those embayments. With an increased proportion of bioavailable N from manure, the highly sensitive  $ssPO_4^{3-}$  assay may have identified the resulting increase in P when other measurements (i.e., N-debt or particulate nutrient ratios) did not. Finally, the difference detected between the

light environment in the main channel and the embayments is a function of relative depths, not anthropogenic activities.

## **CHAPTER 4 – LIGHT VS P LIMITATION**

### **4.1. Introduction**

Phosphorus (P) is generally considered the primary limiting nutrient in most freshwater systems (Edmondson, 1970; Schindler, 1974; Schindler et al., 2008; Vollenweider, 1970). Based on my results this also appears to be the case in Lake Diefenbaker. Chapter 2 highlights the strength of P limitation within this reservoir. However, phytoplankton growth and reproduction can also be limited by the availability of light (Guildford et al., 2000; Thrane et al., 2014; Wozniak et al., 2002). Photosynthesis is the means of obtaining the energy required for the uptake and assimilation of nutrients and therefore, if light is not available then the nutrients cannot be utilized (Hecky and Guildford, 1984; Venables and Moore, 2010). Sterner et al. (1997) suggested that in a “high” light-to-nutrient environment, autotrophs are more likely to be limited by P, and in a “low” light-to-nutrient environment they are more likely to be limited by light. Although I have established that P is often the limiting nutrient within LD, determining the importance of light as a potential limiting factor is vital to fully understanding the response of the reservoir to climate change.

Global drought and water scarcity are expected to intensify with increasing worldwide temperatures (Prudhomme et al., 2014; Schewe et al., 2014). With declining flows and increased water temperatures associated with climate change, algal biomass is predicted to increase (Costa et al., 2016; Jeppesen et al., 2015; Yasarer and Sturm, 2016). The SSR has been designated as Canada’s most threatened river and experts describe the potential for intensifying water scarcity in the region as an emerging water crisis (WWF, 2009). Increases in extreme weather conditions, and associated floods, are also expected (Fischer and Knutti, 2015), which bring large amounts of turbidity into the system (Hudson and Vandergucht, 2015; Yip et al., 2015). Both drought and flood conditions have the potential to affect the light conditions within the reservoir. Turbidity

associated with floods has the potential to limit light availability and therefore biomass production as shown by the positive relationship between Secchi disk depths and chlorophyll *a* concentrations (Yip et al., 2015). Conversely, drought conditions may increase light availability with a reduction in turbidity.

Increases in extreme flows also have the potential to affect nutrient loading within the reservoir due to greater surface runoff and groundwater discharge (Paerl and Huisman, 2009). A greater P load entered LD from the SSR during the higher peak flows in 2011 than 2012 (June P loads ~950 tons and ~225 tons respectively; personal communication, Jess Johansson, University of Saskatchewan). The majority of this P is retained in the reservoir as LD has some of the highest P retention rates (58-91%) in the Saskatchewan River sub-basin (Donald et al., 2015; North et al., 2015b). Conversely, decreased flows combined with warmer water temperatures associated with climate change will result in prolonged stratification, resulting in more potential for anoxic hypolimnia and internal P loading from the sediments (North et al., 2015b). Furthermore, if elevated spring flows deliver increased nutrient loads and are immediately followed by low flows the potential for blooms increases within that season (Paerl and Huisman, 2009).

Given the uncertainty of the future conditions for LD, it is important that we better understand how this reservoir will respond to each possible stressor, be it changes to the light environment with more extreme flows, increased P loads from the SSR or potential for P loading from the sediments (internal loading). This requires a better understanding of the relationship between the most prominent limiting factors in the reservoir, light and P. As the largest source of moderate water quality in Saskatchewan, it is imperative that we have a better understanding of

how this system will respond to changes in nutrient loading and light availability. In this chapter I aim to clarify and refine the light-nutrient limitation relationship.

## 4.2. Methods

Field sampling procedures are described in section 2.2.1. Water chemistry, nutrient bioassays, and light measurements are described in sections 2.2.2, 2.2.3, and 2.2.4 respectively.

### 4.2.1. Statistical Analyses

Water column irradiance data ( $\bar{E}_{24}$ ) from the main channel of LD for both years were combined and then separated into light limited and sufficient based on the threshold of 2.5 mmol m<sup>-2</sup> min<sup>-1</sup> according to Guildford et al. (2000). Mann-Whitney U tests were performed on all nutrient limitation parameters to determine if nutrient status is affected by the presence or absence of light limitation. Finally, the relationship between light and nutrient limitation indicators are graphically examined to further add to our understanding of the association between these parameters.

## 4.3. Results

Nutrient limitation indicators were often different ( $P < 0.05$ ) when grouped according to Guildford et al. (2000). That is, I found a significant difference between  $TT_{PO_4}$ ,  $ssPO_4^{3-}$  concentrations, APA rates, and PN:PP and PC:PN molar ratios when light limited samples were compared to light sufficient samples (Table 4.1). When light was deemed sufficient ( $\bar{E}_{24} > 2.5$  mmol m<sup>-2</sup> min<sup>-1</sup>),  $TT_{PO_4}$  and  $ssPO_4^{3-}$  concentrations were significantly lower and APA rates and PN:PP molar ratios were significantly higher. Each of these suggests a tendency towards stronger P limitation when light was sufficient and relaxed P limitation when light became limiting. Molar PC:PP ratios were also higher when light was sufficient however the difference was not found to be significant ( $P > 0.05$ ). In contrast, when light was sufficient, PC:PN ratios were

lower, suggesting N limitation is relaxed when adequate light was available. It should be noted that both PN:PP and PC:PN ratios were well under the limit to suggest P or N limitation in either case (PN:PP < 22; PC:PN < 8.3). Although not significant, N-debt rates were also lower when light was sufficient, further supporting the results of the PC:PN ratios.

**Table 4.1** Mean (M) and standard error (SE) of nutrient limitation indicators separated into light limited and light sufficient based on Guildford et al. (2000). *n* = number of samples. Each set of variables (light limited and light sufficient) were compared with Mann-Whitney Rank Sum Tests, significantly different from Light Limited indicated with \*\*\*  $P \leq 0.001$ ; \*\*  $P \leq 0.01$ ; \*  $P \leq 0.05$ .

