

**SPATIAL AND TEMPORAL VARIATION IN THE HABITAT QUALITY
AND RESOURCE UTILIZATION OF FISHES IN A LARGE LAKE
ECOSYSTEM**

by

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*Dedicated to my parents, Matthew and Shelli Tellier, my brother, Jacob Tellier, my fiancé,
Emmalee Caisse, and my grandmother, Carol Houle.*

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ABSTRACT

The prevalence of hypoxia in aquatic systems has increased in recent decades and climate change is expected to worsen the extent and severity of hypoxic phenomena worldwide. Moreover, aquatic hypoxia has produced adverse ecological consequences and stimulated research interest within the Laurentian Great Lakes. The physiological stress imposed by hypoxia reduces habitat quality for most aquatic biota and causes changes in patterns of resource use and food web dynamics. We conducted a review of the primary literature to identify trends in prevalence of Great Lakes hypoxia research and broadly classify the unique hypoxic conditions afflicting Great Lakes ecosystems. We found that the majority of research effort toward Great Lakes hypoxia is focused on the Lake Erie central basin. Our review further revealed that this does not characterize the breadth of hypoxic phenomena that occur throughout the Great Lakes region. We then utilized a long-term monitoring dataset provided by the U.S. Environmental Protection Agency Great Lakes National Program Office to quantify the impact of Lake Erie central basin hypoxia on habitat quality of several fish species. We found that bioenergetics-based growth-rate potential models have a potential application as the framework for the development of biological endpoints that measure the effects of hypoxia on aquatic biota. Finally, we utilized stable isotope analysis to look for broad spatial and temporal trends in resource utilization within distinct regions of the Lake Erie central basin, with hypoxia and large-scale hydrodynamic patterns serving as potential driving patterns for spatial differences.

CHAPTER 1. WIDESPREAD PREVALENCE OF HYPOXIA AND THE CLASSIFICATION OF HYPOXIC CONDITIONS IN THE LAURENTIAN GREAT LAKES

1.1 Introduction

Hypoxia is a widespread phenomenon throughout freshwater and marine ecosystems. Hypoxia is harmful to aquatic organisms that rely on aerobic respiration, from single-celled plankton to complex vertebrates (Abdel-Tawwab et al., 2019; Roman et al., 2012). The development and presence of hypoxia has long been monitored and studied in vulnerable coastal systems; for example, the Gulf of Mexico and Chesapeake Bay “dead zones” have received broad attention in both popular press and peer-reviewed journals. Both these high-profile systems are located near areas of high human population density, have potential links to climate change (Du et al., 2018; Dubravko et al., 1996, 2005; Najjar et al., 2010), and have experienced increased severity of hypoxia in recent decades (Du et al., 2018; Turner et al., 2008). However, hypoxia is also prevalent and potentially deleterious in freshwater systems (Jane et al., 2021), including the Laurentian Great Lakes (herein referred to as the Great Lakes). While select locations characterized by hypoxia in the Great Lakes have been subject to concentrated research and monitoring interest (e.g., central basin of Lake Erie), there is a paucity of programs describing and mapping the extent of hypoxia relative to the size and diversity of systems across the Great Lakes. It is therefore useful to assess the range of hypoxic conditions that occur throughout the Great Lakes and for resource managers to understand and identify the attributes of different hypoxic phenomena, the mechanisms leading to such phenomena and the potential consequences of hypoxic conditions.

Hypoxia is a naturally occurring process in many aquatic systems, but the global prevalence and extent of hypoxia has been exacerbated by nutrient loading, habitat alteration, and climate change in both marine (Altieri and Gedan, 2015; Meire et al., 2013; Rabalais et al., 2010) and freshwater (Collingsworth et al., 2017; Jenny et al., 2016; North et al., 2013) systems. Since the 1960's, incidences of hypoxia in coastal marine systems have increased over thirtyfold, with the number of recognized dead zones doubling every ten years over the same time period (Diaz and Rosenberg, 2008). Inland water bodies throughout the world have concurrently experienced increases in the presence and severity of hypoxia (Saari et al., 2018) and the Great Lakes are no exception to this trend. Increased frequencies of hypoxia have been reported in the central basin of Lake Erie (Scavia et al., 2014) since the 1990's, and extensive seasonal hypoxia has recently been documented in Muskegon Lake (Biddanda et al., 2018), Green Bay (Klump et al., 2018), and Saginaw Bay (NOAA GLERL Technical Report, 2013). The intensification of hypoxia in the Great Lakes has also led to new U.S. legislation and increased international efforts to improve our understanding of hypoxia in the United States and Canada, including the Harmful Algal Bloom and Hypoxia Research and Control Act (1998; Amendments: 2004, 2014) and the binational Great Lakes Water Quality Agreement (1972; Amendments: 1983, 1987, 2012), each of which explicitly list hypoxia as a major concern for ecosystem health in the Great Lakes.

The direct and indirect effects of hypoxia on aquatic ecosystems and the services provided by these ecosystems are prolific and include the degradation of benthos and zooplankton community health (Goto et al., 2012; Hale et al., 2016), loss of fish habitat (Budnik et al., 2021), changes in the efficiency of commercial fishing (Chamberlain et al., 2020), and drinking water taste and odor problems (Diaz and Rosenberg, 2011; Ruberg et al., 2008). Many of these consequences are perceived as negative, but hypoxia can have more complicated effects on

organisms when it occurs at sub-lethal levels. Hypoxic zones may provide refuge for zooplankton from planktivorous fish (Vanderploeg et al., 2009a, 2009b), may increase feeding efficiency and consumption by piscivorous fish (Brandt et al., 2011), and may increase commercial fishing catches by concentrating target species in smaller areas (Chamberlain et al., 2020; Kraus et al., 2015). Hypoxia may rise to an issue of concern for aquatic resource managers when the duration, magnitude, or extent of the phenomenon increases beyond natural levels. The annual economic cost of elevated levels of hypoxia is difficult to estimate, but the ecosystem services (e.g., recreational boating, fishing, tourism, drinking water) that are threatened by hypoxia in Lake Erie alone generate an annual income of over \$50 billion (LEIA, 2012). As such, documenting where hypoxia occurs in the Great Lakes and understanding the mechanisms by which hypoxia has developed or intensified in recent decades is informative for the management of Great Lakes ecosystems and may allow for better direction of management actions.

Several distinct types of hypoxia (alternatively, hypoxic conditions) occur throughout the Great Lakes. While the seasonal hypolimnetic hypoxia that develops annually in the central basin of Lake Erie appears to receive the greatest research and monitoring attention, other hypoxic conditions are also common. Complex combinations of physiochemical and biological phenomena result in the development of diverse hypoxic conditions with unique spatial and temporal dynamics. The purpose of this review is to categorize and describe the diversity of hypoxic conditions present within the Great Lakes and to characterize the physical and anthropogenic processes that can cause hypoxia to develop. In doing so, we hope to expand the focus of research and management effort to encompass all hypoxic conditions that affect this freshwater system. Importantly, this review examines the processes that cause hypoxia to develop but intentionally avoids discussing the ecological effects of hypoxia in order to present a more focused analysis. Specifically, our

objectives are to (i) classify the different types of hypoxic conditions that occur throughout the Great Lakes, (ii) examine the documented physical extent of hypoxia and the breadth of related research within the Great Lakes region, and (iii) identify key knowledge gaps as areas for future research.

1.2 Classification of hypoxic conditions

Several studies have defined hypoxia thresholds (e.g., 2.0 mg O₂ L⁻¹, Diaz and Rosenberg, 2008; 3.0 mg O₂ L⁻¹, Howell and Simpson, 1994; 4.0 mg O₂ L⁻¹, Paerl et al., 2006) but the exact concentration below which dissolved oxygen has meaningful biological effects varies depending on the organism of interest, the environment, and the duration of exposure (e.g., Hrycik et al., 2017). In practice, the term hypoxia represents a spectrum of oxygen concentrations ranging from slightly depleted oxygen levels to complete anoxia. Hypoxia is sometimes defined in terms of measurable consequences reflected upon the ecosystem, such as the oxygen concentration at which fisheries collapse (Renaud, 1986) or a particular biological function becomes impaired (Diaz and Rosenberg, 1995). Generally, fishes experience sub-lethal effects of hypoxia (e.g., decreased consumption and growth) at oxygen concentrations much higher than those that lead to direct mortality. The range of oxygen levels likely to negatively impact the population biomass of fishes varies widely among taxa (Hrycik et al., 2017). This variation is evident even within the Great Lakes. For example, yellow perch (*Perca flavescens*) have demonstrated a relatively high tolerance for hypoxic conditions in both experimental and field studies (Almeida et al., 2017; Roberts et al., 2011), while lake trout (*Salvelinus namaycush*) are adversely affected by oxygen concentrations at or below 7.0 mg O₂ L⁻¹ (Evans, 2007). The duration of exposure and the physiology of the organism are important factors in determining the impact of hypoxia on aquatic fauna. Whereas most fishes succumb to hypoxic conditions relatively quickly, many invertebrate species can

survive severe hypoxia for days to weeks (Vaquer-Sunyer and Duarte, 2008). For this review, we recognize that any single dissolved oxygen concentration cannot accurately describe the scope of negative consequences for all aquatic fauna. Instead, we define the term “hypoxia” as any scenario in which decreased dissolved oxygen concentrations have demonstrable effects on the organisms or ecological functions of an ecosystem.

Hypoxic conditions in aquatic systems can develop through a variety of processes. Oxygen can be depleted, and a system can become hypoxic, if a) oxygen consumption rates exceed rates at which dissolved oxygen is generated (e.g., if aerobic respiration exceeds photosynthesis) and b) if depleted oxygen concentrations cannot be adequately replenished from external sources (e.g., if density stratification or ice cover limit oxygen replenishment through diffusion at the air-water interface). Conditions that cause hypoxia can be cyclic, recurring on a seasonal or daily basis, or highly dynamic and spatiotemporally variable. For example, rapid movement of water can lead to a given location quickly shifting from oxygenated to hypoxic conditions. Such phenomena are well-documented in nearshore marine systems where offshore hypoxic waters may rapidly intrude nearshore and displace oxygenated water (e.g., Booth et al., 2012; Fennel and Testa, 2019; Grantham et al., 2004).

Although the specific mechanisms by which hypoxia occurs depend on the system of interest, we can identify four broad categories of hypoxic conditions that occur in the Great Lakes region: hypolimnetic hypoxia, over-winter hypoxia, diel hypoxia and episodic hypoxia. Below, we describe each of these categories, as well as some of the different hypoxia manifestations within each category. Importantly, we focus on hypoxic conditions evident in the Great Lakes and do not discuss other types of phenomena that may lead to hypoxia in other systems.

1.2.1 Hypolimnetic hypoxia

The mechanisms and factors that contribute to the development of hypolimnetic hypoxia have been understood since at least the early 20th century (e.g., Yoshimura, 1933; Edmondson et al., 1956). Warm summer air temperatures generate thermal density stratification throughout the water column, producing a distinct thermocline that separates the cooler hypolimnetic waters near the lakebed from the warmer epilimnetic waters near the lake surface, where oxygen is readily replenished through atmospheric diffusion. Mixing between the lake layers is inhibited by strong, temperature-dependent water density gradients, which suppress the transfer of heat and dissolved gas from the surface layer to the benthos. Vertical mixing is further suppressed by the characteristically weak winds that occur during the stratified summer (Cannon and Troy; 2018; Hamidi et al., 2013) and the well-mixed surface layer rarely extends to depths greater than 20m. High primary productivity in the nutrient- and light-rich surface layer increases oxygen demand in the hypolimnion as organic material settles to the bottom. The respiratory activity of microbial decomposition depletes oxygen faster than it can be replenished due to either mixing with surface waters or primary production in the hypolimnion, which remains low due to limited light and nutrient availability. Dissolved oxygen concentrations in the hypolimnion gradually decrease as the available oxygen supply is exhausted. This degradation continues throughout the stratified summer until surface waters cool and trigger a lake turnover event in the fall, allowing mixing of the stratified layers and a subsequent restoration of hypolimnetic oxygen levels. We define hypolimnetic hypoxia as a gradual, persistent reduction in the dissolved oxygen concentration of bottom waters following the development of a cline (e.g., thermocline) that reduces the vertical mixing of the water column (Figure 1A).

Once established, hypolimnetic hypoxia often persists for the duration of the stratified summer period (e.g., Lake Erie central basin) but considerable variation in the spatial and temporal

dynamics of the phenomenon have been reported among systems. Even relatively shallow systems (e.g., Muskegon Lake, 24m, Biddanda et al., 2018; Western Lake Erie, 11m, Loewen et al., 2007; Green Bay, 10m, Figure 2A) can develop stratification and subsequent hypoxia when wind-driven mixing is reduced and surface water temperatures rise. However, in shallow systems and systems receiving pulsed upstream discharges, stratification may not be maintained throughout the summer and thereby hypolimnetic hypoxia may establish for a period of time, then break down and subsequently reestablish. Wind and current patterns can also influence the spatial dynamics of hypolimnetic hypoxia after it develops. Seiches and gyres can drive oscillatory transport of hypoxic water over variable time scales (e.g., Saginaw Bay, NOAA, 2013; Lake Erie central basin, Bouffard et al., 2013; Saylor and Miller 1987). Fine-scale observational data and predictive models of Lake Erie's central basin show substantial inter-annual variability in the development, movement, and extent of seasonal hypolimnetic hypoxia (Del Giudice et al., 2018; Kraus et al., 2015; Zhou et al., 2013). Even the shape of the thermocline may affect the dynamics of hypolimnetic hypoxia. For example, the thermocline in the Lake Erie central basin develops a bowl-like depression in offshore waters, thereby reducing the volume of isolated hypolimnetic water and increasing the time for which oxygen is depleted (Beletsky et al., 2012). Moreover, benthic sinkholes throughout the Great Lakes are prone to stratification, which is often followed by the seepage and accumulation of hypoxic groundwater (Voorhies et al., 2012). Hypolimnetic hypoxia occurs in diverse and variable forms, and the examples given here are likely not comprehensive of the entire array of hypoxic phenomena that fall into this category.

