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Lower food web dynamics in lakes Michigan and Huron: Spatial and temporal responses to recent oligotrophication

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Approved by Major Professor(s): Dr. Paris Collingsworth & Dr. Tomas Höök

Approved by: Dr. Robert Wagner   11/18/2016

Head of the Departmental Graduate Program   Date

LOWER FOOD WEB DYNAMICS IN LAKES MICHIGAN AND HURON:

SPATIAL AND TEMPORAL RESPONSES TO RECENT

OLIGOTROPHICATION

A Thesis

Submitted to the Faculty

of

Purdue University

by

Margaret Hutton Stadig

In Partial Fulfillment of the

Requirements for the Degree

of

Master of Science

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West Lafayette, Indiana

I dedicate this to my husband, Eric. You have been my rock and my light. We have been

through so much together, both the ups and the downs. You definitely make brights

brighter, chocolate chocolatier, and shinies shinier. I cannot thank you enough for all

your support. As always *lassiez les bon temps rouler*!

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

Stadig, Margaret Hutton M.S., Purdue University, December 2016. Lower Food Web Dynamics in Lakes Michigan and Huron: Spatial and Temporal Responses to Recent Oligotrophication. Major Professors: Paris D. Collingsworth & Tomas O. Höök.

Nutrient abatement programs, originally enacted to counter eutrophication have successfully suppressed nutrient loads and relative primary production in marine and freshwater systems. Recently, the additive impacts of invasive filter feeders have further reduced offshore primary production in several aquatic systems throughout the world. It has been hypothesized that the biological activity of these invasive species may sequester nutrients within the nearshore benthic environment, creating steep gradients in primary production between nearshore and offshore habitats. In the Laurentian Great Lakes, past studies of oligotrophication have primarily focused on food web responses in offshore habitats. Organisms at higher trophic levels have been impacted by reduced productivity in offshore waters and may now rely more heavily on nearshore production pathways. This study analyzed long-term changes in surface chlorophyll *a* concentrations along a nearshore to offshore gradient and the subsequent responses in physiological condition of the secondary consumer *Bythotrephes longimanus* (hereafter referred to as *Bythotrephes*). First, we examined long-term (1998-2013) seasonal and regional trends in surface chlorophyll *a* concentrations in the main basins of lakes Michigan and Huron using satellite imagery. Contrary to the pronounced declines in offshore areas, nearshore

chlorophyll *a* concentrations increased or remained stable throughout time for most seasons. While no regional trends were observed in Lake Huron, nearshore trends were not homogeneous across regions in Lake Michigan. From 1998 to 2013, Chlorophyll *a* concentrations increased in nearshore areas in the southeast and northwest quadrants of Lake Michigan, most likely due the influence of large adjacent agricultural watersheds and warmer surface water temperatures that characterize these regions. These results were in contrast to the southwest region where nearshore chlorophyll *a* concentrations declined over the course of 16 years. Increases in nearshore chlorophyll *a* concentrations and subsequent increase in prey availability, may corroborate the recent reliance of nearshore resources by some fish species in the Great Lakes. The second aspect of this study focused on whether increased nearshore food web subsides would affect the condition of *Bythotrephes* along a nearshore to offshore gradient and regionally in Lake Michigan. No nearshore to offshore differences in lengths, RNA content, and relative fatty acid content were observed; however, regional differences were, again, prominent. Regional variation in surface water temperature facilitated larger sizes and overall condition of *Bythotrephes* on the eastern shores of Lake Michigan during the spring and summer. By the fall, surface water had warmed sufficiently lake-wide to allow for comparable size and condition in *Bythotrephes* across southern Lake Michigan. Overall, responses to oligotrophication at lower trophic levels have differed in both time and space in lakes Michigan and Huron. Further description of how lower trophic levels respond to oligotrophication can help improve our understanding of how nutrient abatement programs and the establishment of invasive filter feeders are influencing food webs across the Great Lakes.

CHAPTER 1. INTRODUCTION

Oligotrophication has recently become a global issue linked to overfishing

(Kohler et al., 2013; Sanni and Wærvågen, 1990), climate change (Cushing, 1989;

Henderson et al., 1992), and land use change (Stockner et al., 2000a; Wolf, 1960).

Nutrient abatement programs enacted to counter the effects of excess nutrient loading on

water quality are a major contributor to the oligotrophication processes in many marine

and freshwater systems. Additionally, the spread and establishment of invasive filter

feeding invertebrates also contributes to oligotrophication because of the large amount of

nutrients these organisms filter from the water column (Edwards et al., 2005; Ozersky et

al., 2012). Taken together, nutrient abatement programs and invasive filter feeders limit

nutrients available for primary producers in lakes (Fahnenstiel et al., 2010; Strayer,

1991), bays (Strayer et al., 1996; Strayer, Hattala, & Kahnle, 2004), estuaries (Paerl,

2006; Paerl et al., 1998), and riverine systems (Strayer et al., 1996; Zhulidov et al., 2004)

and contribute to declines in primary production in offshore locations.

The effects of oligotrophication are observed not only in offshore locations but

also nearshore. The large amount of nutrients taken in by filter feeders is recycled and

excreted back into the benthos, sequestering nutrients in nearshore habitats (Edwards et

al., 2005; Ozersky et al., 2012; Schneider, 1992). This "nearshore shunt" of nutrients

away from offshore areas, coupled with continued high nutrient loadings from tributaries

into nearshore areas has altered food web dynamics in aquatic systems such as the Chesapeake Bay and the Baltic Sea (Hecky et al., 2004; Lindegren, Blenckner, & Stenseth, 2012; Rennie, Evans, & Young, 2013; Strayer et al., 2004).

In recent years, oligotrophication has become an increasingly important topic in the Laurentian Great Lakes of North America. Elevated anthropogenic nutrient inputs in the 1950s through the 1970s had detrimental effects on the food web and water quality. The Clean Water Act and the Great Lakes Water Quality Agreement were enacted to counter the effects of eutrophication and attempt to restore water quality to historic standards by limiting nutrient input from point source pollution (The Great Lake Water Quality Act, 1972). This resulted in rapid decreases in nutrient loadings and chlorophyll *a* concentrations and restored oligotrophic conditions to many of the Great Lakes (Dolan, 1993; Hartig et al., 1991). In conjunction with nutrient abatement programs, the establishment of zebra (*Dreissena polymorpha*) and then quagga mussel (*D. bugensis*, hereafter both are referred to collectively as dreissenids) during the 1990s and early 2000s further altered nutrient dynamics in the Great Lakes. Both species are aggressive filter feeders with the potential to filter large amounts of nutrients from the water column (Edwards et al., 2005; Ozersky et al., 2015; Ragueneau et al., 2005). Relatively dense colonies of dreissenid mussels in midshore locations filter nutrients as they arrive from nearshore areas and have exacerbated declines in midshore and offshore primary production in lakes Ontario (Hall et al., 2003a), Erie (Leach, 1993; Nicholls and Hopkins, 1993), Michigan (Bunnell et al., 2014; Mida et al., 2010; Pothoven & Fahnenstiel, 2013; Vanderploeg, Liebig, Nalepa, Fahnenstiel, & Pothoven, 2010), and Huron (Fahnenstiel, Bridgeman, Lang, McCormick, & Nalepa, 1995). Locally sequestered nutrients

combined with tributary nutrient inputs culminate in greater food resources nearshore (Lowe and Pillsbury, 1995; Stewart et al., 1998; Stewart and Haynes, 1999) and ultimately increase the general abundance of fish species and their reliance on nearshore subsides (Bunnell et al., 2006; Turschak et al., 2014; Foley et al. *in press*). This may further indicate a nearshore shunt in nutrients is shifting food webs in the Great Lakes.

While decreases in offshore primary production around the Great Lakes have been well documented, few studies have analyzed the effects of sequestered nutrients on nearshore primary production. Studies that have considered nearshore primary productivity dynamics, have typically been limited to water depths greater than 30 m for both field sampling and remote sensing analysis (Fahnenstiel et al., 2010; Yousef, Kerfoot, Shuchman, & Fahnenstiel, 2014), but these areas may not adequately represent trends in more shallow areas. Peak dreissenid mussel densities occur at depths greater than 30 m (Nalepa, Fanslow, & Pothoven, 2010) in areas that are also prone to stratification during summer months (Beletsky & Schwab, 2001), which may isolate surface dwelling phytoplankton from the filtering activity of dreissenid mussels (Boegman et al., 2008). Thus, nearshore trends in primary production from studies based on depths greater than 30 m may be biased and mask the true responses of primary production to oligotrophication and a nearshore shunt in the Great Lakes.

Studies focusing on response of food webs to oligotrophication in Lake Michigan have focused on higher trophic consumers such as yellow perch (*Perca flavescens*) and spottail shiner (*Notropis hudsonius*) for example (Happel et al., 2015a, 2015b; Turschak et al., 2014) with relatively few studies considering the responses of lower trophic level consumers (Turschak and Bootsma, 2015). Secondary consumers such as larval fish,

predatory zooplankton, and the increasingly important invasive cladoceran, *Bythotrephes longimanus* (hereafter referred to as *Bythotrephes*), play a vital role in the food web of the Great Lakes, providing a link between primary production and pelagic consumers (Brandt, Mason, Macneill, Coates, & Gannon, 1987; Bur & Klarer, 1991; Mordukhai-Boltovskaia, 1958; Pothoven & Vanderploeg, 2004; Pothoven, 2005). Spatial gradients in primary production from a nearshore to offshore habitats may influence the physiological condition of these secondary consumers, further highlighting how the entire ecosystem in the Great Lakes are responding to oligotrophication.

The overall objective of this study was to quantify the responses of lower trophic levels to oligotrophication, specifically along a nearshore to offshore gradient in the Great Lakes. We first assessed long term trends in surface chlorophyll *a* concentrations in lakes Michigan and Huron from satellite imagery. Secondly we used field samples and biochemical laboratory techniques to assess the condition of *Bythotrephes* along a nearshore to offshore gradient in southern Lake Michigan. We also investigated heterogeneity in tributary nutrient inputs, surface water temperatures, and bathymetry in nearshore areas of lakes Michigan and Huron as these may cause regional differences in the effects of oligotrophication (Robertson & Saad, 2013; Yurista, Kelly, Cotter, Miller, & Van Alstine, 2015).

Seasonal satellite imagery revealed that nearshore chlorophyll *a* concentrations are not declining uniformly as they are in offshore waters of lakes Michigan and Huron. Instead, chlorophyll *a* concentrations increased in nearshore locations during the spring and remained stable during the summer and fall from 1998 to 2013. In contrast, offshore chlorophyll *a* concentrations declined consistently throughout all regions of lakes

Michigan and Huron during the same time period. Comparing across lakes, chlorophyll *a* concentrations in the nearshore of Lake Michigan varied across broad geographic regions, but similar regional variation was not evident in Lake Huron. In Lake Michigan, the southeast and northwest regions are adjacent to large, primarily agricultural watersheds that input large amounts of nutrients that influence nearshore primary production. In contrast, chlorophyll *a* concentrations decreased throughout the time series in the southwest region of Lake Michigan - a region that is characterized by few, small watersheds and is prone to upwellings that bring cold benthic waters to the surface (Beletsky and Schwab, 2001). Temporal trends in chlorophyll *a* concentrations were relatively consistent across all regions of Lake Huron. Overall, our results indicate that the nearshore shunt may be facilitating general increases in nearshore primary production, though this trend may not be ubiquitous throughout regions.

The regional trends that we identified in chlorophyll *a* concentrations in Lake Michigan may be influencing the physiological condition of *Bythotrephes*. *Bythotrephes* were larger and in better condition along the eastern shoreline of Lake Michigan, particularly in early spring. However, by late summer and early fall, the size and condition of *Bythotrephes* was comparable across regions. This time lag in development of *Bythotrephes* along western shores is most likely due to variations in surface water temperature. Temperatures along the western shores of Lake Michigan are typically colder throughout most of the year (Yurista et al., 2015) but once temperatures surpass lower thresholds of optimal growth along western shores in the late summer, the size and physiological condition of *Bythotrephes* were not different between regions. Comparatively, no differences in the condition of *Bythotrephes* were observed along a

nearshore to offshore gradient despite distinct gradients in chlorophyll *a* concentrations derived from satellite analyses. Historically, *Bythotrephes* have been considered a primarily offshore species, but increases in nearshore abundances and sizes of *Bythotrephes* have been recently documented. This may indicate that either offshore populations are declining due to the recent deficiency in food resources or nearshore subsides can now sustain *Bythotrephes* populations where previously they could not.

The spatial and temporal trends observed in this study reflect other trends detected in similar systems experiencing oligotrophication. Shifts in the Great Lakes from primarily pelagic based food webs to ones that rely more heavily on nearshore and benthic production pathways could have important implications for understanding and managing aquatic communities. With declining primary and secondary production in the offshore zone, nearshore resources may become more important for zooplankton and fish communities. However, the spatial trends that we described in both primary production and *Bythotrephes* condition indicate that the effects of oligotrophication are not homogeneous across large, complex systems. As a result, management agencies may need to develop spatially explicit plans to manage nutrient loading and fish communities throughout the lake. Further studies should further explore the regional responses of lower trophic levels to oligotrophication in the Great Lakes.

CHAPTER 2. SPATIOTEMPORAL VARIATION OF CHLOROPHYLL *A*
CONCENTRATIONS IN LAKES MICHIGAN AND HURON

2.1   Introduction

The detrimental impacts of cultural eutrophication due to increased anthropogenic nutrient loading to streams, lakes, marine, and estuarine systems are well established (Carpenter et al., 1998; Smith, Tilman, & Nekola, 1998; Smith, 1998). Nutrient abatement programs enacted to limit excessive anthropogenic nutrient loading in aquatic systems from both point- and non-point-sources, have generally been effective at improving water quality (Guildford & Hecky, 2000; Smith, 2006). Yet, responses to rapid nutrient declines have varied across systems and regions. In many aquatic systems, dramatic declines in nutrient loadings have resulted in the reverse of cultural eutrophication i.e. oligotrophication (Lindegren et al., 2012; Ney, 1996; Stockner et al., 2000b; Yurk and Ney, 1989).

In addition to nutrient abatement, other anthropogenic activities can contribute to oligotrophication. Overfishing can promote oligotrophication by decreasing nutrients subsidies from migratory fish (Kohler et al., 2013) or by decreasing zooplanktivorous fish populations that prey on herbaceous zooplankton, which can lead to overgrazing primary producers (Sanni and Wærvågen, 1990). Climate change can lead to warmer and more strongly stratified lake conditions and intensify the effects of oligotrophication by limiting nutrient exchange and habitat volume for primary producers for longer portions

of the year (Stockner et al., 2000b). The introduction of invasive species can interrupt

production pathways and exacerbate oligotrophication causing lasting effects throughout

the food web. Specifically, intensive filter feeding bivavles have been shown to interrupt

nutrient cycling (Gergs, Grey, & Rothhaupt, 2011; Nalepa, Hartson, Fanslow, Lang, &

Lozano, 1998), facilitate decreases in primary production, and restructure food webs

(Boltovskoy et al., 2015; Boltovskoy and Correa, 2014; Eby et al., 2005) within coastal

marine (Alpine and Cloern, 1992), inland river (Sylvester et al., 2005; Vaughn and

Hakenkamp, 2001), and large and small lake systems (Beaver et al., 1991).

Two particular invasive species, zebra and quagga mussels (*Dreissena*

polymorpha and *D. rostriformis bugensis*, respectively, here after dreissenid mussels),

have contributed to oligotrophication in a variety of ecosystems worldwide (Gergs et al.,

2011). Both species are efficient filter feeders limiting nutrients and removing primary

producers from the water column (Edwards et al., 2005) and thus have been linked to

declines in primary production in streams (Horvath and Lamberti, 1999), rivers (Strayer

et al., 1996; Zhulidov et al., 2004), and lakes (Nalepa et al., 1998; Strayer, 1991). In

particular, dreissenid mussels have had noticeable effects on primary production and food

webs throughout the Laurentian Great Lakes. It has been hypothesized that relatively

high densities of dreissenid mussels at mid-depth locations (30-90 m in depth) may divert

nutrients into benthic habitats before these nutrients can reach offshore pelagic areas

(Cha, Stow, Nalepa, & Reckhow, 2011; Nalepa et al., 2010; Yousef et al., 2014).

Coupled with nutrient abatement programs around the Great Lakes (Dolan, 1993; Hartig

et al., 1991), dreissenid mussels have caused drastic declines in offshore primary

production in lakes Erie (Leach, 1993; Nicholls and Hopkins, 1993), Ontario (Hall et al.,

2003a), Michigan (Bunnell et al., 2014; Fahnenstiel et al., 2010; Mida et al., 2010; Pothoven & Fahnenstiel, 2013), and Huron (Fahnenstiel et al., 1995).

While primary production has decreased in offshore areas of the Laurentian Great Lakes (Nalepa et al., 2010, 1998; Yousef et al., 2014), nearshore habitats may continue to receive relatively high nutrient inputs from tributaries. Along shore currents limit offshore exchange of water from tributaries, concentrating nutrients in the nearshore zone (Yerubandi Rao & Schwab, 2007). Moreover, filtering by dreissenid mussels may cause nutrients to be trapped in nearshore benthic habitats where primary producers may benefit from excretion of dreissenid feces and pseudofeces (Ozersky et al., 2015). This accumulation of nutrients in the nearshore benthos may have brought about a nearshore shunt in production (Hecky et al., 2004; Turschak et al., 2014). As such, sequestration of nutrients in the nearshore zones though time would suggest that long-term trends in nearshore primary production may have diverged from offshore trends, resulting in a food web that relies more heavily on nearshore production pathways (Turschak et al., 2014; Turschak and Bootsma, 2015). However, it is an open question as to whether nearshore primary production has simply declined at slower rates compared to offshore production or if nearshore primary production has actually increased despite reduction in nutrient loading.

Nearshore habitats throughout the Great Lakes are not homogenous due to differences in tributary input, bathymetry, substrate, riverine input, and other environmental characteristics. Tributary size and dominant land uses in adjacent watersheds influence the amount of nutrients and the timing of nutrient delivery into nearshore areas of the Great Lakes (Yurista, Kelly, & Miller, 2011; Yurista, Kelly,

Miller, & Van Alstine, 2012). This can have direct effects on the level of primary

production within nearshore habitats (Dillon and Kirchner, 1975; Lougheed et al., 2001).

Seasonal water temperatures and exchange with shallow embayments such as Green Bay,

Saginaw Bay, and western Lake Erie may also play an important role in driving primary

production within adjacent nearshore regions. Spatial variation in food web subsides

have also been observed around the Great Lakes. A higher reliance of pelagic food web

subsides has been observed in areas adjacent to agricultural watersheds where

chlorophyll *a* concentrations and subsequent food resources may be sustained in pelagic

nearshore locations. Comparatively, in areas associated with smaller, urban watersheds,

many consumers rely on benthic production pathways (Happel et al., 2015a, 2015b;

Foley et al., *in press*). The limited amount of nutrients that is inputted into these areas

may be immediately sequestered by dreissenid filtering, thus forcing consumers to shift

to more benthic food sources. Ultimately this may lead to spatial variation in nearshore

chlorophyll *a* concentrations and subsequently food resources throughout nearshore areas

of Great Lakes as a result of oligotrophication.

For this study we quantified long-term (1998-2013) changes in chlorophyll *a*

concentrations as a proxy for primary production in lakes Michigan and Huron. Surface

chlorophyll *a* concentrations were inferred from satellite imagery from the Sea-Viewing

Wide Field-of-View Sensor (SeaWiFS) and Moderate Resolution Imaging

Spectroradiometer (MODIS) sensors to increase spatial and temporal coverage

throughout both lakes compared to the limited spatiotemporal extent of *in situ* sampling.

We focused on seasonal trends in chlorophyll *a* concentrations along nearshore to

offshore gradients, and compared temporal trends around distinct regions of lakes

Michigan and Huron. We also discuss various environmental factors (i.e. water

temperature, size and majority land use of adjacent tributaries, and driessenid mussel

densities) to help explain observed seasonal and regional trends. We hypothesized that 1)

nearshore zones have experienced slower declines of chlorophyll *a* concentrations

relative to offshore zones, and 2) regional trends in nearshore chlorophyll *a*

concentrations may diverge based on proximity to high nutrient loading watersheds.

2.2   Materials and Methods

2.2.1   Satellite Imagery and Standardization

Chlorophyll *a* concentrations (mg • m^{-3}) were estimated from daily images

produced by the SeaWiFS (1998 to 2010) and MODIS (2002 to the present) ocean color

sensors. Both satellites have an approximate pixel resolution at nadir of 1 km by 1 km.

A tuned band-ratio algorithm was used to estimate the chlorophyll *a* concentrations in

both lakes including nearshore areas (typically areas <30m in depth; Lesht et al., 2015,

2013). This particular band-ratio retrieval method eliminates areas with low blue/green

band ratios which includes areas dominated by the benthic algae *Cladophora*, and

focuses on changes in chlorophyll *a* concentrations (Higgins et al., 2008). The algorithm

also accounts for days with missing data due to cloud cover and suspended sediment by

calculating monthly average chlorophyll *a* concentrations for each 1 x 1 km pixel.

Monthly averages were natural log transformed before analysis due to the lognormal

distribution exhibited by chlorophyll *a* concentrations (Campbell, 1995; O'Reilly et al., 1998; O'Reilly & Maritorena, 2000).

The SeaWiFS and MODIS sensors use different spectral bands to estimate chlorophyll *a* concentrations. The newer MODIS sensor has higher sensitivity and precision than the older SeaWiFS sensor. Previous studies have identified deviations between the SeaWiFS and MODIS sensors especially at high and low chlorophyll *a* concentrations (Kwiatkowska and Fargion, 2003; Zhang et al., 2006). Therefore, it was necessary to standardize the estimated chlorophyll *a* concentrations between satellites to facilitate analyses throughout the entire time series of this study (1998 to 2013). While previous studies in marine systems have already standardized chlorophyll *a* for the two satellites (Zhang et al., 2006; Zibordi et al., 2006), few have standardized estimates in nearshore locations (Schaeffer, 2013). In this study we successfully standardized the SeaWiFS sensor estimates to match the newer MODIS sensor estimates creating a comparable data set with standardized SeaWiFS data from 1998 to 2002 and MODIS data from 2003 to 2013 (see appendix)

2.2.2   Spatiotemporal Analysis

Analyses of chlorophyll *a* concentrations focused not only on the main basin of lakes Michigan and Huron as a whole, but also on different regions that were characterized by specific geographic and bathymetric attributes such as benthic substrate, adjacent watershed size, and prominent land use cover (Table 2.1). Lake Michigan was divided into four regions: a warm, shallow southern basin and a cold, deep northern basin

separated by the Two Rivers Ridge with each basic split from east to west in the middle of the lake (Figure 2.1). Lake Huron was similarly separated but into three different regions with a shallow southern basin and a deep northern basin separated by the Alpena-Amberley Ridge. The northern basin was divided into two sections (northwest and northeast) at the middle of Manitoulin Island (Figure 2.1).