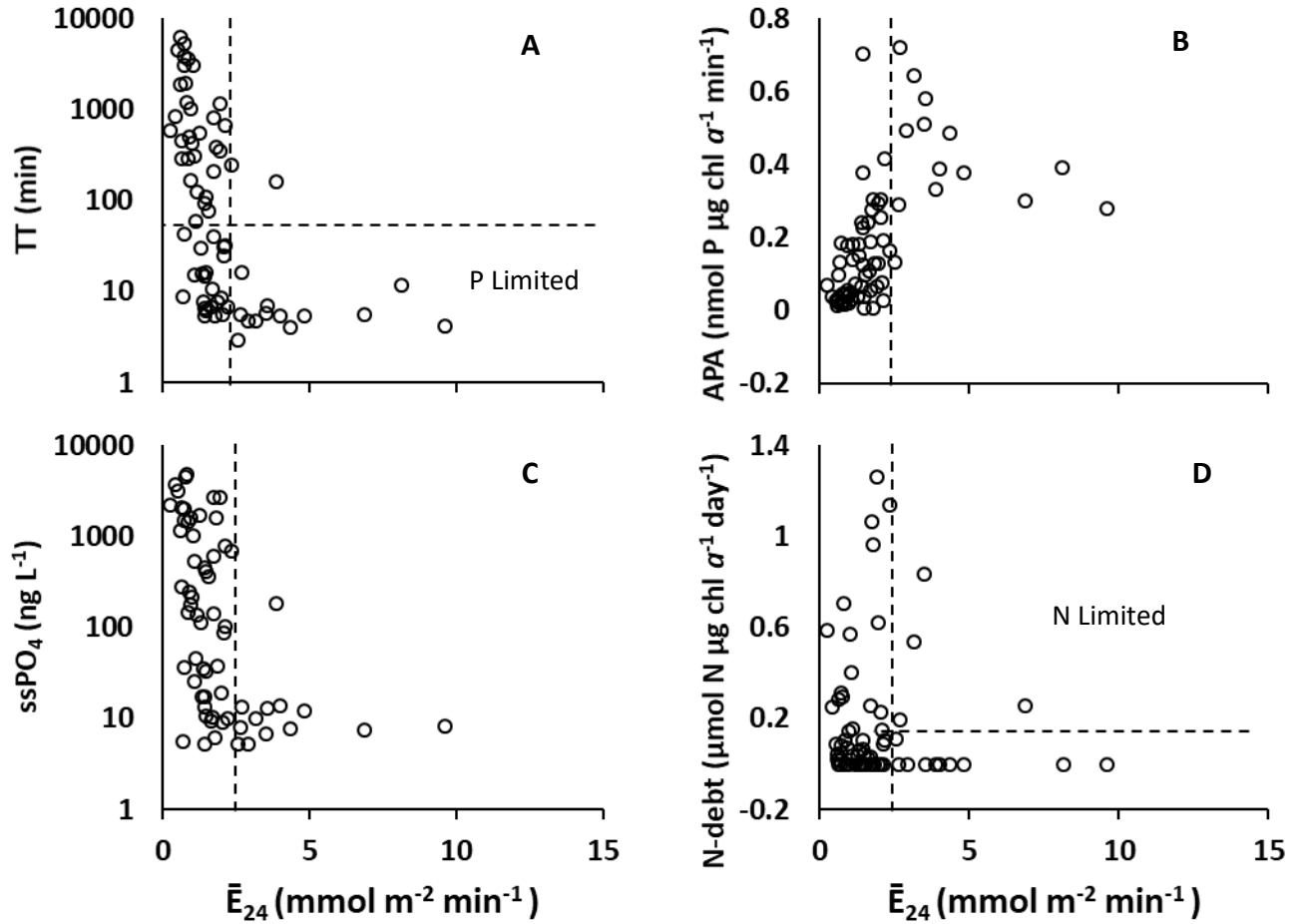
Limitation Indicators	Units	Light Limited		Light Sufficient	
		$\bar{E}_{24} < 2.5^a$	$\bar{E}_{24} > 2.5^a$	$\bar{E}_{24} < 2.5^a$	$\bar{E}_{24} > 2.5^a$
		<i>n</i>	M ± SE	<i>n</i>	M ± SE
P limitation indicators					
TT <sub>PO4</sub>	minutes	57	797 ± 186	14	17.4 ± 11.0*
ssPO <sub>4</sub>	ng L <sup>-1</sup>	57	910 ± 171	13	22.5 ± 13.3**
APA	nmol P μg Chl <i>a</i> (μg) <sup>-1</sup> min <sup>-1</sup>	55	0.13 ± 0.02	14	0.42 ± 0.04***
PC:PP	molar ratio	55	107.6 ± 7.16	14	121 ± 14.9
PN:PP	molar ratio	55	14.9 ± 0.81	14	19.1 ± 2.08*
N limitation indicators					
N-debt	μmol Chl <i>a</i> (μg) <sup>-1</sup> day <sup>-1</sup>	57	0.19 ± 0.04	13	0.14 ± 0.07
PC:PN	molar ratio	55	7.17 ± 0.17	13	6.25 ± 1.09**

<sup>a</sup> mmol m<sup>-2</sup> min<sup>-1</sup>

To further examine these relationships, I have plotted the nutrient limitation indicators as a function of  $\bar{E}_{24}$  (Figs. 4.1 and 4.2). The most interesting of these graphs are TT<sub>PO4</sub>, ssPO<sub>4</sub><sup>3-</sup> and APA. The inverse relationship between  $\bar{E}_{24}$  and TT<sub>PO4</sub> and ssPO<sub>4</sub><sup>3-</sup> shows that when  $\bar{E}_{24}$  increases and light is not limiting then TT<sub>PO4</sub> and ssPO<sub>4</sub><sup>3-</sup> decrease to levels suggesting P limitation (Figure 4.1 B and D). A positive relationship is shown between  $\bar{E}_{24}$  and APA rates, such that as light



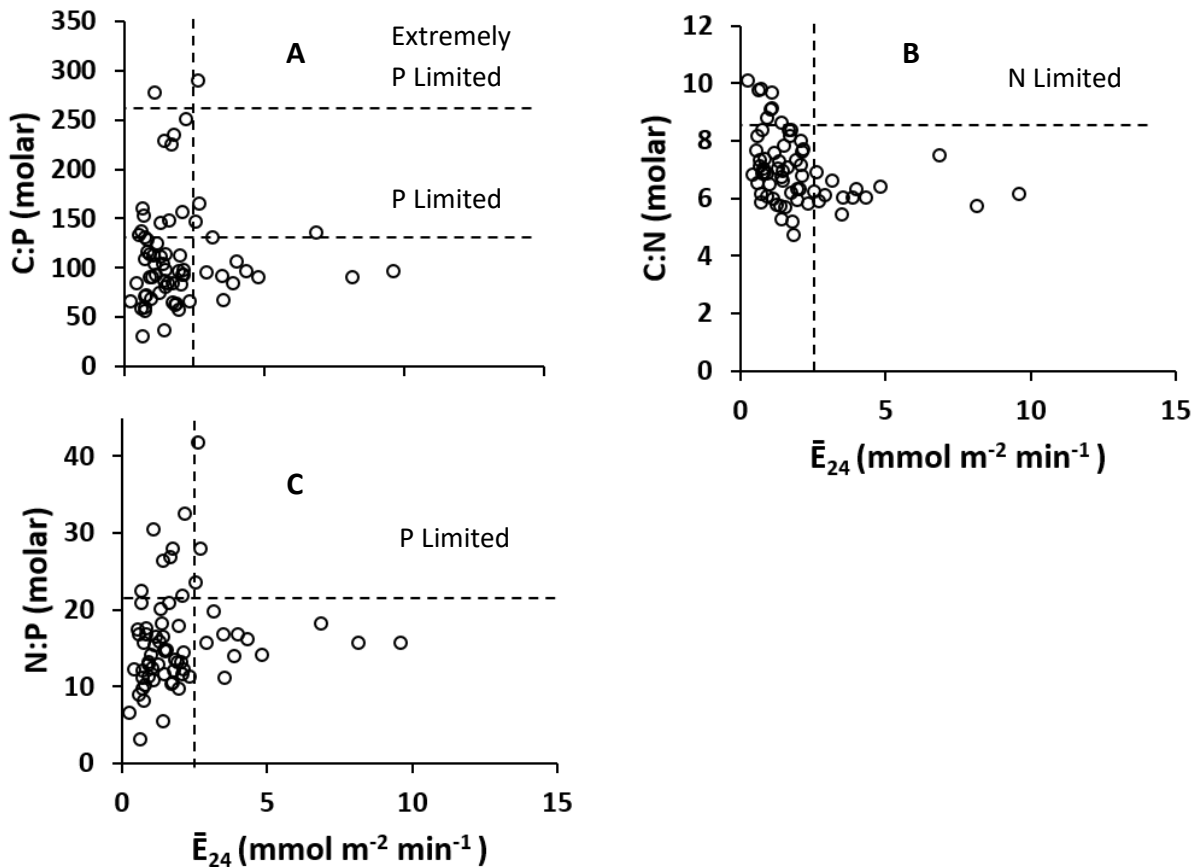
limitation is relaxed ( $\bar{E}_{24}$  increases), then APA rates increase (Fig. 4.1A); this pattern is in agreement with  $TT_{PO_4}$ , and  $ssPO_4^{3-}$ .



**Figure 4.1.** Graphs showing various nutrient limitation parameters as a function of  $\bar{E}_{24}$ . Values to the left of the vertical dashed line ( $\bar{E}_{24} < 2.5$  mmol m<sup>-2</sup> min<sup>-1</sup>) indicate light limitation. Values above or below horizontal dashed lines indicate P or N limitation where noted and thresholds exist. Note that the y axis is logged (A and C). Note that the x axis crosses at a negative value (B and D) to better illustrate the spread of data.