1.2.2 Over-winter hypoxia

Water bodies located in temperate climates have the potential to experience surface freezing and ice accumulation during winter. Thick layers of ice and snow cover may reduce light

penetration and inhibit the ability of aquatic photosynthetic organisms to produce oxygen (Greenbank, 1945). Similarly, the blocked air-water interface eliminates oxygen renewal from diffusion or wave action at the surface layer (Magnuson et al., 1985). Subsequent respiration by aquatic organisms reduces dissolved oxygen levels under the ice, sometimes generating hypoxic conditions (Greenbank, 1945; Magnuson et al., 1985; Yang et al., 2019). Some freshwater diatom species proliferate during winter months by colonizing the underside of ice (e.g., Bondarenko et al., 2006), but under-ice photosynthesis is only sufficient to meet respiratory oxygen demands in shallow, snow-free lakes with no underlying eutrophication issues (Song et al., 2019). Conversely, in nutrient-rich waters, oxygen consumption may actually increase during the under-ice period as freezing ice releases dissolved nutrients to the liquid water below, fueling increased metabolic activity (Yang et al., 2016). The subsequent rate of oxygen consumption is greater than the rate at which oxygen can be replenished due to the inhibiting characteristics of the ice layer. We define over-winter hypoxia as a reduction in the dissolved oxygen concentration in part or all of the water column following the development of a layer of surface ice at the air-water interface (Figure 1B).

The variability and dynamics of over-winter hypoxia are not often investigated given the difficulty involved in accessing and monitoring the under-ice aquatic environment. Over-winter hypoxia seems to present in one of two ways in freshwater systems. Within shallow or inland systems, the interruption of oxygen transfer at the air-water interface may be sufficient to produce hypoxia throughout most of the water column (Magnuson et al., 1985; Marshall et al., 2021). This can have a devastating effect on aquatic biota, often resulting in substantial winterkills (Greenbank, 1945). However, in deeper systems, over-winter hypoxia only develops near the substrate while waters closer to the surface maintain higher dissolved oxygen concentrations (Epstein et al., 1974; Kalejs, 2017; Figure 2B). As with hypolimnetic hypoxia, this trend is likely related to seasonal

mixing and thermal stratification. Although primary production and oxygen renewal may still occur near the surface, where light penetrates the ice, the absence of wind-induced mixing limits oxygen renewal at depth, with weak inverse stratification near the ice-water interface further restricting mixing due to radiative convection (e.g., Yang et al., 2019). While this form of near-substrate, over-winter hypoxia may not present a high risk of direct mortality to most fishes, it has been implicated in the degradation of spawning habitat, affecting egg survival and recruitment for fall-spawning species (e.g., Kalejs, 2017; Madenjian et al., 2008).

1.2.3 Diel hypoxia

Diel hypoxia is a natural phenomenon that can develop in highly productive, shallow, aquatic habitats during warmer months. It is a common occurrence in wetlands and estuaries where it is driven by the interaction between variable rates of primary production and consistently high respiration-induced oxygen demand (Cheek et al., 2009). During the day, high levels of photosynthesis can adequately offset the oxygen consumed during respiration. However, as photosynthesis ceases at night, the high biological oxygen demand rapidly depletes dissolved oxygen concentrations to low levels, and atmospheric diffusion cannot adequately keep pace with demand. Dissolved oxygen is then replenished the next day when photosynthesis resumes. Furthermore, warm temperatures experienced in shallow waters limits oxygen solubility and contributes to rapid deoxygenation. The rates of oxygen consumption and renewal within these shallow, isolated systems are in such delicate balance that the nocturnal cessation of photosynthesis results in decreased dissolved oxygen within hours of sunset (Cornell and Klarer, 2008). We define diel hypoxia as a daily pattern of oscillating dissolved oxygen concentrations driven by rapidly fluctuating levels of oxygen demand and production within a shallow aquatic system (Figure 1C).

The typical presentation of diel hypoxia is less variable than the other hypoxic conditions described above because the specific conditions required to produce diel hypoxia only occur in shallow, productive environments throughout the Great Lakes (e.g., Old Woman Creek estuary, Huron, Ohio). However, temporal variations in the severity of daily dissolved oxygen oscillations have been observed. After severe rainfall or flooding events, changes in water depth and hydrodynamic mixing may reduce the severity of diel hypoxia for several days (Cornell and Klarer, 2008). Coastal inlets are often transformed by nearshore currents and sedimentation patterns. As such, the connections between coastal wetlands and the main lakes are in a constant state of flux, altering the susceptibility of these systems to the development of diel hypoxia.

1.2.4 Episodic hypoxia

All of the forms of hypoxia described thus far develop because of seasonal or diurnal patterns. However, there are two mechanisms which cause hypoxia to arise suddenly in a less periodic, and therefore less predictable, manner. Rapid oxygen depletion may occur in slow-flowing systems that experience a sudden influx of organic material following heavy precipitation (e.g., combined sewer overflow events), especially in urban systems with high densities of impervious drainage areas and channelized tributaries (Gaulke et al., 2015; Kreutzberger et al., 1980). The acute pulse of nutrient-rich water leads to a strong increase in biological oxygen demand and hypoxia. Locally reduced oxygen concentrations can persist for several days to weeks after instances of sudden allochthonous input (Gaulke et al., 2015). The severity of these events depends largely on the duration of exposure, water depth, and the nutrient load into the system (Bell, 2008). In addition, abrupt nearshore intrusions of hypoxia can occur when strong winds generate coastal upwellings, where warm, oxygen-rich water is pushed offshore and replaced by cooler, potentially hypoxic waters from the offshore hypolimnion. (Kraus et al., 2015; Rao et al.,

2014). Such events usually occur between lake layers within a single basin, but examples of inter-basin transfer of oxygen depleted waters have been documented (Jabbari et al., 2019). We define episodic hypoxia as a reduction in dissolved oxygen concentration following a discrete event that results in the sudden intrusion of hypoxic water or allochthonous nutrients into a system (Figure 1D).

1.3 Hypoxia throughout the Great Lakes

Individual studies have documented occurrences of hypoxia throughout the Great Lakes since the early 20th century. However, to our knowledge, there is no comprehensive assessment of the extent of hypoxia within the Great Lakes and surrounding wetlands. As such, researchers and managers may not be aware of the widespread prevalence of hypoxia phenomenon. To evaluate recent patterns of research related to hypoxia in the Great Lakes, we conducted an analysis of published papers. On March 8, 2021, we searched all databases of ISI Web of Science using the topic search query for hypoxia and specific Great Lakes (“Lake Erie” OR “Lake Huron” OR “Lake Michigan” OR “Lake Ontario” OR “Lake Superior”) AND hypoxia) over the period of 2000-2020. This search demonstrated a general increase in the number of Great Lakes hypoxia papers published over this time period (Figure 3A). We corrected for the general trend of increasing number of indexed publications and found a gradual increase in the proportion of Great Lakes hypoxia articles published over the period ($+2.4 \times 10^{-7}$ % of all published articles per year, Adj. $R^2 = 0.553$, $p < 0.001$; Figure 3B). We then normalized by including only Great Lakes articles (as defined by the search query “Lake Erie OR Lake Huron OR Lake Michigan OR Lake Ontario OR Lake Superior”) and still found an increase in the proportion of hypoxia articles among Great Lakes articles published each year ($+0.07\%$ of all Great Lakes articles per year, Adj. $R^2 = 0.658$,

$p < 0.001$; Figure 3C). Not surprisingly, Lake Erie was overrepresented among these articles, with 78% of articles specific to Lake Erie. (Figure 3).

The central basin of Lake Erie is the most intensively studied hypoxic system within the Great Lakes region, and perhaps all the inland waters of North America. Poor water quality and hypoxia have been a major problem in Lake Erie for decades (Conroy et al., 2011; Edwards et al., 2005), with phosphorus-induced eutrophication considered the main driver of central basin hypolimnetic hypoxia since the late sixties (Mortimer, 1987; Vollenweider, 1968). Despite Lake Erie receiving the majority of the research effort, hypolimnetic hypoxia has been identified in other areas of the Great Lakes region (e.g., Lake Simcoe, Nuernberg et al., 2013; Green Bay, Hamidi et al., 2013, 2015; Muskegon Lake, Biddanda et al., 2018; Onondaga Lake, Tango and Ringler, 1996) and the phenomenon is likely present, but generally underrepresented, in many more Great Lakes systems.

Compared to hypolimnetic hypoxia, relatively few studies have attempted to document the presence of over-winter hypoxia in the Great Lakes. This is likely due, at least in part, to the difficulty associated with taking accurate measurements of the under-ice environment and the hazards of field sampling in freezing conditions. Recent advances in optical dissolved oxygen loggers have made it possible for researchers to conduct water quality sampling throughout the under-ice period and recent studies have explored the presence of over-winter hypoxia on coregonine rocky reef spawning grounds (e.g., Kalejs, 2017). Conversely, diel hypoxia has been observed in several shallow and semi-isolated Great Lakes coastal wetlands, such as those associated with the drowned river mouth lakes of eastern Lake Michigan (Parker et al., 2012) and river mouths of southern Lake Erie (NOAA NERRS data; Figure 2C).

Episodic hypoxia in the Great Lakes occurs in response to storm-driven upwellings, longshore currents, severe rainfall runoff events, and direct nutrient input in and around population centers. Offshore hypolimnetic hypoxic water occasionally intrudes into nearshore areas of central Lake Erie when strong wind events displace the surface layer through Ekman transport (Figure 2D; Kraus et al., 2015; Valipour et al., 2021). Upwellings of hypoxic water can be induced or exacerbated elsewhere within the system by large storms or cross-basin currents (Dunstall et al., 1990; Jabbari et al., 2019; Rao et al., 2014). River-input nutrients have also been identified as the cause for severe algal blooms and subsequent episodic hypoxia in several coastal urban centers (Bellinger et al., 2016; Gaulke et al., 2015; Zhang et al., 2016). Lake Erie experiences the greatest abundance and diversity of hypoxic phenomena and so is afforded the majority of research and management focus. However, hypoxia occurs in all five of the Great Lakes and novel hypoxic phenomena have been documented within many systems historically assumed to be normoxic (free of hypoxia) as the practice of regularly monitoring dissolved oxygen conditions has become more affordable and commonplace (Figure 4, Table 1).

1.4 Key knowledge gaps

The study of aquatic hypoxia is inter-disciplinary and the potential knowledge gaps span a broad range of categories (e.g., ecological interactions, municipal water treatment, land-use and nutrient runoff, etc.). Various municipal, state, provincial, tribal and federal agencies are involved with monitoring water quality, including dissolved oxygen, in the Great Lakes, with different agencies fulfilling distinct monitoring aspects; e.g., the EPA Great Lakes National Program Office conducts monitoring and surveillance activities in the US offshore waters of the Great Lakes in support of the U.S. – Canada Great Lakes Water Quality Agreement. Given limited resources, these agencies must make trade-offs when prioritizing monitoring activities. To this end, we draw

attention to three frontiers in monitoring and research that are directly related to the occurrence and prevalence of Great Lakes hypoxia in an effort to encourage further study and broaden awareness of the need to investigate the true breadth of hypoxia within the region.

1.4.1 Spatial and temporal extent

The extent and magnitude of hypoxia outside of the Lake Erie central basin currently represents a major knowledge gap for the Great Lakes. It is likely that many locations throughout the Great Lakes periodically experience hypoxic conditions despite the lack of scientific reporting, with adverse consequences for the aquatic environment and a potential mismatch between present and best-course management practices. For example, current nutrient management plans focus mainly on the reduction of phosphorus to inhibit eutrophication and combat hypoxia (U.S. EPA, 2018). However, some studies have indicated that nitrogen, not phosphorus, limits primary production in Great Lakes coastal wetlands (Cooper et al., 2016; Hill et al., 2006; McCarthy et al., 2007). Anaerobic processes occur naturally in wetlands, which act as global reduction areas for the biosphere, offsetting and balancing terrestrial oxidation reactions. Nutrient enrichment can cause extreme diel fluctuations in oxygen saturation and depletion that disturb this biogeochemical process (Zhang et al., 2015). As such, regulations may need to be adapted to also address anthropogenic nitrogen contributions to more effectively manage naturally occurring hypoxia in coastal wetlands. Similarly, hypoxic phenomena may detract from recent research and management efforts focused on the conservation of habitats that sustain recruitment of native species (e.g., McLean et al., 2015; Kalejs, 2017). Undetected or underestimated hypoxia affecting rocky reefs or other critical spawning habitats may drastically reduce the effectiveness of current and planned improvements to habitat quality, mitigating any potential benefit such measures may have for ecologically and economically important species. The ability to enact informed and

effective management strategies is predicated on improved understanding of the breadth of Great Lakes ecosystems and organisms that are currently experiencing or vulnerable to hypoxia.

Key considerations in monitoring potential hypoxic systems will include both how to measure oxygen concentrations and how to summarize hypoxic measurements. Traditionally, oxygen has been monitored using punctuated point or vertical profile measurements. More recently, oxygen concentrations in the Great Lakes have been quantified using towed sensors (e.g., Xu et al., 2017), autonomous vehicles (e.g., Dawson and Allison, 2021) or longer term, *in situ* loggers (e.g., Karatayev et al., 2018), thereby facilitating broader spatial and temporal quantification of oxygen conditions. Such data can be summarized in a variety of ways to index the magnitude, frequency, spatial coverage and temporal extent of hypoxia. Again, we suggest that setting a strict threshold for hypoxia may not always be appropriate given that organisms differ greatly in terms of their response to low oxygen. Nonetheless, if a single threshold or multiple thresholds are selected, data could be presented based on oxygen concentrations dropping below a threshold, for example, amount of time below threshold, frequency of events below threshold, and spatial area or volume below threshold. Data could also be presented as mean values across time or space. Alternatively, models can be used to represent the combined effects of oxygen and temperature on habitat quality for specific organisms (e.g., Arend et al., 2011). Ultimately, a combination of indices may be most appropriate to summarize oxygen conditions in a particular system as no single index may adequately capture all aspects of hypoxia.