The combined satellite estimations from 1998 to 2013 were used to assess seasonal trends in chlorophyll *a* concentrations for Lake Michigan and Lake Huron. Three months (May, July, and September) were analyzed to capture seasonal differences in surface chlorophyll patterns. Average chlorophyll *a* concentrations for each month were calculated for a number of spatial bins, encapsulating a nearshore to offshore gradient. 'Nearshore' has been defined differently across various studies (e.g., Rao and Murthy, 2001a, 2001b; Yousef et al., 2014); therefore our analyzes focused on two commonly used 'nearshore' definitions: depth contour and distance from shore. Depth contour estimations for chlorophyll *a* concentrations were averaged for 10 m depth intervals starting from the shoreline and proceeding out to all areas greater than 90 m in depth (Figure 2.1). Estimates of chlorophyll *a* concentrations were also averaged based on 2.5 km distance intervals from shore. The first bin started at the shoreline and the last bin incorporated all areas greater than 52.5 km from the shore line (Supplemental material, Figure A.1). Regional and whole basin concentrations were averaged for each depth and distance bin around Lake Michigan and Lake Huron.

For each month, average chlorophyll *a* concentration for each depth and distance bin were regressed against year, with the slope of each regression representing the rate of change in chlorophyll *a* concentration (mg • yr^{-1}). To assess if nearshore and offshore

concentrations diverged overtime, the average maximum chlorophyll *a* concentrations

(from the most nearshore concentration), minimum (from the most offshore

concentration), and range (the difference between the most nearshore concentration and

the most offshore concentration) were calculated for four time periods; 1998-2001, 2002-

2005, 2006-2009, 2010-2013. ANCOVAs were used to determine if the rate of change in

chlorophyll *a* concentration differed across depth contour and distance bin. For each

season and region chlorophyll *a* concentration served as the response variable and

predictor variables including: depth (or distance) as a factor, year as a covariate and the

interaction between depth/distance. Significant interaction terms between depth/distance

and year indicated a difference in the rate of change in chlorophyll *a* concentration

among depth and distance bins.

To further analyze the standardization of the two satellites, the ANCOVAs

described above were run with only MODIS information (2003 to 2013). Similar results

would indicate that the standardization at least held the patterns that were observed

despite potential variations in the absolute value of the estimations (results in the

supplemental material). Temporal and spatial means were calculated in ArcGIS 10.2

(ESRI, ArcDesktop: Release 10. Redlands, CA: Environmental Systems Research

Institute). All other analyses were conducted in R Version 3.1.1 (R Code Team (2014)).

2.3   Results

Results of analyses based on depth and distance from shore were qualitatively

similar, thus only the results with depth bins are reported herein (see supplemental

material for distance analysis results). While the magnitude of trends differed between lakes Michigan and Huron, both lakes had an increase in the range of chlorophyll *a* concentrations between nearshore and offshore zones from 1998-2013(Table 2.2). The range of chlorophyll *a* concentrations around Lake Michigan increased 2× or 3× from 1998 to 2013 (Table 2.2). The range of chlorophyll *a* concentrations in May and July in Lake Huron increased from 1998 to 2013 but the increases were not to the same magnitude as those in Lake Michigan. Comparatively, the range of September chlorophyll *a* concentrations in Lake Huron remained relatively constant.

In May, for both Lake Michigan and Lake Huron, there was a significant interaction between depth and year indicating different rates of change based on depth contours (Figure 2.2 a,d). While chlorophyll *a* concentrations from about 0 to 30m in depth in May did not express strong change overtime (Figure 2.2a,d), offshore chlorophyll *a* concentrations at depths greater than 60 m significantly declined, especially in Lake Michigan. While the interaction of year and depth was significant for Lake Michigan and Lake Huron in July (Figure 2.2 b,e), the overall rate of change for each depth differed compared to May. As opposed to May, chlorophyll *a* concentrations from 0-30m in depth in July increased over time while concentrations in areas greater than 60m in depth neither increased nor decreased for both lakes Michigan and Huron (Figure 2.2 b,e). Trends in September in Lake Michigan were similar to July with increases nearshore and fairly stable concentrations offshore. In contrast, there was not a significant interaction between depth and year in Lake Huron in September indicating no difference in the rate of change of chlorophyll *a* concentrations across depth contours (Figure 2.2 f).

We observed regional differences in rate of change in chlorophyll *a* concentration, particularly in Lake Michigan. Specifically, nearshore chlorophyll *a* concentration increased in northwest, northeast, and southeast regions of Lake Michigan for all seasons, while concentrations decreased in southwest Lake Michigan (Figure 2.3 a-c). While offshore areas decreased in chlorophyll *a* concentrations over time across all regions, the southeast and northwest region had relatively less negative slopes in offshore locations indicating relatively slower rates of decline with significant interactions between depth and year (Figure 2.3). Compared to the rest of the lake, the southwest region of Lake Michigan consistently exhibited relatively greater negative slopes in chlorophyll *a* concentrations (Figure 2.3 a-c) and only in May was there a significant interaction between depth and year in the southwest region of Lake Michigan (Figure 2.3 a).

Regional differences in Lake Huron were not as pronounced as in Lake Michigan. The rates of change in chlorophyll *a* concentrations were fairly consistent for all regions in offshore locations in Lake Huron. Nearshore chlorophyll *a* concentrations in southern Lake Huron in general declined more rapidly than in the northwest and northeast regions, but this pattern did not hold across months (Figure 2.3 d,e). Significant interaction terms between depth and year were evident in all three regions of Lake Huron: northeast (May and July), northwest (July), and south (May) (Figure 2.3 d,e). However, in September, there was no significant interaction between depth and year across in any region of Lake Huron (Figure 2.3 f).

2.4 Discussion

Nutrient abatement programs and invasive filter feeders have contributed to decreases in chlorophyll *a* concentrations in offshore locations throughout not only the Great Lakes (Fahnenstiel et al., 2010, 1995; Mida et al., 2010; Pothoven and Fahnenstiel, 2013), but also in various freshwater, marine, and brackish water systems (Kimmerer, 2006; Naddafi, Eklöv, & Pettersson, 2009; Strayer et al., 2004). Declines in offshore primary production have also lead to declines in offshore consumer biomass in other systems (Kimmerer, 2006; Madenjian et al., 2015; Strayer et al., 2004). However primary production trends in nearshore regions of oligotrophic systems many not track offshore trends. As our study demonstrates, nearshore chlorophyll *a* concentrations have increased in some regions, while offshore concentrations have declined. Prominent shifts in the relative importance of nearshore production has seemingly facilitated increases of certain nearshore species (Bunnell et al., 2006; Jude & Tesar, 1985; Lindegren et al., 2012; Stewart et al., 1998; Strayer et al., 2004) and increase overall reliance on nearshore production pathways (Happel et al., 2015a, 2015b; Rennie et al., 2013; Turschak et al., 2014; Turschak and Bootsma, 2015).

Many past studies describing the concentrations of primary producers in the Great Lakes have focused on offshore locations. Studies describing nearshore chlorophyll *a* concentration patterns have relied on either local transect based sampling (Fahnenstiel et al., 2010; Mida et al., 2010) or satellite imagery to assess chlorophyll *a* concentrations across broad spatial scales (Yousef et al., 2014). However such studies do not include areas less than 30 m in depth and thus ignore or potentially misinterpret the effects of

oligotrophication on nearshore areas. The band-ratio retrieval method used by Lesht et al. (2013) allowed us to consider changes in chlorophyll *a* concentrations in true nearshore locations (< 30 m in depth). The increased temporal and spatial extent of this study allowed us to discern that trends in nearshore chlorophyll *a* concentration did not mirror the decreased trends offshore.

In lakes Michigan and Huron, the overall range between nearshore and offshore chlorophyll *a* concentrations increased overtime. However, the mechanism underlying this increase in the range of chlorophyll *a* concentrations differed by season. In May, regular mixing throughout the water column has the potential to expose surface chlorophyll *a* to filtering by benthic dreissenid mussels, which may lead to drastic declines in offshore primary production (Fahnenstiel et al., 2010; Nalepa et al., 2010). Nearshore locations, though, can be supplemented by localized riverine nutrient from spring runoff in a way that sustains chlorophyll *a* concentrations (Nalepa et al., 2010). In July and September, stratification limits the amount of nutrient exchange between the benthos and epilimnion in offshore locations. During these months, nutrients that were sequestered in the nearshore benthos may still become available due to regular mixing in shallow habitats (Nalepa et al., 2010).

While temporal trends of chlorophyll *a* concentrations were similar across Lake Michigan and Lake Huron, the absolute concentration between the two lakes drastically differed. Lake-wide chlorophyll *a* concentrations were consistently higher in Lake Michigan compared to Lake Huron. Lake Michigan has relatively higher retention time and primarily agricultural based watersheds that typically facilitate greater primary production (Beletsky et al., 1999; Lam and Halfon, 1978; Quinn, 1992). The density of

dreissenid colonies in Lake Huron are lower in both nearshore and offshore locations compared to Lake Michigan (Nalepa et al., 2010; Nalepa, Fanslow, Pothoven, Foley III, & Lang, 2007), which could limit the magnitude of change in relative nearshore production (Nalepa, Pothoven, & Fanslow, 2009; Nalepa et al., 2007).

Studies across a variety of systems have also documented that spatial trends in primary production may be heterogeneous within ecosystems (Carstensen et al., 2011; Taylor et al., 2011). Previously, nutrient abatement efforts were expected to have similar homogeneous effects throughout aquatic ecosystem (Guildford and Hecky, 2000). However, variation in spatial responses of phytoplankton to declines in nutrients similar to those detected in this studied have been identified across lakes (Danielsson et al., 2004; Madenjian et al., 2011) and coastal ecosystems (Carstensen et al., 2011). Such spatial structuring of primary production in response to reduced nutrient loads have been attributed to various causes. For example, environmental factors such as tidal range (Fisher et al., 1999)and upwellings (Polis et al., 1997) have been shown to drive spatial differences in primary production by influencing nutrients availability.

Temporal trends of chlorophyll *a* concentrations were more variable across regions in Lake Michigan compared to Lake Huron despite both lakes having similar bathymetry and geographic features. The southeast and northwest regions of Lake Michigan displayed slight decreases in chlorophyll *a* concentrations in offshore areas and increased chlorophyll *a* concentrations in nearshore areas, particularly during July and September. Both regions receive high amounts of nutrient input from large, primarily agricultural watersheds. Specifically in the northwest, current exchange from the nutrient rich waters of Green Bay directly affect nearshore concentrations in Lake Michigan

(Miller and Saylor, 1985). Conversely, chlorophyll *a* concentrations declined in southwestern Lake Michigan across all depth strata and months. Unlike other regions, the southwest region of Lake Michigan has relatively few, small watersheds with lower nutrient inputs and relatively cold surface water temperatures due to prevailing winds pushing warmer surface water towards the eastern shores of the lake (Table 2.1; Beletsky and Schwab, 2001; Mortimer, 1971; Noble and Wilkerson, 1970). Around Chicago, water is diverted from Lake Michigan into the local river system (Lanyon, 2005) and hard substrate on the southwest shores of Lake Michigan also facilitates greater dreissenid colonization further inhibiting primary production at all depth strata (Table 2.1; Boss and Zaneveld, 2003; Zikhali et al., 2015). In Lake Huron, few to no regional differences in temporal trends of chlorophyll *a* concentrations were apparent. The relatively low chlorophyll *a* concentrations of Lake Huron could also obstruct regional and depth trends.

Results from this and other studies are consistent with the theory of the nearshore shunt. Increases in nearshore nutrients due to localized nutrient loading and the sequestration of nutrients to nearshore habitats by dreissenid mussels are most likely increasing nearshore primary production (Hecky et al., 2004; Lindegren et al., 2012). The coupled effects of increased nearshore primary production and benthic nutrients also has the potential to drive an influx of different species to nearshore locations. With increased habitat from their shells and increased nutrients, dreissenid mussel beds have been shown to increase the abundances of some macroinvertebrates (Ward and Ricciardi, 2007). Recent studies have also shown that fish abundances and catch rates in the Great Lakes may be responding to increasing production in nearshore areas (Simpson et al.,

2016; Strayer et al., 2004), but more information is needed to understand whether these trends are ubiquitous throughout the Great Lakes.

The effects of rapid nutrient reduction on primary production will be observed in many ecosystems as current nutrient abatement programs are enforced and future programs are enacted (Scavia et al., 2015; Watson et al., 2016). Climate change will also exacerbate the spread and establishment of exotic species throughout the world (Raitsos et al., 2010), most of which are expected to be planktivores or deposit feeders (Byrnes et al., 2007) similar to the dreissenid mussel in the Great Lakes. Thus the additive effects of nutrient abatement and invasive filter feeders may shift ecosystems worldwide.

Table 2.1. Comparison of different environmental variables in regions of Lake Michigan and Lake Huron. The number of hydrological unit code (HUC) 8 water shed unit information was accessed through Great Lakes Information Network (Wang et al., 2015); Land cover information was obtained through Great Lakes Aquatic Habitat Framework 2016; Phosphorous loadings were estimated through the SPAtially Referenced Regressions On Watershed attributes (SPARROW) Model for 2002 (Schwarz et al., 2006); Substrate information was obtained from (Creque et al., 2010; Thomas et al., 1973).

	The Number of HUC 8 watershed units; Total Area (1000 has) of Watersheds	Top 2 Percent Land Cover	Avg. Phosphorous Loading (kg km^{-2})	Substrate Type
		Lake Michigan		
Northeast	4; 1,273	Forest (46%) Wetland (15%)	50.42	Increased percentage of larger gravel
Northwest	13; 3,214	Forest (32%) Wetland (31%)	512.79	
Southeast	7; 3,669	Agriculture (40%) Forest (25%)	244.12	Sand and silt
Southwest	3 513	Agriculture (35%) Development (35%)	415.72	Hard, Rock Substrate
		Lake Huron		
Northeast	10; 4,843	Forest (54%) Agriculture (21%)	No Loading Estimates Available	bedrock and glacial till
Northwest	US (5) & CAN (3); 2,361	Forest (64%) Wetland (12%)	No loadings available for North Channel	bedrock and glacial till
Southern	US (7): 1,660 CAN (3): 682	Agriculture (49%) Forest (24%)	348.7	Bedrock, glacial till, and sand

Table 2.2. Average chlorophyll a concentrations (mg m^3) of the maximum (most nearshore) minus the minimum (most offshore) and the range (difference between the most nearshore concentration and the most offshore concentration) for four different time periods for the main basin (Whole) and each region of lakes Michigan and Huron. Overall ranges of chlorophyll *a* concentrations increased overtime for most regions of both Lake Michigan and Lake Huron.

		1998-2001	2002-2005	2006-2009	2010-2013
			Lake Michigan		
May	Whole	1.28 - 0.84 (0.44)	1.22 - 0.68 (0.54)	1.29 - 0.54 (0.75)	1.33 - 0.46 (0.87)
	NE	1.04 - 0.82 (0.22)	1.02 - 0.61 (0.41)	1.09 - 0.54 (0.56)	1.08 - 0.46 (0.62)
	NW	1.32 - 0.79 (0.53)	1.35 - 0.64 (0.71)	1.39 - 0.55 (0.84)	1.53 - 0.48 (1.05)
	SE	1.57 - 0.88 (0.69)	1.46 - 0.66 (0.79)	1.67 - 0.54 (1.13)	1.68 - 0.44 (1.24)
	SW	1.20 - 0.87 (0.33)	1.05 - 0.73 (0.32)	1.01 - 0.55 (0.46)	1.03 - 0.45 (0.58)
July	Whole	1.16 - 0.66 (0.50)	1.17 - 0.59 (0.58)	1.26 - 0.49 (0.77)	1.28 - 0.43 (0.85)
	NE	1.07 - 0.77 (0.30)	1.18 - 0.68 (0.50)	1.11 - 0.54 (0.57)	1.15 - 0.48 (0.67)
	NW	1.25 - 0.70 (0.55)	1.38 - 0.69 (0.69)	1.45 - 0.58 (0.87)	1.53 - 0.54 (0.99)
	SE	1.30 - 0.60 (0.70)	1.26 - 0.52 (0.74)	1.59 - 0.42 (1.17)	1.54 - 0.36 (1.18)
	SW	1.02 - 0.56 (0.47)	0.87 - 0.48 (0.38)	0.89 - 0.43 (0.46)	0.91 - 0.36 (0.55)
September	Whole	1.15 - 0.69 (0.46)	1.19 - 0.60 (0.59)	1.27 - 0.55 (0.72)	1.29 - 0.60 (0.68)
	NE	1.14 - 0.79 (0.35)	1.25 - 0.67 (0.58)	1.26 - 0.62 (0.65)	1.25 - 0.65 (0.60)
	NW	1.16 - 0.76 (0.40)	1.33 - 0.68 (0.65)	1.34 - 0.63 (0.71)	1.51 - 0.70 (0.81)
	SE	1.16 - 0.61 (0.55)	1.18 - 0.52 (0.65)	1.49 - 0.48 (1.01)	1.38 - 0.55 (0.83)
	SW	1.14 - 0.60 (0.53)	1.00 - 0.54 (0.46)	1.01 - 0.47 (0.53)	1.01 - 0.52 (0.49)

