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Effects of multiple stressors on primary production in Lake Erie

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EFFECTS OF MULTIPLE STRESSORS ON PRIMARY PRODUCTION IN LAKE ERIE

By

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DECLARATION OF CO-AUTHORSHIP

I hereby declare that this thesis incorporates material that is result of joint research, as follows: Chapter 2, with contributions from Chapter 1 and Chapter 4, is being prepared to submit as a peer-reviewed article to Limnology and Oceanography, with Anne M. McLeod, Marguerite A. Xenopoulos, and G. Douglas Haffner as co-authors. The author performed the sampling and lab work, data analysis, interpretation, and writing. G. Douglas Haffner contributed to the experimental design and guidance with field and lab work, while Anne M. McLeod assisted with statistical analysis. Both G. Douglas Haffner and Marguerite A. Xenopoulos contributed funding support. All co-authors contributed by revising manuscript drafts.

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ABSTRACT

An unnatural increase in primary production is the main driver of accelerated eutrophication, which causes negative impacts in aquatic systems around the world. Studying factors regulating primary production is therefore critical in systems such as Lake Erie, which experiences eutrophication and has been impacted by many stressors. In this thesis, I investigated factors regulating primary production in Lake Erie on both a long-term temporal scale (by comparing summer values from 1970 to 2014/15 in the western basin) and a spatial scale (by comparing nearshore and offshore sites among the three basins). Both studies suggested that multiple stressors, such as changes in nutrient loading, dreissenid grazing, and light penetration, are likely regulating primary production in Lake Erie. Dreissenid grazing and phosphorus loading reductions may have contributed to a long-term decrease in volumetric primary production in the western basin, as well as to similar volumetric primary production between near and offshore sites in all three basins. Meanwhile, a long-term increase in light penetration in the western basin resulted in no significant change in areal primary production since 1970. Increased light penetration in the eastern basin also resulted in no significant difference in areal primary production compared to the other basins, despite significantly lower volumetric primary production in the eastern basin. In the future, nutrient enrichment experiments and annual primary production measurements are needed. This study demonstrates the complexity of factors regulating primary production and the importance of studying these factors to understand drivers of eutrophication and food web dynamics in Lake Erie.

DEDICATION

To my parents Bryan and Joanne Hillis, for your continuous support.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Introduction

One of the largest global threats to freshwater resources is accelerated eutrophication, which is an unnatural increase in primary production resulting in high phytoplankton biomass in aquatic ecosystems (Richardson and Jorgensen 1996). High phytoplankton biomass causes declines in water clarity and dissolved oxygen, and has been associated with a loss of fish habitat (Paerl and Otten 2013) and increasing incidences of fish kills (Hall et al. 1999). A decline in the perceived aesthetics of a lake associated with increased phytoplankton biomass also has negative economic impacts. For example, in 2014, the total economic cost of eutrophication in Lake Erie was estimated to be $65 million (USD), as a result of decreased property values, declines in tourism revenue and recreational opportunities, and increased costs for drinking water treatment (Bingham et al. 2015).

Accelerated eutrophication often leads to a shift in phytoplankton community composition towards bloom-forming phytoplankton such as cyanobacteria, some of which are potentially toxic. Cyanobacterial blooms occur in freshwater systems on all inhabited continents, some examples which include Lake Winnipeg, North America (Schindler et al. 2012), Tabocas Reservoir, South America (Carmichael et al. 2001), Lake Niewe Meer, Europe (Jöhnk et al. 2008), Lake Taihu, Asia (Paerl et al. 2011), Lake Victoria, Africa (Sitoki et al. 2012) and Lake Mokoan, Australia (Davis and Koop 2006). In the western basin of Lake Erie, high levels of the toxin microcystin resulted in a three-day drinking water ban in 2014 for 500,000 residents of Toledo, Ohio (Carmichael and Boyer 2016). Furthermore, cyanobacterial blooms are often composed of species which are resistant to zooplankton grazing, resulting in changes in energy

and nutrient flow in aquatic food webs (Paerl and Otten 2013). In systems with economically important commercial fisheries, such as Lake Erie, food web effects are particularly concerning.

The environmental, economic, and human health impacts associated with accelerated eutrophication necessitates the need to study the relative importance of factors regulating primary production. Primary production is not just a driver of accelerated eutrophication, it also is the most important source of energy in aquatic food webs. Rates of primary production at the cellular level are typically regulated by a combination of factors which include temperature, light, grazing, and nutrient bioavailability (Fig. 1.1, Richardson and Jorgensen 1996, Carpenter et al. 1987). Human activities, however, can modify rates of primary production in aquatic ecosystems through stressors such as climate change (O'Reilly et al. 2003), overfishing (Scheffer et al. 2005), species invasions (Fahnenstiel et al. 1995) as well as nutrient enrichment (Goldman 1988). These multiple stressors are often interactive and interdependent, making it difficult to predict changes in primary production with respect to change in a single factor.

Although multiple factors are important, attempts are often made to identify the main limiting factor of primary production, which according to Liebig's law of the minimum is the resource that is least abundant relative to the needs of the organism (Wetzel 2001). A comparison of the supply and demand of nutrients in freshwater systems suggests that phosphorus, followed by nitrogen, are usually the first nutrients to limit primary production (Vallentyne 1974). There have also been analyses of multiple lakes which found strong positive correlations between chlorophyll *a* (chl *a*) concentrations (a proxy measurement for phytoplankton biomass) and total phosphorus (TP) concentrations (Schindler 1977; Dillon and Rigler 1974). These empirical models of chl *a* vs TP have been used globally to predict and manage phytoplankton biomass (Schindler et al. 2016), and often assume primary production is

primarily driven by nutrient loadings (Vollenweider et al. 1974). In order to manage eutrophication in different aquatic ecosystems, the relationship between phytoplankton biomass, primary production and nutrient inputs is used to determine target loads for key nutrients such as TP (Dolan and McGunagle 2005).

For example, Lake Erie experienced many symptoms associated with eutrophication during the 1960s and 1970s such as high phytoplankton biomass, western basin cyanobacteria blooms, eastern basin *Cladophora* blooms, and central basin hypoxia (Steffen et al. 2014; Watson et al. 2016). Based on the Vollenweider et al. (1974) model relating TP loadings to annual areal primary production, target TP loadings were set for the Laurentian Great Lakes (LGL) in the 1972 Great Lakes Water Quality Agreement (GLWQA, IJC 1978) to combat these issues. These targets were largely met by the mid-1980s (Maccoux et al. 2016), which corresponded with a decline in phytoplankton biomass and chl *a* across all three basins (Makarewicz and Bertram 1991). However, since the mid-1990s, water quality problems returned in the form of cyanobacteria and *Cladophora* blooms in the western and eastern basins, respectively (Conroy et al. 2005; Watson et al. 2016). Summer hypolimnetic oxygen concentrations in the central basin also decreased after 1996 (Scavia et al. 2014).

While the decrease in phytoplankton biomass and chl *a* from the 1970s to the mid-1980s suggests that declining TP loadings were improving water quality, primary production on either a volumetric (PP_{vol}) or areal (PP_{areal}) scale was not measured during this time (Millard et al. 1999). It is therefore unknown whether primary production decreased at the same rate as phytoplankton biomass or chl *a*. Change in the ratio of PP_{vol} to chlorophyll *a*, known as the assimilation efficiency, would reflect algal adaptation to environmental changes, mainly by changing pigmentation in response to changes in light and nutrient availability (Behrenfeld et al. 2002).

The scarcity of primary production measurements also makes it difficult to determine whether factors regulating primary production changed on a long-term basis among the three basins. While phosphorus is often considered the main regulating factor of primary production, grazing by invasive dreissenid mussels in Lake Erie may decrease phytoplankton biomass (Fig. 1.1) or increase light penetration (Leach 1993), both of which are factors that can regulate PP_{vol} and PP_{areal} (Fahnenstiel et al. 1995, Fitzpatrick et al. 2007). There is also evidence that dreissenids may be contributing to a greater decrease in PP_{vol} and PP_{areal} at nearshore versus offshore sites in the LGL (Depew et al. 2006).

The objective of this thesis was to quantify spatial and temporal variation of primary production and potential regulating factors in Lake Erie. Chapter Two addressed whether PP_{vol} and PP_{areal}, along with chl *a*, phytoplankton biomass and community composition, light penetration, water temperature, and nutrient concentrations (TP and nitrate) changed on a long-term basis (from 1970 to 2014 and 2015) in the western basin. Chapter Three addressed spatial variation both among the three basins and between nearshore and offshore sites for the same factors as in Chapter Two (minus phytoplankton biomass and community composition). Chapter Four synthesized the results from both chapters and considered future research that should be conducted in Lake Erie. More knowledge of the effects of multiple stressors on primary production is needed to address eutrophication issues while maintaining sustainable fisheries in Lake Erie.

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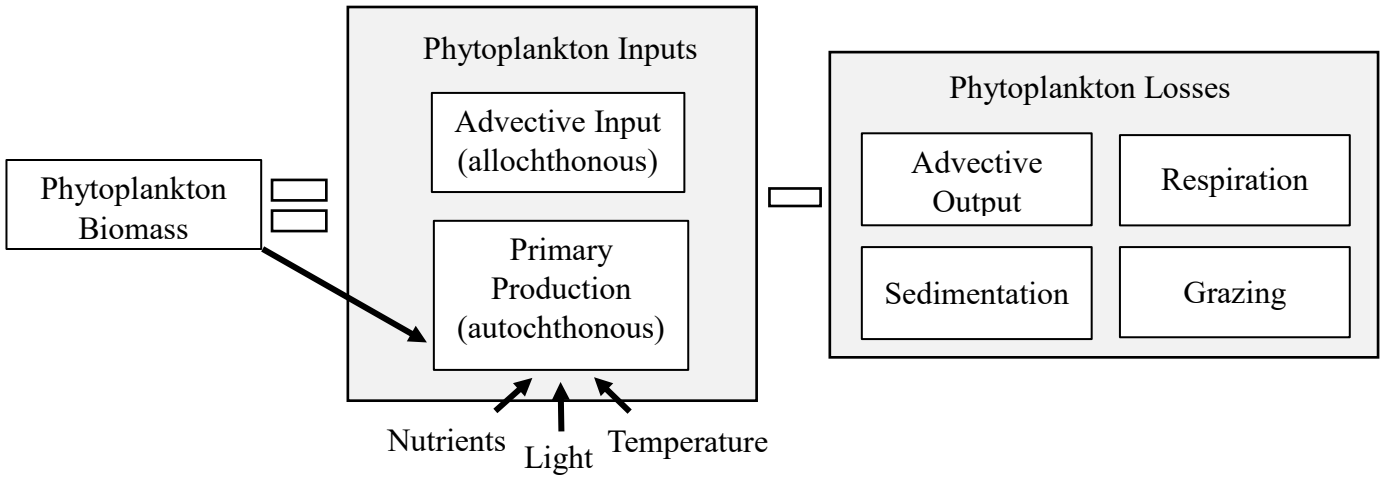

Figure 1.1. Conceptual model showing the phytoplankton inputs and losses in a water body contributing to phytoplankton biomass. Accelerated eutrophication is defined here as an increase in primary production beyond natural levels.

CHAPTER 2

FACTORS REGULATING LONG-TERM CHANGES IN PRIMARY PRODUCTION IN THE WESTERN BASIN OF LAKE ERIE

2.1 Introduction

Despite the recognition of the many effects of multiple stressors on lakes, few studies have been conducted that examine long-term variability of primary production and its response to multiple stressors. A 25-year study at meso-oligotrophic Castle Lake concluded that meteorological factors such as ice breakup date and spring precipitation, as well as top-down effects from variation in rainbow trout catch, regulated inter-annual variability in seasonal PP_{vol} (Jassby et al. 1990). In ultra-oligotrophic Lake Tahoe, an increase in PP_{areal} from 1973 to 1987 correlated with an increase in nitrate (NO_3^-) (Goldman 1988) while a study from Lake Kinneret found no change in PP_{areal}, chl *a* or phytoplankton biomass over 22 years (Berman et al. 1995). These studies suggested that different lakes vary in the relative importance of different stressors regulating long-term primary production. The deficiency of long-term primary production studies is often because such measurements are considered difficult, time-consuming, and expensive to implement. As a result, interannual variability in the relative importance of factors regulating primary production remains unknown for many important aquatic ecosystems.

Primary production in the western basin of Lake Erie not only is the primary driver of eutrophication (Fig. 2.1; Vollenweider et al 1974), it is also critical to sustaining fish production (Fitzpatrick et al. 2008), especially considering that Lake Erie has one of the largest freshwater commercial fisheries in the world. The management of eutrophication in Lake Erie in the 1970s-80s became a global example of a successful restoration of a large lake ecosystem through nutrient control. The TP target load for Lake Erie of 11 000 metric tonnes per annum, which was

set under the 1972 GLWQA, was met by the mid-1980s by reducing levels of phosphates in laundry detergents and upgrading wastewater treatment plants to decrease TP in wastewater (Dolan and McGunagle 2005). Phytoplankton biomass and chl *a* declined in the western basin by the mid-1980s, corresponding with the P reductions (Makarewicz and Bertram 1991).

Since the mid-1990s, however, the western basin has experienced an increase in cyanobacteria biomass (Conroy et al. 2005). Climate change may be playing a role since cyanobacteria tend to have higher optimal temperatures compared to other phytoplankton such as diatoms or chlorophytes (Jöhnk et al. 2008). Extreme precipitation events in the spring of 2011 also contributed to the largest harmful algal bloom in the western basin at the time, demonstrating how climate change is involved in modifying nutrient inputs (Michalak et al. 2013). Although the average annual TP loadings into Lake Erie have not significantly changed from 1987 to 2013 (Maccoux et al. 2016), soluble reactive phosphorus (SRP) has increased in the Maumee River due to intensive agricultural practices (Stow et al. 2015; Michalak et al. 2013). In response to these cyanobacteria blooms, a recent binational report (Annex 4 Objectives and Targets Task Team 2015) used a modeling ensemble approach (Obenour et al. 2014; Stumpf et al. 2012) to recommend a 40% decrease in spring TP and DRP (dissolved reactive phosphorus) loadings in priority watersheds in the western basin.

Lake Erie has also experienced many other important stressors, one example being the invasion of zebra mussels (*Dreissenia polymorpha*) in 1988 (Leach 1993) followed by quagga mussels (*Dreissenia rostriformis bugensis*) in 1989 (Mills et al. 1993). Dreissenid mussels have been shown to modify nutrient cycling (North et al. 2012), light penetration (Leach 1993) and phytoplankton composition through selective grazing (Vanderploeg et al. 2001). Considerable concern has been expressed for the future of the fisheries in the Laurentian Great Lakes (LGL) as

a result of nutrient and energy diversions associated with the dreissenid invasion (Hecky et al. 2004; Fera et al. 2017). Fitzpatrick et al (2008) concluded that current (2000-2002) PP_{areal} rates in the western basin of Lake Erie were just sufficient to meet the primary production required (PPR) to sustain the fisheries. Measuring carbon turnover time (the ratio of phytoplankton carbon to PP_{vol}) is another way to determine whether primary production is replacing the phytoplankton carbon pool at a constant rate, which would support upper levels of the food web.

Despite the importance of primary production to regulate phytoplankton biomass and sustain fisheries, primary production studies in the western basin of Lake Erie are rare. There was only one study in 1970 (Glooschenko et al. 1974a) and five studies during the 1990s and early 2000s (Dahl et al. 1995; Smith et al. 2005; Fitzpatrick et al. 2007; Porta et al. 2005; Ostrom et al. 2005). It is therefore unknown whether PP_{vol} and PP_{areal} decreased at the same rate as phytoplankton biomass or chl *a* from the 1970s to the mid-1980s (Millard et al. 1999; Makarewicz and Bertram 1991). Change in the ratio of PP_{vol} to chlorophyll *a*, known as the assimilation efficiency, would reflect algal adaptation to environmental changes, mainly by changing pigmentation in response to changes in light and nutrient availability (Behrenfeld et al. 2002). The lack of consistent monitoring of primary production also makes it difficult to determine the relative importance of factors regulating primary production on a long-term scale, and whether multiple stressors such as changes in nutrient loading, climate change, and species invasions have affected primary production.

The aim of this study was to determine if primary production rates in the western basin of Lake Erie changed between 1970 and 2015 with respect to declining nutrient loads and the invasion of dreissenid mussels. Specifically, we addressed two main questions:

1) Have the rates of PP_{vol} and PP_{areal} changed in the Western Basin of Lake Erie on a long-term scale (1970 - 2015), and

2) How have factors potentially regulating primary production (specifically light penetration, assimilation efficiency, chl *a*/biomass ratios, phytoplankton composition and carbon turnover rates) changed during this time?

These objectives were met by implementing a study of primary production in 2014 and 2015 using techniques and methods that were comparable to historic studies.

2.2 Methods

Sampling Design

Sampling occurred at a nearshore (N41°58.801', W 82°56.183') and an offshore site (N41°51.396', W 82°59.137') in the western basin of Lake Erie approximately once a month from May to October in 2014 and 2015 (Fig. 2.2). Water samples were collected at 5 depths throughout the water column (0, 1, 2, 3 and 4m for the nearshore site; 0, 1, 3, 5 and 7m for the offshore site) and analyzed for nutrient concentrations (TP and NO_3^-), primary production, chl *a*, phytoplankton biomass, and phytoplankton community composition. The average maximum depths (Z_{max}) during 2014 and 2015 were 7.2 ± 0.2 m at the nearshore site and 10.3 ± 0.1 m at the offshore site (± SE). Water column profiles were also taken for temperature and irradiance.