In contrast, these trends were not as apparent when I examined the relationship between molar ratios and  $\bar{E}_{24}$  graphically (Fig. 4.2). As  $\bar{E}_{24}$  increases and light becomes less limiting, there

is a slight increase in PC:PP and PN:PP ratios, and a decrease in PC:PN ratios (Table 4.1 and Fig. 4.2). However, P limitation is not immediately apparent once light becomes sufficient.



**Figure 4.2.** Graphs showing various nutrient limitation parameters as a function of  $\bar{E}_{24}$ . Values to the left of the vertical dashed line ( $\bar{E}_{24} < 2.5 \text{ mmol m}^{-2} \text{min}^{-1}$ ) indicate light limitation. Values above or below horizontal dashed lines indicate P or N limitation where noted and thresholds exist.

#### 4.4. Discussion

Based on the separation criteria of Guildford et al. (2000), when light was sufficient, P deficiency increased (Table 4.1). However, when the light environment was less favourable (limited), P deficiency was relaxed. In 2013, Dubourg et al. (2015) also found this to be the case in LD. Plotting the nutrient limitation indicators against  $\bar{E}_{24}$  clarified these relationships. When

light was limiting, P limitation indicators were variable, but when light was sufficient, then the proximate P limitation indicators (APA,  $TT_{PO_4}$ , and  $ssPO_4^{3-}$ ) suggested strong P deficiency. This suggests light is the primary limiting factor in LD, followed by P, at least on shorter timescales. A similar relationship was found between light and the phosphorus deficiency index (PDI) in Lake Ontario (Millard et al., 1996). Lean and Pick (1981) developed the PDI as an alternative measurement of P deficiency to the  $^{14}C$  bioassay, the PDI takes into account the ratio of optimal rate of C uptake at full light saturation and the maximum uptake velocity of P. Millard et al. observed PDI values suggesting extreme P limitation occur more often when light was deemed sufficient. When light was limiting the PDI was variable. The measurement of light limitation used here ( $\bar{E}_{24}$ ) reflects immediate changes in the light environment and therefore works on similar timescales to the proximate P limitation indicators. Ultimate measurements of nutrient limitation (particulate molar ratios) take longer to reflect changes in nutrient availability, therefore the relationship between these parameters and  $\bar{E}_{24}$  may be more difficult to determine due to the difference in timescales. Changes in molar nutrient ratios may be occurring with changes to the light environment, however, they may be separated in time and not discernable due to the difference in timescales, thus making the relationship more difficult to detect. However, there is still good separation in the data to suggest that when light is sufficient then PC:PP and PN:PP ratios increase.

In contrast to the P limitation indicators, N limitation indicators showed the opposite trend as seen with P. They suggest stronger N limitation (higher N-debt and PC:PN) when light is deemed limiting than when it is sufficient. This may be due to increases in algal N requirements during low light situations (Healey, 1985), increased bacterial activity when turbidity was high (Goosen et al., 1999; Lind and Dávalos-Lind, 1991; Lind et al., 1997), or a combination of both.

Understanding the relationship between these growth-limiting factors within LD is not only important for management implications for the future of LD but can also serve to inform management decisions for other reservoirs or lakes.

Reservoirs such as LD are largely understudied relative to their importance and abundance. However, they can serve as excellent models to study light and nutrient limitation due to the spatial and temporal dynamics and large gradients in turbidity and light conditions that are present. Due to the strong spatial and temporal gradients present in LD, these relationships became evident. During my two years of study, the separation of data for all P limitation indicators based on Guildford et al.'s (2000) criteria for light limitation, was significant ( $P < 0.05$ ) with the exception of PC:PP ratios, which trended in the same direction (stronger P limitation when light was sufficient) but were not statistically different (Table 4.1). Furthermore, when light was sufficient,  $TT_{PO_4}$  fell well within the range for moderate P limitation ( $TT_{PO_4} = 17.4 \pm 11.0$  min), or extreme P limitation ( $TT_{PO_4} < 10$  min). Moreover, some of the lowest concentrations of  $ssPO_4^{3-}$  ( $< 25$  ng L<sup>-1</sup>) corresponded with the highest  $\bar{E}_{24}$  values in LD (Fig. 4.1D), and were well within the range expected in P deficient systems (Hudson et al., 2000; Vandergucht et al., 2013). The good agreement between multiple P limitation indicators suggests that LD is primarily limited by light and secondarily by P. Hence, the planktonic assemblage was co-limited by light and P in LD during the 2011-12 study. A similar conclusion was reached by Dubourg et al. in 2013. This type of co-regulation of planktonic growth has been shown both in situ (Xenopoulos et al., 2002) and in laboratory experiments (Hessen et al., 2002).

Both nutrient and light availability need to be adequate for significant algal growth to occur. I did not see significant blooms during my sampling periods even though nutrient concentrations were comparable to other systems, such as Lake Champlain (Smeltzer et al.,

2012), Lake Erie (Rockwell et al., 2005), and Lake Simcoe (Nicholls, 2001) that do experience frequent algal blooms. A major difference between LD and Lake Champlain is the light environment; Secchi disk depths are much deeper in Lake Champlain (5 m; Smeltzer et al. 2012) than in LD (3 m; Yip et al., 2015; Dubourg et al. 2015) suggesting that Lake Champlain does not experience light limitation as in LD. Therefore, if light penetration increases in LD an increase in algal growth and the possibility for cyanobacteria blooms and associated odour and toxin issues may develop. With the predicted decrease in flows with climate change (WWF, 2009), light may become more available in LD in the coming years due to decreased non-algal turbidity. Increasing global temperatures will lead to warmer surface waters, earlier onset of stratification, and prolonged stratification (Paerl et al., 2011b), which can lead to anoxia in the lower hypolimnion as was seen during low flows in 1984 (WQB, 1988). This, coupled with the reservoir acting as a sink for P, and the potential for legacy P in the sediments to contribute to internal P loading (North et al., 2015b) renders LD susceptible to a future of poorer water quality. Therefore, future management of this important reservoir should consider P loading and light availability. Light would be difficult to manage, hence the obvious factor that needs current and future attention is the loading of P to the reservoir.

## **CHAPTER 5 - GENERAL DISCUSSION**

### **5.1. Nutrient and Light Limitation in Lake Diefenbaker, Implications for the Future**

A complete understanding of the factors controlling eutrophication requires consideration of the interaction between light and nutrients. Assessing the role of light availability as a regulator of eutrophication is required to fully understand the potential impact of anthropogenic nutrient loading to reservoirs and lakes. Within the boundaries of the LZC we expect to see a longitudinal gradient in nutrient and light availability within a reservoir. In the riverine zone, the LZC predicts high nutrient availability and low light due to relatively high flows carrying suspended solids and non-algal turbidity. In the transition zone the flow is reduced as the suspended load begins to settle thus reducing nutrient availability and increasing light availability. Finally, in the lacustrine zone the expectation is that nutrient supply will be lower, and the relatively clear water column means that light is more available. LD followed most of these expectations; the upstream sites were representative of the riverine zone with high nutrients and suspended solids resulting in a very poor light environment. The next few sites represented the transition zone where the reduced flow resulted in the particulate matter settling out of the water column and consequently reductions in phosphorus and an increase in light penetration. The lacustrine zone is where I saw some deviations from the expectations of the LZC. In the lacustrine zone I did see a further decrease in P concentrations and an increase in water transparency. However, I still saw significant light limitation due to the deep mixing depths, instead of nutrient limitation as predicted by the LZC. Understanding the interaction of these factors and how they control growth of the phytoplankton community within LD is paramount to properly manage this vital resource to the province of Saskatchewan.