1.4.2 Predictive modeling

Large-scale monitoring programs often present logistical and budgetary challenges as they span great distances and require expensive equipment and maintenance. Recent advances in hydrological modeling have allowed researchers to circumvent these issues by projecting hypoxia

risk given a suite of physical and biological variables (e.g., Bocaniov et al., 2016). Hydrological predictive models have been applied to both large (e.g., Rucinski et al., 2014) and small (e.g., Liu et al., 2018) systems throughout the Great Lakes, with varying degrees of success and accuracy. All models require periodic cross-referencing with observational data to ensure their validity and it is important for models to demonstrate agreement with historical data. Specialized hypoxia forecast models would allow researchers to identify systems that are potentially vulnerable to hypoxia using a set of commonly measured environmental variables. An improved ability to quantify hypoxia risk without committing the funds necessary for *in situ* monitoring would be a valuable tool for resource managers looking to allocate finite effort over a large area or among many systems.

1.4.3 Climate change

Much work is needed to accurately forecast the effect of projected climate change on hypoxia in the Great Lakes. Precipitation and average water temperatures in the region have increased over the last century (Barlage et al., 2002; Collingsworth et al., 2017; Höök et al., 2020; McBean, 2008; Trumpickas et al., 2009) and are expected to continue increasing in the future due to climate change (Fang and Stefan, 2009; Kalcic et al., 2019; Trumpickas et al., 2009; Wuebbles and Hayhoe, 2004). Warmer temperatures stimulate biological activity, reduce the solubility of oxygen in water, and lead to longer and more intense periods of stratification. Coupled with intensive land use and widespread use of fertilizers in agricultural areas, these changes will likely increase the extent, severity, and duration of bouts of hypoxia (Bendtsen and Hansen, 2013; Darko et al., 2019; Ludsin and Höök, 2013). Moreover, warming temperatures may reduce the spring mixing potential of large lakes (Anderson et al., 2021), increasing the likelihood of persistent offshore hypoxia in the absence of full lake turnover events. Given these trends, some systems that

do not have a history of hypoxia may develop hypoxic conditions in the future. Specifically, given the direction of predicted future climatic trends, the prevalence of hypolimnetic, diel, and episodic hypoxia will likely increase, while the prevalence of over-winter hypoxia may decrease as warming temperatures reduce the extent of ice- and snow-cover. Increased research effort toward the development of models that track the predicted changes in hypoxia strength with climate change could be useful tools to ensure that management practices will remain beneficial under future conditions.

1.5 Conclusion

Hypoxia is potentially much more widespread throughout the Laurentian Great Lakes than currently reported. Furthermore, climatic shifts in prevailing temperature and precipitation patterns will likely increase the prevalence and severity of hypoxic phenomena, particularly in temperate regions. Contemporary gaps in knowledge combined with the threat of more common and pervasive hypoxia could negatively affect the ecological integrity of the Great Lakes. The first step toward increased appreciation of hypoxia in the Great Lakes is an increased awareness of the range and extent of hypoxic phenomena that occur throughout the system. Our review suggests that the current focus and intensity of research effort does not accurately characterize the magnitude or diversity of hypoxic conditions affecting the Great Lakes. Rather, the relative scarcity of studies investigating hypoxia outside of the Lake Erie central basin may currently limit the ability of resource managers to apply effective conservation measures within systems experiencing unreported hypoxia or those vulnerable to the development of hypoxia.

1.6 Tables and Figures

Table 1.1. Select primary literature articles documenting the presence of hypoxia throughout the Great Lakes region. Numbers in the first column correspond to identifying values on Figure 1.4.

Number	Paper	Location	Type
1	Bellinger et al., 2016	St. Louis River Estuary	Episodic
2	Hamidi et al., 2013, 2015; Klump et al., 2018	Green Bay, Lake Michigan	Hypolimnetic
3	Kreutzberger et al., 1980	Milwaukee River	Episodic
4	Gaulke et al., 2015	Chicago River	Episodic
5	Chubb and Liston, 1986	Pentwater Lake Estuary	Hypolimnetic
6	Nelson et al., 2009	White Lake Estuary	Diel
7	Parker et al., 2012	Muskegon Lake Estuary	Diel
8	Biddanda et al., 2018; Weinke and Biddanda, 2018	Muskegon Lake	Hypolimnetic
9	Voorhies et al., 2012	Lake Huron sinkhole	Hypolimnetic
10	NOAA GLERL Technical Report, 2013	Saginaw Bay, Lake Huron	Hypolimnetic
11	Kalejs, 2017	Saginaw Bay, Lake Huron	Over-winter
12	Voss et al., 2014	Kawkawlin River	Episodic
13	Jabbari et al., 2019	Lake Erie western basin	Episodic
14	Loewen et al., 2007	Lake Erie western basin	Hypolimnetic
15	Conroy et al., 2011	Lake Erie Sandusky subbasin	Hypolimnetic
16	Cornell and Klarer, 2008	Old Woman Creek Estuary	Diel
17	Rao et al., 2014; Rowe et al., 2019; Valipour et al., 2021	Lake Erie central basin	Episodic
18	Conroy et al., 2011; Edwards et al., 2005; Smith and Matisoff, 2008; among others	Lake Erie central basin	Hypolimnetic

Table 1.1 Continued

19	Kraus et al., 2015	Near Fairport Harbor, Lake Erie	Episodic
20	Bowen and Currie, 2017; Flood et al., 2021; Hiriart-Baer et al., 2009	Hamilton Harbour	Hypolimnetic
21	Marshall et al., 2021	Lake Ontario coastal wetlands	Over-winter
22	Klumb et al., 2004	Irondequiot Bay, Lake Ontario	Hypolimnetic
23	Ahrnsbrak and Wing, 1998	Lake Ontario Kingston Basin	Hypolimnetic
24	Marshall et al., 2021	Lake Ontario coastal wetlands	Episodic

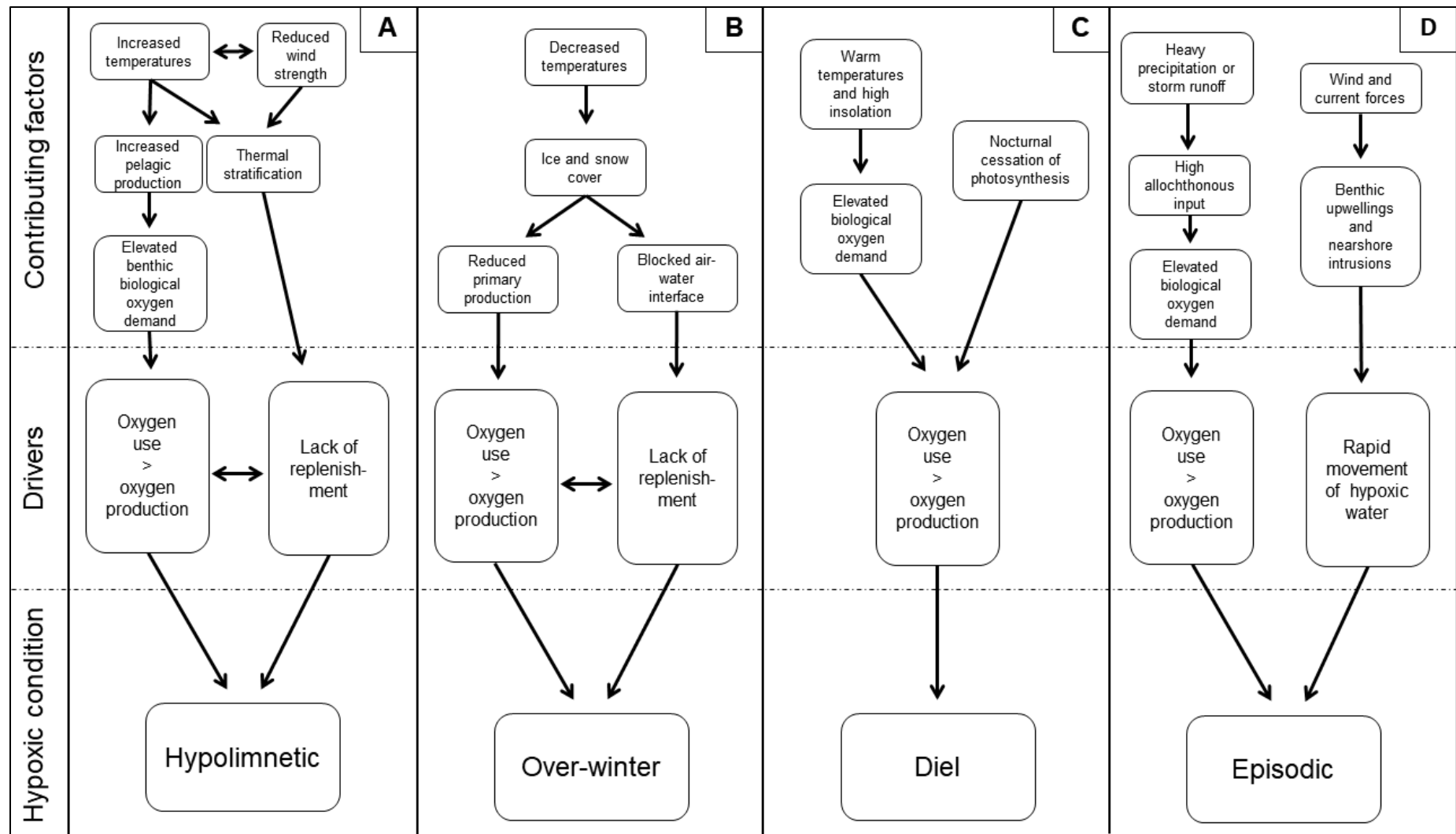


Figure 1.1. Conceptual diagram illustrating the physical and biological principles driving diverse hypoxic conditions throughout the Laurentian Great Lakes, including a) hypolimnetic, b) over-winter, c) diel and d) episodic hypoxia. Vertical arrows indicate logical flow of progression from driving factors to conditions. Horizontal arrows indicate an interaction of factors within a hierarchical level.

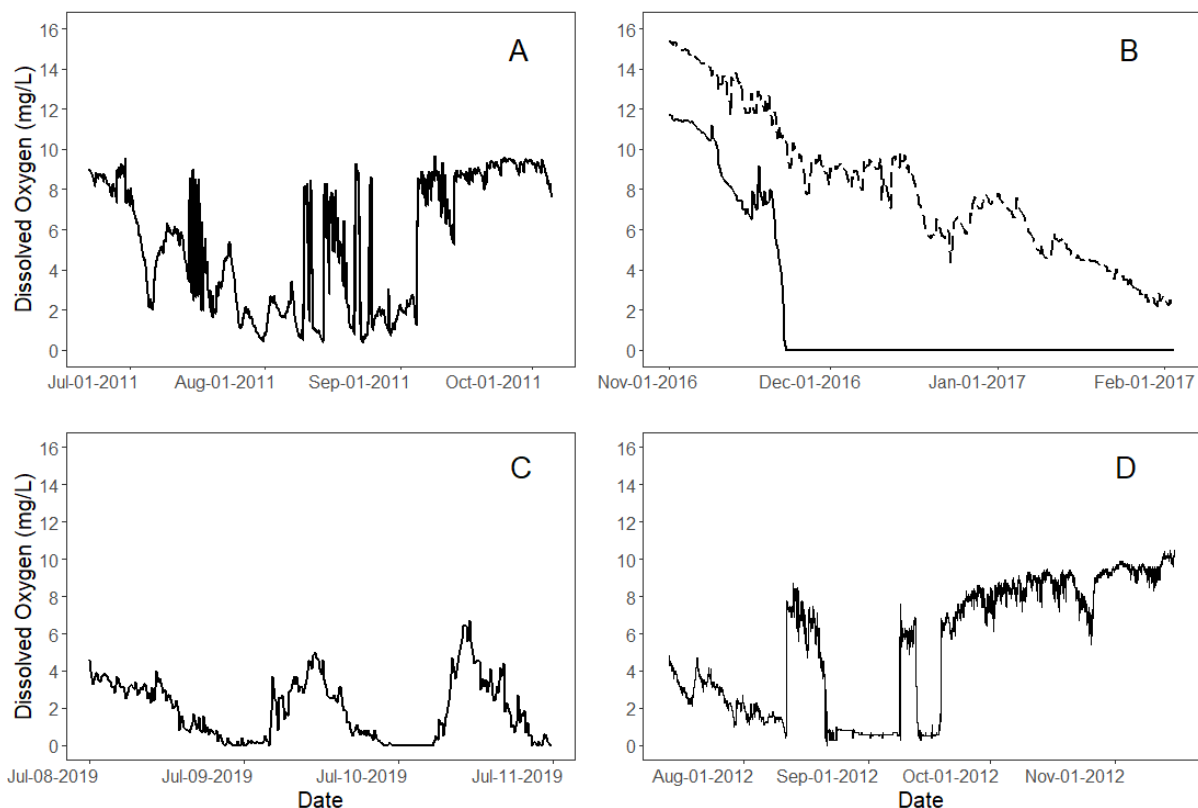


Figure 1.2. Hypoxia observed in long-term monitoring datasets in various locations throughout the Great Lakes. A) Ten-minute hypolimnetic oxygen concentration (mg/L) in Green Bay, Lake Michigan from June 21st to October 5th, 2011 (data courtesy Dr. Val Klump of University of Wisconsin). B) Average 6-hour hypolimnetic oxygen concentration (mg/L) directly at the sediment-water interface (solid line) and 0.5 m above the substrate (dotted line) at Corey Reef in Saginaw Bay during the winter of 2016. C) Fifteen-minute dissolved oxygen values at the mouth of Old Woman Creek estuary, Huron, Ohio from July 8th to July 11th, 2019 (NOAA NERRS data). D) Ten-minute hypolimnetic oxygen concentration (mg/L) within Fairport Harbor, Ohio from July 13th to November 15th, 2012 (data courtesy Kraus et al., 2015).