Lake Physical Characteristics

Water temperature was measured from the surface to Z_{max} using a RBR *maestro* logger. Irradiance measurements were taken at 1m intervals using a LI-250A light meter attached to a LI-193 spherical quantum sensor. The Beer-Lambert Law (Richardson et al. 1983, Scheffer 1998) was used to calculate the light attenuation coefficient such that

(eq. 1) $$I_z = I_0 e^{-\varepsilon_{par} z}$$

where I represents irradiance at the surface (I_0) and at depth Z (I_z) and ε_{par} is the vertical attenuation coefficient. One can then solve for ε_{par}:

(eq. 2) $$\varepsilon_{par} = \frac{(lnI_0 - lnI_z)}{Z}$$

Here, irradiance at 2m was used for surface irradiance (I_0) since wave action can cause irradiance to vary greatly right at the surface (Wetzel 2001). The deepest depth where irradiance was greater than 1 µmol s^{-1} m^{-2} was used for I_z.

Euphotic depth (Z_{eu}) was defined as the depth at which irradiance is equal to one percent of surface irradiance (or $I_{Zeu} = 0.01I_0$), below which net photosynthesis does not occur. Thus, equation 1 can be re-written as:

(eq. 3) $$0.01I_0 = I_0 e^{-\varepsilon_{par} Z_{eu}}$$

simplifying to:

(eq. 4) $$Z_{eu} = \frac{4.60517}{\varepsilon_{par}}$$

Nutrients

The ascorbic acid method (Eaton et al. 1995) was used to determine TP concentrations on a Beckman DU-530 spectrophotometer at the Great Lakes Institute for Environmental Research, University of Windsor. The cadmium reduction method was used to determine NO_3^- concentrations (Eaton et al. 1995) at the Stable Isotope Ecology Lab, Center for Applied Isotope Studies, University of Georgia.

Primary Production

Primary production was measured using the in situ light and dark bottle C^{14} method (adapted from Vollenweider 1974). Two transparent 300 mL BOD (biological oxygen demand) bottles and one black BOD bottle were filled with lake water from each depth. The bottles were injected with 10 µCi of C^{14} contained in a sodium bicarbonate solution at a pH of 9.5 and

incubated at their respective depths for 2 - 4 hours. Incubations took place in the morning, when carbon uptake is greatest (Verduin 1957). From each bottle, 250 mL of lake water was filtered through a Millipore nitrocellulose membrane filter (pore size 0.45 µm). The filter was rinsed with 0.01N HCl to remove carbonate material (Fitzpatrick 2003) and placed in a scintillation vial with 15 mL of EcoLite liquid scintillation cocktail (MP Biomedicals) for at least 24 hours. The vials were run on a Beckman LS6500 Scintillation Counter to obtain radioactive counts per minute (CPM).

For each depth, the dark bottle CPM value was subtracted from the average of the two light bottles, converted to mg C by dividing by a correction factor of 20,943,396 and multiplied by 4 to obtain C^{14} uptake in mg C L^{-1}. Primary production was calculated according to the following equation, adapted from Fitzpatrick (2003) and Vollenweider (1974):

(eq. 5) $$Primary\ production = \frac{C^{14}\ uptake \times C^{12} available \times 1.06}{incubation\ time}$$

where C^{12} available is the amount of carbon available for photosynthesis and 1.06 is the isotope correction factor. For C^{12} available, 21 mg C L^{-1} was used to remain comparable with previous studies (Fitzpatrick et al. 2007, Porta et al. 2005, Glooschenko et al. 1974a). Based on carbonate alkalinity, temperature, and pH reported in Sheffield et al. (1975) and the United States Environmental Protection Agency's Great Lakes Environmental Database (GLENDA, US EPA), average C^{12} available (calculated according to Figure 3.1 in Vollenweider 1974) ranged from 20 to 22 mg C L^{-1} from 1974 to 2014.

Chl *a*

Acetone pigment extraction was used to determine chl *a* concentrations (Eaton et al. 1995, Strickland and Parsons 1968). Between 0.25 - 1L of lake water from each depth was filtered through Whatman GF/C filters (pore size 1.2 µm). The filters were extracted using 30

mL of magnesium carbonate acetone solution prepared according to Eaton et al. (1995), and run on a Beckman DU-530 spectrophotometer, recording absorbances at four wavelengths (630, 645, 665 and 750 nm). MilliQ water was also filtered and the filter was extracted and run as a blank. The following equation from Strickland and Parsons (1968) was used to calculate chl *a* in the sample according to:

(eq. 6) $chla_s = 11.6(ab_{665} - ab_{750}) - 1.31(ab_{645} - ab_{750}) - 0.14(ab_{630} - ab_{750})$

where $chla_s$ is the chl *a* in the sample and ab is the absorbance at the specified wavelength. Using $chla_s$, the concentration of chl *a* in the lake water (chl *a*; in mg m^{-3}) was calculated as follows:

(eq. 7) $chla = \frac{chla_s \text{ x } volume_{ex}}{volume_{fi} \text{ x } p_{length}}$

where $volume_{ex}$ is the volume of magnesium carbonate acetone solution used to extract the chl *a* (30 mL), $volume_{fi}$ is the volume of lake water filtered (between 0.25 - 1 L) and pl_{engh} is the path length of the cuvette used in the spectrophotometer (10 cm).

Phytoplankton biomass and community composition

The inverted microscope technique, modified from Utermöhl (1958), was used to determine phytoplankton biomass and community composition. From each depth, 250 mL of lake water was collected in an Amber Boston bottle and preserved with 5 mL of Lugol's Iodine, prepared according to Eaton et al. (1995). Each bottle was shaken thoroughly before placing 5 mL in a settling chamber for at least 24 hours to allow phytoplankton cells to settle to a bottom slide. The cells were observed under 400x magnification on a Leica DM IRB microscope and identified to their taxonomic group using Wehr et al. (2015), Prescott (1954), and Bellinger and Sigee (2010) as references.

Cell dimensions were measured using a Leica EC3 camera and Leica Application Suite Version 4.5 software, which was calibrated using a stage micrometer. These measurements were applied to standard geometric shapes to obtain biovolumes, using Hillebrand et al. (1999) as a reference. Some exceptions to this approach include the chlorophyte *Pediastrum*, where each cell in a colony was measured as a rod (i.e. a prolate spheroid) per Vadrucci et al. (2007). In other cases, such as centric and pennate diatoms (e.g. *Stephanodiscus,* and *Navicula* respectively), the formulas from Hillebrand et al. (1999) could not be used because the third dimension (depth) was not visible. When this occurred, it was assumed that depth equals width (Sun and Liu 2003), and so the centric diatom was measured as a sphere instead of a cylinder, while the pennate diatom was measured as a rod instead of an elliptic prism.

For each slide, the cells in 10 field of views were identified and measured, and average biovolume based on these was extrapolated to the entire slide. Biovolume was converted to wet weight of biomass by assuming phytoplankton cells have a specific gravity of one, so 10^9 μm^3 of phytoplankton have a mass of 1 mg (Strickland 1960). Biomass of each taxonomic group (Bacillariophyta, Chlorophyta, Cyanophyta, Cryptophyta, and Chrysophyta) was calculated and summed to obtain total biomass.

Wet weight of biomass (in g m^{-3}) was converted to phytoplankton carbon using the equation of Rocha and Duncan (1985):

(eq. 8) $$Phytoplankton\ carbon\ pool = 0.12\ (wet\ weight\ biomass)^{1.051}$$

The phytoplankton carbon pool was calculated for each taxonomic group and then summed.

Calculations for areal and volumetric water column estimates

Volumetric water column averages were calculated for primary production, chl *a*, phytoplankton biomass for each taxonomic group, and nutrients based on trapezoidal integration (Knap et al. 1996). Primary production vs depth was plotted using the Paleontological Statistics Software Package for Education and Data Analysis (PAST) software (Hammer et al. 2001). The points were fit to either a linear or a non-linear (between quadratic, gaussian or logistic) regression, which was determined by choosing the curve with the lowest AIC (Akaike Information Criterion) value. Primary production at the euphotic depth was estimated based on this curve, and areal primary production (PP_{areal} in mg C m^{-2} h^{-1}) was calculated by integrating from the surface to the euphotic depth. Dividing PP_{areal} by the euphotic depth resulted in a weighted volumetric average of the water column (PP_{vol} in mg C m^{-3} h^{-1}).

As a result of isothermal mixing, phytoplankton biomass and nutrients are mixed below the euphotic depth, and therefore water column areal estimates for chl *a*, phytoplankton biomass, and nutrients were calculated using trapezoidal integration from the surface to Z_{max}. Values at Z_{max} were estimated according to the equation of the biomass (or chl *a*, TP or NO_3^-) vs depth curve, which was chosen as described earlier. Weighted average volumetric estimates were calculated by dividing the areal values by Z_{max}. The average water temperature was simply an average from the surface to Z_{max}

Estimating daily and annual primary production

Daily primary production (areal and volumetric) was estimated by multiplying PP_{vol} and PP_{areal} by day length. This was assumed to be 9 hours for spring and fall (March 20- June 20, and September 23 – December 21, respectively), and 12 hours for summer (June 21-September 22), following the conversion factors in Glooschenko et al. (1974a). Carbon turnover time (days) was calculated by dividing the phytoplankton carbon pool by daily PP_{vol}.

Annual PP_{areal} was also estimated from daily PP_{areal} to compare with the 1970 values used in the Vollenweider et al. (1974) model. In 1970, PP_{areal} was integrated from April to December (Glooschenko et al. 1974a) and then increased by 10% to estimate annual PP_{areal} (Vollenweider et al. 1974). However, in 2014 and 2015 sampling only took place from May to October. To correct for the shorter sampling season, 1970 PP_{areal} was integrated from May 1 to October 31 and then compared to annual PP_{areal} to approximate a conversion factor of 27%. Therefore, PP_{areal} in 2014 and 2015 was integrated from May 1 to October 31 and then increased by 27% to estimate annual PP_{areal}. PP_{areal} on May 1 and October 31 was estimated by fitting the points to a quadratic or gaussian curve.

Statistical analysis for long-term trends (1970 - 2015)

To quantify long-term trends, June to September values for $\varepsilon_{par,}$ average water column temperature, hourly PP_{vol} and PP_{areal}, TP and NO_3^- concentrations, phytoplankton biomass, chl *a*, and relative biomass of diatoms, cyanobacteria and chlorophytes were compared to historical studies, which are listed in Table 1. The ratios of PP_{vol} to chl *a* (assimilation efficiencies), chl *a* to biomass, and phytoplankton carbon pool to PP_{vol} (carbon turnover times) were also compared to earlier years. The studies selected all had to have measured primary production in the Western Basin, along with either chl *a* or phytoplankton biomass (or both). Primary production was measured using either *in situ* or incubator C^{14} methods, methods which Fitzpatrick et al. (2007) concluded were comparable in the Western Basin. All chl *a* data were uncorrected for phaeopigments. Sampling also usually took place from at least June to September. Two exceptions were 1997 (Smith et al. 2005), when September sampling did not occur, and ε_{par} in 1970, when only June and September data were available. 1970 secchi depth data was converted to ε_{par} using the following equation (Poole and Atkins 1929):

(eq. 9) $$\varepsilon_{par} = \frac{1.7}{secchi\ depth}$$

Data from separate stations was obtained for all the variables except 1970 PP_{areal}, where instead the average daily PP_{areal} for the Western Basin in Glooschenko et al. (1974a) was divided by the day length conversion factors in Glooschenko et al. (1974a) (listed previously) to obtain hourly PP_{areal}. M. Fitzpatrick provided the rest of the 1970 separate station data from the Environment Canada STAR database, which is summarized as Western Basin averages in Glooschenko et al. (1974a and b), Munawar and Munawar (1996), and Gächter et al. (1974). Daily cloudless PP_{areal}, which was reported for 1993 (Dahl et al. 1995) and 1997 (Smith et al. 2005) using the computer program of (Fee 1990), was also divided by the Glooschenko et al. (1974a) conversion factors to obtain hourly PP_{areal}. These values were then divided by Z_{eu} to obtain PP_{vol}. Finally, PP_{vol} in 2001 and 2002 (Fitzpatrick et al. 2007) and 2003 (Porta et al. 2005) was multiplied by Z_{eu} to obtain PP_{areal}.

When required, data were obtained from figures using the online software WebPlotDigitizer v. 3.11 (Rohatgi 2017). An ordinary least squares regression was conducted using PAST software (Hammer et al. 2001) to determine if there was a significant change in the slope. The significance level was set at $\alpha = 0.05$.

Statistical analysis of seasonal primary production patterns (May- October)

AIC stepwise backwards model selection was used to determine the relative importance of chemical, physical, and biological factors regulating PP_{vol}, chl *a* and biomass at depth in 2014 and 2015. Initial factors included: year (2014 or 2015), location (nearshore or offshore), depth (as related to light attenuation), average water column temperature, nutrient concentrations (TP and NO_3^-), and two phytoplankton variables (among PP_{vol}, phytoplankton biomass, and chl *a*). Final factors were then run as generalized linear models (GLMs) to compare multiple R^2 values

and determine those factors most strongly correlated to primary production and algal biomass. These analyses were performed using RStudio Team (2015). GLMs for chl *a* and phytoplankton biomass and multiple R^2 values for all three variables are summarized in the Supporting Information (Table S1 and Table S2).

2.3 Results

There was a significant decrease in PP_{vol} from a June-September mean of 45 ± 13 mg C m^{-3} h^{-1} in 1970 to 24 ± 2 mg C m^{-3} h^{-1} in 2014 and 2015 (mean of both years, Table 2.1a, Fig. 2.3a). However, PP_{areal} did not change significantly, ranging from 146 ± 64 mg C m^2 h^{-1} in 1970 to 196 ± 24 mg C m^2 h^{-1} in 2014 and 2015 (Table 2.1a, Fig 2.3b). The increase in Z_{eu} from a mean of 3.0 ± 0.5 m in 1970 to 8.3 ± 0.5 m in 2014 and 2015 (Table 2.1a) maintained a constant PP_{areal} relative to the decrease in PP_{vol}. The significant decrease in the vertical attenuation coefficient (ε_{par}) from 1.8 ± 0.4 m^{-1} in 1970 to 0.5 ± 0.1 m^{-1} in 2014 and 2015 (Table 2.1a, Fig. 2.3c) also shows the increase in light penetration on a long-term scale.

A significant decrease in chl *a* occurred from 15.0 ± 2.1 mg m^{-3} in 1970 to 4.2 ± 0.5 mg m^{-3} in 2014 and 2015 (Table 2.1a, Fig. 2.4a). Similarly, there was a significant decrease in phytoplankton biomass from 4.5 ± 1.0 g m^{-3} in 1970 to 2.3 ± 0.3 g m^{-3} in 2014 and 2015 (Table 2.1a, Fig. 2.4b). However, chl *a* decreased more rapidly than biomass, resulting in a significant decrease in the chl *a*: biomass ratio from 5.6 ± 0.7 mg g^{-1} in 1970 to 2.2 ± 0.3 mg g^{-1} in 2014 and 2015 (Table 2.1a, Fig. 2.4c). Chl *a* also decreased more rapidly than PP_{vol}, indicating a significant increase in the assimilation efficiency from 2.5 ± 0.3 mg C mg chl a^{-1} h^{-1} in 1970 to 7.2 ± 0.9 mg C mg chl a^{-1} h^{-1} in 2014 and 2015 (Table 2.1a, Fig. 2.4d).

Carbon turnover time has remained relatively constant, not changing significantly from 1.8 ± 0.4 days in 1970 to 1.2 ± 0.2 days in 2014 and 2015 (Table 2.1a, Fig. 2.4e). Both daily

PP_{vol} (converted from Fig. 2.3a) and the phytoplankton carbon pool (converted from phytoplankton biomass in Fig. 2.4b) decreased at similar rates, resulting in the constant carbon turnover time.

Despite the occurrence of HABs, the phytoplankton assemblage in the Western Basin of Lake Erie has shifted to being more diatom dominated. The relative abundance of diatoms increased from 36 ± 5% of the total phytoplankton biomass in 1970 to 68 ± 7% in 2014 and 2015 (Table 2.1b, Fig. 2.5a). The relative abundance of cyanobacteria in the total phytoplankton assemblage revealed no significant change from 1970 to 2015 (Fig. 2.5b), although the highest relative abundances were observed during 2014 and 2015 (29 ± 10% and 17 ± 8%, respectively, Table 2.1b). Chlorophytes did not significantly change in relative abundance in the phytoplankton assemblage, although there was a decreasing trend from 16 ± 5% in 1970 to 7 ± 2% in 2014 and 2015 (Table 2.1b, Fig. 2.5c).

Average water column temperature did not significantly change from a June-September mean of 21 ± 0.5 °C in 1970 to 21 ± 0.5 °C in 2014 and 2015 (Table A3, Fig. A1a). TP decreased from an average of 38 ± 3 µg L^{-1} in 1970 to 23 ± 2 µg L^{-1} in 2014 and 2015, although this decrease was not significant ($p = 0.07$, Table A3, Fig. A1b). Average TP has remained higher than the target of 15 µg L^{-1} set for the Western Basin in the 1972 GLWQA despite the fact that phosphorus target loads were achieved by the mid-1980s (Dolan and McGunagle 2005). Nitrate had the opposite trend of TP, increasing significantly from 143 ± 30 µg L^{-1} in 1970 to 281 ± 30 µg L^{-1} in 2014 and 2015 (Table A3, Fig. A1c), suggesting significant changes in lake nutrient stoichiometry.