		1998 – 2001	2002 - 2005	2006 - 2009	2010 – 2013
		Lake Huron			
May	Whole	0.51 - 0.31 (0.21)	0.48 - 0.25 (0.22)	0.51 - 0.19 (0.32)	0.49 - 0.16 (0.33)
	NW	0.45 - 0.30 (0.25)	0.47 - 0.25 (0.21)	0.47 - 0.20 (0.27)	0.48 - 0.16 (0.31)
	NE	0.47 - 0.29 (0.18)	0.49 - 0.24 (0.25)	0.56 - 0.19 (0.37)	0.53 - 0.15 (0.37)
	S	0.52 - 0.33 (0.19)	0.48 - 0.27 (0.21)	0.49 - 0.19 (0.30)	0.46 - 0.15 (0.31)
July	Whole	0.44 - 0.21 (0.23)	0.43 - 0.16 (0.27)	0.47 - 0.15 (0.32)	0.48 - 0.12 (0.36)
	NW	0.45 - 0.24 (0.21)	0.48 - 0.20 (0.27)	0.46 - 0.18 (0.28)	0.53 - 0.15 (0.38)
	NE	0.40 - 0.20 (0.19)	0.39 - 0.15 (0.24)	0.46 - 0.13 (0.32)	0.45 - 0.11 (0.35)
	S	0.47 - 0.18 (0.19)	0.42 - 0.13 (0.29)	0.48 - 0.13 (0.36)	0.45 - 0.10 (0.35)
September	Whole	0.48 - 0.21 (0.27)	0.48 - 0.18 (0.30)	0.48 - 0.16 (0.32)	0.47 - 0.16 (0.31)
	NW	0.45 - 0.23 (0.21)	0.48 - 0.23 (0.25)	0.47 - 0.19 (0.27)	0.46 - 0.20 (0.27)
	NE	0.47 - 0.20 (0.27)	0.46 - 0.16 (0.30)	0.46 - 0.13 (0.32)	0.45 - 0.14 (0.30)
	S	0.54 - 0.21 (0.33)	0.52 - 0.16 (0.36)	0.50 - 0.15 (0.35)	0.50 - 0.15 (0.36)
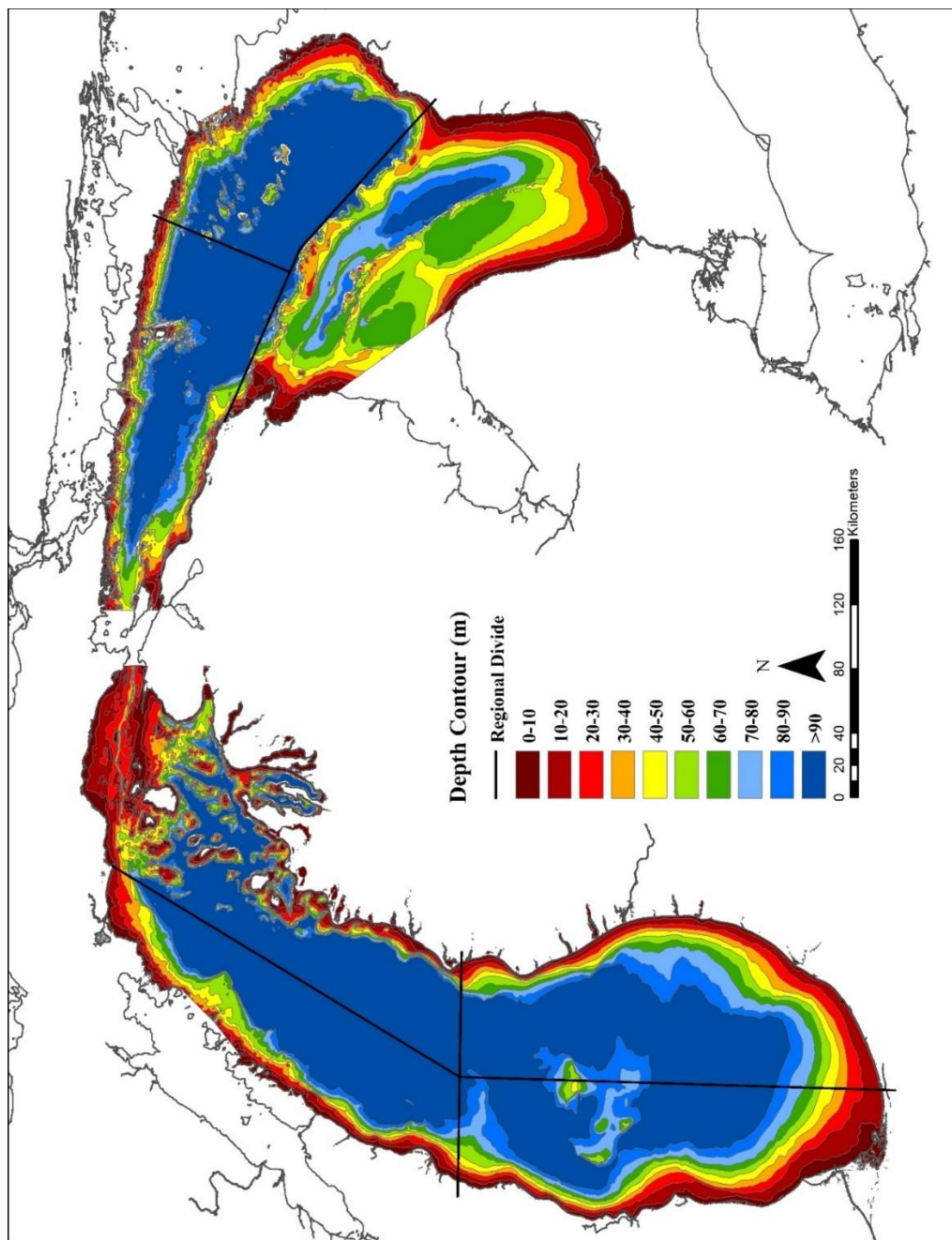
Figure 2.1. Map of Lake Michigan and Lake Huron. Depth contour bins are 10m depth intervals and indicated by different colors in the legend. Black lines divides regions around both lakes. Lake Michigan is divided into southeast, southwest, northeast, and northwest. Lake Huron is divided into south, northeast, and northwest.
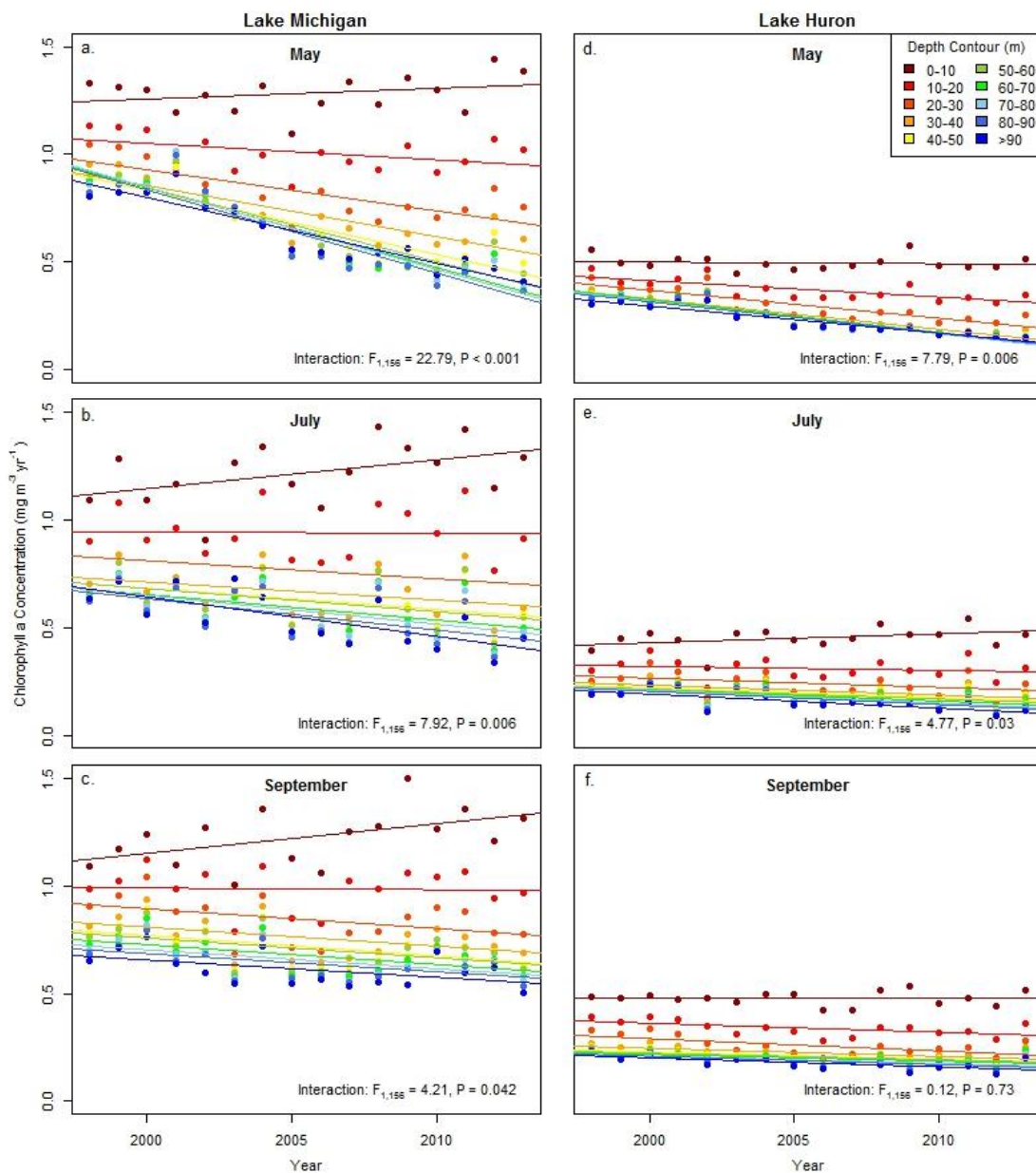
Figure 2.2. Mean seasonal chlorophyll *a* concentrations for the main basins of Lake Michigan (left) and Lake Huron (right) from 1998 to 2013 by depth contour. Graphs (a) and (d) plot concentrations in May. Graphs (b) and (e) plot concentrations in July. Graphs (c) and (f) plot concentrations in September. *F*- and *P*- values are associated with the interaction term between depth and year from that particular lake and month.
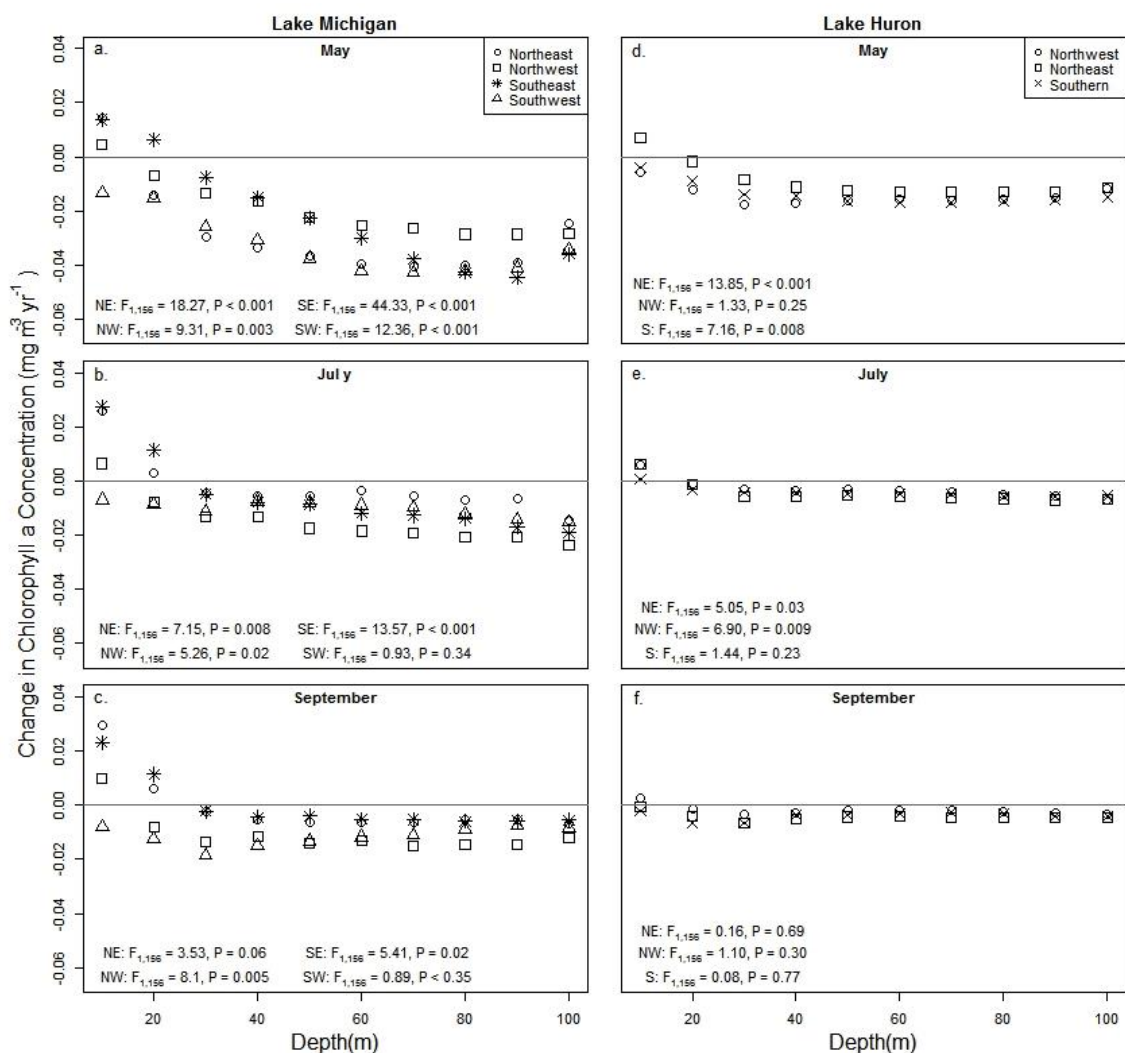
Figure 2.3. The rate of change of chlorophyll *a* concentrations overtime (i.e. the slope of each regression) from 1998 to 2013 for each depth contour in May (a,d), July (b,e), and September (c,f). Values for different geographic regions of each lake are symbolized differently. Grey lines indicate a slope of 0. *F*- and *P*- values are associated with the interaction term between depth and year from the region specified for that particular lake and month.

CHAPTER 3. SPATIOTEMPORAL TRENDS IN THE CONDITION OF A
SECONDARY CONSUMER, *BYTHOTREPHES*, IN SOUTHERN LAKE
MICHIGAN

3.1   Introduction

Natural variations and gradients of nutrient input, currents, temperature, and food

availability can create spatial structuring in food webs of large and small aquatic systems.

Oceanic currents and upwellings drive large amounts of nutrients into specific coastal

regions causing broad spatial differences in the concentration of primary producers

(Barry and Dayton, 1991; Polis et al., 1997). Similarly, riverine inputs can lead to spatial

variations in the concentration of primary producers in bays and lakes (Yurista et al.,

2015, 2012). Spatial patterns of other environmental variables can also structure trophic

responses. For example, temperature gradients across the Atlantic Ocean have been

shown to influence the physiological condition of Atlantic cod populations (*Gadus*

morhua; Rätz and Lloret, 2003) and spatial variations in food availability can influence

growth and condition of different fish species in smaller lakes and bays (Grecay &

Targett, 1996; Paperno, Targett, & Grecay, 2000; Wang, Höök, Ebener, Mohr, &

Schneeberger, 2008). Gradients in temperature and food resources have been linked to

spatial differences in the physiological condition of higher trophic consumers throughout

large aquatic systems, e.g. yellow perch (*Perca flavescens*) in the Laurentian Great Lakes

(Collingsworth and Marschall, 2011; Horns, 2001; Miller and Holey, 1992; Roswell et al., 2013).

The additive effects of nutrient abatement programs and invasive filter feeding mussels have facilitated declines in nutrients within offshore areas of marine (Alpine & Cloern, 1992; Smith, 1998), freshwater (Beaver et al., 1991; Carpenter et al., 1998; Sylvester et al., 2005; Vaughn and Hakenkamp, 2001), and estuarine systems (Smith, 2006) and changed the spatial structuring of food web components (Carstensen et al., 2011; Madenjian et al., 2011). In the Laurentian Great Lakes, and Lake Michigan specificially, rigorous nutrient abatement programs coupled with intensive filter feeding by invasive zebra (*Dreissena polymorpha*) and quagga mussels (*Dreissena bugensis*; here after dreissenid mussels) have contributed to the recent spatial restructuring of food webs along a nearshore to offshore gradient (Madenjian et al., 2011; Turschak et al., 2014; Turschak and Bootsma, 2015). Dreissenid mussels have the capacity to reach relatively high densities in mid-shore depths of the Great Lakes (Nalepa et al., 2010; Yousef et al., 2014) intercepting nutrients and sequestering them within the benthic zone (Edwards et al., 2005; Hecky et al., 2004; Ozersky et al., 2012). This "shunt" in nutrients to the nearshore benthic zone has been implicated in declines in offshore primary production across the entire Great Lakes basin (Fahnenstiel et al., 2010; Fahnenstiel et al., 1995; Hall et al., 2003b; Leach, 1993; Mida et al., 2010; Nicholls & Hopkins, 1993). Yet the combination of sequestered benthic nutrients along with nutrients from tributary input has resulted in stable to increasing primary production in nearshore areas (Fahnenstiel et al., 2010; Vanderploeg et al., 2010, 2002; Chapter 2). Consequently, consumers throughout the Great Lakes have shifted from a historically pelagic forage base to one that relies

more heavily on the increased benthic nearshore resources (Turschak et al., 2014; Turschak and Bootsma, 2015).

Heterogeneity in tributary input, temperature, substrate, and bathymetry along the Great Lakes coastline could promote large scale regional differences in production pathways (Chapter 2). For example, along the western shoreline of Lake Michigan, areas characterized by low nutrient loading from tributaries and relatively cold surface water temperatures have low levels of pelagic primary production (Yurista et al., 2015; Hutton et al. in prep). In these oligotrophic locations, fish species such as yellow perch, spottail shiner (*Notropis hudsonius*), and the round goby (*Neogobius melanostomus*) rely more heavily on benthic production pathways (Happel et al., 2015a, 2015b; Foley et al., 2016). Along the eastern shores of Lake Michigan, higher nutrient input from large, agricultural watersheds coupled with warmer surface water temperatures contribute to higher nearshore primary production and fish communities that rely more heavily on nearshore pelagic production pathways (Happel et al., 2015a, 2015b; Turschak et al., 2014; Turschak and Bootsma, 2015; Chapter 2).

Spatial variation in the concentration of primary producers (e.g. phytoplankton) and the growth rates and production pathway dependence of tertiary consumers (e.g. adult fish) have received considerable attention around the Great Lakes due to the recent effects of oligotrophication (Happel et al., 2015a, 2015b; Hecky et al., 2004; Turschak et al., 2014; Chapter 2). In contrast, relatively few studies have explored spatiotemporal changes in lower trophic consumers such as zooplankton (Turschak and Bootsma, 2015). Secondary consumers, such as larval fish and predatory zooplankton, play an important, intermediary role in the Great Lakes' food web acting as both predators to herbaceous

zooplankton (Bremigan and Stein, 1994; Confer and Lake, 1987; Crowder et al., 1987)

and as prey for planktivorous fish (Brandt et al., 1987; Luecke, Rice, Crowder, Yeo, &

Binkswski, 1990; Wells, 1980). The invasive predatory cladoceran, *Bythotrephes*

longimanus (hereafter *Bythotrephes*), has become an increasingly important secondary

consumer in the Great Lakes. Similar to larval fish, *Bythotrephes* is a pelagic predator

primarily feeding on herbaceous zooplankton (Mordukhai-Boltovskaia, 1958) while

simultaneously serving as an increasingly important prey for many fish species (Brandt et

al., 1987; Bur & Klarer, 1991; Pothoven & Vanderploeg, 2004; Pothoven, 2005).

Bythotrephes also display adaptive responses in length, fecundity, and physiological

condition to changing environmental conditions (Burkhardt, 1994; Miehls et al., 2013)

similar to the plastic responses of zooplankton and larval fish species (Black, 1993;

Straile and Hälbich, 2000). Thus, spatial variations in the condition of *Bythotrephes*

could serve as an indicator of the condition of other secondary consumers while

providing information about the implications for predatory fish species that rely on

Bythotrephes for food and nutrients.

　　　　The aim of this study was to assess spatiotemporal patterns in *Bythotrephes*

condition across Lake Michigan. Specifically, we measured *Bythotrephes* population

density and condition indices including length-at-age, nucleic acid concentrations (RNA),

and concentrations of essential fatty acids along a nearshore to offshore gradient on the

eastern and western shorelines of southern Lake Michigan. We used RNA concentrations

to assess spatiotemporal variations in short-term growth and condition. RNA

concentrations are an indicator of protein synthesis within actively growing cells and

have been shown to fluctuate with growth and starvation in many organisms, including

zooplankton (Buckley, 1984; Bulow, 1970; Clemmesen, 1996; Dahlberg, 1989; Haines, 1973; Kato et al., 2011). We also used fatty acids to analyze condition of *Bythotrephes*. The concentrations of essential fatty acids, such as eicosapentaenoic acid (22:6*n*-3; EPA), have been documented to be important for growth, development, and reproduction of *Bythotrephes* (Iverson et al., 2004; Smyntek et al., 2008). As many predatory fish species either do not or cannot efficiently produce fatty acids requiring them to ingest these nutrients from their food (Sargent et al., 1999; Tocher, 2010). Thus spatiotemporal variations in the amount of essential dietary fatty acids may elucidate differences in the trophic pathways supported by *Bythotrephes* in southern Lake Michigan. Being primarily offshore pelagic feeders, we expected relatively smaller densities and reduced condition of *Bythotrephes* along the western shores of Lake Michigan where primary production is reduced and production pathways are reliant on benthic resources (Happel et al., 2015a, 2015b; Hutton et al. in prep). Along the eastern shores, we hypothesized that the condition of *Bythotrephes* will be enhanced in nearshore areas due to increased food resources in these habitats.

3.2   Materials and Methods

3.2.1   *Bythotrephes* Life History

Bythotrephes is an invasive predatory cladoceran that became established in Lake Michigan in 1986 (Evans, 1988). Although they are spatially distributed throughout most of Lake Michigan for most of the year, they have been categorized as an offshore, pelagic

species that reaches peak densities in the late summer and fall (Cavaletto et al., 2010).

They are aggressive predators that feed primarily on other cladoceran species

(Mordukhai-Boltovskaya 1958) and have been attributed to declines in native cladocerans

throughout the Great Lakes (Bunnell et al., 2012, 2011; Hoffman et al., 2001). The

lifecycle of *Bythotrephes* consists of four different instar stages that can be distinguished

by the number of lateral barbs at the base of the caudal spine (Yurista, 1992; Figure 3.1).

Typically the second, third, and fourth instars are considered adults and females

reproduce parthenogenetically for most of the year. Sexual reproduction occurs in late

fall when males are produced and resting eggs are created (Ketelaars et al., 1995;

Mordukhai-Boltovskaia, 1958). *Bythotrephes* only reach the fourth instar when

reproduced sexually, thus fourth instars are generally only abundant early in the season

when over winter resting eggs hatch and are rarely captured later in the season when

asexual reproduction is common.

3.2.2   Sample Collection

Bythotrephes were collected during the 2015 Cooperative Science and Monitoring

Initiative (CSMI) in Lake Michigan. Monthly samples were collected from June to

September from eastern and western transects with sample sites arranged along a

nearshore to offshore gradient (Figure 3.2). The western transect, located near Racine,

WI, was sampled by the Environmental Protection Agency- Great Lakes National

Program Office (EPA-GLNPO) R/V Lake Guardian during June, July, and September.

Additional samples were collected in July and August by Purdue University aboard a 7m

workskiff. The eastern transect, located near Muskegon, MI, was sampled monthly by the National Oceanic and Atmospheric Association- Great Lakes Environmental Research Laboratory (NOAA-GLERL) R/V Laurentian from June to September. Three different depth contours were sampled along each transect: nearshore (15-18 m in depth), midshore (45 m in depth), and offshore (100-110 m in depth; Figure 3.2). Each depth contour was sampled during the day and night. Weather, time, and vessel capabilities dictated which specific depth contours were sampled during each trip.

Two gears types were used to sample *Bythotrephes*: bongo nets (0.5 m diameter, 333 μm and 505 μm mesh) and neuston nets (2 x 3 m frame, 500um mesh). Prior to sample collection, a conductivity, temperature, and depth (CTD) cast was made to estimate the depth of the metalimnioin. During daytime sampling, bongo nets were towed at roughly 2 knots for ten minutes at each depth contour. Tows at the midshore and offshore location were towed obliquely starting in the metalimnion and raised sequentially to the epilimnion. At nearshore locations, the oblique bongo net tows started at depths close to the bottom to allow for sampling most of the water column. During night time, the same methods were used to deploy bongo samples but with neuston nets which were towed at roughly 2 knots at the surface for ten minutes at each depth contour.

On each sampling occasion, we aimed to collect ten complete samples for biochemical analysis with each sample consisting of three to twenty individual *Bythotrephes* per instar. Due to sampling time constraints along the Racine transect, singular bongo and neuston tows were completed along each depth contour depending on time. Instars were identified under a dissecting microscope within six hours of sampling and three to twenty individuals were combined into a single cryovial for fatty acid

analysis. Vials were flash frozen in liquid nitrogen for transport back to the lab where they were stored at -80°C until further fatty acid analysis could be performed. The remainder of the sample was stored in RNA*later* (10:1 ratio), kept at room temperature for 12 hours, and placed in dark storage at 4°C until further RNA analysis. Along the Muskegon transect, duplicate neuston or bongo tows were performed along each depth contour. The first tow was immediately preserved in RNA*later* and individuals were picked from the second tow for fatty acid analysis. Preservation techniques for the first tow at Muskegon were identical to the Racine samples. The remainder of secondary tows were preserved in either RNA*later* or ethanol.

3.2.3   Laboratory Analysis

Densities and Lengths

In the lab, *Bythotrephes* samples stored in RNA*later* were sorted under a dissecting microscope. Up to 30 individuals of each instar were imaged with Micrometrics 318CU camera software (Accu-scope, Inc. Commack, NY), randomly placed in separate Eppendorf tubes with ~1.0ml of RNA*later*, and stored at 4°C until further RNA analysis. Images were measured for total, body, and spine length to the nearest 0.1mm using the line segment tool in the Image J analysis software (Figure 3.1; Rasband 2009). Samples collected in the 333μm bongo net were completely picked for *Bythotrephes* densities following methods described by Pothoven and Höök (2014). A Folsom plankton splitter was used for samples with large *Bythotrephes* abundances. The

number of *Bythotrephes* per instar was recorded along with the presence or absences of resting eggs and black eye staged embryos.

To account for shrinkage due to preservation time in RNA*later*, we used methods similar to Foley et al. (2010) to calculate a length correction factor. Live individuals were collected on October 30th, 2015, from Lake Michigan near Michigan City, IN. Thirty-seven live individuals of varying instars were photographed then preserved and stored in RNA*later* as described above. Preserved specimens were reimaged again after 70 and 137 days in RNA*later* solution. Total, body, and spine lengths were measured similar to the above mentioned methods at each time period and percent change in length was calculated from the initial to the next two time periods. A repeated measures, mixed model ANOVA was conducted for the total, body, and spine length, with length as the response variable and day measured as the within-subject factor. The final correction factor calculated between Day 0 and Day 137 (a 30% decrease) was applied to each length (see supplemental material for complete analyses).