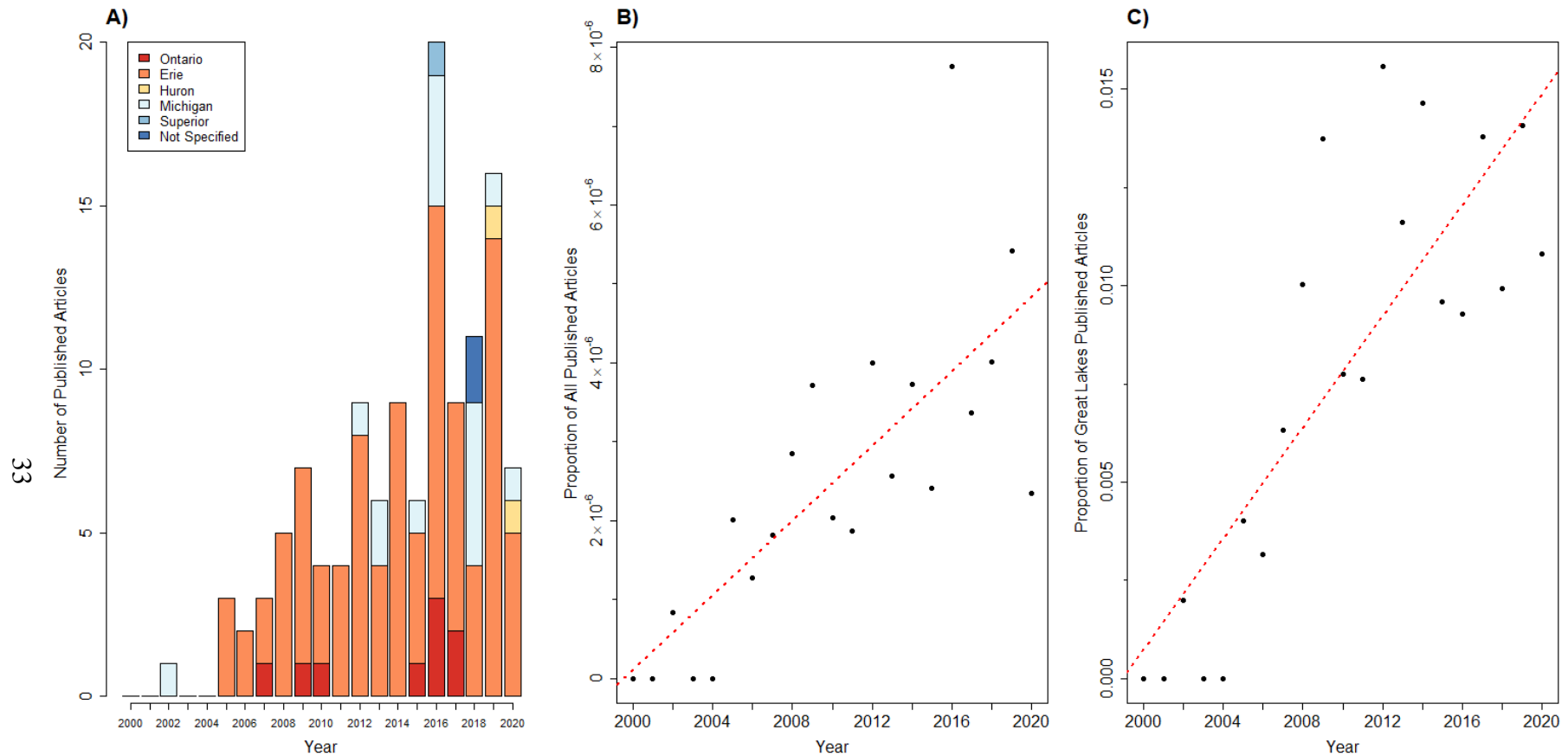


Figure 1.3. A) Number of published articles related to hypoxia returned by the topic search query “Lake X hypoxia” (where X is one of: Ontario, Erie, Huron, Michigan, or Superior) per year, separated by lake of interest, from all databases accessible by ISI Web of Science from 2000-2020. B) Yearly proportion of hypoxia articles relative to all published articles returned from all databases accessible by ISI Web of Science from 2000-2020. C) Yearly proportion of hypoxia articles relative to all Great Lakes articles (as defined by the search query “Lake Erie OR Lake Huron OR Lake Michigan OR Lake Ontario OR Lake Superior”) in all databases accessible by ISI Web of Science from 2000-2020.

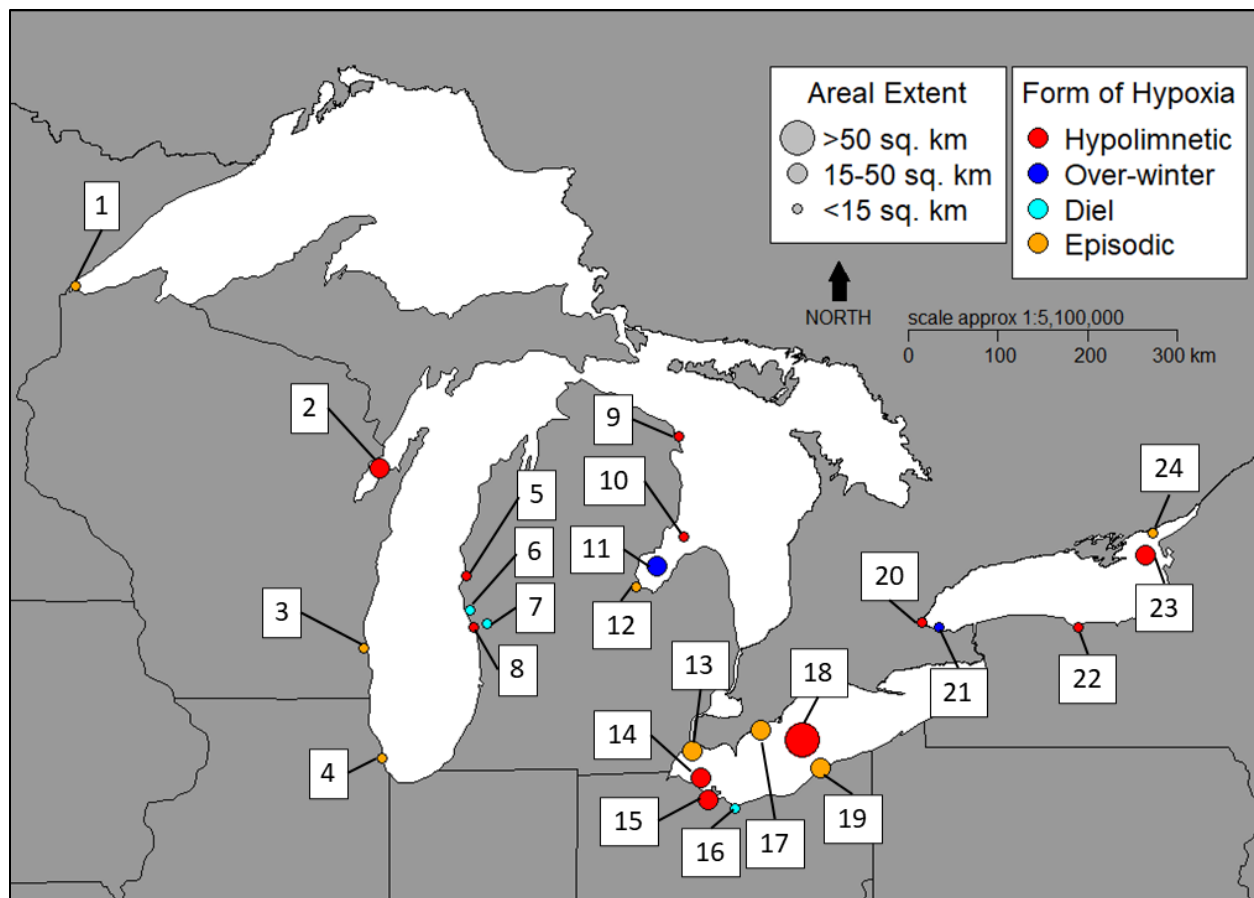


Figure 1.4. Select examples of systems throughout the Great Lakes with documented hypoxia from a primary literature source. Numbers on points correspond to the relevant paper in Table 1. Size of circle denotes relative areal extent of hypoxic phenomena.

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CHAPTER 2. QUANTIFYING OXYTHERMAL FISH HABITAT QUALITY IN A LARGE FRESHWATER ECOSYSTEM

2.1 Introduction

Hypoxia occurs when biological and hydrodynamic processes cause the concentration of dissolved oxygen (DO) within a water body to decrease below a defined threshold. The exact DO concentration used to classify a system as hypoxic varies widely among studies, but reported values generally range between 2 and 3.5 mg L⁻¹ O₂ (Gray et al., 2002; Hofmann et al., 2011). The likelihood that a body of water will become hypoxic increases with increasing nutrient loading (Scavia et al., 2014), biological productivity (Justic et al., 1993) and duration of thermal stratification (Valle-Levinson et al., 1995; Klump et al., 2018). Factors that contribute to the development of hypoxia in aquatic systems are widespread. Though it occurs naturally in both freshwater and marine systems around the world, hypoxia has the potential to negatively impact biota and ecosystem services when the duration, extent, or severity of the phenomenon are elevated beyond natural levels.

Many organisms that reside in naturally hypoxic systems have developed physiological or behavioral adaptations to minimize metabolic losses to oxidative stress or to thrive in low-oxygen environments (Soares et al., 2006; Richards, 2011; Tian et al., 2017). However, anthropogenic activities may exacerbate naturally occurring hypoxia or cause it to develop in previously normoxic systems (Jenny et al., 2016; Collingsworth et al., 2017). Organisms that live in systems with increased hypoxic severity or novel hypoxia due to human activity may lack the adaptations necessary to survive in a low-oxygen environment and face an increased risk of mortality. Mobile organisms, such as fish, will frequently vacate areas with low DO concentrations (Aku et al., 1997;

Eby and Crowder, 2002; Stone et al., 2020), but sessile organisms cannot quickly relocate and instead experience increased mortality during hypoxic conditions (Riedel et al., 2012). Anthropogenic hypoxia regimes alter the biotic community of aquatic ecosystems by negatively impacting population abundances, food web dynamics and species distributions (Hrycik et al., 2017; Chamberlin et al., 2020; Stone et al., 2020). Furthermore, climate change is predicted to alter nutrient loading and thermal stratification patterns in aquatic systems, which will likely increase the frequency, duration, and severity of hypoxic episodes. (Jenny et al., 2016; Collingsworth et al., 2017). Hypoxia, therefore, presents a growing problem for resource managers as it is predicted to increase in prevalence throughout freshwater (Jane et al., 2021; Jenny et al., 2016; North et al., 2013) and marine (Breitburg et al., 2018; Diaz and Rosenberg, 2008; Schmidtko et al., 2017) environments.

Because of the growing prevalence of hypoxia, resource managers are increasingly interested in quantifying the effects of hypoxia on aquatic organisms. The persistence of hypoxia in some high-profile systems, such as the Gulf of Mexico “Dead Zone” and the Lake Erie central basin, has prompted management and legislative action in an effort to mitigate further ecological and economic damage. Despite this, there is currently no consensus among scientists and resource managers on how to best measure the biological impact of hypoxia on aquatic organisms and ecosystems. Current management programs addressing hypoxia often lack specific endpoints to gauge their effectiveness, especially with regard to the effects of hypoxia on ecosystem services such as fisheries. International legislative efforts usually provide direction for monitoring and mitigation of factors that lead to hypoxia (e.g., nutrient annex in the Great Lakes Water Quality Agreement), but these measures often do not inform or consider the biological consequences of hypoxia. Prior studies have demonstrated that hypoxia may affect abundance (e.g., Breitburg, 2002;

Weinke and Biddanda, 2018), growth and condition (e.g., Campbell and Rice, 2014; Casini et al., 2016), behavior and spatial distribution of fishes (e.g., Vanderploeg et al., 2009; Zhang et al., 2009), and susceptibility to fishery harvest (e.g., Kraus et al., 2015, Thambithurai et al., 2019) by fundamentally changing the availability and distribution of high-quality habitat. As such, any comprehensive indicator intended to measure the influence of hypoxia in aquatic ecosystems should consider the effect of hypoxia on habitat quality. Recent studies have made progress toward the establishment of habitat-related endpoints through modeling approaches (e.g., Arend et al. 2011; Budnik et al., 2021), but most systems lack specific endpoints that are broadly used to measure hypoxia-related management targets. The development of reliable, measurable endpoints is especially valuable for systems that contain species assemblages with diverse life histories and ecological responses to hypoxia.

Hypoxia alters the spatial and temporal distribution of high-quality habitat for all aerobic organisms. Low dissolved oxygen negatively impacts habitat quality by acting as a metabolic stressor (Chabot and Dutil, 1999; Wu, 2002; Fitzgibbon et al., 2007), acting as a barrier between organisms and their preferred food sources (Ludsin et al., 2009; Zhang et al., 2009), or forcing organisms to inhabit locations outside of their optimal thermal range (Coutant, 1985; Stone et al., 2020). Hypoxia thus forces organisms into a tradeoff between satisfying respiratory demands and fulfilling other crucial metabolic needs like foraging and thermoregulation (Aku and Tonn, 1999; Roberts et al., 2009; 2012). However, the influence of hypoxia on habitat quality is heavily dependent upon species-specific physiological and metabolic requirements. For example, yellow perch (*Perca flavescens*) are relatively tolerant of hypoxia (Almeida et al., 2017) and have been known to make foraging excursions into hypoxic habitat to access energy-rich prey (Roberts et al., 2012) whereas lake trout (*Salvelinus namaycush*) experience oxidative restrictions at dissolved

oxygen concentrations as high as 7.0 mg L⁻¹ (Evans, 2007). Both species may inhabit the same ecosystem yet exhibit contrasting responses to hypoxic conditions. Within Lake Erie and the Gulf of Mexico, hypoxia and temperature interact to modify habitat quality among species with diverse thermal tolerances (Arend et al., 2011; Zhang et al., 2014). Moreover, species-specific responses to the effect of hypoxia on habitat quality can alter community composition in aquatic ecosystems by modifying the spatial distribution of predators and prey (Neuenfeldt, 2002; Pothoven et al., 2012; Zhang et al., 2009) or by causing species with adaptations to hypoxia to outcompete less-adapted species (Bajer and Sorensen, 2010; Froehlich et al., 2015). As the above examples illustrate, the ecological consequences of hypoxia are often intricate and difficult to predict. An adaptive hypoxia severity indicator would be a useful tool for resource managers charged with predicting the effects of new or worsening hypoxia on habitat quality for complex and varied aquatic communities.