The factors affecting primary production varied depending on the scale of study. On a short-term seasonal scale (May-October), chemical factors (TP and NO_3^- concentrations) were

not key factors correlating to primary production in the GLMs (Table 2.2). TP was a significant negative factor once, and NO_3^- was a significant negative factor twice (Table 2.2). Physical factors (location, temperature, and depth), however, were consistently identified as factors regulating primary production (Table 2.2). Location was always positive, such that primary production was significantly higher at the offshore site (Table 2.2, Fig. A2). Temperature revealed a strong positive relationship with primary production (Table 2.2), demonstrating the effects of variation in May-October temperature (Fig. A3) on primary production (Fig. A2). Finally, depth was always a significant negative factor (Table 2.2), indicating that primary production was strongly regulated by changes in light with depth. Short-term trends for all variables in 2014 and 2015 are summarized in Appendix A, Fig. A2- A4.

2.4 Discussion

Based on the Vollenweider et al. (1974) model, the decrease in annual average chl *a* from 11 mg m^{-3} in 1970 to 4.2 and 2.9 mg m^{-3} in 2014 and 2015 (using May to October values) should have resulted in a decline in annual PP_{areal} from 340 g C m^{-2} y^{-1} in 1970 to 194 and 144 g C m^{-2} y^{-1} in 2014 and 2015, respectively. However, annual PP_{areal} instead remained stable at 402 g C m^{-2} y^{-1} in 2014 and 502 g C m^{-2} y^{-1} in 2015. This observation cautions using the Vollenweider et al. (1974) model, since other factors appeared to be interfering with the relationship between annual PP_{areal} and chl *a*.

One of these factors was the increase in light penetration from 1970 to 2015, which resulted in no significant long-term change in PP_{areal} despite a significant decrease in PP_{vol} (Table 2.1a, Fig. 2.3). This increase in light penetration in the western basin has been seen in other studies, such as Dove and Chapra (2015) (Fig. 2.6). It has also previously been associated with the 1988 dreissenid invasion (Charlton et al. 1999), although phosphorus reductions have likely

had an impact as well. In shallower systems, primary production has been shown to respond differently to increases in light penetration. For example, at inner Saginaw Bay in Lake Huron (mean depth of 5 m, Fahnenstiel et al. 1995), both PP_{vol} and PP_{areal} decreased as light penetration increased, suggesting that the basin was not deep enough for an increase in light penetration to make up for the decrease in PP_{vol} (Fahnenstiel et al. 1995).

Another reason PP_{areal} remained high compared to chl *a* was the significant long-term increase in assimilation efficiency, caused by a greater long-term decrease in chl *a* compared to PP_{vol} (Fig. 2.4d). Changes in assimilation efficiency can be a result of physiological adaptations or changes in phytoplankton community composition (Richardson et al. 1983). Diatoms did significantly increase in relative abundance since 1970 in this study (Fig. 2.5a) and other studies have reported an increase in diatom abundance, although primarily in the central basin in the spring (Reavie et al. 2014). Studies comparing the carbon assimilation efficiencies of different types of phytoplankton in the western basin are needed to further address this question.

In addition to the significant long-term decrease in chl *a* relative to PP_{vol}, there was also a significant decrease in the chl *a*: biomass ratio (Fig. 2.4c). The long-term increase in light penetration (Fig. 2.3c) could be contributing to this significant decrease in chl *a*: biomass through photoacclimation. Photoacclimation is a physiological adaptation typically resulting in a decline in photosynthetic pigments, including chl *a*, in response to increased irradiance (MacIntyre et al. 2002). This can be a dramatic change, as chl *a* cell content can vary up to 5 to 10 times with change in irradiance (Falkowski and Raven 1997). Photoacclimation has been suggested in other dreissenid invaded systems, such as Lake Simcoe (Guildford et al. 2013) and the eastern basin of Lake Erie (North et al. 2012). In both studies, high mean light irradiance corresponded with higher particulate C: chl *a* ratios at nearshore versus offshore sites (Guildford

et al. 2013, North et al. 2012). On a seasonal scale in 2014 and 2015, chl *a* also usually increased with depth as light decreased (Table A1a) while phytoplankton biomass either decreased or did not change with depth (Table A1b), providing support for photoacclimation occurring throughout the water column.

The long-term decrease in chl *a*: biomass (Fig. 2.4c), combined with the fact that chl *a* was not a good predictor of seasonal phytoplankton biomass (Table A1b), raises the question of whether chl *a* is a reliable proxy for phytoplankton biomass estimation. A weak predictive relationship between chl *a* and phytoplankton biomass ($R^2 = 0.04$) was found from 1996-2002 across Lake Erie (Conroy et al. 2005). Other studies in different systems suggest variable conversion factors should be used to predict phytoplankton biomass from chl *a* (Kasprzak et al. 2008). As chl *a* is a key indicator of overall lake trophic status in management models used to set new target loads for Lake Erie (Annex 4 Objectives and Targets Task Team 2015) factors regulating the chl *a*: biomass ratio need to be further elucidated.

The drivers of the long-term decline in summer PP_{vol} (Fig. 2.3a) are not entirely known; however, a couple hypotheses are suggested below. The decrease in TP loadings since 1970 likely played a role (Maccoux et al. 2016), although the decrease in TP concentration since 1970 was not significant (Fig. A1b) and PP_{vol} in 2014 and 2015 was more regulated by the physical factors of location, temperature, and depth than nutrients (Table 2.2). Dreissenid mussels also may have contributed to the decrease in PP_{vol}, as was suggested in the spring in the western basin (Fitzpatrick et al. 2007) and at inner Saginaw Bay (Fahnenstiel et al. 1995). Although the exact reasons for the decline remain unknown, this study suggests that the increase in cyanobacteria biomass since the mid-1990s (Conroy et al. 2005) is not related to an increase in PP_{vol} and is instead likely more associated with a change in phytoplankton community composition.

Overall, the western basin of Lake Erie continues to give mixed signals with respect to environmental health. Although the frequency and intensity of HABs have increased since the mid-1990s, commercial and sport fisheries are in excellent shape, as shown by an increase in walleye and yellow perch quotas in 2017 (Great Lakes Fishery Commission 2017). This second outcome can be linked to the fact that the phytoplankton carbon pool turnover time of 1.8 days has not changed significantly since 1970 (Table 2.1a, Fig. 2.4e). Stable carbon turnover times are good news for the commercial fisheries in the western basin, since they suggest that the primary production required to support the fisheries (PPR) is sustainable (Fitzpatrick et al. 2008).

2.5 Conclusions

Physical factors (light penetration and temperature) played important roles in regulating seasonal primary production during 2014 and 2015 in the western basin of Lake Erie. Although PP_{vol} and chl *a* have significantly declined from 1970 to 2015, PP_{areal} has remained stable as a result of increased light penetration and increases in the carbon assimilation efficiency. Because of these adaptations, carbon turnover time in the western basin has not changed significantly from 1.8 days in 1970 and continues to support upper levels of the food web. Overall, the factors governing primary production in the western basin of Lake Erie are complex and require more knowledge on the interaction and interdependencies of key physical and chemical variables.

2.6 References

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Table 2.1. Sources for historical data from the western basin of Lake Erie used for long-term comparisons in Fig. 2.3- 2.5. June-September means and ranges (in parentheses) are shown. (-) indicates there was no June-September data for that variable. EC = Environment Canada, PP_{vol} and PP_{areal} are volumetric and areal primary production (respectively), Z_{eu} is euphotic depth, ε_{par} is the vertical attenuation coefficient, and chl *a* is chlorophyll *a*. Z_{eu} was converted from ε_{par} using eq. 4: $Z_{eu} = 4.6 / \varepsilon_{par}$. All variables are shown in a) except for phytoplankton community composition, which is shown in b).

a)								
Sampling Year	**1970**	**1993**	**1997**	**2001**	**2002**	**2003**	**2014**	**2015**
Source	EC STAR database	Dahl et al. 1995	Smith et al. 2005	Fitzpatrick et al. 2007	Fitzpatrick et al. 2007	Porta et al. 2005	Hillis et al. (this study)	Hillis et al. (this study)
PP_{vol} (mg C m^{-3} h^{-1})	45 (3- 227)	11 (4-17)	17 (3-49)	26 (4-64)	21 (9-34)	4 (2-6)	23 (11-38)	26 (15-37)
PP_{areal} (mg C m^{-2} h^{-1})	146 (44-397)	94 (8-179)	88 (14-184)	188 (73-261)	135 (65-204)	27 (11-42)	174 (83-298)	222 (182-312)
Z_{eu} (m)	3.0 (1.4-4.0)	8.4 (1.8-10)	6.3 (1.6 – 10)	8.0 (5.1-10)	7.1 (4.2-10)	7.1 (5.7-8.2)	8.0 (2.0-10.7)	8.6 (7-10.4)
ε_{par} (m^{-1})	1.8 (1.1-3.4)	0.7 (0.3-2.6)	1.1 (0.4 – 2.8)	0.6 (0.1-0.9)	0.7 (0.3-1)	0.7 (0.5-0.8)	0.6 (0.3-2.3)	0.4 (0.2-0.5)
Chl *a* (mg m^{-3})	15.0 (3.5-44.6)	4.1 (1.5-9.8)	5.7 (1.3-15.5)	9.0 (2.0-23)	4.2 (1.1-9.4)	7.2 (2.8-9.8)	4.7 (1.0-8.5)	3.5 (1.0-5.0)
Phytoplankton biomass (g m^{-3})	4.5 (0.6-19)	0.8 (0.2-2.7)	-	4.6 (3.6-5.3)	-	-	2.8 (1.2-5.1)	1.6 (0.4-3.4)
Chl *a*: biomass (mg g^{-1})	5.6 (0.6-13)	7.3 (1.9-13)	-	1.7 (0.9-2.9)	-	-	2.0 (0.3-4.5)	2.5 (1.5-4.9)
Assimilation efficiency (mg C mg chl a^{-1} h^{-1})	2.5 (0.5-7.0)	3.3 (1.1 – 7.7)	3.8 (1.1 – 10.7)	2.7 (0.8-3.9)	6.9 (1.8-11)	0.8 (0.2-1.9)	5.5 (1.8-10)	8.4 (4.5-15.2)
Carbon turnover time (days)	1.8 (0.4-8)	1.0 (0.2-3.0)	-	1.9 (1.3 - 2.5)	-	-	1.6 (0.4 - 3.0)	0.7 (0.2 - 1.3)

Table 2.1 (continued)

b)								
Sampling Year	**1970**	**1993**	**1997**	**2001**	**2002**	**2003**	**2014**	**2015**
Source	EC STAR database	Dahl et al. 1995	Smith et al. 2001	Fitzpatrick et al. 2007	Fitzpatrick et al. 2007	Porta et al. 2005	Hillis et al. (this study)	Hillis et al. (this study)
% Chlorophyta	16 (0-96)	0	-	28 (13-37)	-	-	8 (0-31)	4 (0-11)
% Bacillariophyceae	36 (2-87)	55 (22-90)	-	40 (29-53)	-	-	62 (1-98)	75 (42- 98)
% Cyanophyta	14 (0-63)	3 (0-28)	-	13 (10-17)	-	-	29 (0-92)	17 (0-53)

Table 2.2. Factors influencing seasonal (May – October) PP_{vol} at each depth in 2014 and 2015. The factors were selected through stepwise backwards Akaike Information Criterion (AIC) model selection, and run as generalized linear models (GLMs). For each variable, five different datasets were used: all combined (both years and locations), 2014, 2015, nearshore and offshore. The relationship of each factor with the predictive variables is shown as positive (+), negative (-) or no relationship (x). Factors that are not applicable have been shaded gray. (+) for location indicates that the variable was higher at the offshore location compared to the nearshore. TP = total phosphorus concentration, NO_3^- = nitrate concentration, chl *a* = chlorophyll *a* concentration and biomass = phytoplankton biomass (wet weight).

	Factors							
Dataset	**Year**	**Location**	**Depth**	**Temperature**	**TP**	**NO_3^-**	**Chl *a***	**Biomass**
All combined	+	+	-	+	x	x	+	x
2014		+	-	+	x	x	+	x
2015		+	-	+	-	-	+	x
Nearshore	x		-	+	x	x	+	x
Offshore	+		-	+	x	-	+	x

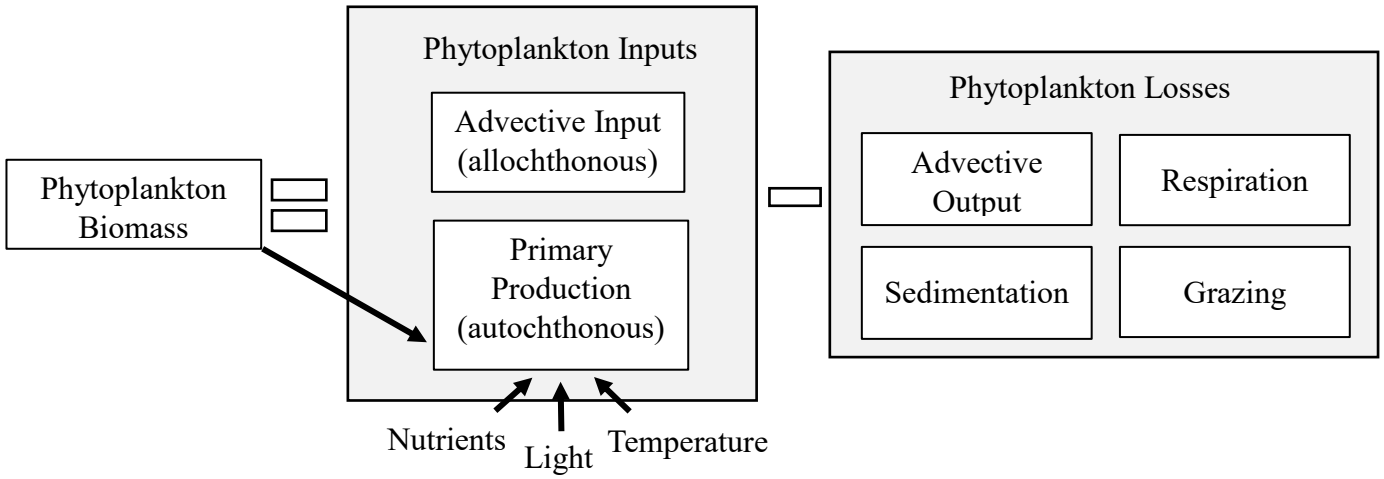

Figure 2.1. Conceptual model showing the phytoplankton inputs and losses in a water body contributing to phytoplankton biomass. Accelerated eutrophication is defined here as an increase in primary production beyond natural levels.

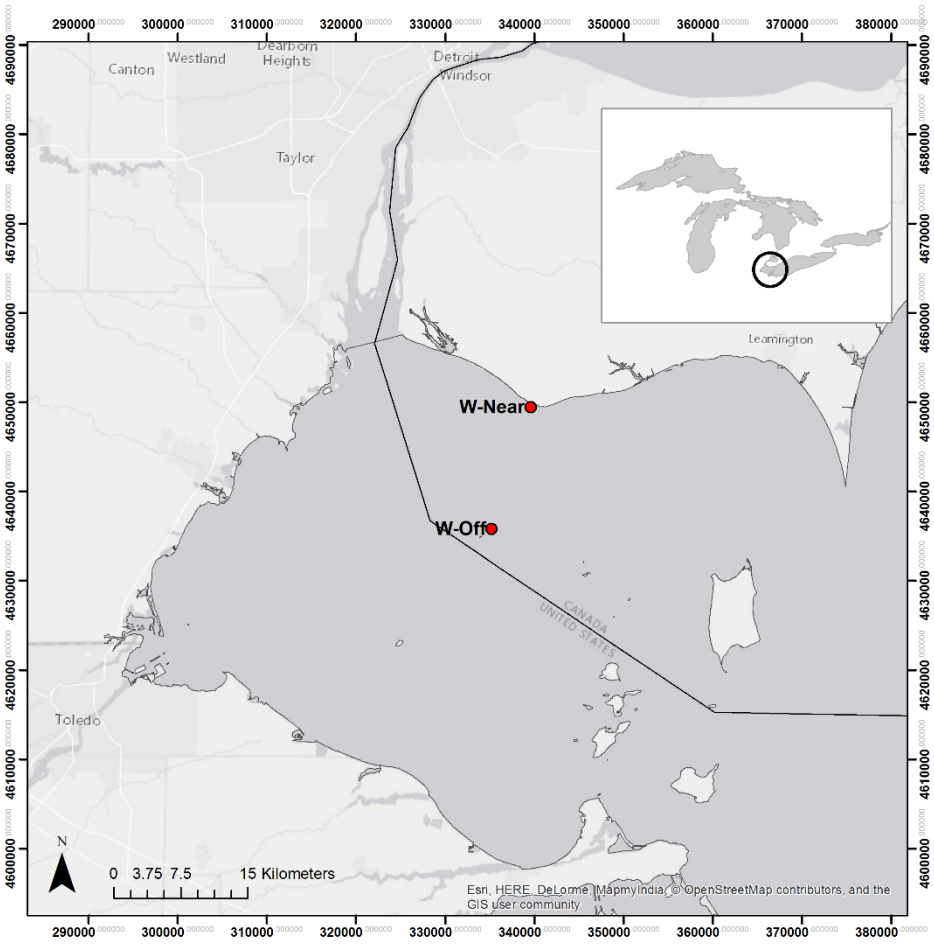

Figure 2.2. Sampling locations in the western basin of Lake Erie. W-Off = the offshore location (N41°51.396', W 82°59.137') and W-Near = the nearshore location (N41°58.801', W 82°56.183').