RNA Concentration

RNA samples were analyzed within 7 months of collection, following methods described in Ryan et al. (2012) with a few modifications. Total length for each *Bythotrephes* was measured as described above, and individuals were placed in 0.1-1.0 ml of extraction buffer of 1% N-Lauroylsarcosine sodium salt (w/v) in TE buffer based on total length. For individuals <1.0mm, two *Bythotrephes* were analyzed together to produce a sufficient sample to detect RNA. Samples were homogenized using an RNAse free pestle and placed in a sequence of 30-second ultrasonic treatment and 1-minute ice

bath for 5 cycles. Samples that were <1.0mm in length were not homogenized due to loss

of mass during pestle crushing but immediately placed in the ultrasonic, ice bath

sequence. After the ice bath, the samples were shaken on an orbital shaker for 1 hour.

To estimate the amount of nucleic acid in an organism, 3 to 4 replicates (10μL each) of

the homogenized sample stock were analyzed fluorometrically after treatment with

Ribogreen. Flouresence was measured using a FLx800 multi-microplate reader (BioTek

Instruments, Inc.) together with RNA and DNA standards (Quant-iT^{TM} and D4522

SIGMA, respectively). To digest RNA, 10μL of endoribonuclease RNase (Thermo

Scientific) was added to each sample and standard and left to incubate for 30 minutes at

approximately 37.5°C before flourescense were quantified again. *Bythotrephes* with eggs

or embryos along with 4th instars were also excluded from further analyses due to

potential biases in RNA content and small sample sizes, respectively (Gorokhova and

Kyle, 2002).

Fatty Acid

The fatty acid composition of *Bythotrephes* was evaluated using a method similar

to that described by Feiner et al. (2016), with modifications for low sample mass.

Bythotrephes, which were frozen in groups of three to twenty individuals, were thawed

and transferred as a group to a 15 ml glass tube filled with 8 ml chloroform plus 0.01%

(w/v) butylated hydroxytoluene (BHT) added as an antioxidant. The sample was then

sonicated for 20-45 seconds using an Ultrasonic Power Corporation Model 1000L

sonicator, after which 4 ml of methanol was added, and the samples were vortexed and

left to soak overnight. Following this lipid extraction, the method described by Feiner et

al. (2016) was followed. Percent composition was calculated for each fatty acid from the total amount of fatty acids. While 38 fatty acids were described, only relative proportions of omega 3 (ω3) and omega 6 (ω6) fatty acids as well as EPA and arachidonic acid (ARA) were used for analysis of fatty acid as indicators of an organism's condition (Kim et al., 2014; Smyntek et al., 2008; Taipale et al., 2014).

Analysis

To consider variation in *Bythotrephes* body length, we analyzed three subsets of date (due to unbalanced sample size; see supplemental material for all sample sizes, Table B.1-B.3), and compared body lengths across: transects (Racine/Muskegon), depth contour (nearshore/midshore/offshore), and sampling months. For each subset, linear models including the primary variable of interest and subsequent covariates and interactions with the primary variable were all included to evaluate which factors were associated with spatio-temporal differences in *Bythotrephes* lengths. The first subset analyzed transect differences in body length using samples collected from nearshore and midshore depths at Racine and Muskegon during July, August, and September. We excluded offshore samples from this analysis due to due sample sizes and the spatial proximity of offshore sites to the other sample depths. The linear regression model included transect as the independent variable and month and instar as additional variables including all subsequent interactions. The second subset analyzed the effects of depth contour on *Bythotrephes* length using Muskegon samples collected during June, July, and August at nearshore, midshore, and offshore depth contours. The linear model included depth contour as the main variable with instar as an additional variable along with the

subsequent interactions of instar or month with depth. The third subset analyzed the effect of month on *Bythotrephes* lengths using nearshore and offshore samples from Muskegon collected from June through September. The linear model included month as the main independent variable with instar as an additional variable and subsequent interactions between instar or depth with month.

Before analyzing spatio-temporal variation of *Bythotrephes* RNA content, a linear regression was used to measure the degradation of RNA content in the samples due to preservation duration (Gorokhova, 2005). To account for the covariation of body length to RNA content, the residuals of a linear regression between the natural log of body length and the natural log of RNA content were regressed over the preservation duration period. A significant decline was observed in the RNA content with increasing preservation duration (t = -4.73, $P < 0.001$). Thus all subsequent RNA analyses include preservation duration as a covariate to avoid loss of sample size. Finally, as body length is also related to instar with older instars typically being longer, we analyzed RNA content separately for each of the three instar (i.e. due to strong correlation between instar and size).

Linear regressions were used to assess effects of transect, depth, and month on the natural log of RNA content in *Bythotrephes* using the same three data subsets as the models conducted for body length. The linear model to assess transect effects on *Bythotrephes* RNA content included transect and month as the main independent variables along with the subsequent interaction. The second subset analyzing depth effects on *Bythotrephes* RNA content had depth as the main independent variable along with the interaction between depth and month. Finally, the third subset analyzed the

effect of month on RNA content in *Bythotrephes* with month as the main independent

variable along with the interaction between month and depth.

Five fatty acid indices were measured to assess the physiological condition and

the quality of *Bythotrephes* as a potential food source. Percent of EPA within

Bythotrephes has been linked to growth and reproduction (Kim et al., 2014; Smyntek et

al., 2008) and was thus used to assess the physiological condition of *Bythotrephes* instars.

Arachidonic acid (20:4n-6; ARA), ω3, and ω6 fatty acids as well as ω3:ω6 were used to

assess *Bythotrephes* potential quality within the food web. Many juvenile and adult

freshwater fish species either cannot produce or inefficiently produce ARA, ω3, and ω6

fatty acids and primarily rely on their diets as a source of essential fatty acids (Tocher,

2010). Increased percentages in these fatty acids within *Bythotrephes* could indicate a

relatively higher quality food source for local fish species.

Due to small sample sizes, three different subsets were used to analyze variations

in fatty acid percentages across transect, depth contour, and sampling month (see

supplemental material for sample sizes). All fatty acid percentages were arcsine square

root transformed prior to analysis.   To analyze the effects of transect on the five different

fatty acids, only 1st instars collected at midshore sites during July were used for analysis.

Variations in the analysis method resulted in a slight correlation with a few fatty acids

proportions. Thus the date the fatty acids were extracted from the sample was included

as a covariate within each linear model. To test the effects of depth on fatty acid

percentages, samples collected in August along Muskegon at nearshore, midshore, and

offshore sites were used and extraction date was again included as a covariate. As EPA

was the only fatty acid used to assess physiological condition of *Bythotrephes,* instar was

included as an independent variable for the analysis on EPA percentages along with its subsequent interaction with depth. To analyze effects of month on *Bythotrephes* fatty acid percentages, offshore samples along Muskegon collected from June through September were used. The date of extraction was included for all five analyses but instar and its interaction with month was only included for the analysis of EPA by month.

All analyses used an α level of 0.05 to denoted significance and were conducted in R version 3.1.1 (R Core Team (2014)).

3.3   Results

Densities of *Bythotrephes* ranged from 0 m^{-3} at nearshore Racine in June and July to 17.5 m^{-3} at offshore Muskegon during August. Muskegon consistently had relatively higher densities of *Bythotrephes* for all depth contours and months compared to Racine (Figure 3.3). The density of *Bythotrephes* along the Muskegon transect generally increased overtime with a few exceptions. Nearshore, densities decreased from June to July and offshore densities decreased from August to September (Figure 3.3). Offshore locations along Muskegon consistently had higher densities than the other two depth contours except in September when nearshore locations were higher. The number of *Bythotrephes* throughout the Racine transect gradually increased overtime with peak density of *Bythotrephes* in September in nearshore locations at 6.5 m^{-3} (Figure 3.3). Unlike Muskegon, the offshore location of Racine typically had the lowest density of *Bythotrephes* for all months except June (Figure 3.3).

Along Racine, 1st instar *Bythotrephes* dominated early in the season during June and July (Figure 3.3) but 2nd instar *Bythotrephes* were more prominent in later months. Along Muskegon all three instars were present throughout the season except for 2nd instars, which were not observed at the midshore location in June (Figure 3.3).

While there was no significant difference between the Racine and Muskegon transects in overall variation of *Bythotrephes* lengths, the overarching trends in body length may be masked by the significant interaction term between transect and month (Table 3.1). Body lengths were shorter along Racine earlier in the season compared to Muskegon. However, *Bythotrephes* along Racine grew over time to lengths comparable to Muskegon by August and September (Figure 3.4 a,b,c).

At Muskegon, depth contour was not a significant factor in explaining variation in *Bythotrephes* body length (Figure 3.4 b,c,d; Table 3.1). The interaction between depth contour and month was significant (Table 3.1) though no distinquishable pattern between month and depth contour existed (Figure 3.4 b,c,d). Month was a significant factor in explaining variation in body lengths of *Bythotrephes* throughout the sampling season along Muskegon (Table 3.1). Overall, there was a general increase in body lengths for all instars from June through August before lengths decreased in September (Figure 3.4 b,d).

Transect was a significant factor for all three instars when explaining the variation in RNA content (Table 3.2). Similar to body length, RNA content for all three instars were relatively lower along Racine compared to Muskegon in July but comparable in August and September with significant interaction between transect and month (Figure 3.4 e,f,g; Table 3.2).

Along the Muskegon transect, depth contour was not a significant factor explain RNA content of 1st and 2nd instars. However, depth contour was significantly related to RNA content at 3rd instars and the interaction between depth contour and month was significant for all instars (Table 3.2). Despite the interaction between depth and month very few patterns were observed (Figure 3.4 f,g,h). Finally, month was a significant factor for RNA content in 2nd and 3rd instars with significant interactions between depth and month for all three instars (Table 3.2).   Overall, *Bythotrephes* generally had higher RNA content early in the season and lower content later (Figure 3.4 f,h). RNA content was relatively lower in July and September at nearshore locations compared to June and August (Figure 3.4 f,h).

We measured significantly higher proportions of EPA along the Muskegon transect compared to Racine ($F_{1,26}= 8.41$, $P = 0.008$; Figure 3.5). EPA percentages did not differ significantly along the depth contour ($F_{2,91}= 1.59$, $P = 0.21$) but we did detect a significant interaction between depth contour and instar ($F_{4,97}= 3.73$, $P = 0.007$). EPA percentages at the midshore location were relatively lower than the other two transects but had higher standard errors around the mean. EPA percentages in offshore Muskegon samples did differ significantly by month ($F_{1,111}= 5.725$, $P = 0.018$). Yet unlike increases overtime in body length and length-adjusted RNA content, decreases in EPA percentages were observed from June through September (Figure 3.5). The interaction between month and instar was significant ($F_{6,111}= 5.52$, $P < 0.001$). Overall the percentage of EPA in 1st and 3rd instars decreased overtime, yet 2nd instars had relatively similar percentages of EPA from July through September.

When considering the potential quality of *Bythotrephes* within the food web, only the percentage of ω6 fatty acids differed by transect. Proportions of ω6 fatty acids were significantly higher in *Byhotrephes* along Muskegon compared to Racine ($F_{1,26}$= 5.40, *P* = 0.03; Figure 3.6). Month was also not significantly related to any of the four fatty acid indices at offshore Muskegon sites (Figure 3.6). Percentages of ARA and ω6 fatty acids were significantly higher in nearshore areas compared to offshore areas along Muskegon in August (*t* = 3.14, *P* = 0.006; *t* = 2.58, *P* = 0.03, respectively; Figure 3.6). However, there was no significant difference for ω3 fatty acid or the ratio between ω3 and ω6 between depth contours (*P* = 0.10; *P* = 0.21, respectively).

3.4   Discussion

Broad spatial differences in the abundance and condition indices of *Bythotrephes* were observed in southern Lake Michigan. Densities of *Bythotrephes* were consistently greater along Muskegon throughout the entire year compared to densities along Racine. Similarly most condition indices including body length, RNA content, and EPA percentages had greater values along Muskegon compared to Racine early in the season. Yet unlike the consistent spatial differences in densities, the spatial differences in condition indices were not ubiquitous throughout the entire sampling season.

Surface water temperature has been positively correlated to *Bythotrephes* densities in Lake Michigan and other Great Lakes (Keeler et al., 2015). Surface water temperatures along Muskegon are consistently warmer throughout most of year compared to Racine (Yurista et al., 2015; Figure 3.7). Field and laboratory studies have indicated

that peak *Bythotrephes* abundances occur between 16 and 22°C (Allan, 1976; Keeler et al., 2015) coinciding with water temperatures in Muskegon from June to September (Figure 3.7). The eastern shore of Lake Michigan also receive higher nutrient inputs from large agricultural watersheds (Table 2.1) that lead to consistently higher chlorophyll *a* concentrations (Chapter 2). Regular westerly winds propagate warmer waters along eastern shores of Lake Michigan pushing colder water to the surface along the southwest region of the lake (Allender and Saylor, 1979). The southwestern region including Racine also experiences frequent periods of upwelling (Beletsky & Schwab, 2001). Unlike upwellings in marine systems that tend to bring nutrient rich waters to the surface facilitating phytoplankton production (Abbott and Zion, 1985), upwelling events in the Great Lakes tend to bring nutrient poor waters to the nearshore (Haffner et al., 1984). This may further inhibit *Bythotrephes* densities along Racine while warmer water temperatures and relatively higher available nutrients may promote greater *Bythotrephes* densities near Muskegon.

Suitable water temperatures likely facilitated faster growth rates and typically longer *Bythotrephes* along eastern Lake Michigan (Allan, 1976; Miehls et al., 2013). Muskegon water temperatures reached 16°C in late June while Racine waters did not reach 16°C until middle of July (Figure 3.7). It was during this time that the greatest difference in lengths of *Bythotrephes* between the two transects were observed. Once temperatures reached 16°C along Racine, lengths were comparable across transects.

To our knowledge, this is the first study to describe RNA content of *Bythotrephes* overtime and patterns in RNA content generally mirrored temporal trends in body length. Overall increases in RNA content through time were particularly prominent along

Racine. Along Muskegon, RNA content was fairly consistent until late in the season when declines were measured in September. This may indicate a seasonal lag in *Bythotrephes* growth between the eastern and western shores of Lake Michigan.

During late August and September, water temperatures along the Muskegon transect were at or around 22°C, which represents the upper thermal tolerance for *Bythotrephes* (Figure 3.7; Garton et al., 1990; Keeler et al., 2015). Such high ambient temperatures could explain the smaller body lengths and lower RNA content that were observed later in the season in our study. Multiple studies have also observed declines in *Bythotrephes* densities and lengths early in the fall (Cavaletto et al., 2010; Pothoven et al., 2012). However, we did not collect samples after September, and may have missed the late-season declines in densities, body lengths, and RNA content along the Racine transect that were observed along Muskegon. The declines in September may instead be due to the long period of warm water temperatures as opposed to seasonal declines.

Spatial differences in zooplankton densities have been observed in other large aquatic systems similar to the results described here. Regional differences in *Bythotrephes* in southern Lake Michigan are most likely due to surface water temperature and resource availability while regional differences in zooplankton communities in other aquatic systems are effected by factors such as availability of habitat cover, predation, salinity, and turbidity (Dejen et al., 2004; Hansen et al., 2006; Marques et al., 2006).

Some studies have looked at the responses of zooplankton abundance to oligotrophication along a nearshore to offshore gradient and produced inconsistent results (Pace et al., 1998). In some systems, zooplankton densities declined in response to decreases in food resource due to oligotrophication (Manca and Ruggiu, 1998), while

others have shown that zooplankton densities are not effected by oligotrophication unlike primary producers or top level consumers (Hall et al., 2003a; Jack and Thorp, 2000; Jeppesen et al., 2002). One synoptic study by Jeppesen et al. (2005) found that zooplankton densities change in response to oligotrophication were depth dependent. In general, shifts and overall changes to fish communities were greater in shallow areas and lakes causing further shifts in zooplankton densities and compositions. While our study did not find consistent patterns in condition of *Bythotrephes* along the depth stratum, comparisons to previous studies may suggest further responses to oligotrophication.

Bythotrephes are primarily considered a pelagic species. Their densities in nearshore locations have generally been described as lowand patchy with relatively smaller individuals in comparison to offshore populations (Cavaletto et al., 2010; Lehman, 1987; Pothoven et al., 2003). It was hypothesized that high predation pressure from fish in nearshore areas may previously have limited nearshore densities and lengths of *Bythotrephes* (Pothoven et al., 2007; Pothoven and Vanderploeg, 2004). Recent studies, including this one, have observed densities and sizes of *Bythotrephes* in nearshore areas similar to densities and sizes in offshore areas (Keeler et al., 2015). This potentially indicates either an increase in nearshore populations or a decrease in offshore populations. Increases in nearshore primary production, especially along the southeastern region of Lake Michigan, has been linked to an increased reliance on nearshore habitats by higher trophic consumers (Hecky et al., 2004; Turschak et al., 2014; Chapter 2). The same may also be true for *Bythotrephes* populations. Increased nearshore energy subsides may compensate for the amount of energy spent evading predators and still allow for better condition compared to historical populations. Similarly, other studies

have suggested that abundances of offshore zooplankton communities are stable during oligotrophication potentially due to an increased reliance of herbaceous zooplankton on other organic material opposed to phytoplankton (Di Toro et al., 1975). It has also been shown that declines in predators, such as the declines in alewife in offshore locations of Lake Michigan (Madenjian et al., 2002), have a strong positive effect on cladoceran densities and growth rates (Dodson and Brooks, 1965) potentially facilitating the similar density and body lengths of *Bythotrephes* in nearshore and offshore locations.

Conversely, similarities in the density and condition of *Bythotrephes* along a nearshore to offshore gradient may be due to declines in offshore *Bythotrephes* populations. The declines in offshore food web resources may have a negative impact on *Bythotrephes* similar to zooplankton communities in other aquatic systems experiencing oligotrophication (Manca and Ruggiu, 1998). Declines in offshore *Bythotrephes* biomass and condition has the potential to create the similarities between nearshore and offshore populations. More information is required to fully piece together what mechanism is driving the similarity in *Bythotrephes* populations along the depth gradient.

Unlike temporal trends in other measures of condition in *Bythotrephes*, the percentage of EPA decreased overtime along Muskegon (Figure 3.5). Increases in the percentages of EPA within *Bythotrephes* has been linked to increased growth and relatively large quantities of EPA are also required for reproduction (Kim et al., 2014; Smyntek et al., 2008). Studies on other cladoceran species have shown they can regulate their internal concentrations of fatty acids independently from concentrations available within seston and will retain greater amounts of EPA at colder temperatures (Hartwich et al., 2013; Schlechtriem et al., 2006; Sperfeld and Wacker, 2012). EPA percentages in

Lake Michigan's *Bythotrephes* were generally higher in June and July when water temperatures were relatively cold, which may indicate that percentages of EPA in *Bythotrephes* are temperature regulated similar to growth. Earlier life history studies have documented that *Bythotrephes* may allocate less energy towards growth later in the season in favor of producing resting eggs (Burkhardt, 1994) and the percentages of EPA in the body may decline during the production of resting eggs as well (Becker and Boersma, 2005). Thus decreased percentages of EPA and RNA content later in the season may also suggest that *Bythotrephes* are allocating more resources, energy, and fatty acids towards the production of resting eggs.

   Bythotrephes are an important food source for many fish species within the Great Lakes including lake trout (*Salvelinus namaycush*; Madenjian et al., 2011), alewife (*Alosa pseudoharengus*; Pothoven et al., 2007; Pothoven and Vanderploeg, 2004), and yellow perch (*Perca flavescens*; Schneeberger, 1991). We assessed the value of *Bythotrephes* as a prey item using ω3, ω6, ARA as well as EPA fatty acids which are vital to freshwater fish species' growth, reproduction, and egg quality (Henderson, 1996; Tocher, 2010). The prsences of all four fatty acids groups potentially indicating that *Bythotrephes* may be an important source of essential dietary fatty acids necessary for fish species. For most of the fatty acids, especially the ω3 and EPA fatty acids, there was a general decrease in percentages overtime. Laboratory studies of other cladoceran species have found higher concentrations of ω3 are more abundant in colder temperatures (Sperfeld and Wacker, 2012). Thus while the fatty acids are present in *Bythotrephes* for most of the year, individual consumers who prey upon *Bythotrephes* earlier in the season may benefit more from this nutritional aspect as compared to consumers who consume

Bythotrephes later in the season (Bur and Klarer, 1991; Schneeberger, 1991). We did not

detected any dominant spatial trends in fatty acid percentages for *Bythotrephes* in Lake

Michigan. This finding is consistent with other studies that found no apparent spatial

patterns in the compositions of fatty acids in zooplankton communities of other lake

systems (Kainz et al., 2004). Nearshore locations along the depth contour of Muskegon

had relatively higher percentages of ω3, ω6, and ARA fatty acids compared to midshore

and offshore locations. These results are in agreement with increases in nearshore

subsides along the eastern shoreline in other organisms (Happel et al., 2015a, 2015b) due

to relatively higher nutrient and primary production concentrations.

     Bythotrephes was chosen as a study species particularly as a representative for

other secondary consumers such as larval fish. Larval fish species may display similar

trends to what we report for *Bythotrephes,* as some fish species display higher densities

along the eastern shoreline of Lake Michigan (Brandt et al., 1991; Höök et al., 2003).

This comparison suggests that *Bythotrephes* may make a good model organism for broad

spatial scale variations in secondary consumers around Lake Michigan. Further studies

are necessary to understand whether larval fish similarly exhibit a temporal lag in

condition between the eastern and western shorelines of Lake Michigan. Yet unlike

Bythotrephes, larval fish densities can be variable along a nearshore to offshore gradient

pending the species (Heufelder, 1982; Perrone et al., 1983; Tin and Jude, 1983) making a

comparison of the effects of oligotrophication along a nearshore to offshore gradient of

secondary consumers difficult.

     While spatiotemporal trends were apparent, future studies should be conducted to

further understand the effects of oligotrophication and shunted nearshore nutrients on the

Great Lakes ecosystem. Specifically, our study had relatively small *Bythotrephes* sample

sizes at the Racine transect which made it impossible to compare fatty acids and

condition indices along a fine spatial scale (i.e. nearshore to offshore) or throughout time.

More consistent sampling longer into the season may also elucidate whether trends in

fatty acids and other indices of condition along Racine mirror trends observed along

Muskegon with eventual decreases in densities and lengths later in the season. Further

studies along a nearshore to offshore gradient may confirm whether there are shifts in

Bythotrephes to more nearshore locations or simple decreases in offshore locations.