Bioenergetics provides a framework for the establishment of biological endpoints to define habitat quality in aquatic ecosystems that are prone to hypoxia. Bioenergetics equations quantify the effect of ambient environmental conditions, principally temperature, on the metabolism and growth of organisms and can be modified to incorporate other abiotic conditions that may alter metabolism or feeding ecology, such as DO concentration or turbidity. As poikilothermic ectotherms, fish are ideally suited for the application of bioenergetics models because they experience fluctuations in their metabolic rate in response to changes in ambient temperature. The causative relationship between temperature and metabolic rate in fishes has been known and studied for over a century, and many species now have a standard set of equations that define their metabolic demands in response to temperature (Hanson et al., 1997). Bioenergetics provides a link between the metabolic processes of an individual organism and ambient environmental conditions,

but estimating habitat quality using bioenergetics requires applying these principles across a simulated spatial environment. Growth-rate potential (GRP) is an extension of bioenergetics that uses the same equations to measure differences in habitat quality across broad spatial scales. GRP is the theoretical surplus energy available for somatic growth or reproduction after accounting for non-negotiable energy expenditures, namely the metabolic processes (i.e., respiration, excretion, etc.) that an organism must perform to survive. A positive GRP value indicates that an organism can persist in a given location under the ambient conditions in the system, whereas a negative value indicates that environmental conditions in that location are not conducive to long-term survival because the organism cannot fulfill metabolic requirements. The main advantage of using GRP models over other similar approaches is the relative simplicity and limited assumptions that are required during model development. GRP serves as an index of habitat quality, measured in grams of growth per gram of body mass per day, given ambient conditions at discrete locations within a model environment (Brandt et al., 1992). Previous studies have modified GRP beyond ambient temperature to allow for additional environmental factors, such as DO concentration (Arend et al., 2011), to serve as the basis for the biological consequences of hypoxic conditions.

Here, we describe the development of a GRP model to assess inter-specific, seasonal, and annual variation in habitat quality in a well-studied hypoxic system: the central basin of Lake Erie. Lake Erie may have historically experienced some degree of natural hypoxia, but the severity and frequency of seasonal hypoxic events have increased in recent years due to increased nutrient loading into the lake from surrounding watersheds and increased lake temperatures (Watson et al., 2016; Perello et al., 2017; Del Giudice et al., 2018). Hypoxia develops in the central basin late in the summer during periods of thermal stratification that prevent the mixing of hypolimnetic waters with the oxygen-rich epilimnion. Excess nutrient loading from agricultural activities frequently

produces large algal blooms and, as algae eventually settle to the bottom, their decomposition further increases hypolimnetic oxygen demand. Hypoxic conditions generally persist through the late summer until lake turnover in the fall, but the duration and severity of hypolimnetic hypoxia is highly variable from year to year. In this study, we develop a GRP model to examine the effect of inter-annual variability in hypoxia on habitat quality for multiple fish species using historical data collected by a multi-agency DO monitoring program in the central basin of Lake Erie. Our objectives were to (i) develop a three-dimensional GRP model that encompasses the offshore waters of the central basin using historical temperature and DO monitoring data for four ecologically important fish species; (ii); examine the effect of seasonal hypoxia on the spatial distribution of optimal habitat for fish species with different life-history strategies and environmental tolerances; and (iii) use model output to produce biologically-relevant volumetric indicators of hypoxia severity.

2.2 Methods

2.2.1 Dissolved oxygen monitoring data

The U.S. Environmental Protection Agency (EPA) Great Lakes National Program Office (GLNPO), in partnership with the United States Geological Survey (USGS) Great Lakes Science Center, has maintained an ongoing dissolved oxygen monitoring program in the central basin of Lake Erie since 1983 under the authority of the Great Lakes Water Quality Agreement (Burlakova et al., 2018). The program monitors temperature and dissolved oxygen at ten offshore stations in the central basin of Lake Erie during the stratified season (U.S. EPA, 2020). Each year, sites are sampled at approximately three-week intervals starting at the onset of stratification and concluding when water column stratification subsides. Historical samples were collected using several EPA

and USGS research vessels equipped with SeaBird Scientific SBE CTD (Conductivity, Temperature, Depth) Profilers and an integrated SBE43 Dissolved Oxygen Sensor for collecting vertical DO profiles. At each station, CTD and oxygen sensors are slowly lowered through the water column and measurements of water temperature and dissolved oxygen concentration are recorded 16 to 24 times per second from 4 meters below the surface to the respective maximum depth at each site. Quality control (QC) of raw data occurs aboard the research vessel and post-hoc comparative analyses are conducted to ensure data quality when more than one CTD are used within a sampling season (U.S. EPA, 2020). A full description of sampling gear, research vessels, sampling techniques, and QC measures are included within the most recent Lake Erie Dissolved Oxygen Monitoring Program technical report (U.S. EPA, 2020). Only sampling trips from 1993-2018 that contained a complete set of ten (one for each station in Figure 1A) vertical profiles after QC were retained for analysis. In total, the dataset represented 94 sampling excursions of the EPA Lake Erie Dissolved Oxygen Monitoring Program from 1993, 1997-2003, and 2005-2018.

Vertical profiles of temperature and DO from all 10 stations of the Lake Erie Dissolved Oxygen Monitoring Program were combined to produce a three-dimensional volume of estimated ambient water quality conditions. To accomplish this data transformation, the total volume of water within the study area was first converted into a series of 0.91 km by 0.91 km by 1 m grid cells, with each cell representing a water volume of approximately 8.281×10^{-4} cubic km. This cell size was chosen as it maximized the coverage of cube-shaped model cells within the irregularly shaped polygon of the study area. Each meter-depth interval (i.e., 4 to 5 meters below the surface, 5 to 6 meters below the surface, etc.) was treated as a separate raster, resulting in 18 unique geospatial grid planes from 4 to 22 meters below the surface, each containing a total of 3339 cells (Figure 1A). A separate, smaller grid plane containing 518 cells of the same size was constructed

for the 22- to 23-meter depth interval, as only four of the ten monitoring stations recorded a maximum depth below 22 meters (Figure 1B). The depth-specific raster grids were then stacked to produce a three-dimensional gridded polygon containing the entire study volume (Figure 1C), representing a total volume of water of approximately 50 cubic km.

At each of the ten stations, vertical casts of temperature and DO were averaged for each depth increment by calculating the arithmetic mean of all measurements within the corresponding meter of depth of the water column. Observational data were then interpolated within each horizontal grid plane using Shepard's inverse distance weighting, with a power parameter set at 2. Each plane was interpolated separately and had no impact on the interpolated values within adjacent planes. The interpolated grid planes were then stacked and agglomerated into volumes that recreated the water temperature and DO conditions throughout the entire study volume for each of the 94 historical sampling trips. All data transformations were conducted in R Version 3.6.3 (R Core Team, 2020) using RStudio Version 1.1.456 (RStudio Team, 2016) and the *sp* (Bivard et al., 2013), *rgdal* (Bivard et al., 2019), *raster* (Hijmans, 2020), *geosphere* (Hijmans, 2019), *phylin* (Tarroso et al., 2015), and *dplyr* (Wickman et al, 2020) packages.

2.2.2 Bioenergetic growth-rate potential model

A spatial growth-rate potential habitat quality model was built in IDL version 8.7.2 (Exelis Visual Information Solutions, Boulder, Colorado) following the procedure of Arend et al., 2011, with minor modifications to allow for three-dimensional model space. The model was designed upon the principles of bioenergetics in which the growth of an organism can be modeled as:

$$G = C - (R + W)$$

Where G is growth, C is consumption, R is energy lost through respiration, and W is energy lost through wastes (egestion, excretion, and specific dynamic action), with units of grams of growth

per gram of body mass per day ($\text{g g}^{-1} \text{ d}^{-1}$). The details for each component of this equation are outlined in Hanson et al. 1997. The basic bioenergetic model structure was altered to incorporate the addition of a DO modifier on consumption originally developed in Arend et al., 2011. Briefly, the DO modifier equation produces a breakpoint relationship with species-specific minimal DO thresholds, after which further decreasing DO linearly decreases the maximum possible consumption of an organism following the split equation:

$$fDO = \left(\frac{DO}{DO_{crit}} \right); \text{when observed } DO < DO_{crit}$$

$$fDO = 1; \text{when observed } DO > DO_{crit}$$

Where DO is ambient dissolved oxygen (mg L^{-1}), DO_{crit} is a species-specific DO threshold, and fDO is a multiplier (0-1) on the consumption value calculated from the standard bioenergetic equations. DO_{crit} thresholds for each species are also temperature-specific, to account for the fact that hypoxia has a stronger effect on consumption at warmer temperatures. Given the meso- to eutrophic status and consistently high biomass of lower-trophic prey species present within the Lake Erie central basin, prey availability was not factored into the model and instead all metabolic and growth calculations assumed that the model organism consumed prey at a rate of 50% maximum possible consumption. The model utilized depth-specific values for prey species energy density consistent with Arend et al., 2011. A benthic energy density value (3138 J g^{-1}) was allocated to cells less than or equal to two meters from the maximum depth and a pelagic energy density value (2510 J g^{-1}) was allocated to cells greater than two meters from the maximum depth. These values were derived from previous energetics studies of Great Lakes ecosystems which also differentiated between benthic and pelagic forage species (Schaeffer et al., 1999; Arend et al., 2011).

Metabolic responses to changes in temperature, respiratory and energetic requirements and tolerance of hypoxia are all traits that differ among species and life stages of fish. To index growth-rate potential, species-specific bioenergetic equations and parameters were selected from previous studies of adult and young-of-year (YOY) yellow perch, (*Perca flavescens*, Kitchell et al., 1977), adult and YOY rainbow smelt (*Osmerus mordax*, Lantry and Stewart, 1993), adult round goby (*Neogobius melanostomus*, Lee and Johnson, 2005) and adult emerald shiner (*Notropis atherinoides*, Arend et al., 2011). These species and life stages were chosen because their model parameters (Table 1) have been established and used in prior studies (Hanson et al., 1997; Arend et al., 2011) and they represent a range of unique feeding ecologies, preferred habitats and thermal tolerances that are found among the fish community in Lake Erie. Yellow perch are common meso-predators that tolerate a wide range of thermal and DO conditions. Adult yellow perch prefer to forage on energy-rich benthic prey when not engaging in piscivory (Graeb et al., 2006.) and have been shown to exhibit novel feeding strategies in the presence of hypolimnetic hypoxia (Roberts et al., 2012), whereas YOY yellow perch are more dependent upon pelagic resources. Rainbow smelt are coldwater pelagic planktivores and are a widespread forage species found throughout most the Great Lakes. Adult rainbow smelt may experience thermal stress in Lake Erie during summer months and are subsequently often found in high numbers near the thermocline (Pothoven et al., 2012), but YOY rainbow smelt are more tolerant of warm temperatures than adults (Colburn et al., 2012). Emerald shiner are native warmwater benthopelagic fish that are more likely to tolerate high temperatures within Lake Erie (Stone et al., 2020). Round goby are obligate benthic-dwelling omnivores common throughout the Great Lakes. Unlike our other study species, round goby lack a swim bladder which restricts their vertical mobility through the water column. To account for their lack of vertical mobility, the model imposed a flat penalty on energy expenditure

due to respiration (3.3x) when calculating growth-rate potential for round goby greater than two meters from the maximum depth of the lake basin. Interpolated volumes of historical water temperature and DO represented the ambient environmental conditions utilized in the species-specific bioenergetic model equations to calculate growth-rate potential ($\text{g g}^{-1} \text{d}^{-1}$) within each cell of the three-dimensional study volume.

2.2.3 Calculation of habitat quality endpoints

The focus of the present study was to develop a novel indicator that accurately measures the effect of seasonal hypoxia on the habitat available to fish species with contrasting life histories and that can be used to inform hypoxia-related management goals. To accomplish this objective, habitat conditions were modeled and analyzed during two ecologically important time periods: prior to the development of hypoxia (June), and during peak hypoxic conditions (September). A 15-year timeseries was reconstructed from the monitoring data to describe the environmental conditions in the central basin during the relevant time periods. The volumetric proportion of suitable habitat (defined as the volume of water with a GRP value greater than zero divided by the total study volume) was proposed as the primary biological endpoint for measuring the effect of hypoxia on aquatic macrofauna. This endpoint was calculated during both June and September for each year within the dataset for each study species using the three-dimensional volumes of growth-rate potential developed from the model.

2.2.4 Comparison with existing endpoints

Despite the diverse consequences of hypoxia on ecological communities, current hypoxia tracking methods and severity indicators rely solely on abiotic water quality conditions. For example, several studies have tied elevated phosphorus loading to eutrophication and hypoxia

(e.g., Bosch et al., 2013, Scavia et al., 2014, Scavia et al., 2016) and annual phosphorus loading from surrounding catchments is monitored in accordance with the Great Lakes Water Quality Agreement (GLWQA, 2012). International efforts have been made to reduce loading of phosphorus and other nutrients in hopes of simultaneously reducing the extent and severity of late summer hypolimnetic hypoxia in the central basin. Similarly, prior studies have utilized the rate of oxygen depletion in the hypolimnion (Edwards et al., 2005; Rucinski et al., 2010) to define and track the severity of annual central basin hypoxia. All of these endpoints have useful applications, but they fail to consider hypoxia severity in the context of the organisms within the central basin ecosystem. As such, we sought to compare the utility of our novel GRP endpoint with that of existing methods currently used to measure hypoxia severity within Lake Erie.