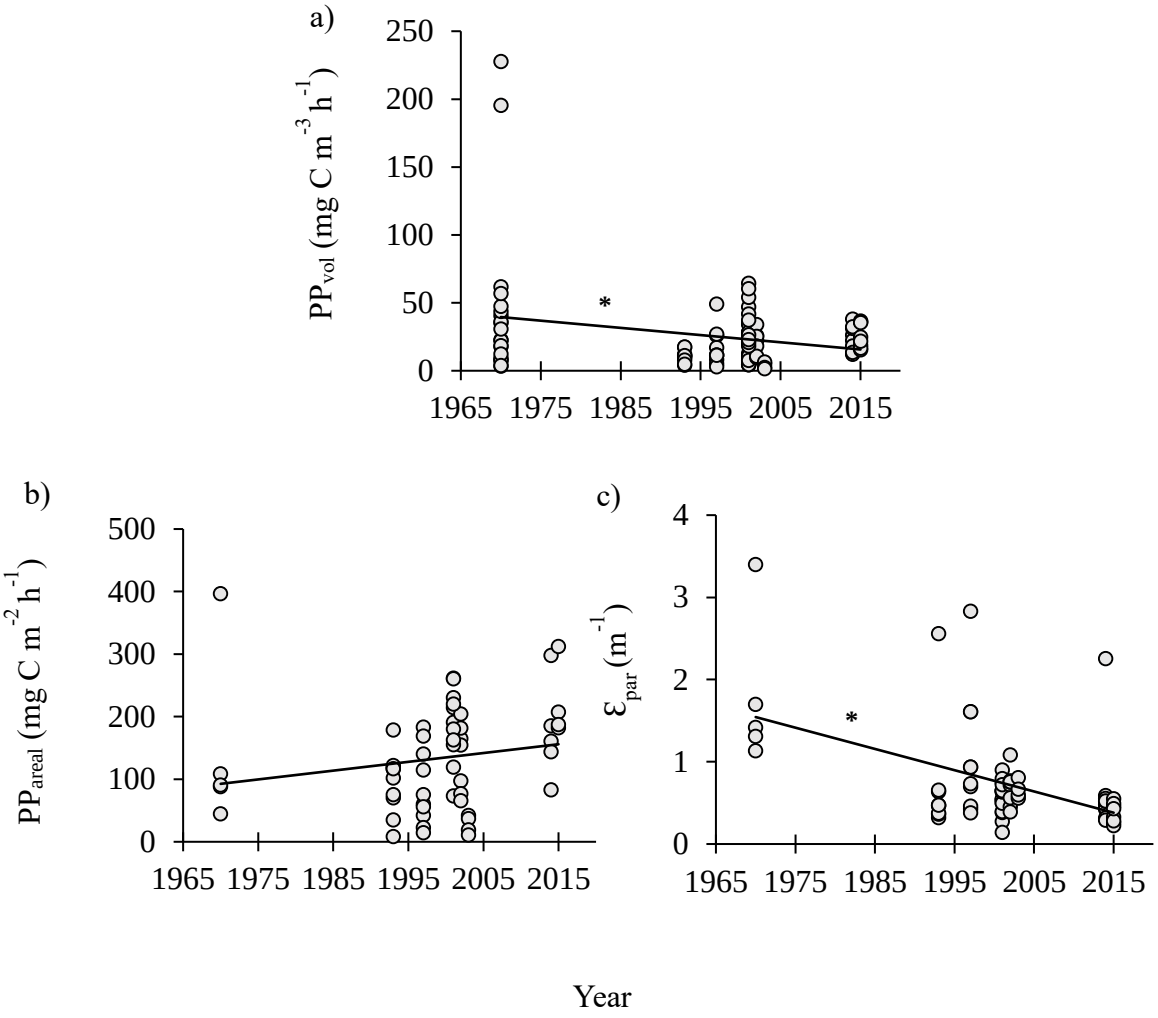

Figure 2.3. Long-term changes in June - September a) volumetric primary production (PP_{vol}) b) areal primary production (PP_{areal}) and c) vertical light attenuation coefficient (ε_{par}) in the western basin of Lake Erie. For a) and c), each point represents a separate station while for b), each point is an average of separate stations to remain consistent with 1970. Sources for each year are listed in Table 2.1a. * = $p < 0.05$ per an ordinary least squares regression.

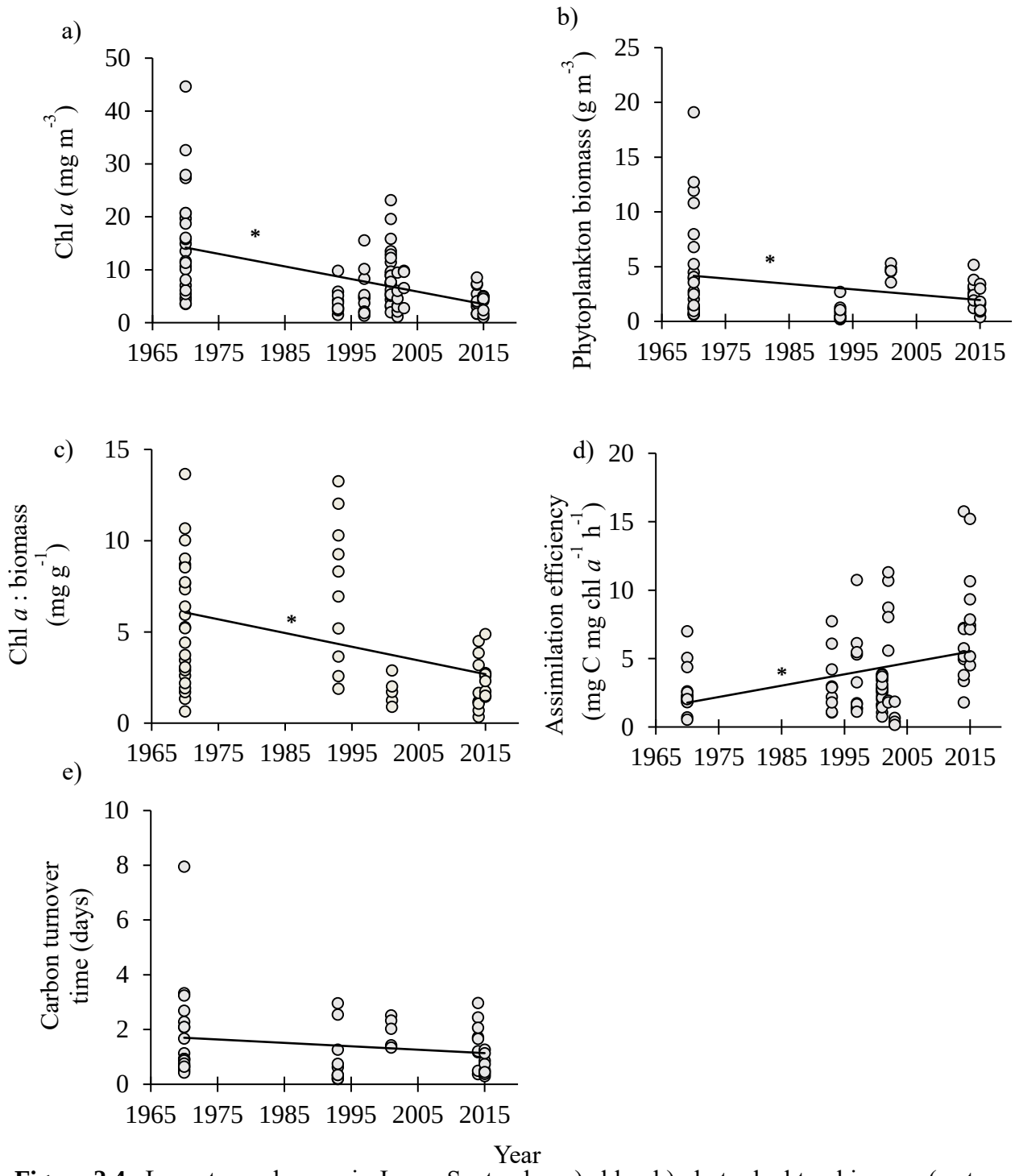

Figure 2.4. Long-term changes in June - September a) chl *a*, b) phytoplankton biomass (wet weight) c) chl *a*: phytoplankton biomass, d) assimilation efficiencies and e) carbon turnover time in the western basin of Lake Erie. Each year includes at least monthly sampling from June-September at separate stations. Sources for each year are listed in Table 2.1a. * = $p < 0.05$, per an ordinary least squares regression.

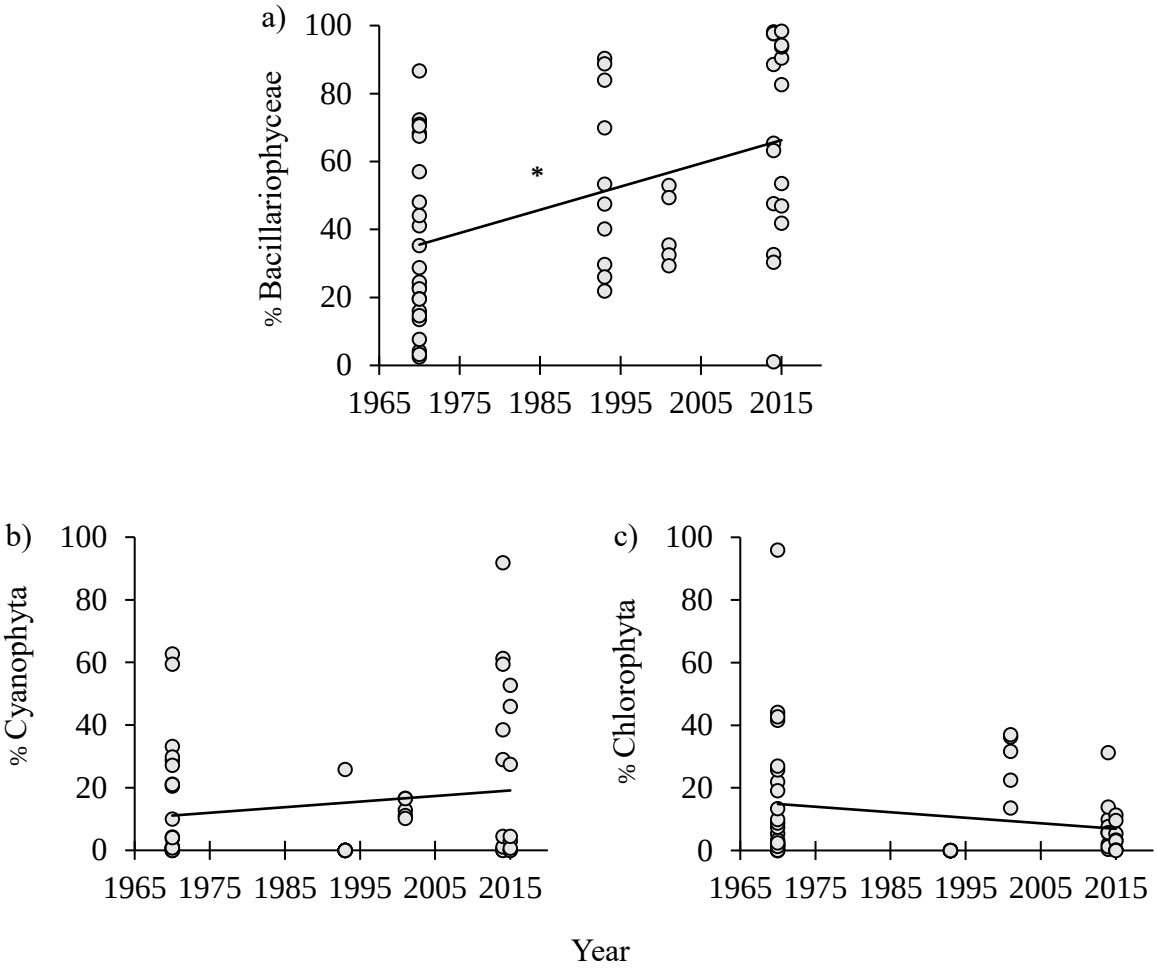

Figure 2.5. Long-term changes in June - September a) % bacillariophyceae (diatoms) b) % cyanophyta (cyanobacteria) and c) % chlorophyta (chlorophytes), all in relation to total phytoplankton biomass in the western basin of Lake Erie. Each point represents at least monthly sampling from June-September at separate stations. Sources for each year, along with ranges and averages, are listed in Table 2.1b. * = $p < 0.05$ per an ordinary least squares regression.

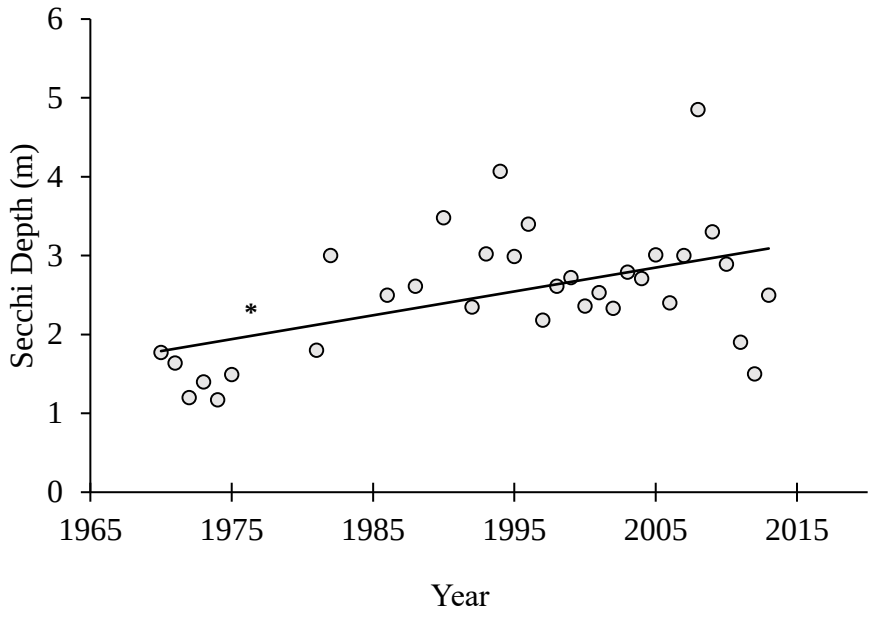

Figure 2.6. Long-term temporal change in summer secchi depth in the Western Basin, obtained from Table 3 in Dove and Chapra (2015). * = $p < 0.05$ per an ordinary least squares regression.

CHAPTER 3

SPATIAL VARIATION OF PRIMARY PRODUCTION AND CHLOROPHYLL *A* IN THE THREE BASINS OF LAKE ERIE

3.1 Introduction

While Chapter Two considered long-term trends of factors regulating primary production in the western basin of Lake Erie, primary production can also be compared across the three basins of Lake Erie. The three basins are an ideal study system to compare primary production as they are all exposed to the same climate, but other factors such as depth and trophic status vary considerably. The western basin is the shallowest (maximum depth 10 m) followed by the central basin (maximum depth 25 m) and the eastern basin (maximum depth 64 m) (Schertzer 1999). In 1970, PP_{vol} and chl *a* were generally highest in the western basin, followed by the central and then eastern basins (Glooschenko et al. 1974a, b). Vollenweider et al. (1974) classified the western basin as highly eutrophic with an annual PP_{areal} of 310 g C m^{-2} $year^{-1}$, central basin as secondary eutrophic (at 210 g C m^{-2} $year^{-1}$), and the eastern basin as mesotrophic (160 g C m^{-2} $year^{-1}$).

Few studies have measured primary production in all three basins of Lake Erie since the 1970s. Lake Erie has undergone many changes such as reductions in P loadings (Maccoux et al. 2016) and the dreissenid invasion (Nicholls and Hopkins 1993). While there were some measurements of primary production in the 1950s and 60s, these were limited to either just the western basin (Verduin 1956) or one lakewide cruise (Parkos et al. 1969). Glooschenko et al. (1974a) was the only study of primary production in Lake Erie prior to P reductions and the dreissenid invasion that sampled throughout the year and across all three basins. It is not known if this study was truly indicative of conditions at the time, but it is the only reference point.

Primary production was not measured again in all three basins until 1993 (Dahl et al. 1995) and 1997 (Smith et al. 2005). In 1997, although PP_{vol} was slightly higher in the western basin, PP_{areal} did not differ significantly between the west and central basins as a result of deeper light penetration in the central basin (Smith et al. 2005).

Unfortunately, different primary production methods have been used throughout the three basins of Lake Erie, making it difficult to determine whether the spatial pattern of primary production has changed. Glooschenko et al. (1974a) used a constant light incubator to measure primary production, while Dahl et al. (1995) and Smith et al. (2005) used a variable light incubator. It is not known how these methods compare to each other or with the *in situ* method, which has not been used in the central or eastern basins. The central and eastern basins are deeper and thermally stratified, and depth is likely an important factor regulating both light attenuation and phytoplankton distributions in the water column, emphasizing the importance of using the *in situ* method. Recycling of nutrients from below the thermocline can also affect primary production in deeper systems, as demonstrated in Lake Lanao in the Philippines (Lewis 1974).

It is also important to consider how assimilation efficiencies (in mg C mg chl a^{-1} h^{-1}) vary across the basins and at different depths. Assimilation efficiency is a function of algal adaptation to light and nutrient availability (Behrenfeld et al. 2002). Glooschenko et al. (1974a) found that the highest assimilation efficiencies occurred in the western basin, which was associated with higher nutrient concentrations (Gächter et al. 1974). Higher assimilation efficiencies were also observed in late summer in Lakes Ontario and Erie when cyanobacteria were abundant, suggesting a strong link between assimilation efficiencies and composition of the phytoplankton community (Glooschenko et al. 1974a). As nutrients remain higher in the western basin

(Charlton et al. 1999) and reports of cyanobacteria are largely focused on the western basin (Watson et al. 2016), one would predict assimilation efficiencies to be highest in the western basin should nutrient availability be playing a limiting role.