Regional differences in *Bythotrephes* have mirrored the differences that have been

observed in chlorophyll *a* concentrations and higher trophic consumers. Along the

western shoreline of Lake Michigan where *Bythotrephes* densities are relatively low,

there were declines in surface chlorophyll *a* concentrations throughout the entire depth

contour (Chapter 2) that may lead higher trophic consumers to rely more heavily on

benthic production pathways (Happel et al., 2015a, 2015b). Thus the general shift to

increases in nearshore biomass may not be ubiquitous throughout the Great Lakes.

Instead, decreases in surface production coupled with the nutrients sequestered in the

benthos due to dreissenid mussels may facilitate more benthic species such as

macroinvertebrates or the invasive round goby (*Neogobius melanostomus*) that primarily

forage in the benthos. Thus communities along the eastern and western shores of Lake

Michigan may diverge in their composition and diversity.   Further studies are required to

understand whether community changes are occurring throughout the Great Lakes due to

oligotrophication and whether these trends are ubiquitous.

Table 3.1. ANCOVA results for body length for the three different subsets that analyze the effects of transect, depth contour, and sampling period. The data included in each subset is in parenthesizes. Significant p-values ($\alpha = 0.05$) are in bold.

	Df	Sum Sq	Mean Sq	F-value	P-value
Transect (Nearshore and Midshore samples were combined. Offshore samples were excluded)					
Instar	2	157.16	78.58	364.8	**<0.001**
Transect	1	0.02	0.02	0.087	0.77
Month	3	116.02	38.67	179.5	**<0.001**
Instar:Transect	2	4.42	2.21	10.25	**<0.001**
Instar:Month	6	1.99	0.33	1.54	0.16
Transect:Month	3	52.38	17.46	81.05	**<0.001**
Residuals	747	160.92	0.22		
Depth Contour (Muskegon samples from June to August)					
Instar	2	69.56	34.78	152.24	**<0.001**
Depth Contour	2	0.03	0.02	0.073	0.93
Instar:Depth	4	2.81	0.7	0.074	**0.016**
Depth:Month	6	91.75	15.29	66.94	**<0.001**
Residuals	516	117.88	0.23		
Sampling Period (Nearshore and Offshore Muskegon Samples from June through September)					
Instar	2	56.64	28.32	146.2	**<0.001**
Month	3	68.88	22.96	118.5	**<0.001**
Instar:Month	6	2.08	0.35	1.79	0.10
Depth:Month	4	3.31	0.83	4.27	**0.002**
Residuals	445	86.21	0.19		

Table 3.2. Results for RNA content for each instar to address the effects of transect, depth contour, and sampling period. Three different subset were used to test the three factors and the data included in each subset is in parenthesizes. Significant p-values (α = 0.05) are in bold.

	Instar	Df	Sum Sq	Mean Sq	F-value	P-value
Transect (Nearshore and Midshore samples were combined. Offshore samples were excluded)						
log(Body Length)	1	1	157.3	157.3	1042.9	**<0.001**
Preservation Duration		1	1.05	1.05	6.97	**0.009**
Transect		1	9.03	9.03	59.88	**<0.001**
Month		3	2.38	0.79	5.26	**0.002**
Depth:Month		3	40.12	13.37	88.65	**<0.001**
Residuals		295	44.50	0.15		
log(Body Length)	2	1	135.6	135.6	758.4	**<0.001**
Preservation Duration		1	3.45	3.45	19.28	**<0.001**
Transect		1	5.90	5.90	33.00	**<0.001**
Month		3	7.59	2.53	14.14	**<0.001**
Depth:Month		2	26.42	13.21	73.89	**<0.001**
Residuals		256	45.77	0.18		
log(Body Length)	3	1	50.32	50.32	289.7	**<0.001**
Preservation Duration		1	1.25	1.25	7.21	**0.008**
Transect		1	5.39	5.39	31.05	**<0.001**
Month		3	5.76	1.92	11.06	**<0.001**
Depth:Month		2	1.15	0.57	3.30	**0.04**
Residuals		186	32.31	0.17		
Depth Contour (Muskegon samples from June to August)						
log(Body Length)	1	1	18.34	18.34	118.2	**<0.001**
Preservation Duration		1	0.00	0.00	0.00	0.96
Depth		2	0.32	0.16	1.02	0.36
Depth:Month		6	8.86	1.48	9.51	**<0.001**
Residuals		154	23.90	0.16		
log(Body Length)	2	1	11.66	11.66	85.07	**<0.001**
Preservation Duration		1	0.30	0.30	2.20	0.14
Depth		2	0.31	0.16	1.14	0.32
Depth:Month		6	10.79	1.80	13.13	**<0.001**
Residuals		207	28.37	0.14		
log(Body Length)	3	1	24.96	24.96	151.24	**<0.001**
Preservation Duration		1	1.67	1.67	10.10	**0.002**
Depth		2	1.71	0.86	5.19	**0.007**
Depth:Month		6	10.49	1.75	10.59	**<0.001**
Residuals		137	22.61	0.17		

Sampling Period (Nearshore and Offshore Muskegon Samples from June through September)						
log(Body Length)	1	1	10.55	10.54	66.96	**<0.001**
Preservation Duration		1	0.03	0.03	0.19	**0.67**
Month		3	1.36	0.45	2.87	0.04
Depth:Month		4	2.32	0.58	3.68	**0.007**
Residuals		131	20.63	0.16		
log(Body Length)	2	1	7.81	7.81	65.31	**<0.001**
Preservation Duration		1	0.39	0.39	3.26	0.07
Month		3	3.40	1.13	9.46	**<0.001**
Depth:Month		4	4.25	1.06	8.87	**<0.001**
Residuals		174	20.81	0.12		
log(Body Length)	3	1	9.73	9.73	53.51	**<0.001**
Preservation Duration		1	2.32	2.32	12.76	**0.001**
Month		3	4.02	1.34	7.37	**<0.001**
Depth:Month		4	5.50	1.38	7.56	**<0.001**
Residuals		126	22.92	0.18		
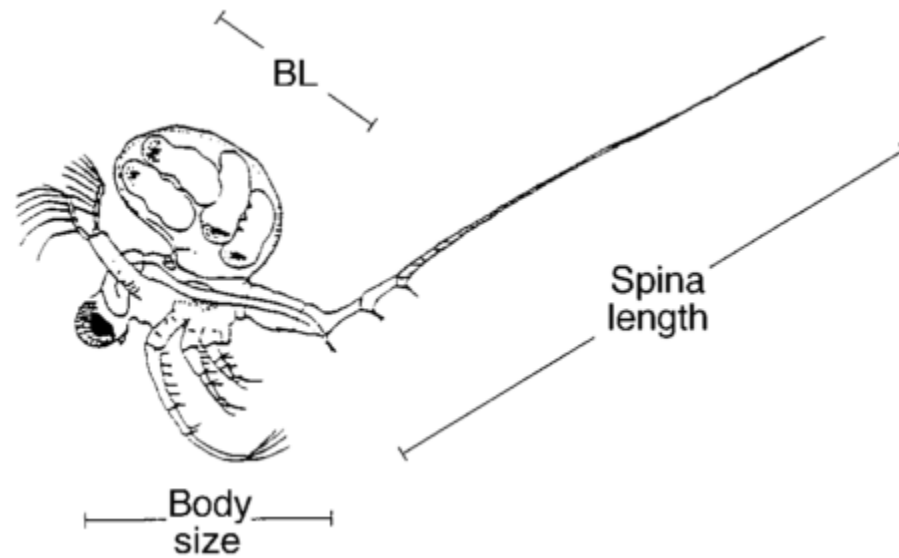
Figure 3.1. Measurements of adult *Bythotrephes*. Instars are counted by the number of barbs on their caudal spine(a) (3 shown). Eggs were counted if black-eye spots were visible in the brood sac length (BL). The total length was also measured (body size + spine length). Image taken from Straile and Hälbich (2000).
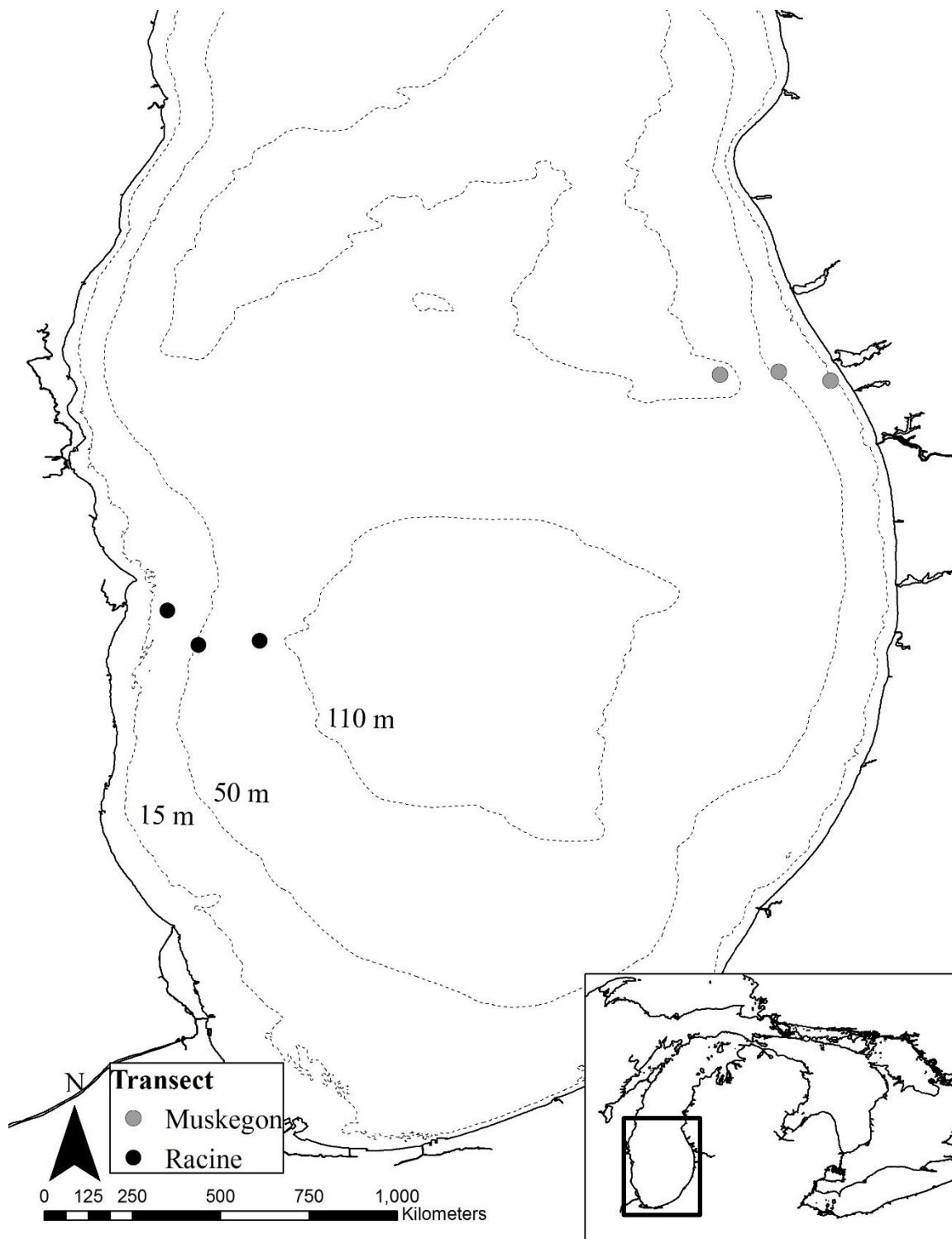
Figure 3.2. Map of sampling locations off Racine and Muskegon in southern Lake Michigan. Dashed lines indicate different contours (in meters).
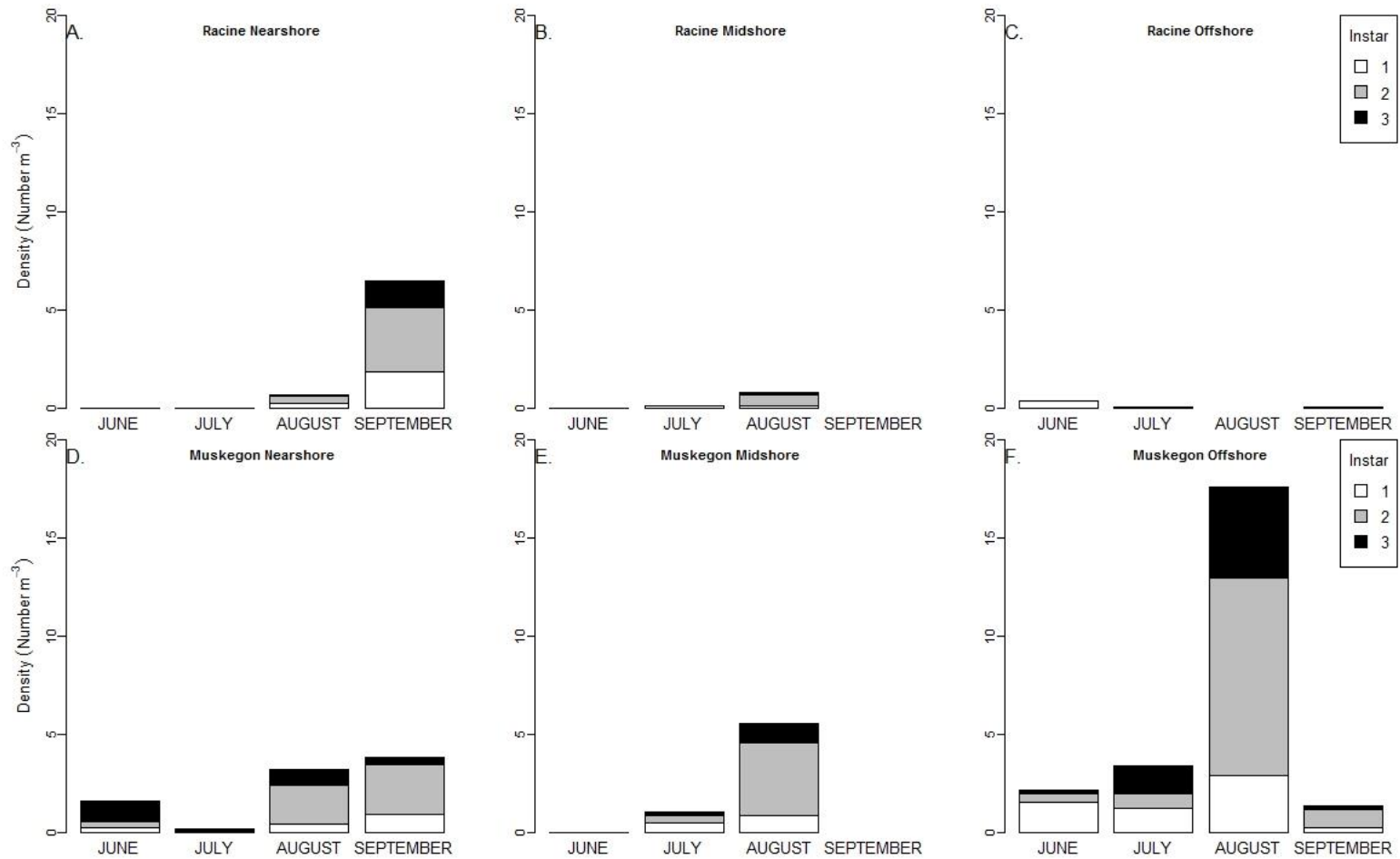
Figure 3.3. Density (# m^{-3}) of *Bythotrephes* (estimated from the Bongo 333 replicate) at nearshore (15 m; a & d), midshore (45 m; b & e), and offshore (110 m; c & f) sites from June to September. Racine densities are on the top (a,b,c), Muskegon densities are on the bottom (d,e,f). Instars are represented by different colors. Samples were not collected at Racine offshore of Muskegon midshore in August nor at Racine midshore in September.
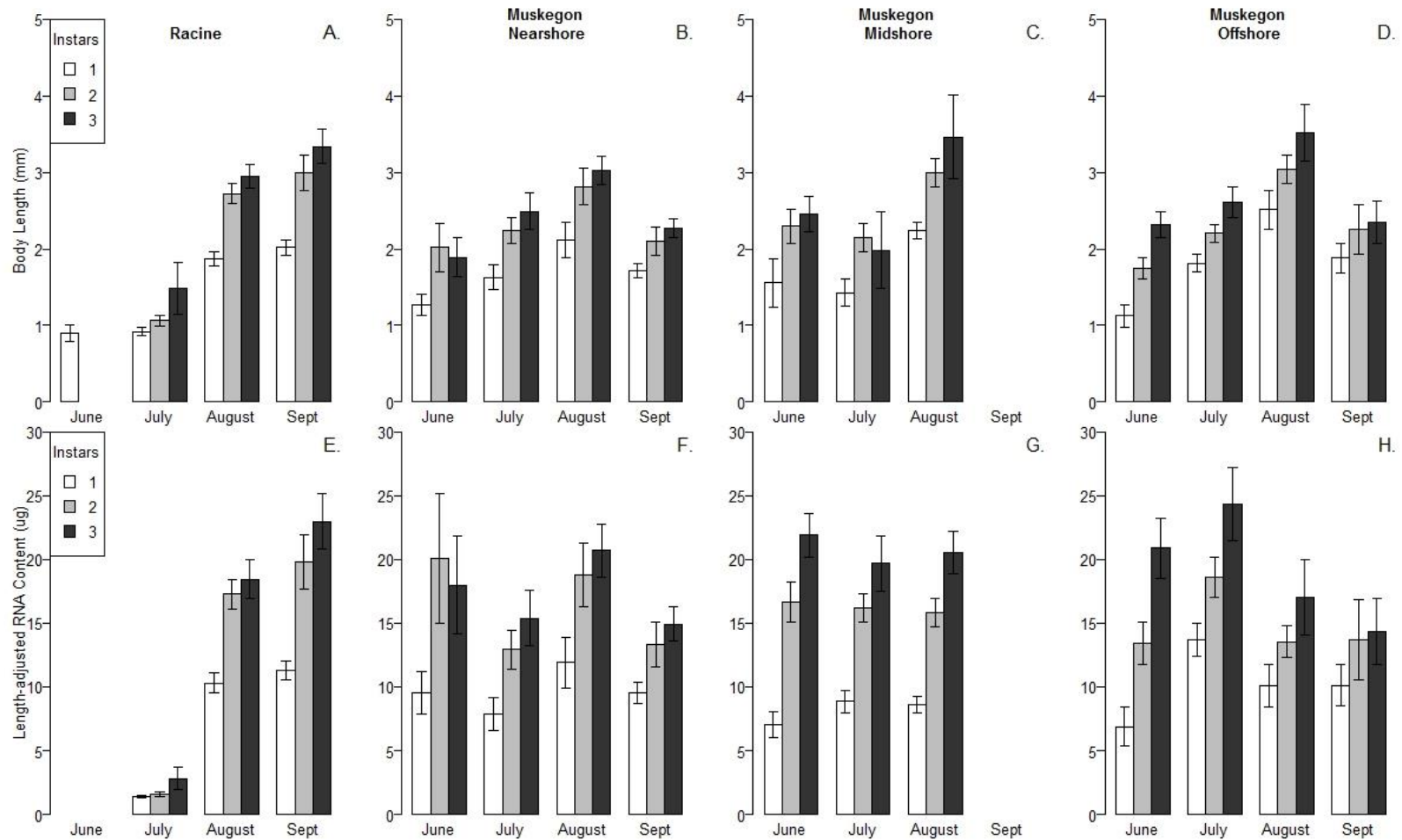
Figure 3.4. Average body length (a,b,c,d) and RNA content (d,e,f,g) for *Bythotrephes* (±SE). To account for the correlation between RNA content and body length to observe apparent spatial patterns, RNA content was estimated for *Bythtotrephes* using the same length creating a length-adjusted RNA content (actual RNA content can be found in the appendix). Averages along Racine include averages of the nearshore and midshore samples.
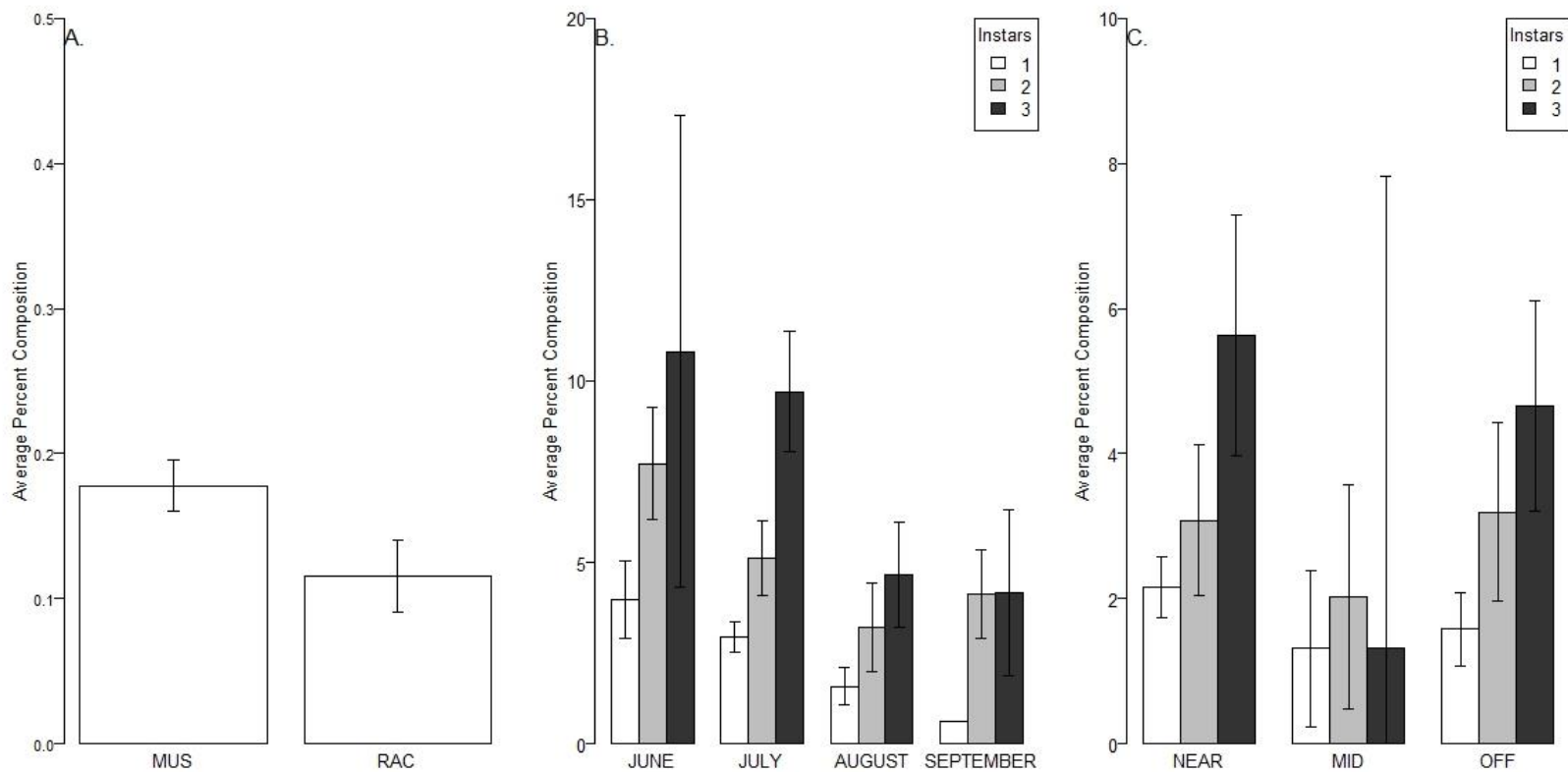
Figure 3.5. Average percentage (±SE) of the EPA fatty acid across transects (A), sampling period (B), and depth contour (C). Samples from plot B and C were only from Muskegon due to sample size.
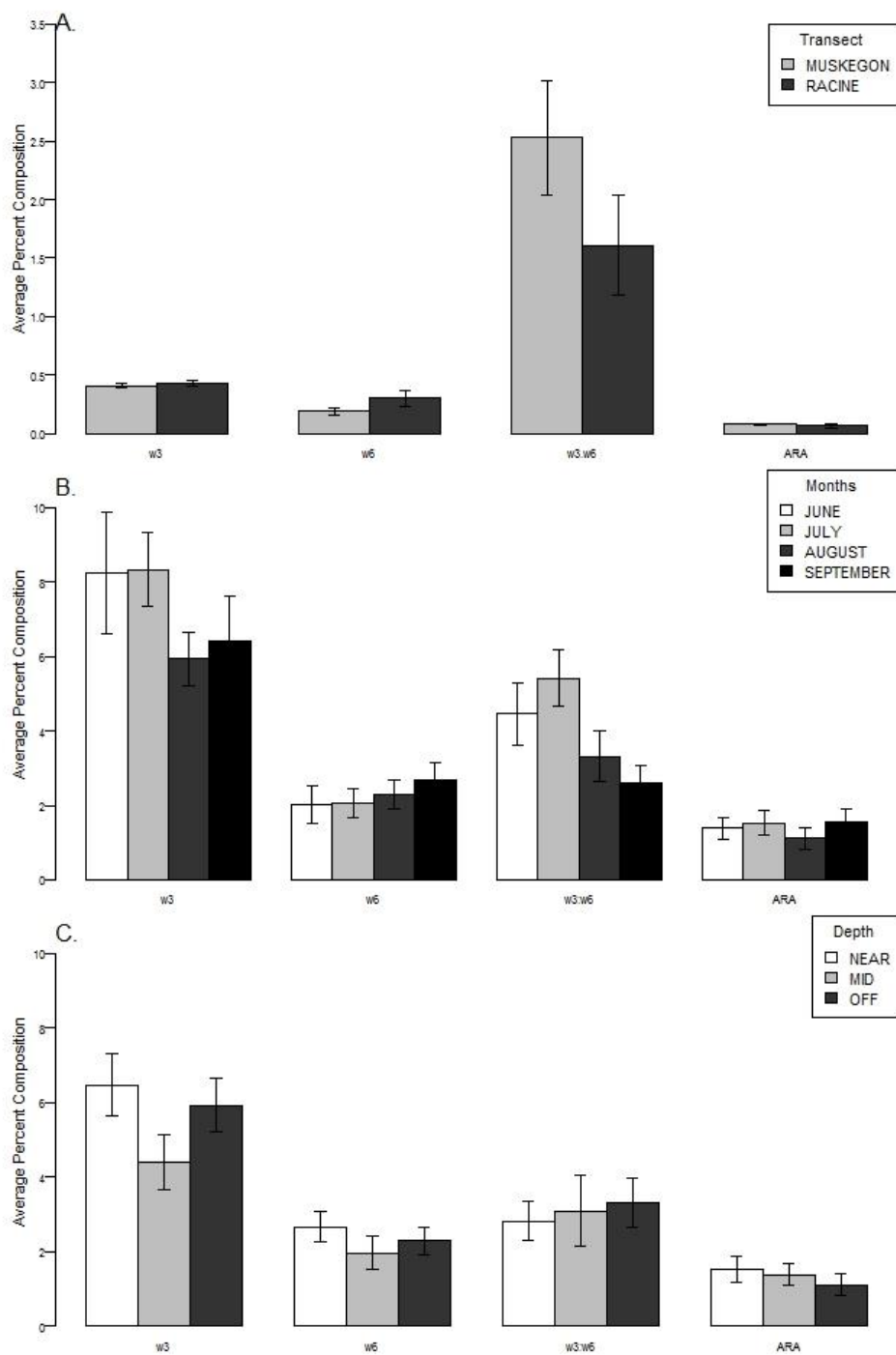
Figure 3.6. Average percentage (±SE) of the four different fatty acid indicators of for *Bythotrephes* value within the food web (ω3, ω6, ω3:ω6, and ARA) across transects (A), sampling period (B), and depth contour (C). Instars were combined.
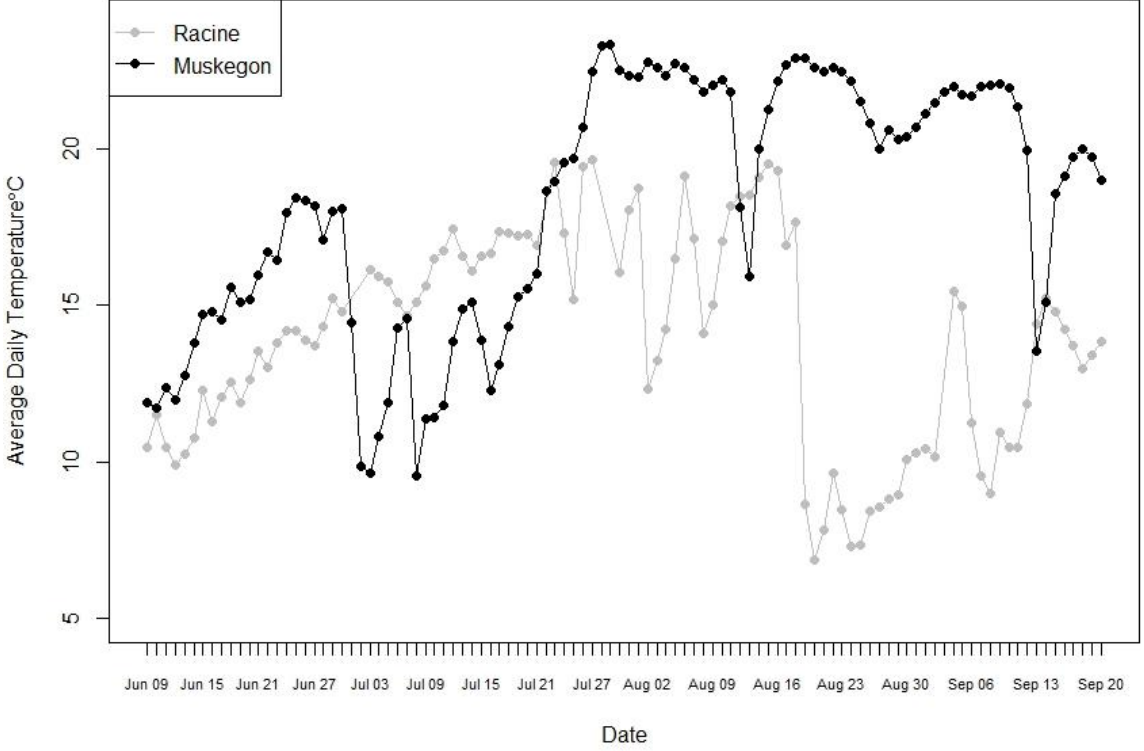
Figure 3.7. Average daily temperature. Muskegon temperatures were collected from the Great Lakes Environmental Research Lab buoy off Muskegon, MI, at station 45161 from the Great Lakes Observing System. Racine daily temperatures were collected from a buoy off the shores of Milwaukee, WI, at station MLWW3 owned by the Great Lakes Environmental Research Laboratory.