We conducted a correlation analysis between our annual measure of proportional suitable habitat in September (during the peak hypoxic season) and three existing metrics associated with central basin hypoxia: annual total phosphorus loading (TP), annual dissolved reactive phosphorus loading (DRP), and median annual hypolimnetic DO depletion rate. Heidelberg University manages and curates an open-access data portal for tributary nutrient loading into Lake Erie known as the Heidelberg Tributary Loading Program (HTLP). This long-term monitoring project has been collecting water quality data in Lake Erie tributaries since 1974. Historical phosphorus loading data with dates matching those available from the GRP model dataset were available for three rivers (Maumee, Sandusky, and Cuyahoga). Annual TP and DRP loading values were summed across all three rivers and tested for correlation with the GRP indicator values in September for each of the six study species using Pearson's correlation test and Kendall's rank correlation test. Prior studies have indicated that oxygen depletion rate in the central basin experiences a time-lagged correlation with nutrient loading (Burns et al., 2005) so correlations were tested both for

direct-year comparisons (i.e., 2018 phosphorus loading vs. 2018 GRP) and with a one-year lag between nutrient loading and our novel hypoxia indicator (i.e., 2017 phosphorus loading vs. 2018 GRP). Hypolimnetic DO depletion rate data were provided by the EPA Great Lakes National Program Office.

2.3 Results

2.3.1 Visualizing model output

Two-dimensional contour plots of GRP reveal complex hydrodynamic phenomena within the central basin of Lake Erie. Across the whole lake, Lake Erie has pronounced temperature and productivity gradients from west to east and in some years, hypoxia does not spread to the eastern edge of the central basin. This phenomenon is visible in several horizontal plots of GRP wherein low DO concentration restricts the ability of fish species to meet energetic demands within only a portion of the hypolimnion stemming from the western edge of the basin (e.g., Figure 2). Vertical contour plots reveal that the thermocline developed at a depth of about 19 meters in all years with a detectable thermocline by September. However, the location of the initial thermocline development (and subsequent hypoxic area) varied spatially from year to year. Stratification had a substantial effect on habitat quality and availability for a number of fish species. To illustrate species-specific spatial variation in the distribution of suitable habitat, we highlight vertical contour plots of growth-rate potential along the southern edge of the study volume before and after the development of the thermocline for the summer of 2012 (Figure 3), a year in which record droughts caused an extensive hypoxic event within the central basin (Zhou et al., 2015). Adult and YOY yellow perch, adult and YOY rainbow smelt, and adult emerald shiner experienced favorable conditions throughout the entire water column during June but were restricted from accessing most

of the cool hypolimnion and benthic prey during September due to the development of hypolimnetic hypoxia. However, a small portion of benthic habitat free from hypoxia in the eastern portion of the study volume offered the highest growth-rate potential during September for all species except adult rainbow smelt. YOY rainbow smelt had a much larger volume of suitable habitat than adult rainbow smelt during September owing to their greater tolerance for warmer temperatures. The thermocline is a defining feature of the water column within all September profiles, representing a distinct barrier between suitable and unsuitable habitat for most species while also serving as a last refuge of suitable thermal habitat for adult rainbow smelt. Round goby experienced favorable conditions for growth in benthic habitats during June but were almost completely excluded from the study volume during September except for the small eastern edge of the benthos that was free from hypoxia. The unique range of thermal and oxidative tolerances experienced by each species and life stage produced spatial and temporal differences in the distribution of suitable habitat within the central basin.

2.3.2 Assessment of novel hypoxia endpoint

Analysis of our GRP-based habitat quality indicator revealed inter-specific and inter-annual differences in the effects of hypoxia and temperature on habitat quality. Time-series plots of the annual proportion of the study volume with positive GRP (i.e., suitable habitat) in June and September (Figure 4) indicated that the total volume of available habitat was generally not restricted in June, however, most species experienced reduced habitat quality during September that coincided with the formation of hypolimnetic hypoxia. The extent of reduced habitat quality varied during year of mild versus severe hypoxia for adult and YOY yellow perch, YOY rainbow smelt, adult round goby and adult emerald shiner. All five of these groups displayed similar inter-annual patterns of proportional suitable habitat. However, adult rainbow smelt experienced severe

reductions in habitat quality during September regardless of year, indicating that warm surface water temperature in the central basin of Lake Erie is equally limiting for this cold-water species during the late summer.

2.3.3 Comparison with existing endpoints

Annual measures of proportional suitable habitat quality were compared to existing indices (annual total phosphorous loading, annual dissolved reactive phosphorous loading, median annual hypolimnetic DO depletion rate) using Pearson's and Kendall's correlation tests. Correlations were tested for year-to-year comparison and with a time lag of one year between the existing index and the novel GRP index. No time series data from existing indices significantly correlated with proportional suitable habitat in September for any of the six species or life stages according to either Pearson's correlation coefficient or Kendall's rank correlation coefficient.

2.4 Discussion

Hypoxia is a growing concern for aquatic resource managers because it reduces habitat quality (Arend et al., 2011; Budnik et al., 2021; Eby et al., 2005), alters feeding ecology (Pothoven et al., 2009; Roberts et al., 2012), and can lead to shifts in community structure (Wu, 2002; Bajer and Sorensen, 2010) and changes in the efficiency of commercial fishing (Chamberlin et al., 2020). As such, managers in many systems have proposed or implemented plans to reduce the extent or severity of hypoxia (e.g., Donner and Kucharik, 2008; GLWQA, 2012; Moore et al., 2010; Tomer et al., 2015). Most of these plans are adopted around monitoring practices that focus primarily on abiotic conditions to measure the relative success of hypoxia mitigation efforts (e.g., nutrient loading). However, the abiotic metrics used in these hypoxia remediation programs lack the ability to inform resource managers about the direct consequences of hypoxia on aquatic organisms. The

framework developed herein will allow natural resource managers to more effectively quantify the effects of hypoxia on fish habitat quality under historical, current, and projected future conditions using readily available environmental data. The three-dimensional GRP model can infer complex spatial patterns of habitat quality among fish species with different life histories and environmental tolerances. Moreover, these methods provide a quantifiable and biologically meaningful endpoint that may be used to track the progress of hypoxia mitigation efforts.

We analyzed the utility of our model-derived biological endpoint in assessing the influence of hypoxia and thermal conditions on fish habitat quality. Assessment of time-series data revealed clear inter-specific and inter-annual differences in late summer habitat quality. Temporal patterns suggested the presence of yearly hypoxia regimes, with some years exhibiting relatively mild hypoxia and other years more severe hypoxia. In June, before the development of hypoxia, habitat conditions were consistently favorable for all species (i.e., positive GRP within a majority of the simulated study volume). Following the onset of hypoxia, habitat quality became much more variable among species. Adult rainbow smelt experienced substantial reductions in suitable habitat during September in all years, but all five other species/ life stages experienced reductions in habitat quality only during severely hypoxic years. In fact, mean GRP throughout the study volume actually increased during the hypoxic season for adult and YOY yellow perch in most years, but always decreased during the hypoxic season for adult rainbow smelt. YOY yellow perch and adult emerald shiner displayed similar patterns, with reduced mean GRP during September only during severely hypoxic years. Inter-annual fluctuations in late summer habitat quality for cool water species confirmed that the extent and severity of hypolimnetic central basin hypoxia is highly variable from year to year; with hypoxia developing throughout the offshore hypolimnion in some years, but occupying only a small portion of the central basin in others.

Our proposed habitat quality endpoint can be used to inform and improve management practices. For example, results indicated that yellow perch, YOY rainbow smelt, and emerald shiner are tolerant of the thermal conditions in the surface waters of the central basin during the summer and only experienced a significant decrease in habitat quality during years of severe hypoxia. In contrast, adult rainbow smelt are thermally excluded from the epilimnion during the late summer (Vanderploeg et al., 2009) and will presumably aggregate offshore in deeper water to find cooler temperatures. However, they cannot survive in the oxygen-depleted hypolimnion and are often restricted to a thin band of habitable water along the thermocline (Vanderploeg et al., 2009; Pothoven et al., 2012; Stone et al., 2020; Figure 3C). There has been a recent interest in re-introducing native cisco, an extirpated cold-water species, to Lake Erie (e.g., Schmitt et al., 2020). Lake Erie presently supports populations of other cold-water species as well, namely lake whitefish, lake trout, and steelhead. If our findings for rainbow smelt are also typical of other cold-water species, all of these coldwater species will likely be excluded from the central basin during the hypoxic summer conditions. By extension, efforts to re-introduce cisco into the central basin may fail unless hypoxia is mitigated and access to cold, hypolimnetic habitat is restored. Managers will have to consider whether sufficient summer holdover habitat exists within the central basin to make allocation of resources and conservation efforts to the re-establishment of cisco worthwhile.

Results suggest that management of warm-water species is also impacted by hypoxia. While round goby and yellow perch are tolerant of the thermal conditions in offshore waters, hypoxia still separates these species from preferred benthic habitats. Yellow perch may alter their behavior (e.g., Roberts et al., 2012) or seek out small pockets of optimal habitat present within the hypolimnion in the offshore (Figure 2A, 2B) rather than feed on lower quality prey items in nearshore habitats. However, round goby, as an obligate benthic species, will be completely

excluded from the offshore waters of the central basin during severely hypoxic years (Figure 3E) because they cannot move upward in the water column to avoid hypolimnetic hypoxia. In both cases, hypoxia will likely alter the distribution of these species, reducing the accuracy of monitoring efforts (e.g., abundance estimates, Kraus et al., 2015) and affecting the efficiency of fishing (e.g., mortality, catch-per-unit-effort, Chamberlin et al., 2020). Accurately modeling the effects of hypoxia and temperature on fish habitat quality may further help resource managers to understand and explain future ecological responses to low DO conditions.

Climate change is expected to cause hypoxia to become more severe and more common locally (Blumberg and Di Toro, 1990) and worldwide (Diaz and Rosenberg 2008; Rabalais et al., 2009; Meire et al., 2013). As such, aquatic resource managers will soon be confronted with the unique challenge of predicting species- and ecosystem-level changes in habitat quality following the development of novel and worsening hypoxia. Historical variations within ambient conditions in the Lake Erie central basin revealed the presence of distinctly mild versus severe years of late summer hypoxia. If, as predicted, climate change causes intensified thermal stratification and earlier onset of hypoxic conditions, organisms within the central basin may be faced with more frequent bouts of severe hypoxia and longer-lasting periods of sub-optimal habitat quality (Collingsworth et al., 2017). During severe years, all species and life stages examined experienced reduced habitat quality relative to mild years (except adult rainbow smelt). However, alternative predictions indicate that climate change may actually reduce the occurrence of hypoxia in the central basin. The Lake Erie central basin exhibits such severe hypoxia because the thermocline develops only a few meters above the sediment, leaving only a small volume of hypolimnetic water which rapidly loses oxygen due to biological oxygen demand from benthic organisms. Increased temperatures and wind strengths predicted to occur with climate change may cause thermoclines

to develop at lower depths within stratified lakes (Schindler, 2009; Gauthier et al., 2014). If this were to occur in the central basin, it would push the depth at which a thermocline was to develop beyond the maximum depth, removing stratification altogether. Regardless of future climatic scenarios, traditional water quality monitoring alone does not address biological responses to hypoxia-induced alterations in habitat quality.

Established indices show no significant correlation with the novel GRP-based endpoint, suggesting that the newly developed GRP endpoint may prove beneficial as a supplemental indicator of hypoxia severity or as a standalone metric. The novel endpoint developed in the present study allows resource managers to quantify ecologically important changes in habitat quality through time and with the changing climate. This methodology also has several advantages over existing monitoring indices. The straightforward, flexible design and low data requirements allow this model to be applied to any aquatic system for which ambient water quality conditions are known. Furthermore, the direct measurement of ecological conditions (i.e., habitat quality) contrasts with traditional monitoring endpoints that solely report on abiotic conditions, providing a new perspective by which resource managers can evaluate their efforts. Finally, three-dimensional volumetric modeling allows for precise analysis of complex spatial phenomena (e.g., variable thermocline depth, pockets of suitable habitat, compression of suitable habitat). Combined with existing indices, the novel habitat quality endpoint and model framework developed herein will allow for more effective and comprehensive management of freshwater hypoxic systems.

Whereas the present study developed a useful new indicator and framework for monitoring hypoxia, further research is likely needed to establish this methodology for widespread use. At present, the model uses only coarse measurements of temperature and DO to inform habitat quality, which is suitable for Lake Erie where prey is abundant but may be too simplistic for systems where

prey is limited (e.g., oligotrophic alpine lakes, Eckmann, 2017) or for which other abiotic water quality variables may also inform habitat quality (e.g., salinity in nearshore coastal estuaries, Vinagre et al., 2006; Shields et al., 2012). Additionally, the present study applied the model to a single, freshwater system over a time span of 25 years, and it should be tested in other systems and for varying temporal scales to assess the utility of widespread use. Of particular interest are systems which have been identified as vulnerable to severe hypoxia or have documented increased hypoxia severity in response to human activities (e.g., northern Gulf of Mexico, Rabalais et al., 2001; Chesapeake Bay, Hagy et al., 2004; Baltic Sea, Carstensen et al., 2014). The ecological consequences of novel or aggravated hypoxia in aquatic systems are diverse, affecting all levels of the ecosystem from primary producers to fish. Resource managers charged with overseeing many freshwater and marine systems are already being confronted with the threat of habitat degradation and the cascading biological effects of hypoxia and the threat of climate change trends will continue to exacerbate these problems worldwide. The methodology presented herein serves as a means to directly quantify and assess the effect of hypoxia on biological endpoints in light of this potential outcome.