Results of Chapter 2 indicate that phosphorus (P) is the main limiting nutrient in Lake Diefenbaker (LD) with nitrogen (N) deficiency appearing at times typically associated with high

flow and low light. Although the reservoir received large loads of both P and N with spring flows, which declined throughout each season, N and P dynamics in the reservoir differed. Particulate P settled quickly out of the water column resulting in declining P concentrations along the length of the reservoir (Fig. 2.2). This agrees with the assessment of North et al. (2015b), that LD acts as a sink for P. This is typical of reservoirs in general (Kimmel et al., 1990). In contrast, N concentrations increased along the length of the reservoir (Fig. 2.3), suggesting that at times, LD is acting as a source for N. Although Scott et al. (2009) found that reservoir transition zones can be hot spots for planktonic N fixation, that does not appear to be the case in LD. Donald et al. (2015) found that LD was sequestering TN and DIN, therefore, the spatial increases observed here may have been an artifact of time between sampling. There may have been a pulse of N that we did not capture in the upstream regions but did measure in the downstream regions, thus giving the appearance of increasing concentrations along the length of the reservoir. Light deficiency played an important role in LD during both years of sampling. Although the light environment may become more favourable with decreasing flows (as expected with climate change), there is still potential for significant light deficiency due to the deep mixing depths in the lacustrine regions of the reservoir.

Chapter 3 examined the effects of cattle operations and recreational activities on nutrient and light limitation within a set of embayments of LD. Results suggest that these activities are not significantly affecting the local light or nutrient environments. Due to the larger than normal flows in both years the embayments may have been well flushed and therefore anthropogenic impacts not detectable.

Results of Chapter 4 suggest that light was the primary limiting factor in LD, with P limitation being secondary, or that the system was co-limited by light and P. When light

deficiency was relaxed (light was sufficient) P deficiency emerged. Although this interaction between light and the proximate P limitation indicators show very interesting relationships, we must also look to the longer-term measurements of nutrient limitation (ultimate limitation) for a more complete understanding of the nutrient status of LD. During my two years of study, particulate molar ratios indicated several instances of moderate P limitation and suggested extreme P limitation on two separate occasions. The majority of these instances were also considered to be light limited and were in the lacustrine sections of the reservoir.

Light and P limitation may have been partly responsible for the absence of major algal blooms in the reservoir in 2011 and 2012. Regardless of whether light or P is considered the ultimate limiting factor, only P can be controlled. Reducing inputs of P is well known to have resulted in significant reductions in eutrophication of many lakes in North America (NRC, 1992; Schindler et al., 2016), and therefore, controlling P inputs into the reservoir is a prudent management strategy to pursue. Upstream sources of P include non-point sources such as run-off from agricultural land and urban centres; point sources may include waste water effluent and industrial release. Programs like the Bow River Phosphorus Management Plan (BRPMP) are vital to the success of reducing P inputs to the SSR and LD. The BRPMP provides information to the public about anthropogenic sources of P, and how changes in behaviour can reduce direct and indirect additions of P to the river. The focus must be placed on public education and both monitoring and management of P inputs to be able to mitigate the potential effects of climate change on this essential resource for the Canadian Prairies. Unfortunately, the anticipated changes to flow and stratification patterns associated with climate change, and the potential for legacy P loading in LD, may lead to significant P inputs through internal loading. If this occurs, we may observe increased cyanobacterial blooms and the development of odours and harmful



toxins. Therefore, P reduction strategies should be implemented immediately to reduce P loading to LD in an effort to mitigate the potential effects of climate change.

## LITERATURE CITED

- Abirhire, O., North, R.L., Hunter, K., Vandergucht, D.M., Sereda, J., and Hudson, J.J. (2015). Environmental factors influencing phytoplankton communities in Lake Diefenbaker, Saskatchewan, Canada. *J. Gt. Lakes Res.* *41*, Supplement 2, 118–128.
- Anzai, H., Wang, L., Oishi, K., Irbis, C., Li, K., Kumagai, H., Inamura, T., and Hirooka, H. (2016). Estimation of nitrogen and phosphorus flows in livestock production in Dianchi Lake basin, China. *Anim. Sci. J.* *87*, 37–45.
- Arvola, L. (1981). Spectrophotometric determination of chlorophyll a and phaeopigments in ethanol extractions. *Ann. Bot. Fenn.* *18*, 221–227.
- Asplund, T.R. (1996). Impacts of motorized watercraft on water quality in Wisconsin lakes (Madison, WI: Wis. Dep. Nat. Res. Bur. Research).
- Asplund, T.R., and Cook, C.M. (1997). Effects of motor boats on submerged aquatic macrophytes. *Lake Reserv. Manag.* *13*, 1–12.
- Bachmann, R., and Canfield, D. (1996). Use of an alternative method for monitoring total nitrogen concentrations in Florida lakes. *Hydrobiologia* *323*, 1–8.
- Beardall, J., Young, E., and Roberts, S. (2001). Approaches for determining phytoplankton nutrient limitation. *Aquat. Sci.* *63*, 44–69.
- Bentzen, E., and Taylor, W.D. (1991). Estimating Michaelis–Menten parameters and lake water phosphate by the Rigler bioassay: importance of fitting technique, plankton size, and substrate range. *Can. J. Fish. Aquat. Sci.* *48*, 73–83.
- Bergmann, M., and Peters, R.H. (1980). A simple reflectance method for the measurement of particulate pigment in lake water and its application to phosphorus–chlorophyll–seston relationships. *Can. J. Fish. Aquat. Sci.* *37*, 111–114.
- Bernardi, R. de, and Giussani, G. (1990). Are blue-green algae a suitable food for zooplankton? An overview. In *Bio-manipulation Tool for Water Management*, R.D. Gulati, E.H.R.R. Lammens, M.-L. Meijer, and E. van Donk, eds. (Springer Netherlands), pp. 29–41.
- Box, G.E., and Cox, D.R. (1964). An analysis of transformations. *J. R. Stat. Society Ser. B Methodol.* *26*, 211–252.
- Capece, J.C., Campbell, K.L., Bohlen, P.J., Graetz, D.A., and Portier, K.M. (2007). Soil phosphorus, cattle stocking rates, and water quality in subtropical pastures in Florida, USA. *Rangel. Ecol. Manag.* *60*, 19–30.
- Carlson, R.E., and Simpson, J. (1996). A coordinator’s guide to volunteer lake monitoring methods. *North Am. Lake Manag. Soc.* *96*, 305.
- Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., and Smith, V.H. (1998). Nonpoint pollution of surface waters with phosphorus and nitrogen. *Ecol. Appl.* *8*, 559–568.