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APPENDICES

Appendix A Satellite Results

Appendix A1: Satellite Standardization

Methods

To standardize the relationship between each monthly SeaWiFS and MODIS chlorophyll *a* estimate, a linear regression was conducted with the individual 1 km x 1 km monthly average SeaWiFS estimates of chlorophyll *a* concentration as the predictor variable and the individual monthly average MODIS estimates of chlorophyll *a* concentration as the response variable. Monthly averages of chlorophyll *a* concentrations for May, July, and September from 2003 to 2007 were used in the standardization as both sensors were operational and working properly during this time. Because the retrieval algorithm is not lake specific, concentrations from Lake Michigan and Lake Huron were regressed together. Chlorophyll *a* concentrations from shallow embayments such as Green Bay, Saginaw Bay, Georgian Bay, and the North Channel were not included in the standardization or any further analysis due to relatively higher chlorophyll *a* concentrations in these areas. Individual average monthly chlorophyll *a* concentrations in nearshore (<30 m in depth) and offshore (>30 m in depth) areas were analyzed separately. The two linear regressions were bootstrapped (999 iterations) using a leave-one-out technique to identify the slope and intercept for both the nearshore and offshore standardization equation. Similar techniques were previously used to standardize offshore chlorophyll *a* concentrations in Lake Michigan (Warner and Lesht, 2015) and nearshore marine areas (Schaeffer, 2013).

An ANCOVA using the combined standardized SeaWiFS concentrations and observed MODIS concentrations as the response variable with the two different sensors as the predictor variable and lake as a covariate was conducted to verify no significant differences were detected between the observed and standardized concentrations. Lake was included as a covariate to confirm that the standardization model was consistent across both lakes. Standardization techniques were successful and the model was applied to chlorophyll *a* concentrations for years when SeaWiFS data were the only data available (i.e. 1998 to 2002) which created a comparable dataset of chlorophyll *a* concentrations that spans from 1998 to 2013 in both Lake Michigan and Lake Huron. Standardization was completed in R version 3.1.1 (R Core Team (2014)) and the R statistical package "boot" (Canty and Ripley 2014).

Results

The standardization equations for nearshore (<30m in depth) SeaWiFS concentrations was

$$SeaWiFS_{St} \ = \ -0.0205 + 1.127 \times SeaWiFS_O$$

With *SeaWiFS$_O$* as the original SeaWiFS concentrations and *SeaWiFS$_{St}$* as the new standardized concentrations. The standard error for the intercept and slope was 0.0019 and 0.0039, respectively. The standardization equation for offshore (>30m in depth) SeaWiFS concentrations was

$$SeaWiFS_{St} \ = \ 0.00498 + 0.988 \times SeaWiFS_O$$

The standard error for the intercept and slope was 0.0006 and 0.00154, respectively.

Verification of the standardized concentrations indicated that there was no significant difference between original MODIS concentration and the newly standardized SeaWiFS concentrations ($F_{1,2140}$=0.061, p=0.805). Also, there was no significant interaction between satellite and lake ($F_{1,2140}$=1.952, p=0.163) indicating the standardization technique was applicable across Lake Michigan and Lake Huron. Future MODIS information can also be included in any prospective analyses.

Results from the seasonal ANCOVAs between depth and year using only MODIS satellite chlorophyll a concentrations were comparable to the results observed using the entire dataset from 1998 to 2013. There were significant interaction terms in both lakes Michigan ($F_{1,116} = 14.09; P < 0.001$) and Huron ($F_{1,116} = 4.28; P = 0.041$) for in May with significant decreases in offshore chlorophyll a concentrations facilitating the different trends. In July, Lake Michigan had a significant interaction term ($F_{1,116} = 4.16; P = 0.044$) due to increases in nearshore chlorophyll a concentrations opposed to decreases in offshore chlorophyll a concentrations. In September, both interaction terms were no longer significant for either Lake Michigan ($F_{1,116} = 1.51; P = 0.22$) and Lake Huron ($F_{1,116} = 0.34; P = 0.56$). Due to similarities in the ANCOVAs with and without the SeaWiFS data, the standardization techniques described were deemed to be sufficient in allowing for analysis of information across the entire time period despite potential variations in absolute values of chlorophyll a concentrations.

Appendix Table A.1 The average maximum, minimum, range of chlorophyll *a* concentrations for each range of years for each lake, month, and region for the distance bins. The maximum value was taken from the most nearshore location, the minimum value was taken from the most offshore location, and the range was the difference between the two.

|		1998-2001	2002-2005	2006-2009	2010-2013
		Lake Michigan			
May	Whole	1.22 - 0.87 (0.35)	1.14 - 0.71 (0.43)	1.20 - 0.50 (0.71)	1.23 - 0.42 (0.81)
	NE	0.95 - 0.77 (0.19)	0.91 - 0.59 (0.32)	0.95 - 0.50 (0.45)	0.92 - 0.43 (0.48)
	NW	1.23 - 0.70 (0.53)	1.19 - 0.54 (0.65)	1.19 - 0.51 (0.68)	1.29 - 0.48 (0.81)
	SE	1.54 - 0.86 (0.69)	1.43 - 0.70 (0.73)	1.66 - 0.52 (1.14)	1.66 - 0.12 (1.54)
	SW	1.18 - 0.88 (0.29)	1.04 - 0.72 (0.32)	1.00 - 0.47 (0.53)	1.05 - 0.39 (0.65)
July	Whole	1.11 - 0.54 (0.56)	1.11 - 0.46 (0.65)	1.18 - 0.40 (0.79)	1.17 - 0.32 (0.85)
	NE	0.96 - 0.72 (0.23)	1.01 - 0.66 (0.34)	1.01 - 0.48 (0.52)	0.96 - 0.43 (0.53)
	NW	1.17 - 0.71 (0.46)	1.29 - 0.69 (0.60)	1.31 - 0.50 (0.80)	1.37 - 0.45 (0.92)
	SE	1.29 - 0.55 (0.74)	1.28 - 0.47 (0.81)	1.54 - 0.39 (1.15)	1.46 - 0.07 (1.39)
	SW	1.02 - 0.54 (0.48)	0.88 - 0.46 (0.42)	0.87 - 0.40 (0.47)	0.89 - 0.32 (0.58)
September	Whole	1.10 - 0.56 (0.55)	1.17 - 0.50 (0.67)	1.20 - 0.45 (0.75)	1.20 - 0.48 (0.72)
	NE	1.08 - 0.78 (0.30)	1.33 - 0.65 (0.68)	1.21 - 0.61 (0.60)	1.15 - 0.63 (0.52)
	NW	1.11 - 0.73 (0.37)	1.25 - 0.65 (0.59)	1.19 - 0.59 (0.60)	1.37 - 0.69 (0.68)
	SE	1.15 - 0.56 (0.58)	1.13 - 0.49 (0.63)	1.41 - 0.46 (0.95)	1.34 - 0.25 (1.08)
	SW	1.09 - 0.56 (0.53)	0.97 - 0.50 (0.47)	1.01 - 0.45 (0.56)	0.96 - 0.48 (0.47)