2.5 Tables and Figures

Table 2.1. Species-specific parameters for Wisconsin bioenergetics equations. Coefficients and equations from Fish Bioenergetics 3.0 (Hanson et al. 1997) unless otherwise noted. *All round goby values, all emerald shiner values, and select smelt values, were taken from Arend et al. 2011. **Gobies have two unique activity multiplier values, based on their position in the water column. A lack of a swim bladder means they incur a significant respiratory penalty (3.3x) for feeding in the pelagic zone.

Parameter	Adult Yellow Perch	Adult Rainbow Smelt	Adult Round Goby*	YOY Yellow Perch	YOY Rainbow Smelt	Adult Emerald Shiner*
Body mass (g)	50.0	6.1	10.0	7.0	1.0	4.5
Consumption equation #	2	3	3	2	3	2
CA	0.25	0.18	0.192	0.25	0.18	0.254
CB	-0.27	-0.275	-0.256	-0.27	-0.275	-0.276
CQ	2.3	3	5.594	2.3	3	2.25
CTO	23	10	24.648	29	10	25.0
CTM	28	14*	25.706	32	21*	30.0
CTL	-	20*	28.992	-	26*	-
CK1	-	0.4	0.113	-	0.4	-
CK4	-	0.01	0.419	-	0.01	-
Respiration equation #	2	1	1	2	1	2
RA	0.0108	0.0027	0.00094	0.0108	0.0027	0.0122
RB	-0.2	-0.216	-0.157	-0.2	-0.216	-0.12
RQ	2.1	0.036	0.061	2.1	0.036	2.35
RTO	28	-	-	32	-	29.0
RTM	33	-	-	35	-	33.0
ACT	1	1	1, 3.3**	1	1	1
SDA	0.172	0.175	0.175	0.172	0.175	0.161
Egestion/ Excretion equation #	2	1	1	2	1	1
FA	0.158	0.16	0.15	0.158	0.16	0.25
FB	-0.222	-	-	-0.222	-	-
FG	0.631	-	-	0.631	-	-
UA	0.0253	0.1	0.1	0.0253	0.1	0.1
UB	0.58	-	-	0.58	-	-
UG	-0.299	-	-	-0.299	-	-
Predator Energy Density	4186	4814	4600	4186	4814	7352
DO Crit Slope	0.168	0.168	0.168	0.168	0.168	0.168
DO Crit Intercept	0.358	1.635	0.358	0.358	1.635	1.635

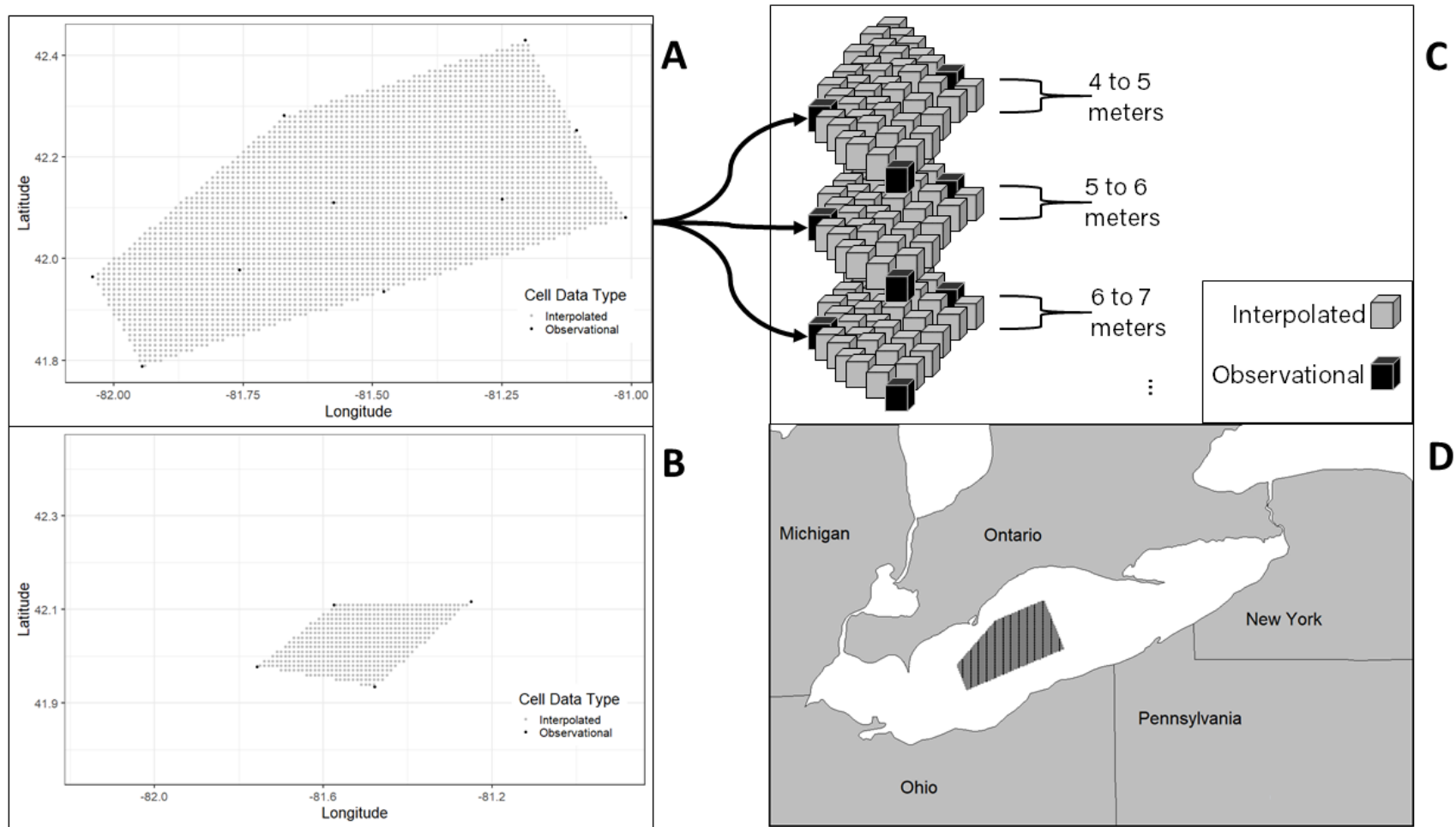


Figure 2.1. Visualization of the steps necessary to create a three-dimensional gridded raster encompassing the sample sites within the central basin of Lake Erie. A) Filled raster grid (for all depth increments except 23 meters) showing distribution of cells with observational and interpolated data. B) Filled raster grid for the lowest depth increment of 23 meters, unique in that only four of ten sites reach this depth and so requiring a different grid shape. C) Conceptual diagram demonstrating the vertical stacking of horizontal raster grids to build the three-dimensional model space. D) Location of the simulated study area within the Lake Erie central basin.

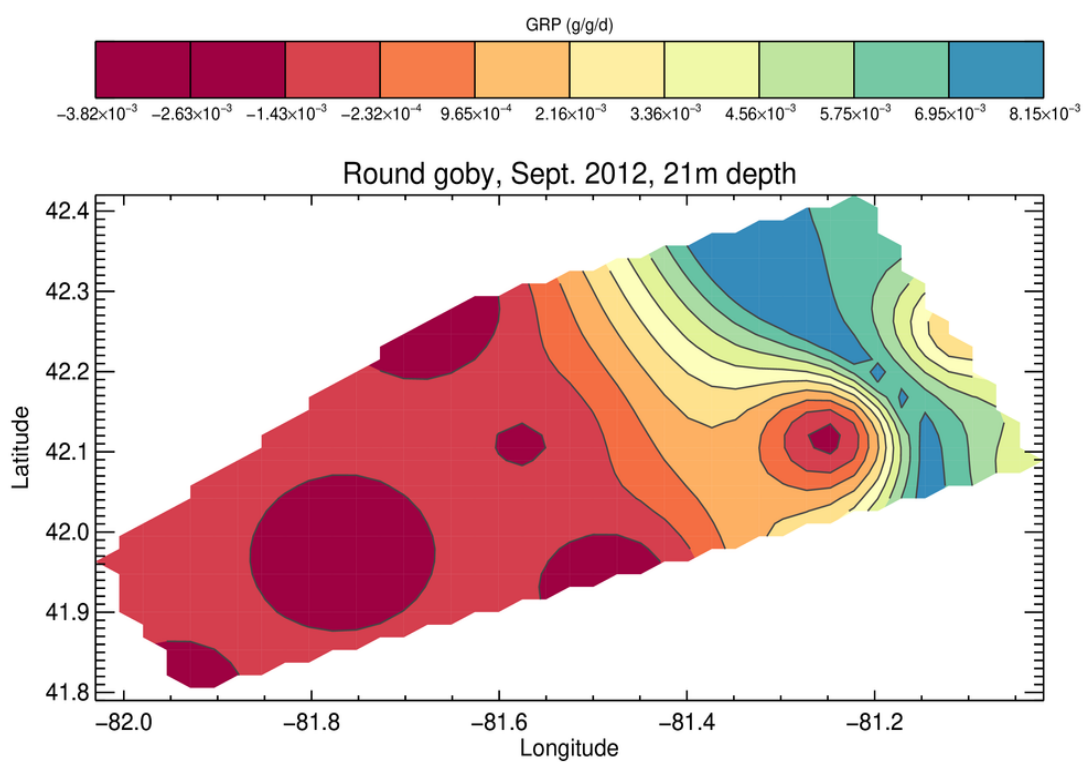


Figure 2.2. Horizontal contour plot displaying round goby growth-rate potential (in grams of growth per gram of body mass per day) within the Lake Erie central basin study volume at 21 meters depth during September 2012.

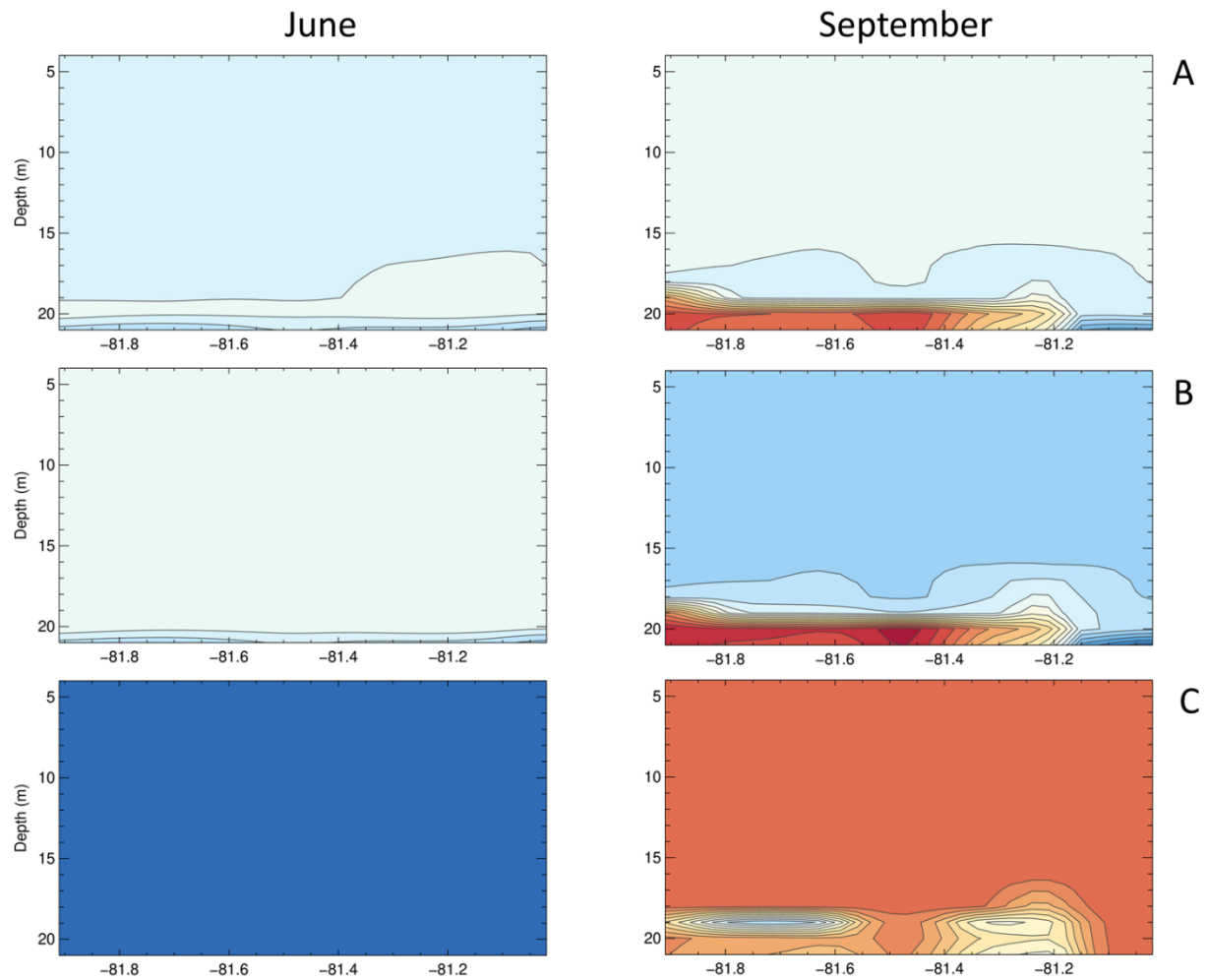
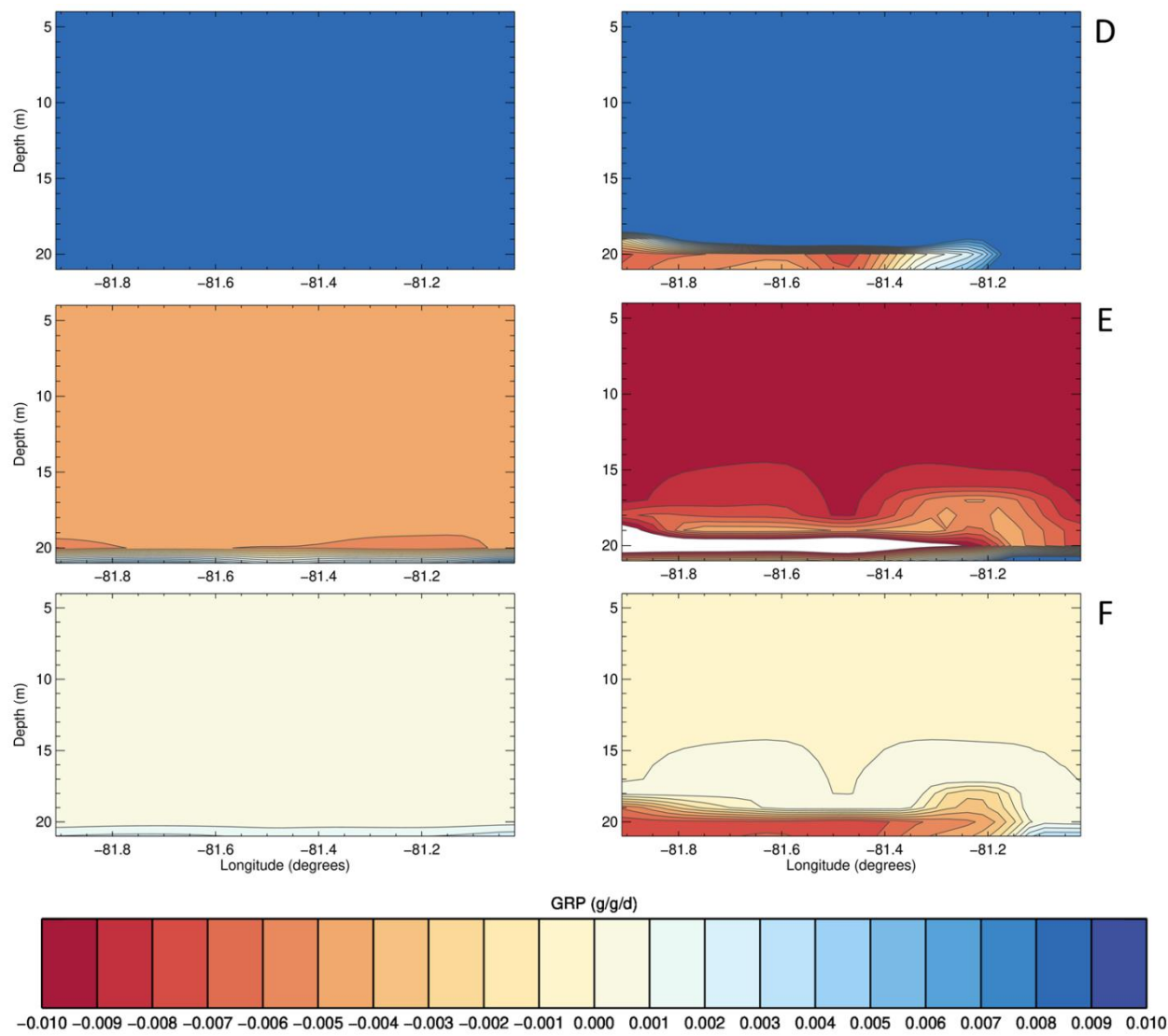