- Centre for Hydrology, University of Saskatchewan (2012). Review of Lake Diefenbaker Operations 2010-2011. Edited by Saskatchewan Water Security Agency, Saskatoon, SK.
- Chrzanowski, T.H., and Grover, J.P. (2001). The light: nutrient ratio in lakes: a test of hypothesized trends in bacterial nutrient limitation. *Ecol. Lett.* *4*, 453–457.
- Conley, D.J., Paerl, H.W., Howarth, R.W., Boesch, D.F., Seitzinger, S.P., Havens, K.E., Lancelot, C., and Likens, G.E. (2009). Controlling eutrophication: Nitrogen and phosphorus. *Science* *323*, 1014–1015.
- Cooke, G.D., Welch, E.B., Peterson, S., and Nichols, S.A. (2005). *Restoration and Management of Lakes and Reservoirs*, Third Edition (CRC Press).
- Costa, M.R.A. da, Attayde, J.L., and Becker, V. (2016). Effects of water level reduction on the dynamics of phytoplankton functional groups in tropical semi-arid shallow lakes. *Hydrobiologia* *778*, 75–89.
- Crompton, W.G., Isenhardt, T.M., and Mitchell, P.D. (1992). Nitrate and organic N analyses with second-derivative spectroscopy. *Limnol. Oceanogr.* *37*, 907–913.
- Currie, D.J., and Kalff, J. (1984). A comparison of the abilities of freshwater algae and bacteria to acquire and retain phosphorus. *Limnol. Oceanogr.* *29*, 298–310.
- Davies, J.-M., Nowlin, W.H., and Mazumder, A. (2004). Temporal changes in nitrogen and phosphorus codeficiency of plankton in lakes of coastal and interior British Columbia. *Can. J. Fish. Aquat. Sci.* *61*, 1538–1551.
- Davies, J.-M., Nowlin, W.H., Matthews, B., and Mazumder, A. (2010). Temporal discontinuity of nutrient limitation in plankton communities. *Aquat. Sci.* *72*, 393–402.
- Dessouki, T.C.E., Hudson, J.J., Neal, B.R., and Bogard, M.J. (2005). The effects of phosphorus additions on the sedimentation of contaminants in a uranium mine pit-lake. *Water Res.* *39*, 3055–3061.
- Dodson, S.I. (2005). *Introduction to limnology*. (New York: McGraw-Hill).
- Donald, D.B., Parker, B.R., Davies, J.-M., and Leavitt, P.R. (2015). Nutrient sequestration in the Lake Winnipeg watershed. *J. Gt. Lakes Res.* *41*, 630–642.
- Dubourg, P., North, R.L., Hunter, K., Vandergucht, D.M., Abirhire, O., Silsbe, G.M., Guildford, S.J., and Hudson, J.J. (2015). Light and nutrient co-limitation of phytoplankton communities in a large reservoir: Lake Diefenbaker, Saskatchewan, Canada. *J. Gt. Lakes Res.* *41*, *Supplement 2*, 129–143.
- Dzialowski, A.R., Wang, S.-H., Lim, N.-C., Spotts, W.W., and Huggins, D.G. (2005). Nutrient limitation of phytoplankton growth in central plains reservoirs, USA. *J. Plankton Res.* *27*, 587–595.
- Easton, Z.M., and Petrovic, A.M. (2005). Effect of hill slope on nutrient runoff from turf. *Golf Course Manage* *73*, 109–113.
- Edmondson, W.T. (1970). Phosphorus, Nitrogen, and Algae in Lake Washington after Diversion of Sewage. *Science* *169*, 690–691.

- Ekholm, P. (1994). Bioavailability of phosphorus in agriculturally loaded rivers in southern Finland. *Hydrobiologia* 287, 179–194.
- Elser, J.J., and Kimmel, B.L. (1985). Nutrient Availability for Phytoplankton Production in a Multiple-Impoundment Series. *Can. J. Fish. Aquat. Sci.* 42, 1359–1370.
- Elser, J.J., Bracken, M.E.S., Cleland, E.E., Gruner, D.S., Harpole, W.S., Hillebrand, H., Ngai, J.T., Seabloom, E.W., Shurin, J.B., and Smith, J.E. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecol. Lett.* 10, 1135–1142.
- Falkowski, P.G., and Raven, J.A. (2013). *Aquatic Photosynthesis*. (Princeton, N.J., USA: Princeton University Press).
- Falkowski, P., Scholes, R.J., Boyle, E., Canadell, J., Canfield, D., Elser, J., Gruber, N., Hibbard, K., Högberg, P., Linder, S., et al. (2000). The Global Carbon Cycle: A Test of Our Knowledge of Earth as a System. *Science* 290, 291–296.
- Fischer, E.M., and Knutti, R. (2015). Anthropogenic contribution to global occurrence of heavy-precipitation and high-temperature extremes. *Nat. Clim. Change* 5, 560–564.
- Fitzgerald, G.P. (1968). Detection of limiting or surplus nitrogen in algae and aquatic weeds. *J. Phycol.* 4, 121–126.
- Galloway, J.N., Townsend, A.R., Erisman, J.W., Bekunda, M., Cai, Z., Freney, J.R., Martinelli, L.A., Seitzinger, S.P., and Sutton, M.A. (2008). Transformation of the Nitrogen Cycle: Recent Trends, Questions, and Potential Solutions. *Science* 320, 889–892.
- Gaudreau, J.E., Vietor, D.M., White, R.H., Provin, T.L., and Munster, C.L. (2002). Response of turf and quality of water runoff to manure and fertilizer. *J. Environ. Qual.* 31, 1316–1322.
- Glibert, P.M. (2017). Eutrophication, harmful algae and biodiversity — Challenging paradigms in a world of complex nutrient changes. *Mar. Pollut. Bull.* 124, 591–606.
- Gloss, S.P., Reynolds, R.C., Mayer, L.M., and Kidd, D.E. (1981). Reservoir Influences on Salinity and Nutrient Fluxes in the Arid Colorado River Basin. (ASCE), pp. 1618–1629.
- Goosen, N.K., Kromkamp, J., Peene, J., van Rijswijk, P., and van Breugel, P. (1999). Bacterial and phytoplankton production in the maximum turbidity zone of three European estuaries: the Elbe, Westerschelde and Gironde. *J. Mar. Syst.* 22, 151–171.
- Government of Alberta (2002). *A Primer on Water Quality: Impact of Livestock Production Practices on Water Quality*.
- Graf, W.H. (1984). *Hydraulics of Sediment Transport* (Highlands Ranch, CO, USA: Water Resources Publication).
- Grove, J.R., Croke, J., and Thompson, C. (2013). Quantifying different riverbank erosion processes during an extreme flood event. *Earth Surf. Process. Landf.* 38, 1393–1406.

- Gu, P., Shen, R.F., and Chen, Y.D. (2008). Diffusion pollution from livestock and poultry rearing in the Yangtze Delta, China. *Environ. Sci. Pollut. Res.* *15*, 273.
- Guildford, S.J., and Hecky, R.E. (2000). Total nitrogen, total phosphorus, and nutrient limitation in lakes and oceans: Is there a common relationship? *Limnol. Oceanogr.* *45*, 1213–1223.
- Guildford, S.J., Bootsma, H.A., Fee, E.J., Hecky, R.E., and Patterson, G. (2000). Phytoplankton nutrient status and mean water column irradiance in Lakes Malawi and Superior. *Aquat. Ecosyst. Health Manag.* *3*, 35–45.
- Guildford, S.J., Hecky, R.E., Smith, R.E.H., Taylor, W.D., Charlton, M.N., Barlow-Busch, L., and North, R.L. (2005). Phytoplankton Nutrient Status in Lake Erie in 1997. *J. Gt. Lakes Res.* *31, Supplement 2*, 72–88.
- Hall, R.I., Leavitt, P.R., Quinlan, R., Dixit, A.S., and Smol, J.P. (1999). Effects of agriculture, urbanization, and climate on water quality in the northern Great Plains. *Limnol. Oceanogr.* *44*, 739–756.
- Hallock, D.D., and Falter, C.M. (1987). Powerboat Engine Discharges as a Nutrient Source in High-Use Lakes. *Lake Reserv. Manag.* *3*, 172–181.
- Harpole, W.S., Ngai, J.T., Cleland, E.E., Seabloom, E.W., Borer, E.T., Bracken, M.E.S., Elser, J.J., Gruner, D.S., Hillebrand, H., Shurin, J.B., et al. (2011). Nutrient co-limitation of primary producer communities. *Ecol. Lett.* *14*, 852–862.
- Hart, R.C. (1988). Zooplankton feeding rates in relation to suspended sediment content: potential influences on community structure in a turbid reservoir. *Freshw. Biol.* *19*, 123–139.
- Havens, K.E., Fukushima, T., Xie, P., Iwakuma, T., James, R.T., Takamura, N., Hanazato, T., and Yamamoto, T. (2001). Nutrient dynamics and the eutrophication of shallow lakes Kasumigaura (Japan), Donghu (PR China), and Okeechobee (USA). *Environ. Pollut.* *111*, 263–272.
- Healey, F.P. (1975). *Physiological Indicators of Nutrient Deficiency in Algae* (Winnipeg, MB, Canada: Research and Development Directorate, Freshwater Institute).
- Healey, F.P. (1979). Short-Term Responses of Nutrient-Deficient Algae to Nutrient Addition. *J. Phycol.* *15*, 289–299.
- Healey, F.P. (1985). Interacting Effects of Light and Nutrient Limitation on the Growth Rate of *Synechococcus Linearis* (cyanophyceae). *J. Phycol.* *21*, 134–146.
- Healey, F.P., and Hendzel, L.L. (1979). Indicators of Phosphorus and Nitrogen Deficiency in Five Algae in Culture. *J. Fish. Res. Board Can.* *36*, 1364–1369.
- Healey, F.P., and Hendzel, L.L. (1980). Physiological Indicators of Nutrient Deficiency in Lake Phytoplankton. *Can. J. Fish. Aquat. Sci.* *37*, 442–453.
- Hecker, M., Khim, J.S., Giesy, J.P., Li, S., and Ryu, J. (2012). Seasonal Dynamics of Nutrient Loading and Chlorophyll A in a Northern Prairies Reservoir, Saskatchewan, Canada. *J. Water Resour. Prot.* *04*, 180–202.