In many lakes, nearshore areas are generally regarded as being more productive than offshore areas (Wetzel 2001). Glooschenko et al. (1974a) reported that PP_{vol} tended to be higher at nearshore vs offshore sites in Lake Ontario. TP concentrations, secchi depth and chl *a* also indicated greater trophic states at nearshore sites in Lakes Ontario, Erie, Huron and Superior (Gregor and Rast 1982). Higher TP and chl *a* along with lower secchi depth were also observed at nearshore versus offshore sites in Lake Michigan (Bartone and Schelske 1982). However, recent studies have indicated that this pattern is changing in the LGL, and has been attributed to both reductions in external nutrient loading in Lake Michigan (Carrick et al. 2001) and the invasion of dreissenid mussels in the eastern basin of Lake Erie (Depew et al. 2006). Not as much is known about the relationship between nearshore and offshore sites in the other two basins of Lake Erie.

The aim of this study was to consider spatial variation of primary production and chl *a* in the three basins of Lake Erie. This involved two questions:

1) Does primary production (both PP_{vol} and PP_{areal}), chl *a* and assimilation efficiency vary among basins?
2) Does PP_{vol}, PP_{areal}, chl *a* and assimilation efficiency vary between nearshore and offshore sites in each basin?

Light penetration, water column temperature, and nutrients (TP and nitrate) were measured to determine how they relate to primary production, chl *a* and assimilation efficiencies. More knowledge on the spatial variation of primary production in Lake Erie will provide insight to re-

eutrophication problems such as cyanobacterial blooms in the western basin (Watson et al. 2016) central basin hypoxia (Scavia et al. 2014).

3.2 Methods

Sampling Design

Sampling occurred at a nearshore and offshore site in each basin of Lake Erie (western, central, and eastern) approximately once a month from May to October in 2014 and 2015. The exact dates are summarized in Table 3.1, and the sites and coordinates are shown in Fig. 3.1. At all the nearshore sites, water samples were collected from 0, 1, 2, 3 and 4m. The sampling depths for offshore sites varied depending on the basin, and are shown in Table 3.2. The nearshore sites were selected at the ~ 7m depth in all basins, while Z_{max} at the offshore sites increased from the western to the eastern basin (Table 3.2). The water samples at each depth were analyzed for nutrient concentrations (TP and NO_3^-), chl *a*, and primary production.

Temperature and Irradiance Profiles

Water temperature was measured at each site using a RBR maestro logger. At the eastern offshore site, temperature was measured from 0 to 30m, while temperature was measured from 0m to Z_{max} at all the other sites. Irradiance was measured at 1 m intervals using a LI-250A light meter attached to a LI-193 spherical quantum sensor from the surface to Z_{max} or until irradiance was < 1 µmol s^{-1} m^{-2}. ε_{par} and Z_{eu} were calculated using eq. 1 - 4 in Section 2.2.

Nutrients

TP and NO_3^- concentrations were determined using the ascorbic acid and cadmium reduction method, respectively (Eaton et al. 1995) as in Section 2.2.

Primary production and chl *a*

Primary production was measured through ^{14}C uptake by phytoplankton using the *in situ* light and dark bottle method (adapted from Vollenweider 1974), which is described in more detail in Section 2.2. Acetone pigment extraction was used to determine chl *a* concentrations (Eaton et al. 1995, Strickland and Parsons 1968) (Section 2.2).

Areal and Volumetric Estimates of Primary Production

Volumetric water column averages were calculated for primary production, chl *a*, and nutrients using the trapezoidal integration method (Knap et al. 1996) as described in Section 2.2. Briefly, primary production vs depth was plotted in PAST software (Hammer et al. 2001), and the points were fit to a linear or non-linear curve with the lowest AIC (Akaike Information Criterion) value. Primary production at Z_{eu} was estimated based on this curve, and areal primary production (PP_{areal} mg C m^{-2} h^{-1}) was calculated by integrating from the surface to the euphotic depth. Dividing areal primary production by the euphotic depth resulted in a weighted volumetric average of the water column (PP_{vol} in mg C m^{-3} h^{-1}).

Water column areal estimates for chl *a*, TP and NO_3^- concentrations were calculated using trapezoidal integration from the surface to the mixing depth (Z_{mix}). Here, Z_{mix} refers to the position of the thermocline in the water column where the change in temperature over 1 m is greater than 1°C (Wetzel 2001). Since the western basin of Lake Erie is isothermal, Z_{mix} never occurred and so $Z_{max} = Z_{mix}$. Values at Z_{mix} were estimated according to the equation of the chl *a*, TP or NO_3^- vs depth curve, chosen again by fitting the curves to a linear or non-linear regression by comparing AIC values in PAST. Weighted average volumetric estimates were calculated by dividing the areal values by Z_{mix}.

At the eastern offshore site, water column average temperature was an average from 0 to 30 m. The average water temperature for all other sites was simply an average from the surface to the bottom of the water column.

Statistical Analysis

In each basin, water column averages were compared between the nearshore and offshore sites, and significant differences ($p < 0.05$) were tested using a two-sample t-test. Meanwhile, for each type of site (nearshore or offshore), significant differences ($p < 0.05$) between the three basins were tested using one-way analyses of variance (ANOVAs). Water column averages from both years were combined in these statistical analyses, and the analyses were conducted in PAST (Hammer et al. 2001). Normality was tested using the Shapiro-Wilk test, and transformed as needed. The transformations required for the t-tests were $\log_{10}(x)$ (PP_{vol} central and east, PP_{areal} east, TP central, and ε_{par} west), $\sqrt{x}$ (NO_3^- west), x^2 (temperature central), $-1/x$ (TP east, ε_{par} central) and $-1/x^2$ (ε_{par} east). For the ANOVAs, the transformations required were $\log_{10}(x)$ (PP_{vol} and PP_{areal} offshore, TP offshore), $\sqrt{x}$ (NO_3^- nearshore), x^2 (temperature offshore), x^3 (temperature nearshore), $-1/x$ (TP nearshore, ε_{par} nearshore) and $-1/x^2$ (ε_{par} offshore).

The F test was used to test for equal variances in the t-tests, and the Welch test was used if variances were unequal. For the ANOVAs, equal variances were tested for using Levene's test and the Welch ANOVA was used instead of the one-way ANOVA if variances were unequal. If the one-way or Welch ANOVA was significant, then Tukey's pairwise post hoc test was used to determine where the significant differences between the basins occurred.

May to August PP_{vol}, chl *a* and assimilation efficiencies for each basin were obtained from previous studies in 1970 (Glooschenko et al. 1974a and b), 1993 (Dahl et al. 1995), and 1997 (Smith et al. 2005). In order to make the data comparable over time, PP_{vol} was calculated

by dividing PP_{areal} by euphotic depth in these studies. Significant differences in PP_{vol}, chl *a* and assimilation efficiencies among basins was tested using one-way ANOVAs in PAST (Hammer et al. 2001) for all studies. As previous studies included both nearshore and offshore sites, nearshore and offshore data were combined in 2014 and 2015. For PP_{vol} and chl *a*, a $\log_{10}(x)$ transformation was required for 1970, 1993, and 1997. For assimilation efficiencies, a $\log_{10}(x)$ transformation was required for 1993, 1997 and 2014. If variances were unequal, the Welch ANOVA was used instead of the one-way ANOVA and Tukey's pairwise post hoc test was used to determine where the significant differences among basins occurred.

3.3 Results

At nearshore sites, during the sampling period of May to October, there was no significant difference in PP_{vol} among the western (17 ± 3 mg C m^{-3} h^{-1}), central (21 ± 6 mg C m^{-3} h^{-1}) or eastern basins (11 ± 2 mg C m^{-3} h^{-1}) (Table 3.3). Nearshore nutrient concentrations decreased from west to east, with significantly higher TP in the western basin (26 ± 3 μg L^{-1}) compared to the eastern basin (20 ± 7 μg L^{-1}). Similarly, there was higher nitrate in the western basin (328 ± 60 μg L^{-1}) compared to the central and eastern basins (215 ± 46 and 99 ± 14 μg L^{-1}, respectively). Light penetration was deepest in the eastern basin, demonstrated by a significantly lower ε_{par} (0.36 ± 0.14 m^{-1}) compared to the central and western basins (0.50 ± 0.14 and 0.61 ± 0.16 m^{-1}, respectively). As Z_{max} was the same among the basins at the nearshore sites (Table 3.2) and light usually penetrated to the bottom of the water column in all basins (Fig. 3.2d), light attenuation did not play a significant role in regulating PP_{areal} among basins at the nearshore sites. There were no significant differences among basins at the nearshore sites for either PP_{areal} (western = 112 ± 23, central = 110 ± 21 and eastern = 79 ± 20 mg C m^{-2} h^{-1}) chl *a* (western = 2.9

± 0.6, central = 3.5 ± 0.9 and eastern = 1.9 ± 0.4 mg m^{-3}) or assimilation efficiencies (western = 7.0 ± 1.2, central = 7.5 ± 1.2 and eastern = 8.0 ± 1.6 mg C mg chl a^{-1} h^{-1}).

At the offshore sites, however, PP_{vol} was significantly lower in the eastern basin (10 ± 2 mg C m^{-3} h^{-1}) compared to the central and western basins (24 ± 6 and 22 ± 3 mg C m^{-3} h^{-1}, respectively) (Table 3.3). The same pattern was observed for chl *a* (eastern = 1.3 ± 0.2, central = 3.6 ± 0.5 and western = 4.4 ± 0.6 mg m^{-3}). TP did not vary significantly among the basins (Table 3.3), although nitrate was significantly higher in the western basin (288 ± 34 μg L^{-1}) compared to the central and eastern basins (150 ± 32 and 134 ± 14 μg L^{-1}, respectively). Offshore light penetration was significantly deeper in the offshore eastern basin (ε_{par} = 0.26 m^{-1}) compared to the central (ε_{par} = 0.37 m^{-1}) or western basins (ε_{par} = 0.50 m^{-1}) (Table 3.2), which resulted in a deeper euphotic depth of 21 m (Fig. 3.3d). This increased light penetration in the eastern basin resulted in primary production deeper in the water column and no significant difference in PP_{areal} among the basins (western = 201 ± 32, central = 262 ± 46, and eastern = 196 ± 28 mg C m^{-2} h^{-1}). Carbon assimilation efficiencies were also similar among the basins (western = 5.6 ± 0.6, central = 6.7 ± 1.2, and eastern = 10.3 ± 1.9 mg chl a^{-1} h^{-1}).

For most of the variables, there were no significant differences between nearshore and offshore sites in each basin (Table 3.3). The only exception was PP_{areal}, which was significantly higher in the offshore sites in each basin as a result of the increased Z_{eu} in offshore versus nearshore sites (Fig. 3.2 and 3.3).

3.4 Discussion

While it is often assumed that the western basin is the most productive in Lake Erie, PP_{vol} did not vary significantly between the western and central basins in 2014 and 2015, at either nearshore or offshore sites (Table 3.3). PP_{vol} was also similar between the western and central

basins in 1997 (Smith et al. 2005, Fig. 3.4a). Studies from 1970 (Glooschenko et al. 1974) and 1993 (Dahl et al. 1995), however, concluded that PP_{vol} was higher in the western basin compared to the eastern and central basins (Fig. 3.4a). In the present study, PP_{vol} was significantly lower in the eastern versus western and central basins at the offshore sites, while PP_{areal} did not differ significantly among the three basins (Table 3.3). This pattern demonstrates how increased light penetration in the offshore eastern basin results in primary production occurring deeper in the water column (Fig. 3.3d).

The lack of consistent methods to measure primary production over time prevents a conclusion of whether the spatial patterns of primary production among the basins have indeed changed on a long-term basis. Future studies should compare the incubator and *in situ* methods in the central and eastern basins, as was done by Fitzpatrick et al. (2007) in the western basin, to see if incubator and *in situ* primary production methods are sufficiently comparable to determine long term trends in primary production. The 2014 and 2015 PP_{vol} and PP_{areal} patterns question the conclusions of Glooschenko et al. (1974a) and Vollenweider et al. (1974) that the western basin is the most productive.

Like PP_{vol}, chl *a* was similar between the western and central basins at both the nearshore and offshore sites (Table 3.3). This again differs from 1970, when chl *a* was significantly higher in the western basin (Glooschenko et al. 1974, Fig. 3.4b). In both 1993 (Dahl et al. 1995) and 1997 (Smith et al. 2005), however, chl *a* also did not change significantly between the western and central basins (Fig. 3.4b).

The high PP_{vol} in the central basin suggests that most of the phytoplankton biomass is originating within the central basin, and does not depend on advective transport of algal material from the western basin. Carbon burial in the western basin of Lake Erie has been quantified to

be 13.6 g C m^{-2} $year^{-1}$ based on 2014 and 2015 data (S. Oni unpublished data), which is relatively high considering that global carbon burial rates are estimated to range from 4.5 to 14 g C m^{-2} $year^{-1}$ (Tranvik et al. 2009). Studies examining the distribution of hydrophobic sediment-bound persistent organic pollutants (POPs) in Lake Erie found higher contamination in the western basin compared to the central and eastern basins (Lu et al. 2015, Letcher et al. 2015) also concluding that little transfer of organic matter occurs between basins. In another example, a mass balance looking at the distribution of 2, 4-di-tert-pentylphenol (24DP) in Lake Erie sediment from its source in the Detroit River concluded that 73% of the sediment-bound 24DP entering Lake Erie remained in the western basin (Carter and Hites 1992).

These examples suggest that the sedimentation of organic carbon (which includes phytoplankton) in the western basin is relatively high, and therefore the high central basin PP_{vol} (21 and 24 mg C m^{-3} h^{-1} at the nearshore and offshore sites, respectively) is driving the high central basin chl *a* (3.5 and 3.6 mg m^{-3} at both the nearshore and offshore sites, respectively, Table 3.3). Phytoplankton biomass and composition measurements in the central basin are required to support this hypothesis. In the future, models predicting hypoxia in the central basin, such as Rucinski et al. (2016), must incorporate measurements of central basin primary production.

The only measured variable that varied significantly between nearshore and offshore sites was PP_{areal} (Table 3.3), which was significantly higher at offshore sites as a result of increases in Z_{eu} (Fig. 3.2 and 3.3). This was also observed in 2001 and 2002 in the eastern basin, where PP_{areal} was higher at offshore sites but PP_{vol} did not vary between nearshore and offshore sites (Depew et al. 2006). Depew et al. (2006) also concluded that chl *a* was significantly higher at offshore sites in the eastern basin, while in the present study there was no difference in chl *a*

between nearshore and offshore sites (Table 3.3). The present results still support the conclusions of Depew et al. (2006), in that both studies reveal no evidence of higher chl *a* or primary production at nearshore sites, a pattern that is often assumed to be typical of large lakes (Wetzel 2001). Some studies have suggested that the filtering effects of dreissenid mussels (Fahnenstiel et al. 1995, Depew et al. 2006) and the reduction of external nutrient loadings (Carrick et al. 2001) have reduced primary production at nearshore sites in the LGL.

Carbon assimilation efficiencies were the same among basins at both nearshore and offshore sites (Table 3.3). This observation differs from 1970 (Glooschenko et al. 1974a), when assimilation efficiencies were significantly higher in the western basin compared to the eastern basin (Fig. 3.4c). Higher nutrient levels and relative cyanobacteria abundances in the western basin would be predicted to contribute to higher assimilation efficiencies (Glooschenko et al. 1974a). While phytoplankton community composition was not measured in the present study, NO_3^- (nearshore and offshore) and TP (just nearshore) concentrations were significantly higher in the western basin compared to the eastern basin (Table 3.3). However, at the offshore sites, TP did not vary significantly among basins (Table 3.3), suggesting that the gradient of increasing TP concentrations from the Western to Eastern Basins may not be as prominent as in 1970 (Gächter et al. 1974), which could be contributing to similar assimilation efficiencies between basins.

Many studies have suggested there are distinct differences in nutrient stoichiometry across Lake Erie. In both 2014 and 2015 (Prater et al. 2017) and 1997 (Guildford et al. 2005), particulate C:P ratios were higher in the eastern basin compared to the western and central basins, indicating that the eastern basin is P limited (Guildford et al. 2005). Further studies have demonstrated that nutrient limitation in aquatic systems varies seasonally (Moon and Carrick

2007), and that assimilation efficiencies can increase with nutrient enrichment when phytoplankton are nutrient limited such as in the late summer (Glooschenko and Curl 1971). It is possible that recycling of nutrients during storms or fall overturn events in the eastern basin can significantly increase assimilation after a period of nutrient limitation. It is of interest to note that the ratio of Z_{eu}/ Z_{mix} was significantly negatively related to TP water column concentrations in the eastern basin (Fig. 3.5a), supporting the hypothesis that sediment resuspension events increased TP concentrations in this system while decreasing light penetration. While determining the effect of TP on assimilation efficiencies is outside the scope of this project, the very high carbon assimilation efficiency observed at the surface on October 5, 2015 at the east offshore site (36 mg C mg chl a^{-1} h^{-1}) may have been influenced by nutrient enrichment associated with the fall overturn as unusually high phosphorus concentrations were also observed (TP ranged from 30 - 77 μg L^{-1} among the depths) (Fig. 3.5b). Although an isolated incident, this demonstrates the importance of further investigating the impact of nutrient recycling associated with mixing events, especially as storms are predicted to increase in number and intensity in the future with climate change (Michalak et al. 2013).