|		1998 – 2001	2002 – 2005	2006 - 2009	2010 - 2013
		Lake Huron			
May	Whole	0.40 - 0.20 (0.20)	0.39 - 0.15 (0.24)	0.42 - 0.13 (0.28)	0.42 - 0.10 (0.32)
	NW	0.41 - 0.28 (0.13)	0.41 - 0.24 (0.17)	0.44 - 0.19 (0.25)	0.42 - 0.16 (0.26)
	NE	0.50 - 0.25 (0.25)	0.42 - 0.22 (0.20)	0.41 - 0.19 (0.21)	0.39 - 0.16 (0.23)
	S	0.51 - 0.33 (0.18)	0.48 - 0.24 (0.24)	0.49 - 0.16 (0.33)	0.46 - 0.16 (0.33)
July	Whole	0.48 - 0.29 (0.19)	0.44 - 0.24 (0.20)	0.45 - 0.18 (0.26)	0.42 - 0.15 (0.27)
	NW	0.34 - 0.21 (0.13)	0.32 - 0.15 (0.16)	0.36 - 0.13 (0.22)	0.36 - 0.10 (0.26)
	NE	0.41 - 0.21 (0.20)	0.44 - 0.15 (0.28)	0.41 - 0.14 (0.28)	0.45 - 0.10 (0.35)
	S	0.46 - 0.20 (0.27)	0.41 - 0.14 (0.27)	0.49 - 0.13 (0.35)	0.45 - 0.10 (0.36)
September	Whole	0.44 - 0.21 (0.23)	0.45 - 0.18 (0.26)	0.43 - 0.16 (0.27)	0.42 - 0.16 (0.26)
	NW	0.39 - 0.21 (0.19)	0.38 - 0.18 (0.20)	0.37 - 0.14 (0.22)	0.36 - 0.15 (0.21)
	NE	0.40 - 0.22 (0.17)	0.44 - 0.21 (0.22)	0.42 - 0.18 (0.23)	0.40 - 0.18 (0.22)
	S	0.53 - 0.19 (0.33)	0.52 - 0.17 (0.35)	0.51 - 0.15 (0.36)	0.51 - 0.16 (0.35)
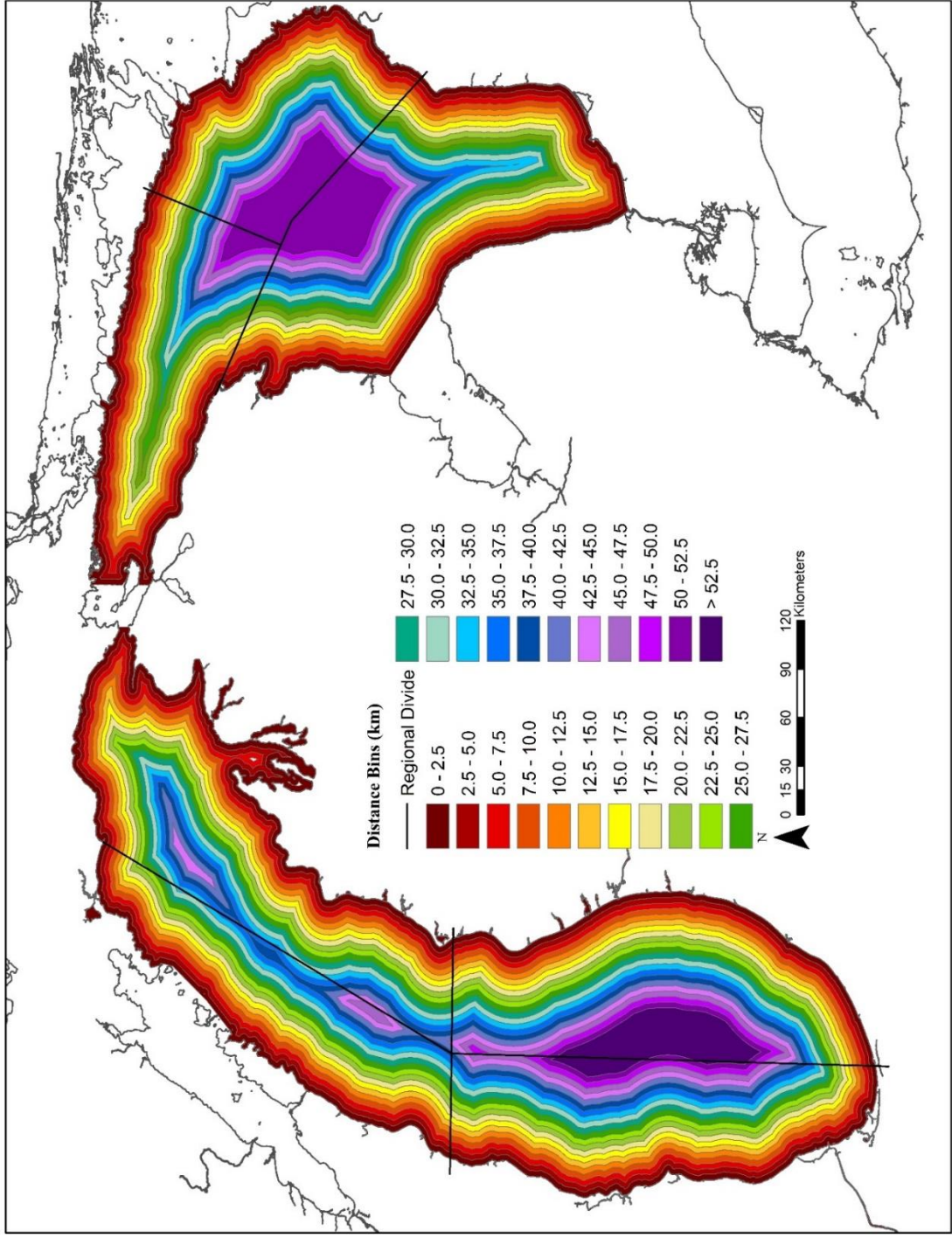
Appendix Figure A.1 Map of Lake Michigan and Lake Huron. Bins are 2.5km distance intervals and indicated in different colors in the legend. Black lines divide regions around both lakes. Lake Michigan is divided into southeast, southwest, northeast, and northwest. Lake Huron is divided into south, northwest, and northeast.
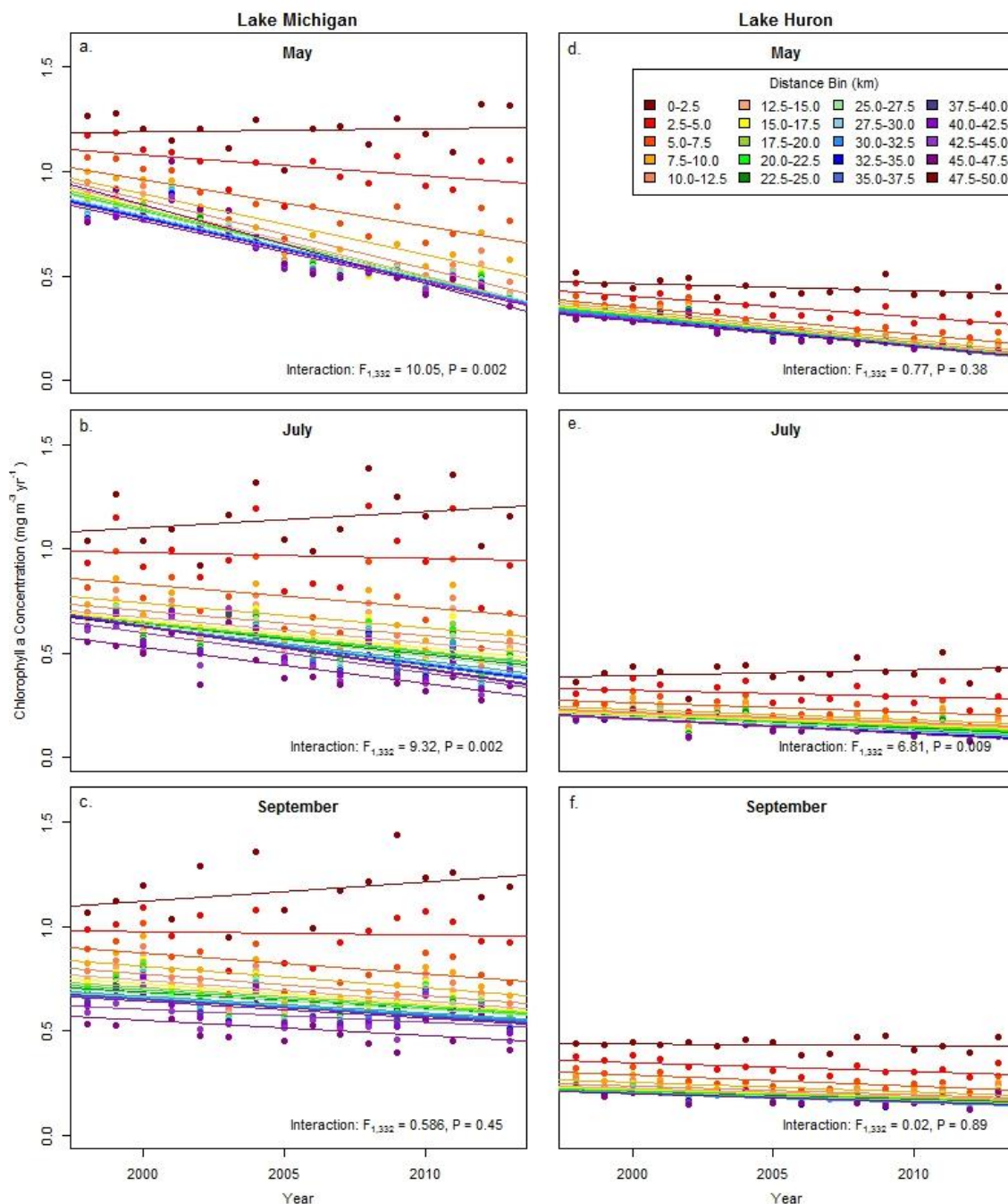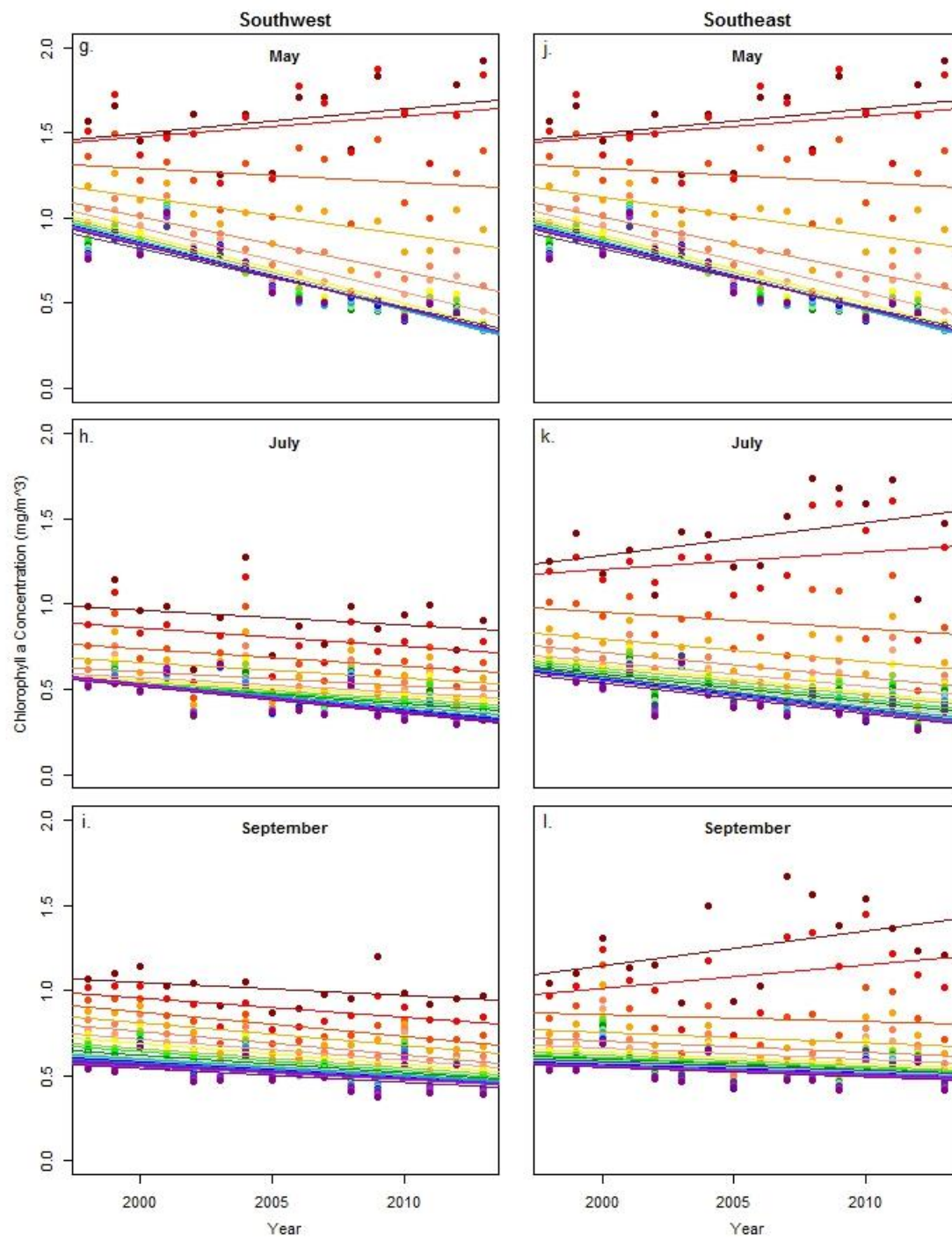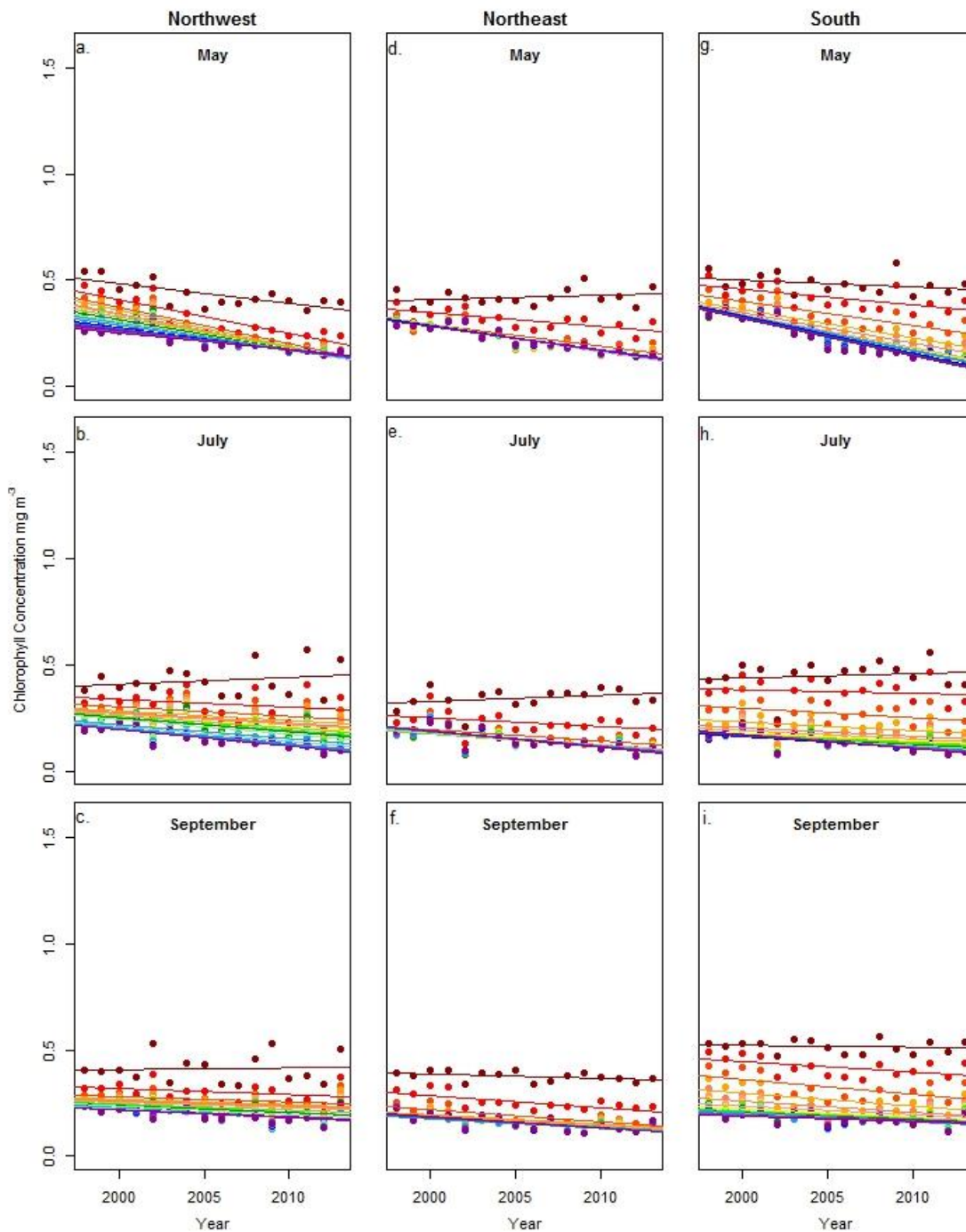
Appendix Figure A.2 The seasonal chlorophyll *a* concentrations averages for the main basin of Lake Michigan (left) and Lake Huron (right) from 1998 to 2013 by distance bins. Graphs (a) and (d) plot concentrations in May. Graphs (b) and (e) plot concentrations in July. Graphs (c) and (f) plot concentrations in September. *F*- and *P*- values are associated with the interaction term between depth and year from that particular lake and month.
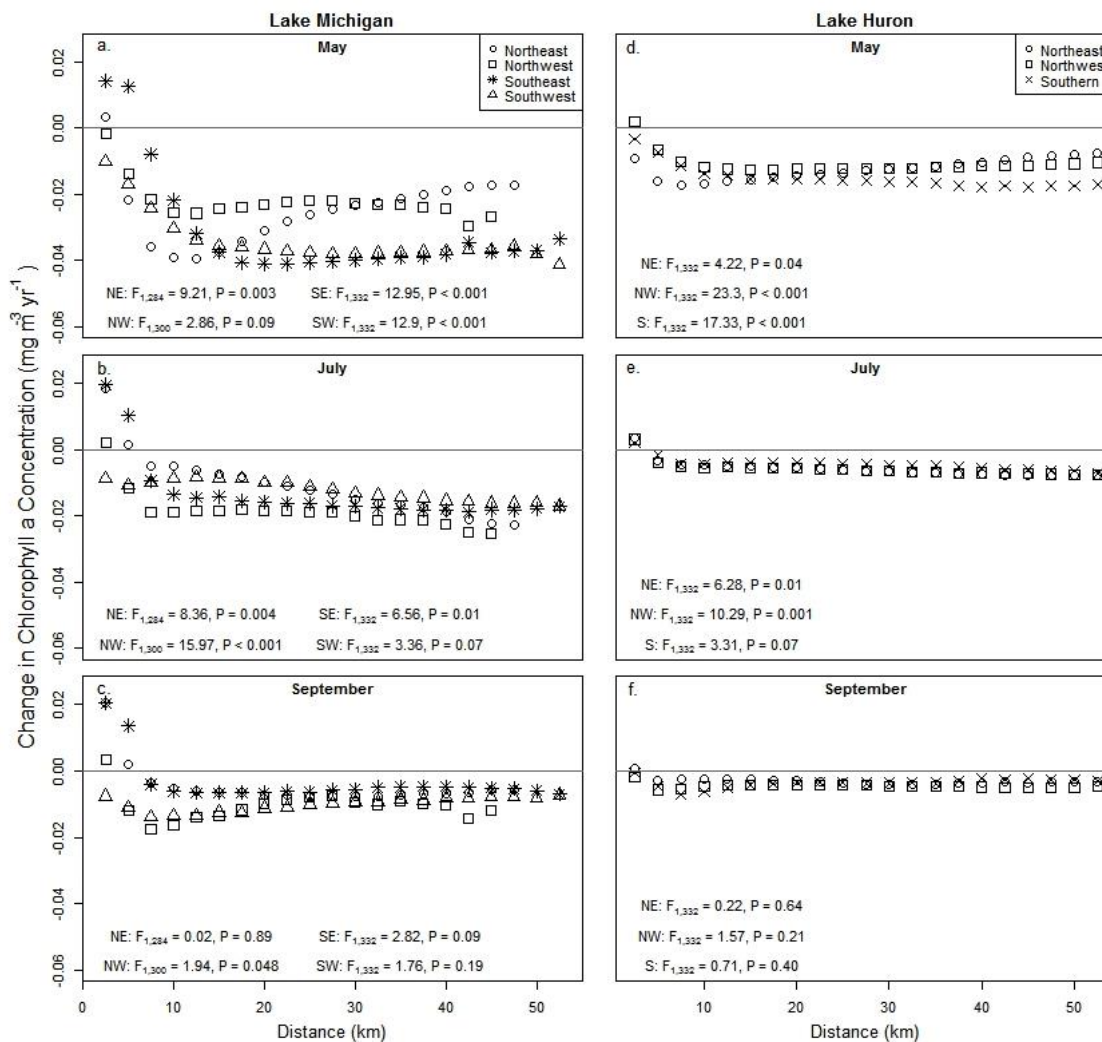
Appendix Figure A.3 The slope of a regression between chlorophyll *a* concentration from 1998 to 2013 (chlorophyll *a* concentrations/year) for each distance bin. Values for different geographic regions of each lake are symbolized differently. Grey lines indicate a correlation of 0. *F*- and *P*- values are associated with the interaction term between depth and year from the region specified for that particular lake and month.
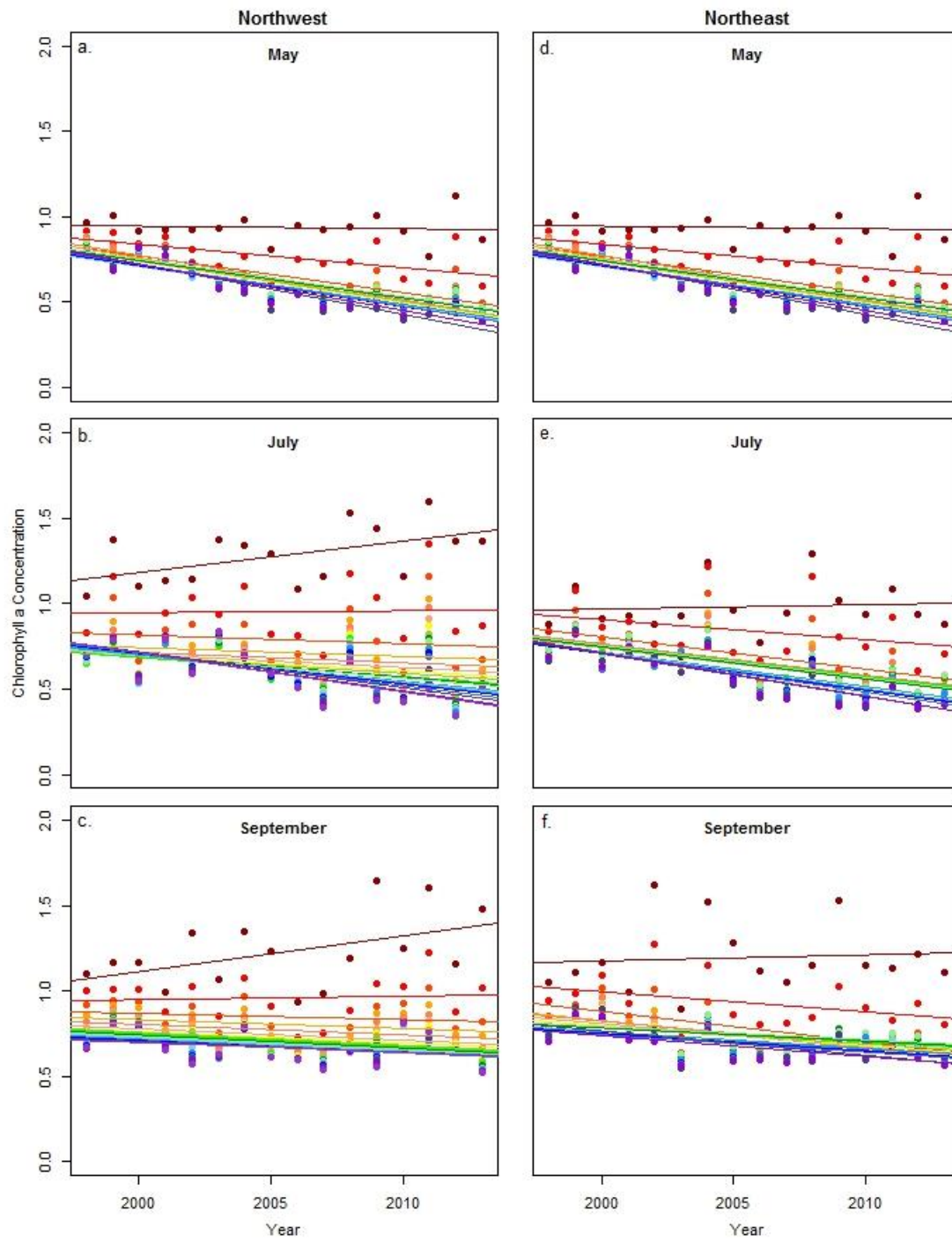
Appendix Figure A.4 The seasonal chlorophyll *a* concentrations averages for each region of Lake Michigan (left) and Lake Huron (right) from 1998 to 2013 by distance bin. Colors correspond to distance bins from map in Figure A.1.
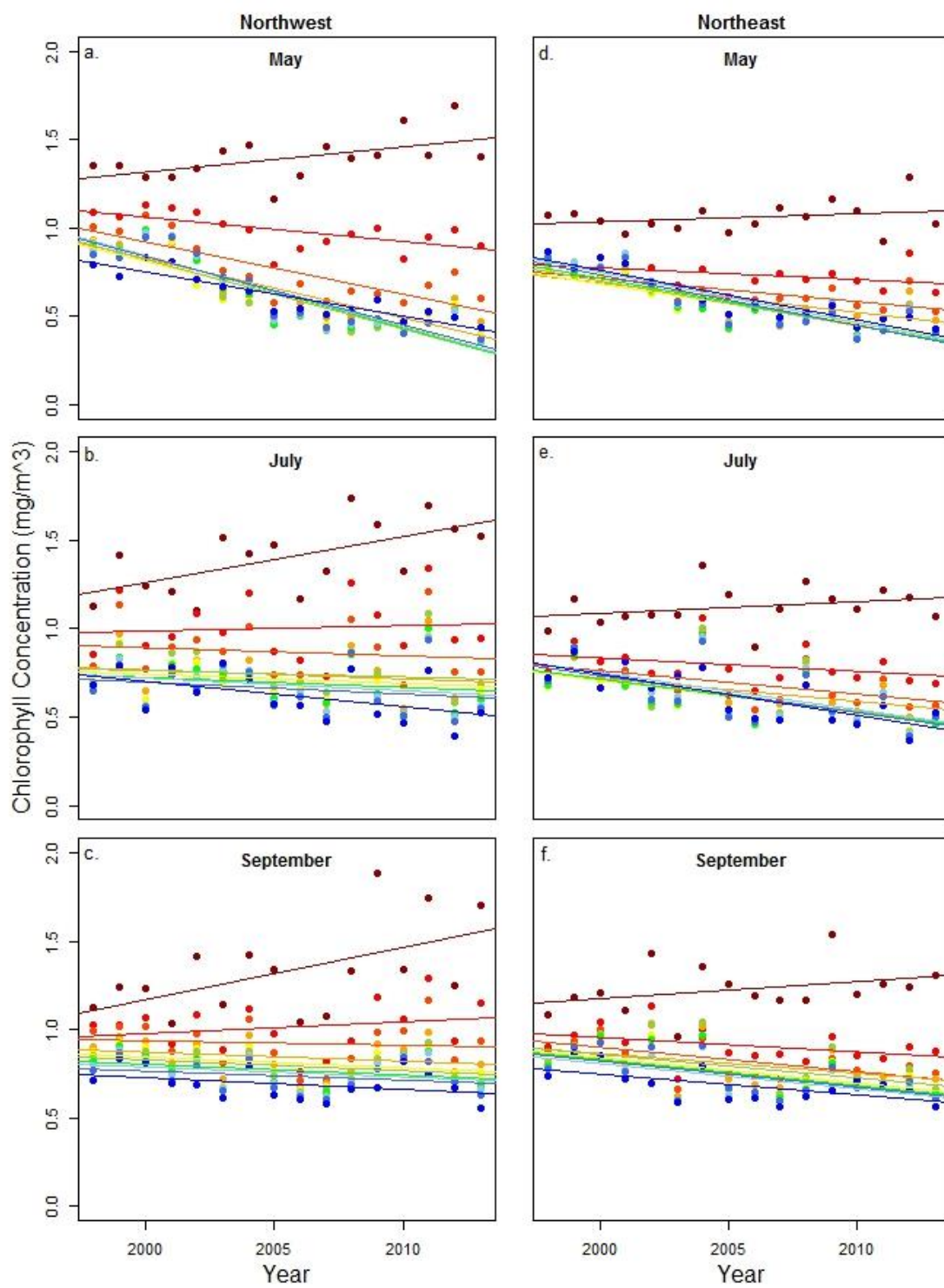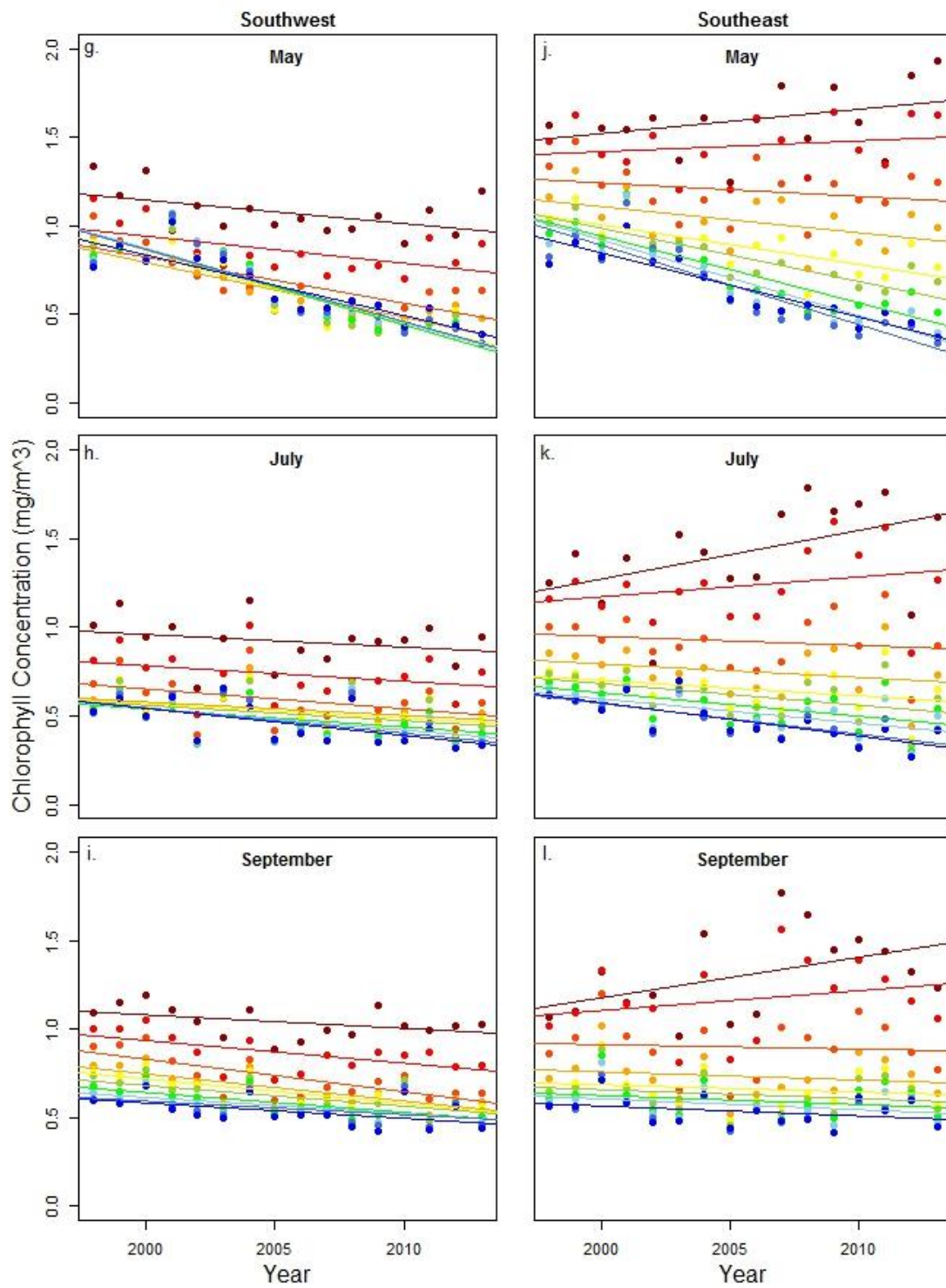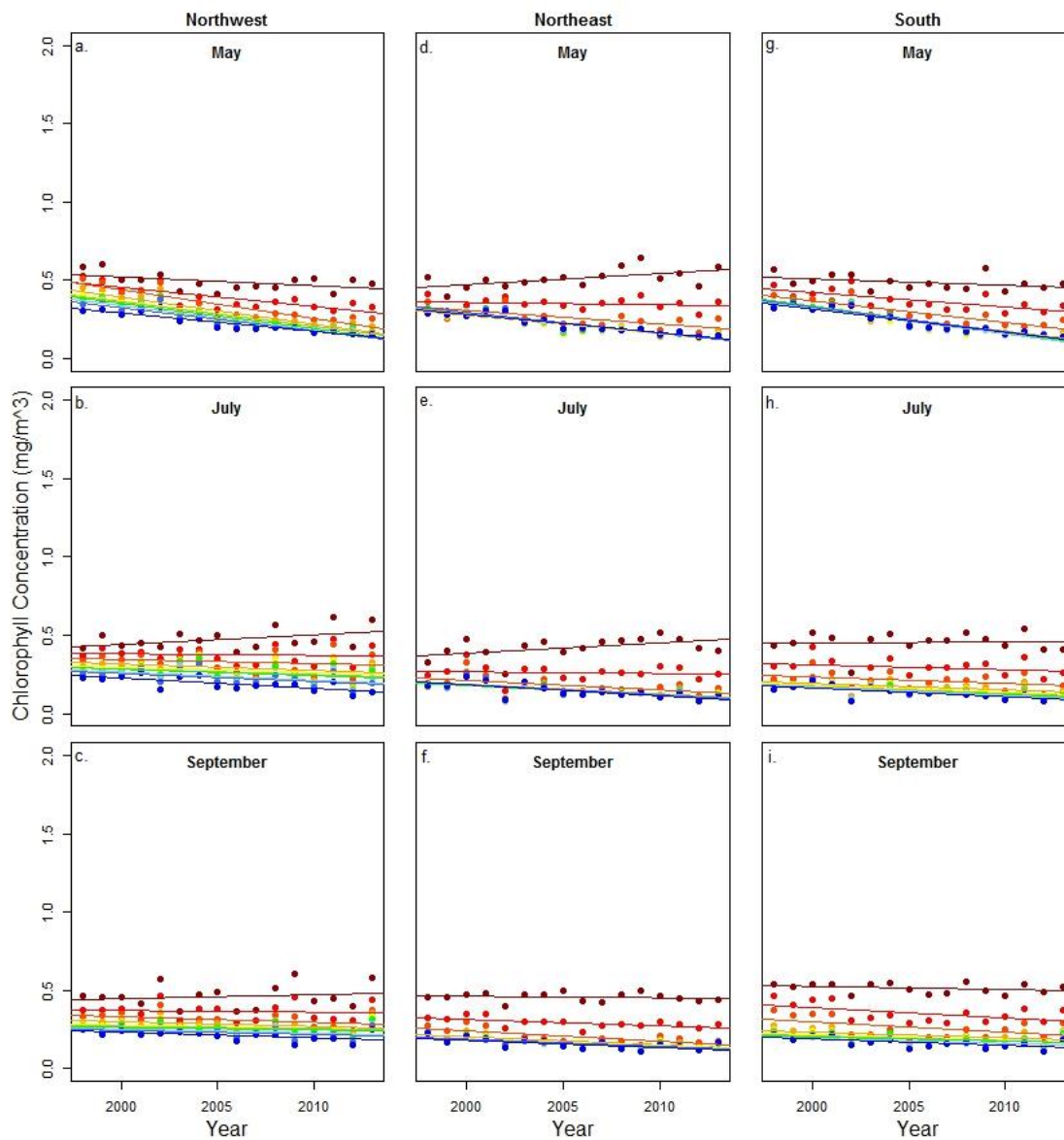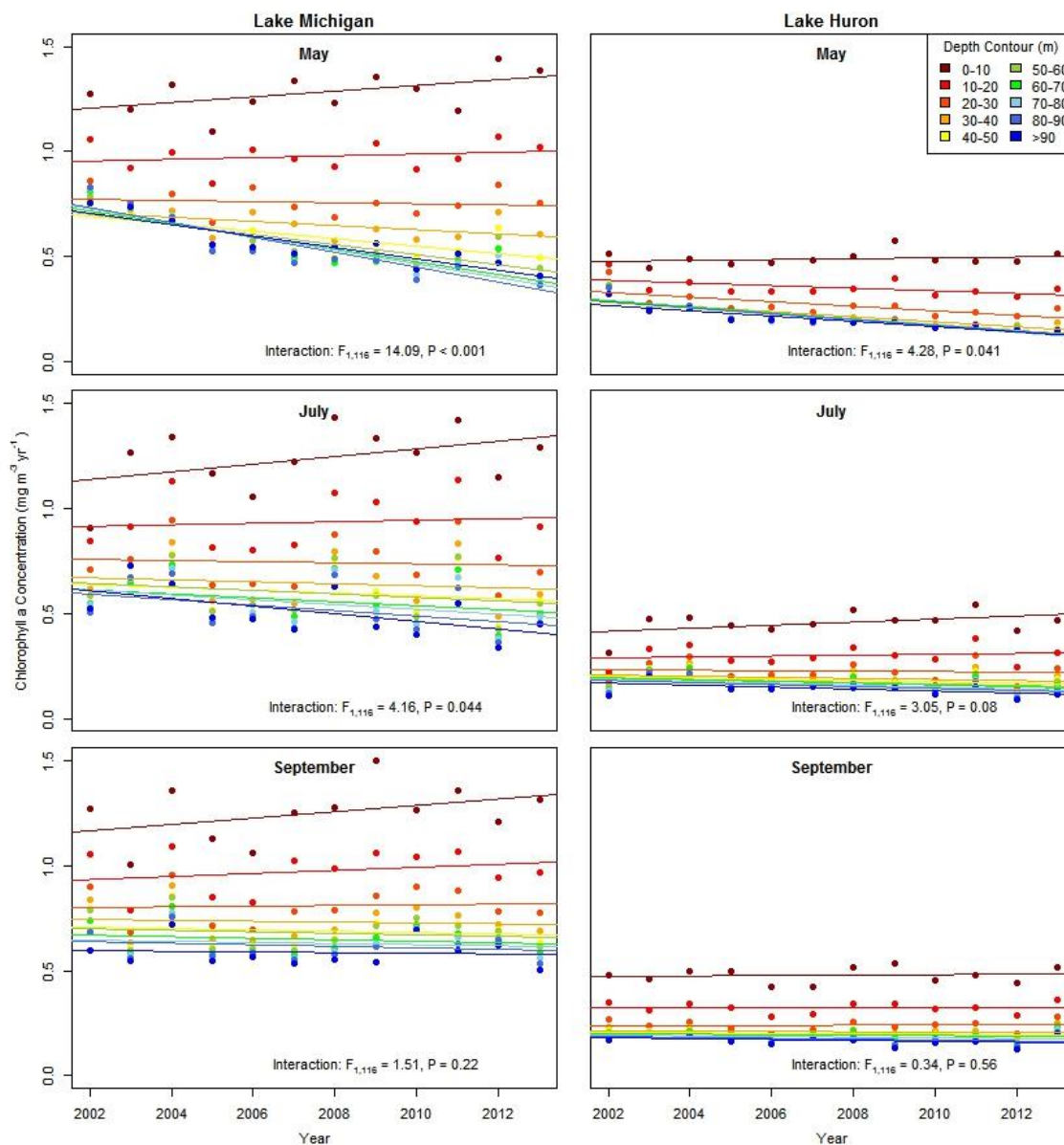
Appendix Figure A.5 The seasonal chlorophyll *a* concentrations averages for each region of Lake Michigan (left) and Lake Huron (right) from 1998 to 2013 by depth contours. Colors correspond to depth bins from map in Figure 1.