Hecky, R.E., and Guildford, S.J. (1984). Primary productivity of Southern Indian Lake before, during, and after impoundment and Churchill River diversion. *Can. J. Fish. Aquat. Sci.* *41*, 591–604.

Hecky, R.E., and Kilham, P. (1988). Nutrient limitation of phytoplankton in freshwater and marine environments: a review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.* *33*, 796–822.

Hessen, D.O., Færøvig, P.J., and Andersen, T. (2002). Light, Nutrients, and P:c Ratios in Algae: Grazer Performance Related to Food Quality and Quantity. *Ecology* *83*, 1886–1898.

Hewlett, C., North, R.L., Johansson, J., Vandergucht, D.M., and Hudson, J.J. (2015). Contribution of shoreline erosion to nutrient loading of the Lake Diefenbaker reservoir, Saskatchewan, Canada. *J. Gt. Lakes Res.* *41*, 110–117.

Higgins, S.N., Paterson, M.J., Hecky, R.E., Schindler, D.W., Venkiteswaran, J.J., and Findlay, D.L. (2017). Biological Nitrogen Fixation Prevents the Response of a Eutrophic Lake to Reduced Loading of Nitrogen: Evidence from a 46-Year Whole-Lake Experiment. *Ecosystems* 1–13.

Hooda, P.S., Edwards, A.C., Anderson, H.A., and Miller, A. (2000). A review of water quality concerns in livestock farming areas. *Sci. Total Environ.* *250*, 143–167.

Hudson, J.J., and Taylor, W.D. (1996). Measuring regeneration of dissolved phosphorus in planktonic communities. *Limnol. Oceanogr.* *41*, 1560–1565.

Hudson, J.J., and Taylor, W.D. (2005). Rapid estimation of phosphate at picomolar concentrations in freshwater lakes with potential application to P-limited marine systems. *Aquat. Sci.* *67*, 316–325.

Hudson, J.J., and Vandergucht, D.M. (2015). Spatial and temporal patterns in physical properties and dissolved oxygen in Lake Diefenbaker, a large reservoir on the Canadian Prairies. *J. Gt. Lakes Res.* *41*, Supplement 2, 22–33.

Hudson, J.J., Taylor, W.D., and Schindler, D.W. (2000). Phosphate concentrations in lakes. *Nature* *406*, 54–56.

International Lake Environment Committee Foundation (ILEC) (1993). Data List | Lake Diefenbaker | World Lake Database - ILEC (Japan).

Jansson, M. (1988). Phosphate uptake and utilization by bacteria and algae. *Hydrobiologia* *170*, 177–189.

Jeppesen, E., Brucet, S., Naselli-Flores, L., Papastergiadou, E., Stefanidis, K., Nöges, T., Nöges, P., Attayde, J.L., Zohary, T., Coppens, J., et al. (2015). Ecological impacts of global warming and water abstraction on lakes and reservoirs due to changes in water level and related changes in salinity. *Hydrobiologia* *750*, 201–227.

Ji, Z.-G. (2017). *Hydrodynamics and Water Quality: Modeling Rivers, Lakes, and Estuaries* (John Wiley & Sons).

Kalff, J. (2002). *Limnology: Inland water ecosystems*. (Upper Saddle River, N.J., USA: Prentice Hall).

Karlsson, J., Byström, P., Ask, J., Ask, P., Persson, L., and Jansson, M. (2009). Light limitation of nutrient-poor lake ecosystems. *Nature* 460, 506–509.

Keenan, J.D., and Auer, M.T. (1974). The Influence of Phosphorus Luxury Uptake on Algal Bioassays. *J. Water Pollut. Control Fed.* 46, 532–542.

Kelly, V.J. (2001). Influence of reservoirs on solute transport: a regional-scale approach. *Hydrol. Process.* 15, 1227–1249.

Khanna, D.R., Bhutiani, R., and Chandra, K.S. (2009). Effect of the Euphotic Depth and Mixing Depth on Phytoplanktonic Growth Mechanism. *Int. J. Environ. Res.* 3, 223–228.

Kimmel, B.L., and Groeger, A.W. (1984). Factors Controlling Primary Production in Lakes and Reservoirs: A Perspective. *Lake Reserv. Manag.* 1, 277–281.

Kimmel, B.L., Lind, O.T., and Paulson, L.J. (1990). Reservoir Primary Production. In *Reservoir Limnology: Ecological Perspectives*, (New York: Wiley-Interscience), p.

King, K.W., Harmel, R.D., Torbert, H.A., and Balogh, J.C. (2001). Impact of a turfgrass system on nutrient loadings to surface water. *JAWRA J. Am. Water Resour. Assoc.* 37, 629–640.

King, K.W., Balogh, J.C., Hughes, K.L., and Harmel, R.D. (2007). Nutrient load generated by storm event runoff from a golf course watershed. *J. Environ. Qual.* 36, 1021–1030.

Kirk, J.T.O. (1994). *Light and Photosynthesis in Aquatic Ecosystems*. (Cambridge, UK: Cambridge University Press).

Kunimatsu, T., Sudo, M., and Kawachi, T. (1999). Loading rates of nutrients discharging from a golf course and a neighboring forested basin. *Water Sci. Technol.* 39, 99–107.

Lean, D.R.S., and Pick, F.R. (1981). Photosynthetic Response of Lake Plankton to Nutrient Enrichment: A Test for Nutrient Limitation. *Limnol. Oceanogr.* 26, 1001–1019.

Lean, D.R.S., Abbott, A.P., Charlton, M.N., and Rao, S.S. (1983). Seasonal Phosphate Demand for Lake Erie Plankton. *J. Gt. Lakes Res.* 9, 83–91.

Lewis, W.M., and Wurtsbaugh, W.A. (2008). Control of Lacustrine Phytoplankton by Nutrients: Erosion of the Phosphorus Paradigm. *Int. Rev. Hydrobiol.* 93, 446–465.

Lind, O.T., and Dávalos-Lind, L. (1991). Association of turbidity and organic carbon with bacterial abundance and cell size in a large, turbid, tropical lake. *Limnol. Oceanogr.* 36, 1200–1208.

Lind, O.T., Chrzanowski, T.H., and Dávalos-Lind, L. (1997). Clay turbidity and the relative production of bacterioplankton and phytoplankton. *Hydrobiologia* 353, 1–18.

Lucas, B.T., Liber, K., and Doig, L.E. (2015). Reconstructing diatom and chironomid assemblages to infer environmental spatiotemporal trends within Lake Diefenbaker, a narrow river-valley reservoir on the Canadian Prairies. *J. Gt. Lakes Res.* 41, *Supplement 2*, 45–55.