3.5 Conclusions

Unlike previous studies in the 1970s, there were no differences in chl *a* and PP_{vol} observed between the western and central basins of Lake Erie during 2014 and 2015. Although the western basin has been considered a carbon source to the central basin, current PP_{vol} and chl *a* concentrations in the central basin were sufficient to develop sufficient algal biomass to drive hypoxia in the hypolimnion. In all the basins, PP_{areal} was higher at offshore versus nearshore sites as a result of increased light penetration, but chl *a* concentrations and PP_{vol} did not vary between nearshore and offshore sites. Finally, carbon assimilation efficiencies did not vary

among the basins in 2014 and 2015. While the reasons for this remain unknown, the effects of nutrient recycling, particularly in the eastern basin, should be investigated further. Consistent monitoring of primary production across the three basins of Lake Erie, along with enrichment experiments looking at the regulating effects of light and nutrients on primary production and chl *a*, are essential to better understand the factors regulating phytoplankton dynamics in Lake Erie.

3.6 References

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Table 3.1. Sampling dates for each basin in a) 2014 and b) 2015.

a) 2014

	Basin		
Month	**West**	**Central**	**East**
May	05-May-14	30-May-14	04-Jun-14
June	21-Jun-14	27-Jun-14	23-Jun-14
July	09-Jul-14	22-Jul-14	11-Jul-14
August	15-Aug-14	28-Aug-14	19-Aug-14
September	15-Sep-14, 29-Sep-14		26-Sep-14
October	16-Oct-14	23-Oct-14	

b) 2015

	Basin		
Month	**West**	**Central**	**East**
May	29-Apr-15	14-May-15	07-May-15
June	04-Jun-15	24-Jun-15	11-Jun-15
July	06-Jul-15	22-Jul-15	06-Aug-15
August	28-Jul-15	16-Aug-15	28-Aug-15
September	16-Sep-15	22-Sep-15	
October	26-Oct-15		05-Oct-15

Table 3.2. Depths sampled and average Z_{max} for each site sampled in 2014 and 2015.

Site	**Depths sampled (m)**	**Average Z_{max} (m)**
W- near	0, 1, 2, 3, 4	7.2
C- near	0, 1, 2, 3, 4	6.9
E- near	0, 1, 2, 3, 4	7.0
W-off	0, 1, 3, 5, 7	10.3
C- off	0, 1, 3, 5, 7, 10, 14	14.8
E- off	0, 5, 10, 15, 20, 25, 30 (except for May and June 2014, which were 0, 1, 5, 7, 10, 15, 20)	52.8

Table 3.3. May to October averages (± SE) of water column averages for each variable in the nearshore and offshore sites in each basin. Both years (2014 and 2015) are combined. The t-test indicates whether there was a significant difference between the nearshore and offshore sites, while the one-way ANOVA tests for differences between the basins. The significance level was set at $\alpha = 0.05$: ns = no significant difference, significant differences are in bold. PP_{vol} = volumetric primary production, PP_{areal} = areal primary production, near = nearshore, off = offshore, W = western basin, C = central basin and E = eastern basin.

		Basin			
Variable	**Site**	**Western**	**Central**	**Eastern**	**One-way ANOVA**
PP_{vol} (mg C m^{-3} h^{-1})	**Near**	17 ± 3	21 ± 6	11 ± 2	ns
	Off	22 ± 3	24 ± 6	10 ± 2	**W, C > E**
	T-test	ns	ns	ns	
PP_{areal} (mg C m^{-2} h^{-1})	**Near**	112 ± 23	110 ± 21	79 ± 20	ns
	Off	201 ± 32	262 ± 46	196 ± 28	ns
	T-test	**off > near**	**off > near**	**off > near**	
Chl *a* (mg m^{-3})	**Near**	2.9 ± 0.6	3.5 ± 0.9	1.9 ± 0.4	ns
	Off	4.4 ± 0.6	3.6 ± 0.5	1.3 ± 0.2	**W, C > E**
	T-test	ns	ns	ns	
Carbon assimilation efficiency (mg C mg chl a^{-1} h^{-1})	**Near**	7.0 ± 1.2	7.5 ± 1.2	8.0 ± 1.6	ns
	Off	5.6 ± 0.6	6.7 ± 1.2	10.3 ± 1.9	ns
	T-test	ns	ns	ns	
TP (µg L^{-1})	**Near**	26 ± 3	21 ± 4	20 ± 7	**W > E**
	Off	24 ± 3	17 ± 2	19 ± 4	ns
	T-test	ns	ns	ns	
Nitrate (µg L^{-1})	**Near**	328 ± 60	215 ± 46	99 ± 14	**W > C, E**
	Off	288 ± 34	150 ± 32	134 ± 14	**W > C, E**
	T-test	ns	ns	ns	
Average temperature (°C)	**Near**	18 ± 2	19 ± 1	16 ± 1	ns
	Off	18 ± 2	16 ± 1	13 ± 2	ns
	T-test	ns	ns	ns	
ε_{par} (m^{-1})	**Near**	0.61 ± 0.16	0.50 ± 0.14	0.36 ± 0.14	**W, C > E**
	Off	0.50 ± 0.04	0.37 ± 0.05	0.26 ± 0.06	**W, C > E**
	T-test	ns	ns	ns	

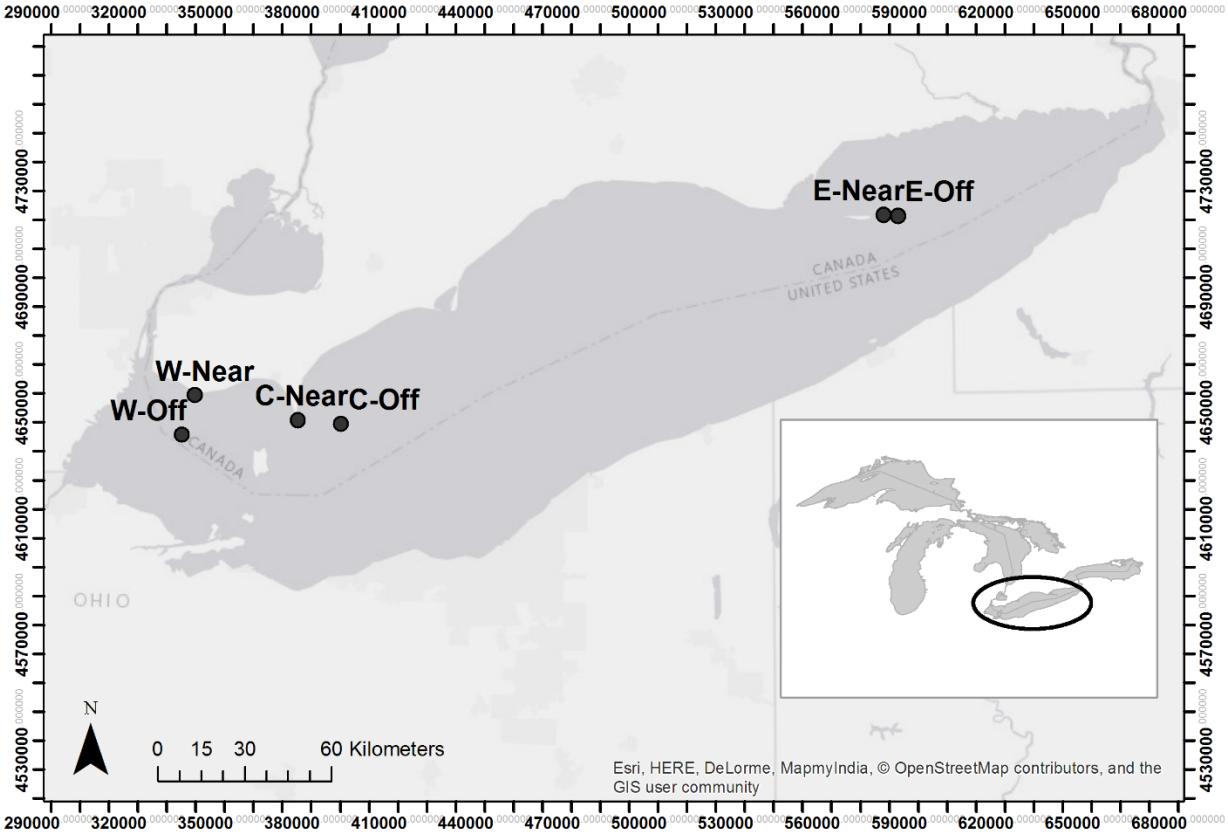

Figure 3.1. Sampling locations in the western, central and eastern basin of Lake Erie. W-Off = the western offshore location (N41°51.396', W 82°59.137'), W-Near = the western nearshore location (N41°58.801', W 82°56.183'), C- near = the central nearshore location (N 41°54.560', W 82°30.270'), C-off = the central offshore location (N41°53.949', W 82°19.373'), E-near = the eastern nearshore location (N42°33.275', W 80°03.031'), and E-off = the eastern offshore location (N 42°33.035', W 79°59.435'). Sampling took place from May to October in 2014 and 2015.

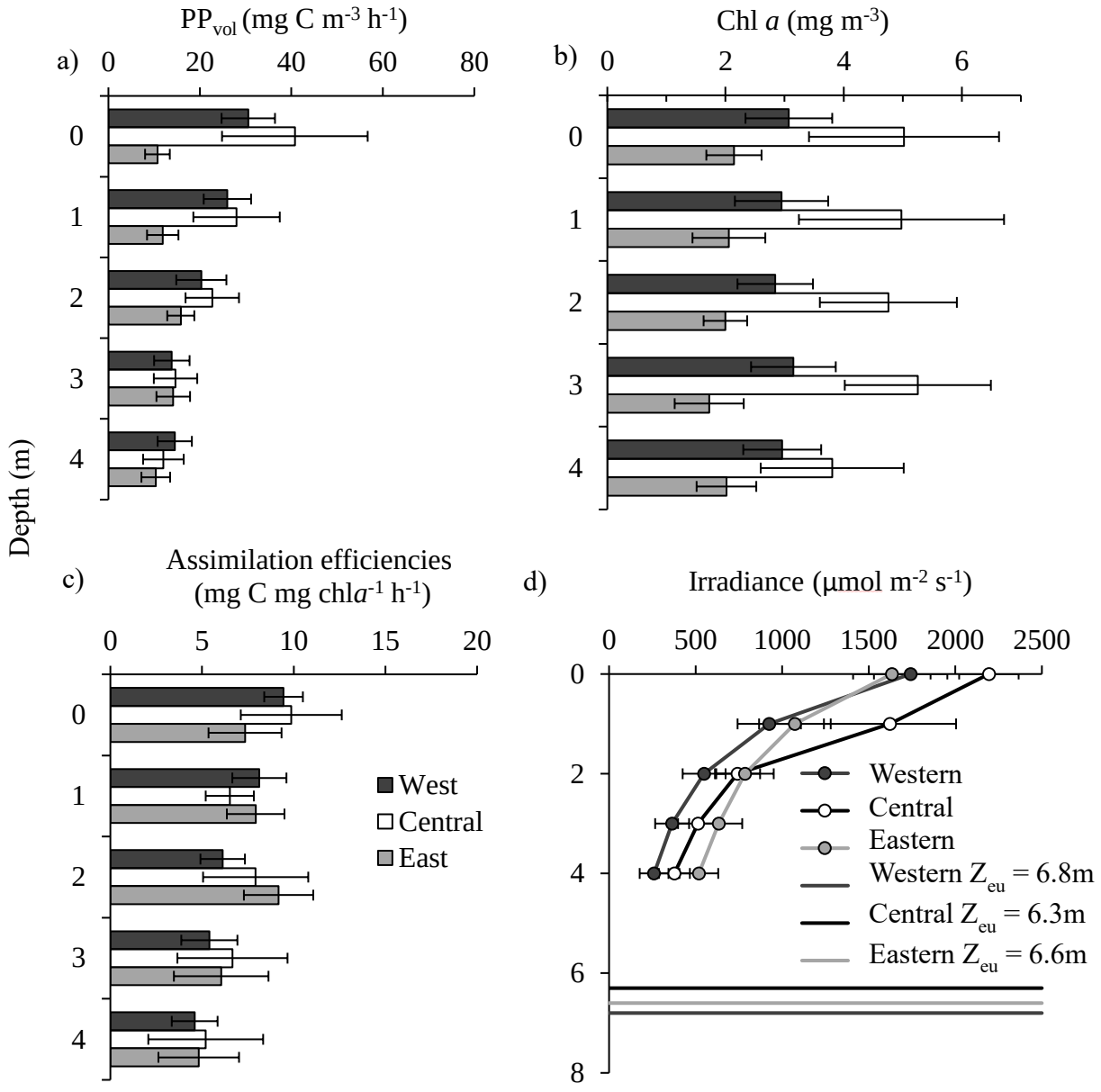

Figure 3.2. Average a) volumetric primary production (PP_{vol}), b) chlorophyll *a* (chl *a*) c) carbon assimilation efficiency and d) irradiance (± SE) at each depth from May to October for nearshore stations in the western, central and eastern basins. Data from both 2014 and 2015 are included. May to October Z_{eu} for each basin are shown in d). These calculations are described in the methods in Chapter 2 (Section 2.2).

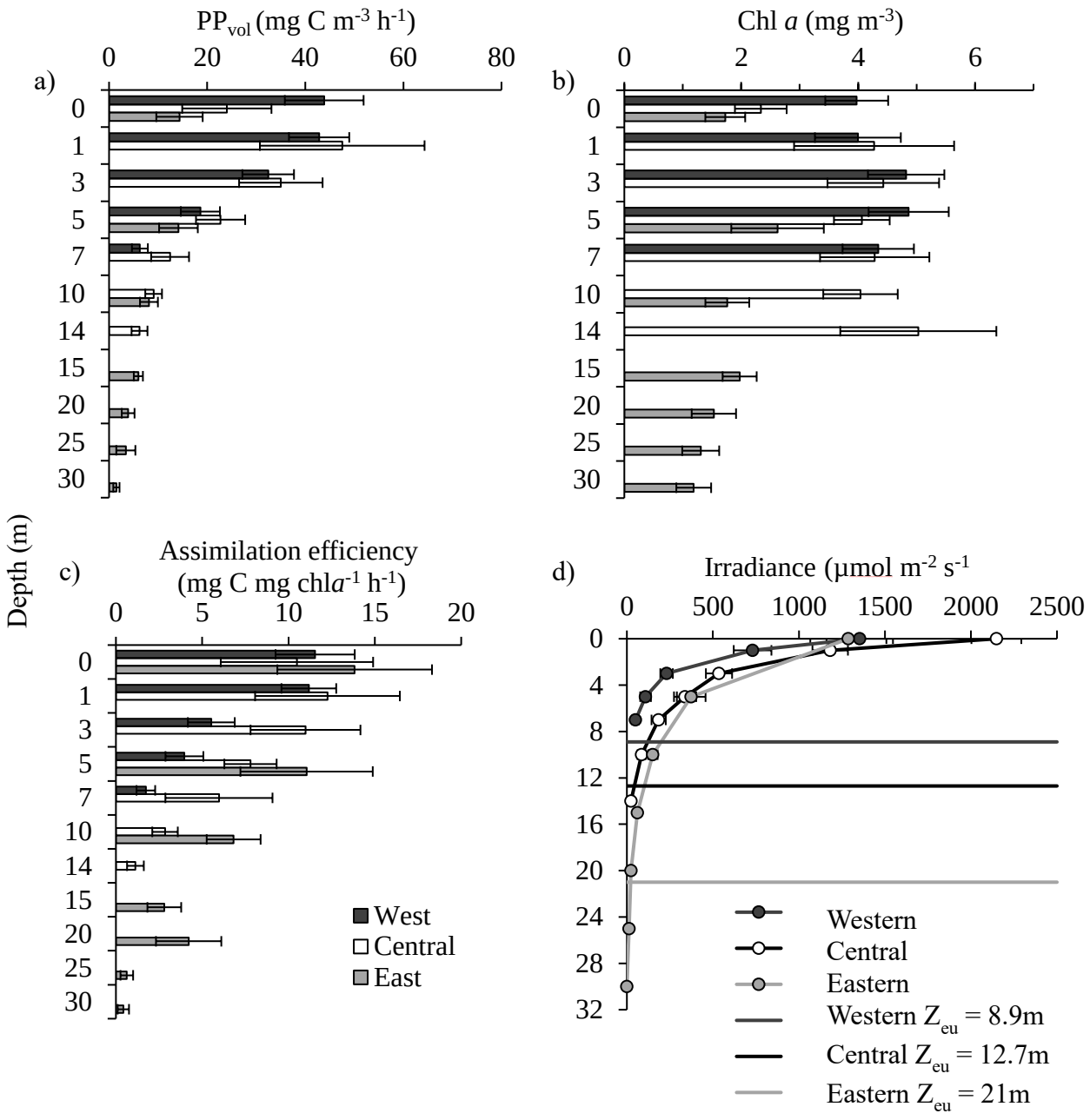

Figure 3.3. Average a) volumetric primary production (PP_{vol}), b) chlorophyll *a* (chl *a*) c) carbon assimilation efficiency and d) irradiance (± SE) at each depth from May to October for offshore stations in the west, central and east basins. Data from both 2014 and 2015 are included. May to October Z_{eu} for each basin are shown in d). These calculations are described in the methods in Chapter 2 (Section 2.2).