Appendix Figure A.6 The seasonal chlorophyll *a* concentrations averages for the main basin of Lake Michigan (left) and Lake Huron (right) for MODIS satellite from 2002 to 2013 by depth contours. Graphs (a) and (d) plot concentrations in May. Graphs (b) and (e) plot concentrations in July. Graphs (c) and (f) plot concentrations in September. *F*- and *P*- values are associated with the interaction term between depth and year from that particular lake and month.
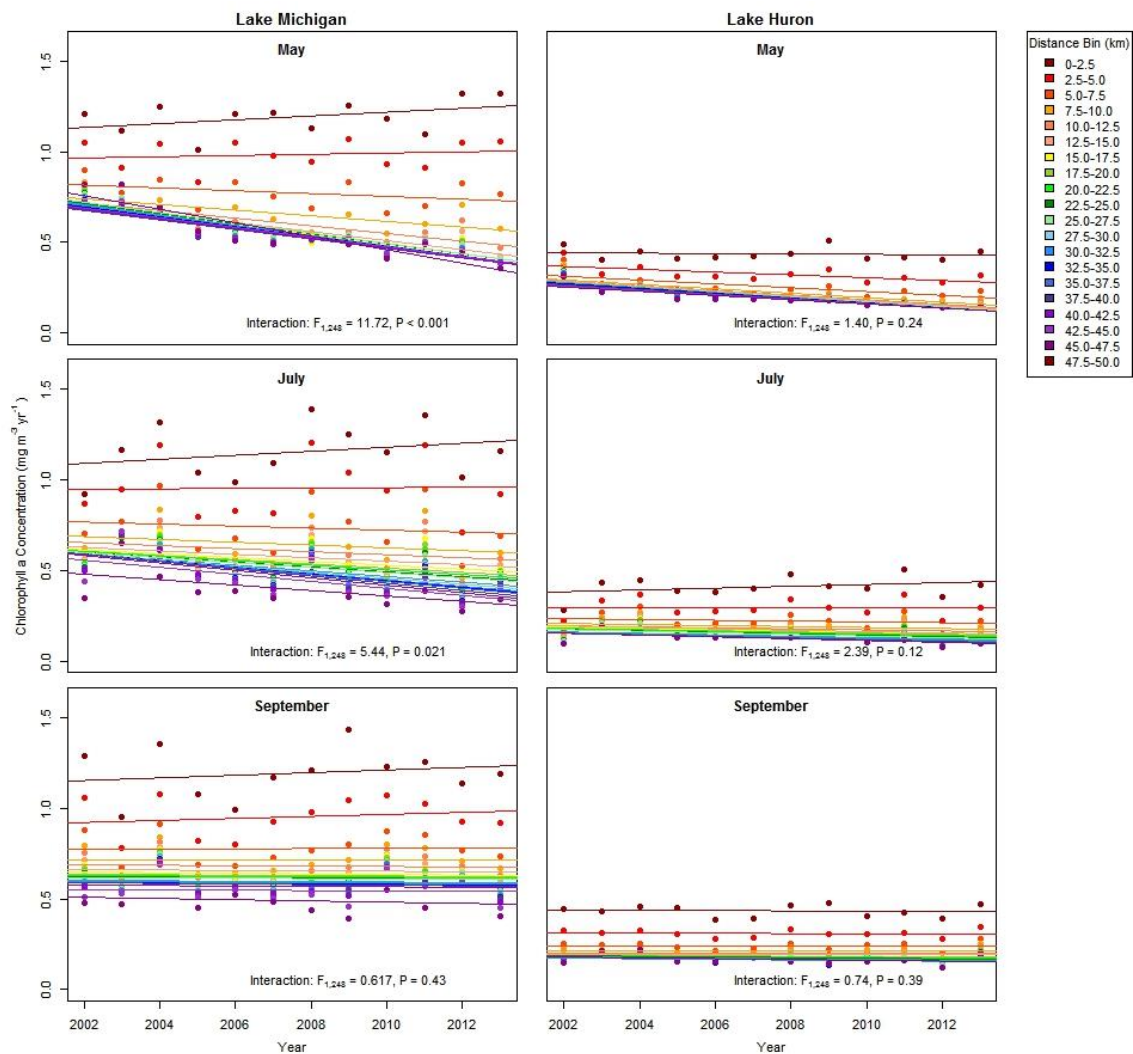
Appendix Figure A.7 The seasonal chlorophyll *a* concentrations averages for the main basin of Lake Michigan (left) and Lake Huron (right) for the MODIS satellite from 2002 to 2013 by distance bins. Graphs (a) and (d) plot concentrations in May. Graphs (b) and (e) plot concentrations in July. Graphs (c) and (f) plot concentrations in September. *F*- and *P*- values are associated with the interaction term between depth and year from that particular lake and month.

Appendix B   Experimental Data

Appendix B1: Length Standardization

Foley et al. (2010) found preservation times longer than 90 days did not significantly change lengths. As all our samples were preserved for greater than 90 days before being measured we used the difference between the initial and final measurement date. There was a significant difference from the initial to the final date for both the total $(F_{2,37} = 12.43; P < 0.001)$ and body length $(F_{2,37} = 13.58; P < 0.001)$. There was not a significant difference in the lengths of the spines over time $(F_{2,37} = 3.037; P = 0.06)$.

Appendix Table B.1 Mean (±SE) percent change in total, body, and spine length of *Bythotrephes* preserved in RNA*later* relative to the initial date of preservation (Day 0). Asterisks indicate significance from initial preservation date.

	Day 70	Day 137
Body Length	-40.38 ± 2.33*	-30.11 ± 1.50*
Spine Length	+6.89 ± 1.49	-3.02 ± 1.66
Total Length	+15.96 ± 0.93*	-11.25 ± 0.78*

Appendix Table B.2 Sample sizes of *Bythotrephes* body lengths along the Muskegon and Racine transects for each instar from June through September. N/A's indicate months and depth contours which were not sampled.

Transect/Depth Contour	Instar	June	July	August	September
Muskegon					
	1	7	28	9	31
Nearshore	2	12	31	30	29
	3	18	39	19	30
	1	10	29	33	0
Midshore	2	24	24	29	0
	3	30	13	21	1
	1	33	22	12	10
Offshore	2	30	23	30	16
	3	30	19	19	11
Racine					
	1	0	0	30	35
Nearshore	2	0	0	30	25
	3	0	0	11	35
	1	0	69	25	N/A
Midshore	2	0	26	30	N/A
	3	14	12	30	N/A
	1	0	18	N/A	1
Offshore	2	0	1	N/A	11
	3	20	0	N/A	2

Appendix Table B.3 Sample sizes of *Bythotrephes* RNA content along the Muskegon and Racine transects for each instar from June through September. N/A's indicate months and depth contours which were not sampled.
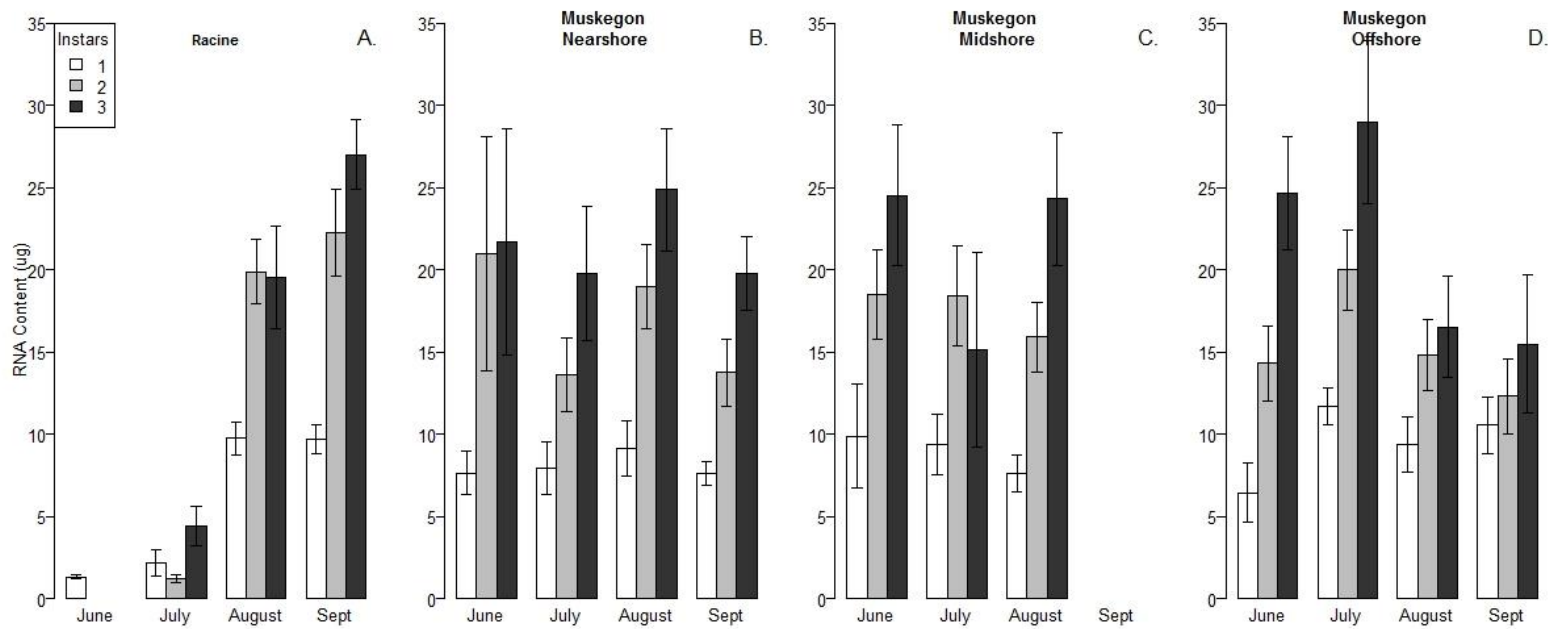
Transect/Depth Contour	Instar	June	July	August	September
Muskegon					
	1	7	25	9	31
Nearshore	2	11	30	29	27
	3	12	29	14	24
	1	9	29	30	0
Midshore	2	24	23	28	0
	3	29	11	4	1
	1	36	22	12	6
Offshore	2	33	23	29	7
	3	27	16	11	7
Racine					
	1	0	0	30	34
Nearshore	2	0	0	29	24
	3	0	0	7	28
	1	14	69	25	N/A
Midshore	2	0	24	23	N/A
	3	0	16	25	N/A
	1	22	18	N/A	1
Offshore	2	0	1	N/A	11
	3	0	0	N/A	1

Appendix Table B.4 Sample sizes of *Bythotrephes* fatty acid proportions along the Muskegon and Racine transects for each instar from June through September. N/A's indicate months and depth contours which were not sampled.

Transect/Depth Contour	Instar	June	July	August	September
Muskegon					
	1	0	2	7	10
Nearshore	2	1	5	16	10
	3	2	6	10	7
	1	1	22	10	N/A
Midshore	2	4	17	9	N/A
	3	4	11	9	N/A
	1	7	20	12	1
Offshore	2	6	12	22	10
	3	2	22	10	11
Racine					
	1	0	0	N/A	1
Nearshore	2	0	0	N/A	4
	3	0	0	N/A	2
	1	1	10	N/A	N/A
Midshore	2	0	2	N/A	N/A
	3	0	1	N/A	N/A
	1	1	0	N/A	1
Offshore	2	0	0	N/A	2
	3	0	0	N/A	0

Appendix Figure B.1 Average observed RNA content for *Bythotrephes* (±SE) using actual lengths. Averages along Racine include averages of the nearshore and midshore samples.

Appendix C   Supplementary References

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