- Mbonde, A.S., Sitoki, L., and Kurmayer, R. (2015). Phytoplankton composition and microcystin concentrations in open and closed bays of Lake Victoria, Tanzania. *Aquat. Ecosyst. Health Manag.* *18*, 212–220.
- McCarney-Castle, K., Voulgaris, G., and Kettner, A.J. (2010). Analysis of Fluvial Suspended Sediment Load Contribution through Anthropocene History to the South Atlantic Bight Coastal Zone, U.S.A. *J. Geol.* *118*, 399–416.
- Menzel, D.W., and Corwin, N. (1965). The measurement of total phosphorus in seawater based on the liberation of organically bound fractions by persulfate oxidation. *Limnol. Oceanogr.* *10*, 280–282.
- Millard, E.S., Myles, D.D., Johannsson, O.E., and Ralph, K.M. (1996). Seasonal phosphorus deficiency of Lake Ontario phytoplankton at two index stations: light versus phosphorus limitation of growth. *Can. J. Fish. Aquat. Sci.* *53*, 1112–1124.
- Milne, J.A. (2005). Societal expectations of livestock farming in relation to environmental effects in Europe. *Livest. Prod. Sci.* *96*, 3–9.
- Morris, J.G.J. (1999). Harmful Algal Blooms: An Emerging Public Health Problem with Possible Links to Human Stress on the Environment. *Annu. Rev. Energy Environ.* *24*, 367–390.
- Nanson, G.C., Von Krusenstierna, A., Bryant, E.A., and Renilson, M.R. (1994). Experimental measurements of river-bank erosion caused by boat-generated waves on the Gordon river, Tasmania. *Regul. Rivers Res. Manag.* *9*, 1–14.
- National Research Council (NRC) (1992). Restoration of aquatic ecosystems: science, technology, and public policy (Washington, D.C., USA: National Academies Press).
- National Research Council (NRC) (2000). Clean Coastal Waters: Understanding and Reducing the Effects of Nutrient Pollution. (Washington, D.C., USA: National Academies Press).
- Nicholls, K.H. (2001). Lake Simcoe water quality update: LSEMS Phase II progress report 1995–1999 with emphasis on phosphorus trends. LSEMS Implement. Tech. Rep. No ImpB19 Lake Simcoe Reg. Conserv. Auth. Newmark. Ont.
- Nogueira, M.G., Henry, R., and Maricatto, F.E. (1999). Spatial and temporal heterogeneity in the Jurumirim Reservoir, São Paulo, Brazil. *Lakes Reserv. Sci. Policy Manag. Sustain. Use* *4*, 107–120.
- North, R.L., Davies, J.-M., Doig, L.E., Lindenschmidt, K.-E., and Hudson, J.J. (2015a). Lake Diefenbaker: The prairie jewel. *J. Gt. Lakes Res.* *41*, *Supplement 2*, 1–7.
- North, R.L., Johansson, J., Vandergucht, D.M., Doig, L.E., Liber, K., Lindenschmidt, K.-E., Baulch, H., and Hudson, J.J. (2015b). Evidence for internal phosphorus loading in a large prairie reservoir (Lake Diefenbaker, Saskatchewan). *J. Gt. Lakes Res.* *41*, *Supplement 2*, 91–99.
- Paerl, H.W. (2009). Controlling Eutrophication along the Freshwater–Marine Continuum: Dual Nutrient (N and P) Reductions are Essential. *Estuaries Coasts* *32*, 593–601.



- Paerl, H.W., and Huisman, J. (2009). Climate change: a catalyst for global expansion of harmful cyanobacterial blooms. *Environ. Microbiol. Rep.* *1*, 27–37.
- Paerl, H.W., Fulton, R.S., Moisander, P.H., and Dyble, J. (2001). Harmful freshwater algal blooms, with an emphasis on cyanobacteria. *Sci. World J.* *1*, 76–113.
- Paerl, H.W., Xu, H., McCarthy, M.J., Zhu, G., Qin, B., Li, Y., and Gardner, W.S. (2011a). Controlling harmful cyanobacterial blooms in a hyper-eutrophic lake (Lake Taihu, China): The need for a dual nutrient (N & P) management strategy. *Water Res.* *45*, 1973–1983.
- Paerl, H.W., Hall, N.S., and Calandrino, E.S. (2011b). Controlling harmful cyanobacterial blooms in a world experiencing anthropogenic and climatic-induced change. *Sci. Total Environ.* *409*, 1739–1745.
- Paerl, H.W., Gardner, W.S., McCarthy, M.J., Peierls, B.L., and Wilhelm, S.W. (2014). Algal blooms: Noteworthy nitrogen. *Science* *346*, 175–175.
- Paerl, H.W., Scott, T.J., McCarthy, M.J., Newell, S.E., Gardner, W.S., Havens, K.E., Hoffman, D.K., Wilhelm, S.W., and Wurtsbaugh, W.A. (2016). It Takes Two to Tango: When and Where Dual Nutrient (N & P) Reductions Are Needed to Protect Lakes and Downstream Ecosystems. *Environ. Sci. Technol.* *50*, 10805–10813.
- Parsons, T.R., Maita, Y., and Lalli, C.M. (1984). *A Manual of Chemical & Biological Methods for Seawater Analysis.* (Oxford: Pergamon Press).
- Perry, M.J. (1972). Alkaline phosphatase activity in subtropical Central North Pacific waters using a sensitive fluorometric method. *Mar. Biol.* *15*, 113–119.
- Pettersson, K. (1980). Alkaline phosphatase activity and algal surplus phosphorus-deficiency indicators in Lake Erken. *Arch. Für Hydrobiol.* *89*, 54–87.
- Pick, F.R. (1987). Interpretations of alkaline phosphatase activity in Lake Ontario. *Can. J. Fish. Aquat. Sci.* *44*, 2087–2094.
- Pinheiro, J.C., and Bates, D.M. (2000). *Mixed-Effects Models in S and S-PLUS.* (New York: Springer).
- Prudhomme, C., Giuntoli, I., Robinson, E.L., Clark, D.B., Arnell, N.W., Dankers, R., Fekete, B.M., Franssen, W., Gerten, D., Gosling, S.N., et al. (2014). Hydrological droughts in the 21st century, hotspots and uncertainties from a global multimodel ensemble experiment. *Proc. Natl. Acad. Sci.* *111*, 3262–3267.
- Redfield, A.C. (1934). *On the proportions of organic derivatives in sea water and their relation to the composition of plankton.* (Liverpool, UK: Liverpool University Press).
- Rockwell, D.C., Warren, G.J., Bertram, P.E., Salisbury, D.K., and Burns, N.M. (2005). The U.S. EPA Lake Erie Indicators Monitoring Program 1983–2002: Trends in phosphorus, silica, and chlorophyll a in the central basin. *J. Gt. Lakes Res.* *31*, 23–34.
- Rose, C., and Axler, R.P. (1997). Uses of alkaline phosphatase activity in evaluating phytoplankton community phosphorus deficiency. *Hydrobiologia* *361*, 145–156.