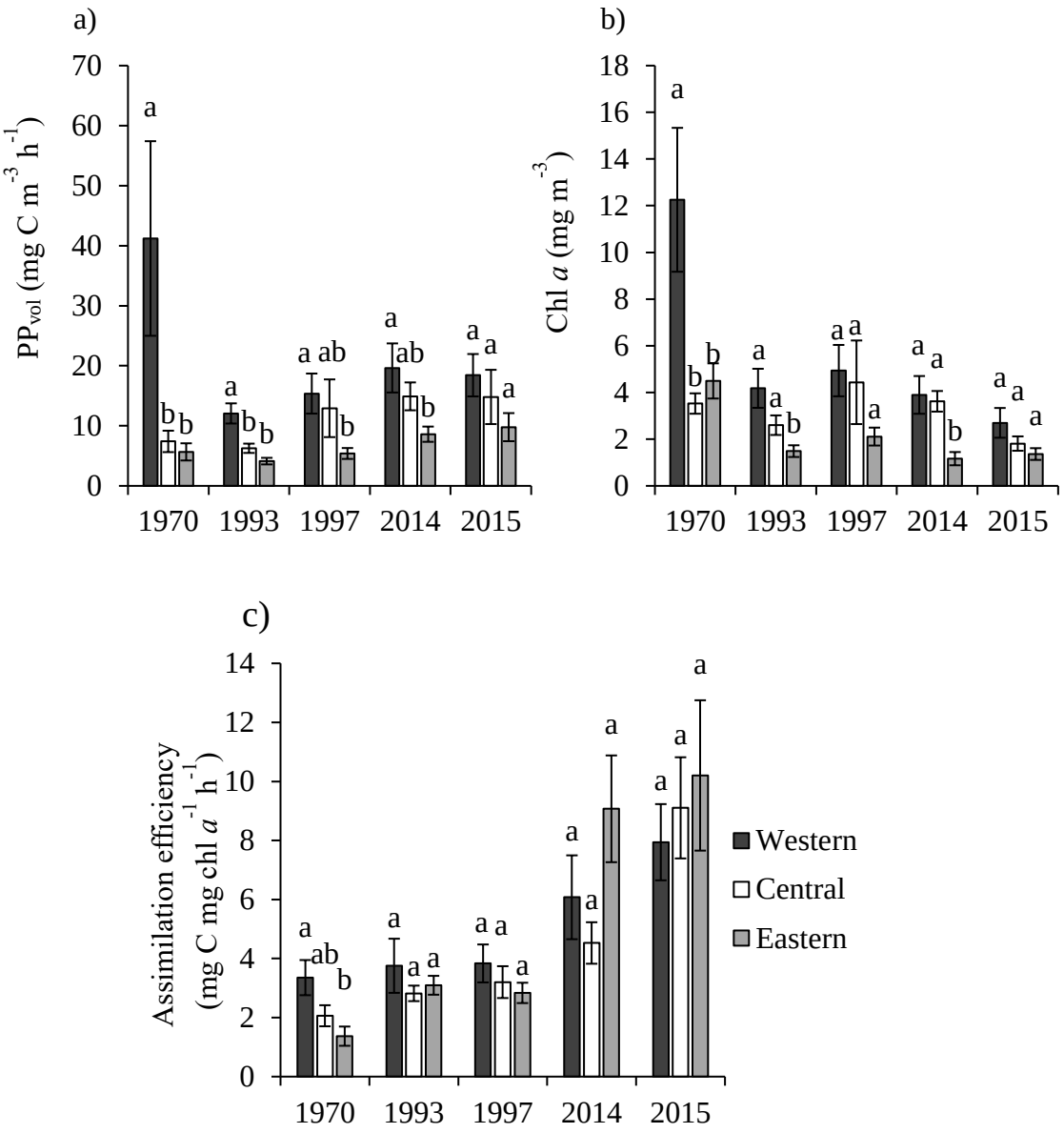

Figure 3.4 Comparison of May to August a) volumetric primary production (PP_{vol}), b) chlorophyll *a* (chl *a*) and c) carbon assimilation efficiencies with previous studies from the three basins of Lake Erie. 1970 data is from Glooschenko et al. (1974), 1993 is from Dahl et al. (1995), 1997 is from Smith et al. (2005) and 2014 and 2015 are from the present study (near and offshore sites). Different letters signify a significant difference between basins per a one-way ANOVA ($p < 0.05$).

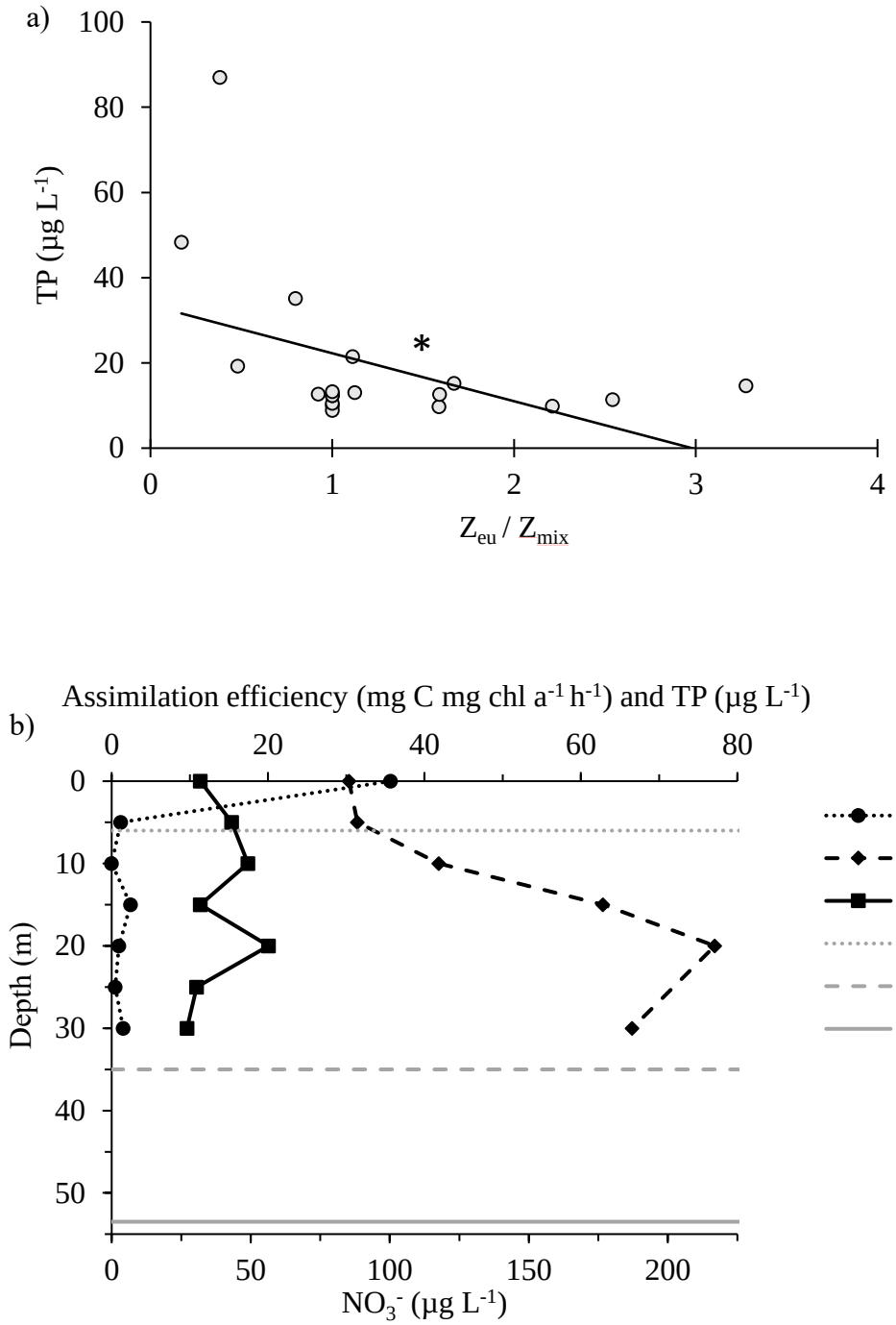

Figure 3.5. a) Ordinary least squares regression between Z_{eu} / Z_{mix} and TP concentrations in the Eastern Basin in 2014 and 2015. * = $p < 0.05$ per an ordinary least squares regression. b) Water column change in assimilation efficiency, TP, and NO_3^- at the east offshore site on October 5, 2015. Z_{eu}, Z_{mix} and Z_{max} are also shown.

CHAPTER 4

GENERAL DISCUSSION

4.1 Discussion

This thesis examined long-term temporal and spatial variation in primary production (both PP_{vol} and PP_{areal}) and potential regulating factors in Lake Erie. Lake Erie is an important system in which to study the effects of multiple stressors on primary production as a result of changing TP loadings to Lake Erie and the invasion of dreissenid mussels in 1988. Although phytoplankton biomass declined from the 1970s to 1980s, eutrophication problems have returned since the mid-1990s (Steffen et al. 2014). As more than 11 million people rely on Lake Erie for drinking water, which was compromised during the Toledo water crisis, there is also high public demand to understand factors driving cyanobacterial blooms in Lake Erie (Watson et al. 2016).

Long-term variation in primary production and other factors in the western basin was addressed in Chapter Two. Summer (June to September) PP_{vol}, phytoplankton biomass and chl *a* all significantly declined from 1970 to 2014 and 2015. Chl *a* and biomass had also declined since 1970 in earlier studies, which was largely associated with the decrease in TP loadings (Makarewicz and Bertram 1991), although the invasion of dreissenid mussels likely played a minor role after 1988 (Charlton et al. 1999). Fitzpatrick et al. (2007) also showed a decrease in spring PP_{vol} since the 1970s, which was attributed to dreissenids. However, this thesis is the first study to demonstrate that summer PP_{vol} has also decreased in the western basin since 1970.

Chapter Three was the first study in Lake Erie to measure both *in situ* primary production and chl *a* at multiple depths across the three basins. Compared to 1970, chl *a* and PP_{vol} did not differ significantly between the western and central basins, while in 1970 both variables were significantly higher in the western basin (Glooschenko et al. 1974a, b). Meanwhile, although

1970 assimilation efficiencies were significantly higher in the western versus eastern basin (Glooschenko et al. 1974a), assimilation efficiencies did not vary significantly across the three basins in 2014 and 2015. Studies comparing primary production methods in the central and eastern basins are needed to determine whether these changes in the spatial pattern were due to a temporal change or a difference in methods.

Both chapters show the importance of considering the effects of multiple stressors, in this case changes in nutrient loading, grazing, and light penetration, on primary production. TP loading reductions and grazing pressure from dreissenids both likely played a part in the long-term decrease in PP_{vol} in the western basin (Chapter Two), as well as the similarities in PP_{vol} between nearshore and offshore sites (Chapter Three). In addition, nutrient recycling during fall overturn in the eastern basin may have led to higher assimilation efficiencies (Chapter Three).

Changes in light penetration also had a very important impact, particularly when comparing PP_{vol} versus PP_{areal}. While offshore PP_{vol} in Chapter Three was significantly lower in the eastern basin versus the western and central basins, there was no significant difference in PP_{areal} as a result of deeper light penetration in the eastern basin. In addition, the long-term increase in light penetration in the western basin maintained PP_{areal} despite a decrease in PP_{vol} associated with declining nutrient levels (Chapter Two). The increase in light penetration also might have contributed to the significant long-term decrease in chl *a*: biomass in the western basin through the physiological process of photoacclimation, ultimately contributing to the increase in assimilation efficiency. Overall, the western basin appears to be moving from a light limited system to a system where other factors such as nutrients, grazing, and temperature are playing a more important role.

Due to the long-term increase in euphotic depth and assimilation efficiency in Chapter Two, annual PP_{areal} did not decrease with chl *a* according to the Vollenweider et al. (1974) model. This suggests that the Vollenweider model should be used with trepidation in the LGL. Future primary production models should quantify TP loadings as well as phosphorus bioavailability to changes in PP_{vol}. As was shown in Lake Erie, human actions such as decreases in TP loadings combined with unexpected stressors such as invasive species can strongly modify the primary production capacities of aquatic ecosystems.

Meanwhile, the stable carbon turnover time and PP_{areal} since 1970 in the western basin (Chapter Two) suggests that there is sufficient primary production to support upper levels of the food web (Fitzpatrick et al. 2008). This is supported by the fact that the fisheries in the western basin of Lake Erie are doing well based on recent increases in fish quotas (Great Lakes Fishery Commission 2017). However, this is not the case in other areas of the LGL. For example, in Southern Lake Michigan, spring PP_{areal} significantly declined from the 1980s and 90s to 2007-2008 (Fahnenstiel et al. 2010). At the same time, there were declines in populations of *Diporeia*, an important fish prey item, as well as fish growth and quality, suggesting that this decrease in PP_{areal} has had negative implications farther up the food web (Evans et al. 2011).

Based on a variety of models, a recent binational report (Annex 4 Objectives and Targets Task Team 2015) called for a 40% reduction in spring TP and DRP loadings to the western basin to combat cyanobacterial blooms. While this recommendation was called a "no regrets" strategy, the declines in PP_{areal} in Lake Michigan and the possible impacts further up the food web (Evans et al. 2011) have revealed significant negative impacts associated with reductions in nutrient loadings and PP_{areal}. If further TP loading reductions contribute to a further decrease in PP_{vol} in the western basin, this might lead to a decrease in PP_{areal} and have negative implications

farther up the food web as a result of a decline in carbon recycling rates at the base of the food web. More research on the factors regulating primary production and phytoplankton community composition are needed to better inform the P loading recommendations.

In the future, nutrient enrichment experiments are also needed in Lake Erie to further study the regulating effects of nutrients on *in situ* primary production and carbon assimilation efficiencies. Because nutrients are quickly taken up by phytoplankton, especially under limiting conditions, nutrient concentrations alone are not sufficient to determine whether nutrients are regulating primary production and carbon assimilation efficiencies. Nutrient enrichment studies conducted in the western (Chaffin et al. 2013), central (Moon and Carrick 2007), and eastern basins (North et al. 2007) have revealed seasonal colimitation of phytoplankton growth involving nutrients such as P, N, Si (silica) and Fe (iron). However, these studies used growth chambers instead of an *in situ* method and considered the response of chl *a* instead of primary production. The interacting effects of nutrients and light also needs to be considered because these variables can change considerably with depth, as discussed in Chapter Three.

Annual measurements of primary production in Lake Erie (and the rest of the LGL) are essential to implement an ecosystem approach to managing the LGL in a manner that integrates watershed and lake management. This approach will require the consideration of factors that regulate both annual and interannual variability of primary production. For example, in a 28-year study at Castle Lake, extreme values of PP_{areal} were more likely to occur in years with strong El Niño/ Southern Oscillation (ENSO) events (Goldman et al. 1989). However, as ENSO and other teleconnections patterns have a time scale of 2-7 years, more than two decades of data are needed to see if these patterns are having a significant effect on primary production (Goldman et al. 1989). The same study found that spring mixing depth can influence interannual variability in

PP_{areal} (Goldman et al. 1989) while ice breakup date and spring precipitation can regulate interannual variability in PP_{vol} (Jassby et al. 1990). These annual climate factors are likely important in the LGL, as suggested in Michalak et al. (2013), where high spring precipitation in 2011 was connected to high P loading and the largest harmful algal bloom at the time. However, more long-term data is needed to study the effects of spring precipitation and other annual climate factors on primary production.

Annual primary production data would also be useful for models connecting TP loadings to central basin hypoxia (Rucinski et al. 2016) western basin cyanobacteria blooms (Obenour et al. 2014) or overall phytoplankton biomass (Verhamme et al. 2016). These models should also consider other factors besides P loadings that may be important, such as the annual climate factors mentioned above, light penetration and other nutrients including N, Si, and Fe.

Primary production was one of the ecosystem processes identified by Sterner et al. (2017) as requiring future research in the LGL. While measuring primary production is expensive and time-consuming, this thesis suggests that multiple stressors, such as differences in nutrient loading, grazing, and light penetration, affect primary production and its relationship with chl *a* in Lake Erie. More research is required to investigate other factors that may be affecting primary production in Lake Erie, such as other nutrients and annual climate factors. A better understanding of the factors regulating primary production is vital to understand the drivers of eutrophication and maintain sustainable fisheries in Lake Erie.

4.2 References

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APPENDICES

Appendix A

Table A.1. Factors influencing seasonal (May – October) a) chlorophyll *a* (chl *a*) and b) phytoplankton biomass (biomass) at each depth in 2014 and 2015. The factors were selected through stepwise backwards Akaike Information Criterion (AIC) model selection, and run as generalized linear models (GLMs). Five different datasets were used: all combined (both years and locations), 2014, 2015, nearshore and offshore. The relationship of each factor with the predictive variables is shown as positive (+), negative (-) or no relationship (x). Factors that are not applicable are shaded gray. (+) for location indicates that the variable was higher at the offshore location compared to the nearshore. PP= primary production, TP = total phosphorus concentration, and NO_3^- = nitrate concentration.

a) Chl *a*	**Factors**								
Dataset	**Year**	**Location**	**Depth**	**Temperature**	**TP**	**NO_3^-**	**PP**	**Chl *a***	**Biomass**
All combined	-	+	+	x	x	-	+		x
2014		x	+	-	x	-	+		+
2015		x	+	x	x	x	+		x
Nearshore	-		x	+	x	-	+		x
Offshore	-		+	x	x	x	+		x
b) Biomass									
All combined	-	+	-	+	x	-	x	x	
2014		x	-	+	-	x	x	+	
2015		x	x	x	x	-	+	x	
Nearshore	x		x	x	x	x	x	+	
Offshore	x		-	+	-	-	x	x	

Table A.2. Multiple R^2 values obtained when running generalized linear models (GLMs) predicting volumetric primary production (PP_{vol}), phytoplankton biomass and chlorophyll *a* (chl *a*). Five different datasets were used: all combined (both years and locations), 2014, 2015, nearshore and offshore. The factors included in the initial models were year (2014 or 2015), location (nearshore or offshore), depth, water temperature, nutrients (TP and NO_3^- concentrations), and the other two phytoplankton variables (between PP_{vol}, phytoplankton biomass, and chl *a*).