- Sadeghian, A., de Boer, D., Hudson, J.J., Wheeler, H., and Lindenschmidt, K.-E. (2015). Lake Diefenbaker temperature model. *J. Gt. Lakes Res.* *41, Supplement 2*, 8–21.
- Saskatchewan Water Security Agency (SWSA) (2010). 2010 State of the Watershed Report.
- Saskatchewan Water Security Agency (SWSA) (2012a). Lake Diefenbaker Reservoir Operations: Context and Objectives (Saskatchewan Water Security Agency).
- Saskatchewan Water Security Agency (SWSA) (2012b). State of Lake Diefenbaker. Prepared for Consultation Meeting on May 30, 2012; revised on October 19, 2012.
- Schewe, J., Heinke, J., Gerten, D., Haddeland, I., Arnell, N.W., Clark, D.B., Dankers, R., Eisner, S., Fekete, B.M., Colón-González, F.J., et al. (2014). Multimodel assessment of water scarcity under climate change. *Proc. Natl. Acad. Sci.* *111*, 3245–3250.
- Schindler, D.W. (1974). Eutrophication and Recovery in Experimental Lakes: Implications for Lake Management. *Science* *184*, 897–899.
- Schindler, D.W. (1977). Evolution of Phosphorus Limitation in Lakes. *Science* *195*, 260–262.
- Schindler, D.W. (2012). The dilemma of controlling cultural eutrophication of lakes. *Proc. R. Soc. B Biol. Sci.* rspb20121032.
- Schindler, D.W., Hecky, R.E., Findlay, D.L., Stainton, M.P., Parker, B.R., Paterson, M.J., Beaty, K.G., Lyng, M., and Kasian, S.E.M. (2008). Eutrophication of lakes cannot be controlled by reducing nitrogen input: Results of a 37-year whole-ecosystem experiment. *Proc. Natl. Acad. Sci.* *105*, 11254–11258.
- Schindler, D.W., Carpenter, S.R., Chapra, S.C., Hecky, R.E., and Orihel, D.M. (2016). Reducing Phosphorus to Curb Lake Eutrophication is a Success. *Environ. Sci. Technol.* *50*, 8923–8929.
- Scott, J.T., and McCarthy, M.J. (2010). Nitrogen fixation may not balance the nitrogen pool in lakes over timescales relevant to eutrophication management. *Limnol Ocean.* *55*, 1265–1270.
- Scott, J.T., Stanley, J.K., Doyle, R.D., Forbes, M.G., and Brooks, B.W. (2009). River–reservoir transition zones are nitrogen fixation hot spots regardless of ecosystem trophic state. *Hydrobiologia* *625*, 61–68.
- Seehausen, O., van Alphen, J.J.M., and Witte, F. (1997). Cichlid Fish Diversity Threatened by Eutrophication That Curbs Sexual Selection. *Science* *277*, 1808–1811.
- Shatwell, T., and Köhler, J. Decreased nitrogen loading controls summer cyanobacterial blooms without promoting nitrogen-fixing taxa: Long-term response of a shallow lake. *Limnol. Oceanogr.* *00*, 1–13. DOI: 10.1002.
- Smeltzer, E., Shambaugh, A. d., and Stangel, P. (2012). Environmental change in Lake Champlain revealed by long-term monitoring. *J. Gt. Lakes Res.* *38*, 6–18.
- Smith, V.H., Tilman, G.D., and Nekola, J.C. (1999). Eutrophication: Impacts of excess nutrient inputs on freshwater, marine, and terrestrial ecosystems. *Environ. Pollut.* *100*, 179–196.

- Sobolev, D., Moore, K., and Morris, A.L. (2009). Nutrients and Light Limitation of Phytoplankton Biomass in a Turbid Southeastern Reservoir: Implications for Water Quality. *Southeast. Nat.* *8*, 255–266.
- Soggie, J. (2011). *Lake Quality Endangered, Star Phoenix*. CanWest MediaWorks Publ. Inc.
- Sonzogni, W.C., Chapra, S.C., Armstrong, D.E., and Logan, T.J. (1982). Bioavailability of Phosphorus Inputs to Lakes. *J. Environ. Qual.* *11*, 555–563.
- Stainton, M.P., Capel, M.J., and Armstrong, F.A.J. (1974). *The Chemical Analysis of Fresh Water* (Research and Development Directorate, Freshwater Institute).
- Sterner, R.W. (2008). On the Phosphorus Limitation Paradigm for Lakes. *Int. Rev. Hydrobiol.* *93*, 433–445.
- Sterner, R.W., and Elser, J.J. (2002). *Ecological Stoichiometry: The Biology of Elements from Molecules to the Biosphere*. (Princeton, N.J., USA: Princeton University Press).
- Sterner, R.W., Elser, J.J., Fee, E.J., Guildford, S.J., and Chrzanowski, T.H. (1997). The light: nutrient ratio in lakes: the balance of energy and materials affects ecosystem structure and process. *Am. Nat.* *150*, 663–684.
- Sun, C., and Wu, H. (2012). Pollution from animal husbandry in China: a case study of the Han River Basin. *Water Sci. Technol. J. Int. Assoc. Water Pollut. Res.* *66*, 872–878.
- Tanzeeba, S., and Gan, T.Y. (2012). Potential impact of climate change on the water availability of South Saskatchewan River Basin. *Clim. Change* *112*, 355–386.
- Thrane, J.-E., Hessen, D.O., and Andersen, T. (2014). The absorption of light in lakes: Negative impact of dissolved organic carbon on primary productivity. *Ecosystems* *17*, 1040–1052.
- Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R., and Polasky, S. (2002). Agricultural sustainability and intensive production practices. *Nature* *418*, 671–677.
- Tse, T.J., Doig, L.E., Leavitt, P.R., Quiñones-Rivera, Z.J., Codling, G., Lucas, B.T., Liber, K., Giesy, J.P., Wheeler, H., and Jones, P.D. (2015). Long-term spatial trends in sedimentary algal pigments in a narrow river-valley reservoir, Lake Diefenbaker, Canada. *J. Gt. Lakes Res.* *41, Supplement 2*, 56–66.
- Vandergucht, D.M., Sereda, J.M., Davies, J.-M., and Hudson, J.J. (2013). A comparison of phosphorus deficiency indicators with steady state phosphate in lakes. *Water Res.* *47*, 1816–1826.
- Vanni, M.J., Andrews, J.S., Renwick, W.H., Gonzalez, M.J., and Noble, S.J. (2006). Nutrient and light limitation of reservoir phytoplankton in relation to storm-mediated pulses in stream discharge. *Arch. Für Hydrobiol.* *167*, 421–445.
- Venables, H., and Moore, C.M. (2010). Phytoplankton and light limitation in the Southern Ocean: Learning from high-nutrient, high-chlorophyll areas. *J. Geophys. Res. Oceans* *115*, C02015.

Vogt, R.J., Sharma, S., and Leavitt, P.R. (2015). Decadal regulation of phytoplankton abundance and water clarity in a large continental reservoir by climatic, hydrologic and trophic processes. *J. Gt. Lakes Res.* *41*, 81–90.

Vollenweider, R.A. (1970). Scientific fundamentals of the eutrophication of lakes and flowing waters, with particular reference to nitrogen and phosphorus as factors in eutrophication (Organisation for Economic Co-operation and Development).

Water Quality Branch (WQB) (1988). Lake Diefenbaker and Upper South Saskatchewan River: Water Quality Study 1984–85.

Webb, J., and Archer, J.R. (1994). Pollution of soils and watercourses by wastes from livestock production systems. In *Pollution in Livestock Production Systems*, (Wallingford, UK: CABI), pp. 189–204.

Winter, J.G., and Dillon, P.J. (2005). Effects of golf course construction and operation on water chemistry of headwater streams on the Precambrian Shield. *Environ. Pollut.* *133*, 243–253.

World Wildlife Fund (WWF) (2009). *Canada's rivers at risk* (World Wildlife Fund).

Wozniak, B., Dera, J., Ficek, D., Ostrowska, M., and Majchrowski, R. (2002). Dependence of the photosynthesis quantum yield in oceans on environmental factors. *Oceanologia* *44*.

Xenopoulos, M.A., Frost, P.C., and Elser, J.J. (2002). Joint effects of UV radiation and phosphorus supply on algal growth rate and elemental composition. *Ecology* *83*, 423–435.

Yasarer, L.M.W., and Sturm, B.S.M. (2016). Potential impacts of climate change on reservoir services and management approaches. *Lake Reserv. Manag.* *32*, 13–26.

Yip, H.D., Johansson, J., and Hudson, J.J. (2015). A 29-year assessment of the water clarity and chlorophyll-a concentration of a large reservoir: Investigating spatial and temporal changes using Landsat imagery. *J. Gt. Lakes Res.* *41*, Supplement 2, 34–44.

Yousef, Y.A., McLellon, W.M., and Zebuth, H.H. (1980). Changes in phosphorus concentrations due to mixing by motorboats in shallow lakes. *Water Res.* *14*, 841–852.

Zarfl, C., Lumsdon, A.E., Berlekamp, J., Tydecks, L., and Tockner, K. (2014). A global boom in hydropower dam construction. *Aquat. Sci.* *77*, 161–170.

Zohary, T., Padisák, J., and Naselli-Flores, L. (2010). Phytoplankton in the physical environment: beyond nutrients, at the end, there is some light. *Hydrobiologia* *639*, 261–269.