	Phytoplankton Variable		
Dataset	**PP_{vol}**	**Phytoplankton biomass**	**Chl *a***
All combined	0.62	0.28	0.56
2014	0.59	0.33	0.54
2015	0.75	0.23	0.62
Nearshore	0.57	0.30	0.68
Offshore	0.69	0.29	0.38

Table A.3. Sources for historical data from the western basin of Lake Erie used for long-term comparisons in Fig. A.1. June- September means and ranges (in parentheses) for each variable are displayed.

Sampling Year	**Source**	**Water column temperature (°C)**	**TP (µg L^{-1})**	**NO_3^- (µg L^{-1})**
1970	EC STAR database	21 (15-25)	38 (17-71)	143 (15-677)
1993	Dahl et al. 1995	23 (16-26)	20 (11-45)	372 (197-659)
1997	Smith et al. 2005	-	25 (14 - 56)	-
2001	Fitzpatrick et al. 2007	23 (22-24)	23 (11-41)	320 (190-568)
2002	Fitzpatrick et al. 2007	23 (19-25)	53 (27-80)	311 (159-506)
2003	Porta et al. 2005	21 (16-24)	82 (58-104)	275 (170-440)
2014	Hillis et al. (this study)	21 (18-23)	18 (12-28)	262 (134-526)
2015	Hillis et al. (this study)	21 (17-25)	28 (16-37)	305 (128-503)

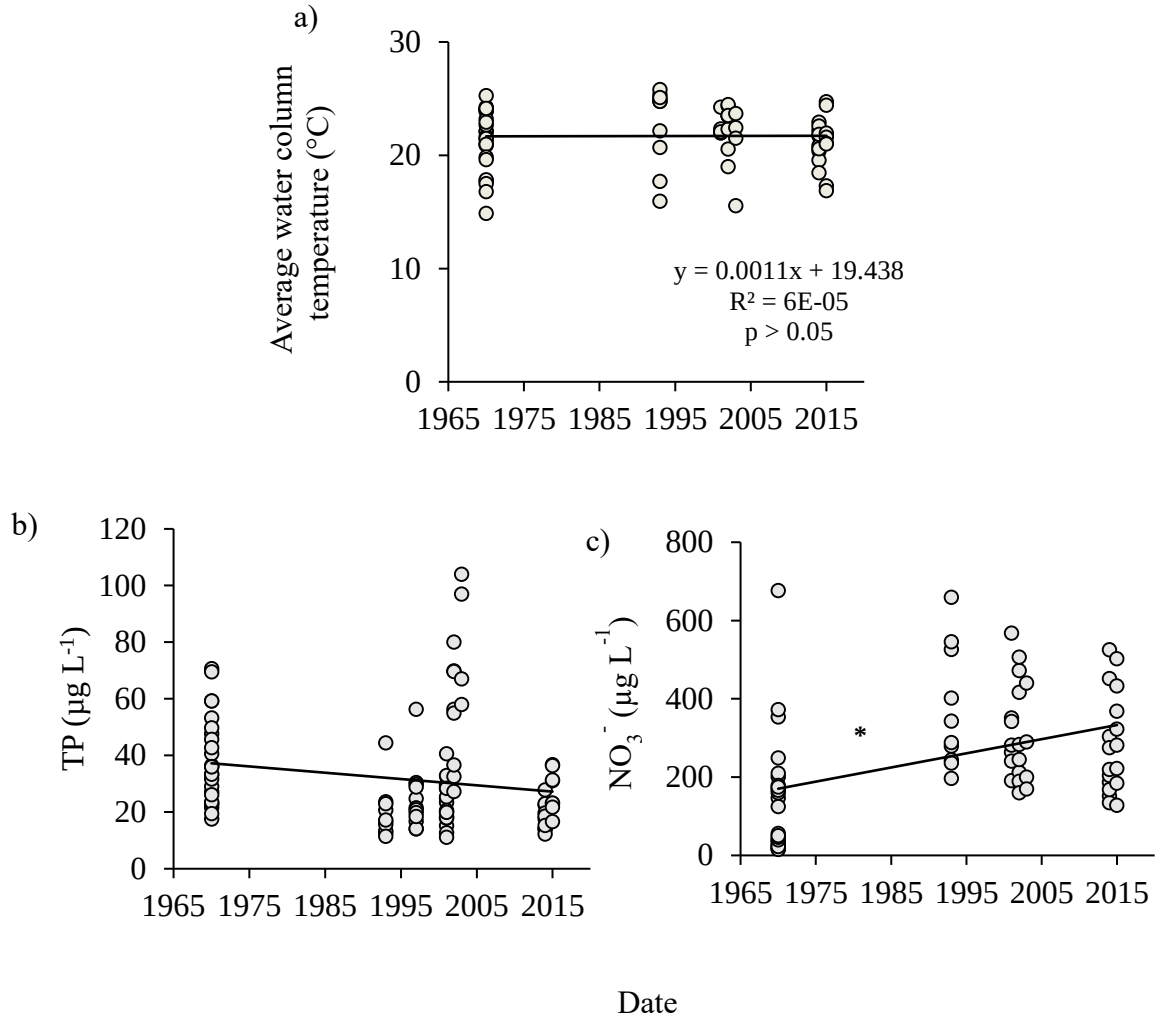

Figure A.1. Long-term temporal change in June - September a) average water column temperature b) TP (total phosphorus) and c) NO_3^- (nitrate) concentrations in the western basin of Lake Erie. Sources, ranges, and averages for each year are listed in Table A.3. Each point represents at least monthly sampling from June-September at separate stations. TP and NO_3^- are volumetric weighted averages of the water column, as described in the methods. * = $p < 0.05$ per an ordinary least squares regression.

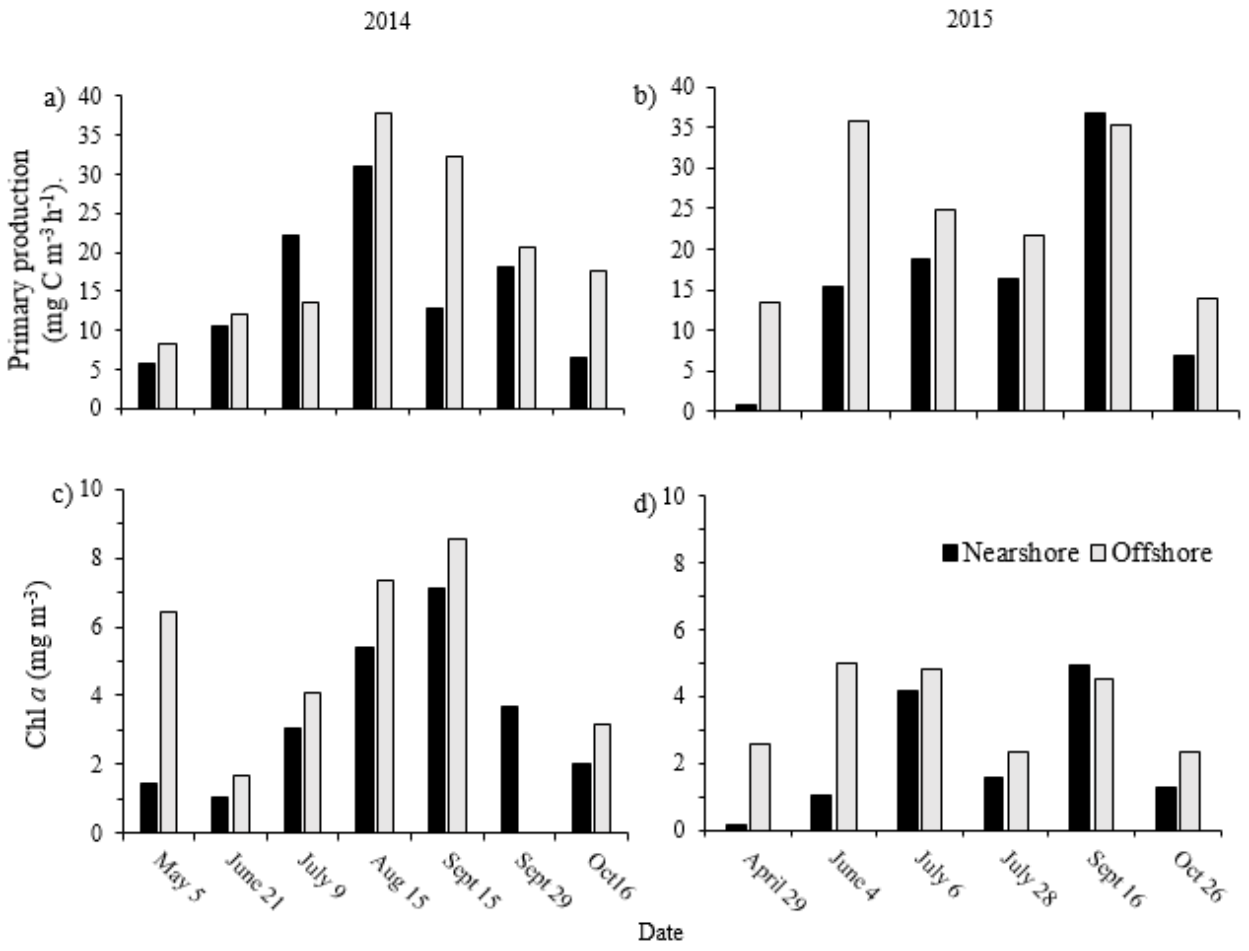

Figure A.2. Seasonal (May- October) trends in a) 2014 and b) 2015 volumetric primary production, as well as c) 2014 and d) 2015 chl *a* at a nearshore (black) and offshore (gray) site in the Western Basin of Lake Erie. Both chl *a* and primary production are volumetric weighted averages of the water column (more details in the methods).

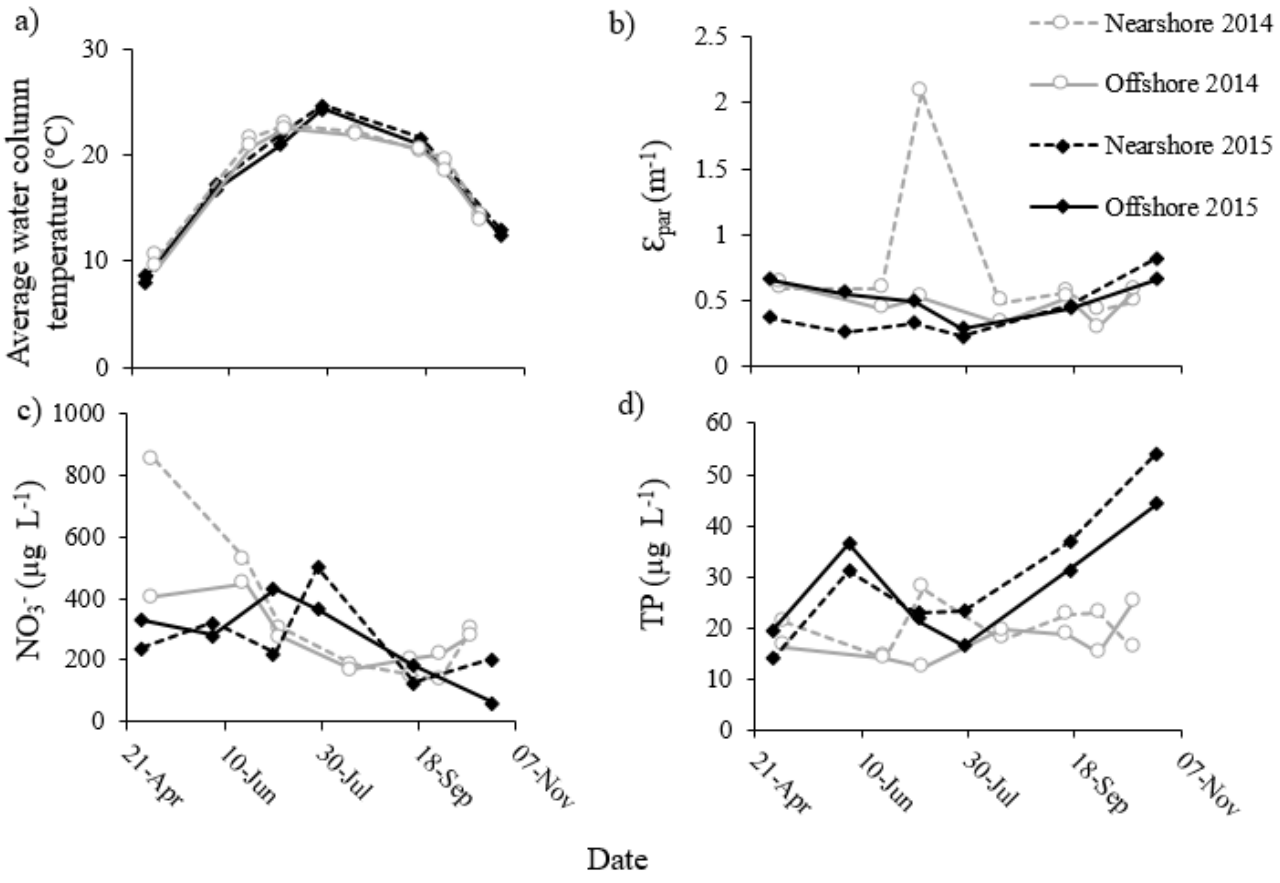

Figure A.3. Seasonal (May – October) trends in a) average water column temperature, b) vertical light attenuation coefficient (ε_{par}), c) NO_3^- concentration and d) TP concentration at a nearshore and offshore site in the western basin of Lake Erie. The two sites and years are indicated in the legend. TP and NO_3^- are volumetric weighted averages of the water column (more details in the methods). ε_{par} was calculated according to equation 2: $\varepsilon_{par} = (\ln I_0 - \ln I_z) / z$.

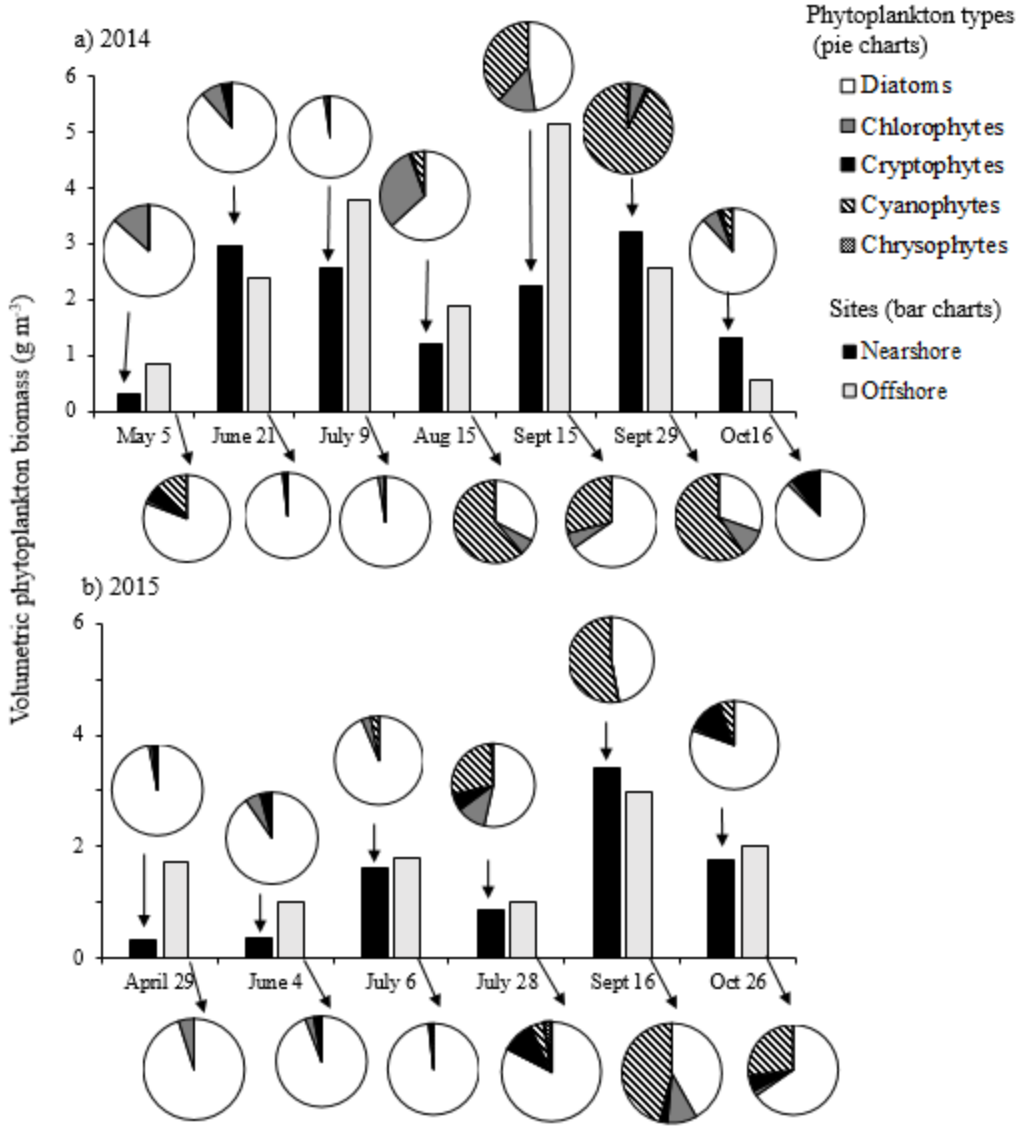

Figure A.4. Seasonal (May- October) trends in phytoplankton biomass (wet weight) and community composition for a) 2014 and b) 2015 in the western basin of Lake Erie. The two sites and types of phytoplankton are indicated in the legend. Nearshore pie charts are above the chart, offshore are below. Biomass is a volumetric weighted average of the water column (more details in the methods).

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