Figure 2.3. Vertical contour plots displaying growth-rate potential (in grams of growth per gram of body mass per day) along the southern edge of the Lake Erie central basin study volume during June and September of 2012 for (A) adult yellow perch, (B) YOY yellow perch, (C) adult rainbow smelt, (D) YOY rainbow smelt, (E) adult round goby, and (F) adult emerald shiner.

Figure 2.3 Continued



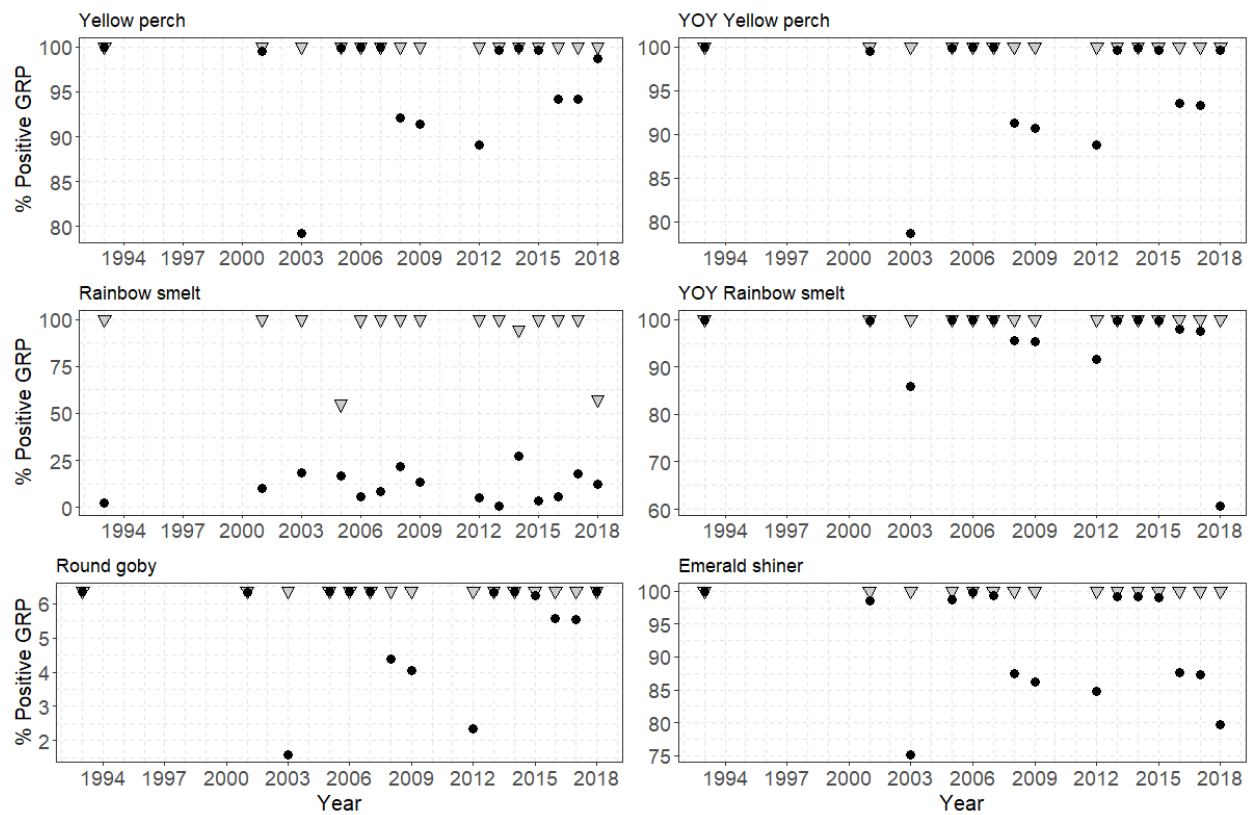


Figure 2.4. Percentage of the study volume exhibiting GRP greater than zero during June (grey triangles) and September (black circles) for years with at least four sampling trips. Note inconsistency in y-axes due to species-specific growth-rate potential calculations.

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CHAPTER 3. SPATIALLY AND TEMPORALLY DISTINCT PRODUCTION PATHWAYS SUPPORTING THE LAKE ERIE CENTRAL BASIN FOOD WEB

3.1 Introduction

While food web structure has traditionally been conceptualized as rather static, it is now widely recognized that food web structure and dynamics can be altered over time in response to discrete events, such as changes in ambient environmental conditions (e.g., Schindler, 2001; Shimoda et al., 2011), invasion of exotic species (e.g., Pothoven and Madenjian, 2008; Strayer, 2010; Turschak et al., 2014), or anthropogenic modifications to habitat (e.g., Kalcounis-Rueppell et al., 2007; Potthoff et al., 2008). Moreover, various studies demonstrate that food webs can be continuously variable across space and time, both in terms of overall food web structure, as well as the primary production pathways supporting food webs. For example, spatial variation in dominant carbon sources supporting freshwater food webs have been detected across varying spatial scales (i.e., 10 to 100 km²; Arantes et al., 2019; Finlay, 2004; Hunt et al., 2012), with spatial patterns potentially varying temporally, e.g., with seasonal patterns of riverine discharge and system productivity. Furthermore, spatiotemporal differences in energy flow and nutrient transfer at lower trophic levels are often reflected in higher trophic level consumers (Doi et al., 2019; Finlay et al., 2002). Spatiotemporal variation in resource use, when underestimated or overlooked, may affect interpretations of food web structure, dynamics and dominant production pathways. As such, it is important for resource managers to consider and characterize the extent of spatiotemporal variation in resource use within aquatic food webs.

The Laurentian Great Lakes have extensively characterized food webs and a long historical record of alterations to food web structure (e.g., Blanke et al., 2018; Bunnell et al., 2014; Mills et

al., 2003). The Great Lakes exhibit seasonal and inter-annual variability in food web dynamics concomitant with resource availability (e.g., Hrycik et al., 2018; Stewart et al., 2017; Zhang et al., 2012). Moreover, intraspecific spatial variation in resource utilization has been detected in several Great Lakes among lower trophic organisms (Camilleri and Ozersky, 2019; Ives et al., 2013) and fishes (Foley et al., 2017; Happel et al., 2015; Happel et al., 2018; Hrycik et al., 2018). However, other studies have found evidence for strong linkages and subsidies among habitats (e.g., Sierszen et al., 2014) or lake-wide similarities in intra-specific prey consumption (Leonhardt et al., 2020) that would homogenize the resource utilization of consumers and weaken any spatial variability in food web dynamics. Apparent spatial variation in resource utilization has been correlated with eutrophication (Camilleri and Ozersky, 2019), habitat heterogeneity (Sierszen et al., 2014), and niche availability (Ives et al., 2013), suggesting a connection between food web dynamics and external environmental factors.

Lake Erie, particularly the central basin, has strong potential for spatial and temporal variations in food web dynamics and dominant energy pathways. Lake Erie has been substantially altered by human activities, principally excess nutrient loading from surrounding land, resulting in eutrophication and nearly annual hypoxia in offshore regions of the central basin (Kane et al., 2014; Smith et al., 2015; Williams and King, 2020). The eutrophication is primarily caused by high concentrations of nutrient loading via many large rivers (e.g., Maumee River, Detroit River, Cuyahoga River). The discharge from these rivers also results in large river plumes that generally flow from west to east along the lake, influencing the hydrological and ecological conditions of affected nearshore habitats (Jarrin et al., 2015; Jiang et al., 2015; Niu et al., 2018). Nutrient concentrations can vary significantly at the margin of these river plumes relative to the lake basin proper, especially during storm runoff events (Baker et al., 2014). Wind- and current-driven

upwelling events also occur regularly in nearshore regions of Lake Erie (Valipour et al., 2019), particularly along the broad northern and southern coastlines within the central basin. These upwellings transport autochthonous benthic nutrients and production into nearshore or pelagic regions, substantially altering the water quality, primary production potential and dominant primary production sources in localized areas (Dunstall et al., 1990; Rowe et al., 2019). There is evidence that both river input and wind-driven hydrological processes contribute to habitat heterogeneity and production within the lake (Jiang et al., 2015). Additionally, the characteristic seasonal hypoxia that occurs within the central basin may represent a barrier to movement for species that principally rely on benthic resources or habitats. Thereby, hypolimnetic hypoxia may limit the potential for organisms to spatially integrate the central basin food web. Moreover, the extent of hypoxic area and the intensity of stratification differ from year to year, thereby potentially altering trophic spatial patterns and connectivity. As such, the food web dynamics and dominant energy pathways that characterize the central basin of Lake Erie are likely to vary on both spatial and temporal scales.

Stable isotope analysis is a well-established approach for quantifying and comparing certain features of aquatic food webs. Isotopic ratios of nitrogen are often used to proxy the relative trophic positioning of organisms within a food web. The lighter isotope of nitrogen (^{14}N) is preferentially eliminated by organisms during protein breakdown and excretion of nitrogenous waste, leading to a pattern of accumulation of the heavier nitrogen isotope (^{15}N) at higher trophic levels. However, it should be noted that baseline values of $\delta^{15}\text{N}$ can vary among and within systems based on the source of nitrogenous compounds entering the ecosystem (Cabana and Rasmussen, 1996; Richards et al., 2020), complicating any analysis of trophic structure across broad spatial scales. Isotopic ratios of carbon do not vary substantially across trophic levels.

Instead, $\delta^{13}\text{C}$ values generally indicate the source of organic compounds utilized by producers or the relative contribution of distinct production pathways to the diets of consumers (in part because different primary producers differentially incorporate carbon isotopes). In aquatic systems, this is often used to measure the relative contribution of benthic versus pelagic or autochthonous versus allochthonous production pathways supporting the system. We employed stable isotope analysis to investigate the possibility of spatially and temporally distinct differences in dominant production pathways and food web dynamics within the Lake Erie central basin. Specifically, the principal objective of the study was to evaluate the potential intraspecific spatial differences in resource utilization among fishes of the Lake Erie central basin.

3.2 Methods

3.2.1 Study species

Four ecologically and economically important fish species of Lake Erie's central basin were chosen for isotopic analysis. These species were chosen because, while they are all primarily invertivorous, they exhibit diverse foraging and habitat preferences. Rainbow smelt (*Osmerus mordax*) are introduced pelagic planktivores that experience seasonal conditions of sub-optimal habitat quality in Lake Erie due to thermal stress and hypoxia (Arend et al. 2011). The central basin hypoxia has altered trophic interactions for rainbow smelt, limiting access to benthic resources and forcing increased reliance on zooplankton (Pothoven et al. 2012; Stone et al. 2020). Round goby (*Neogobius melanostomus*) are an invasive obligate benthic generalist which have become a crucial component of the Lake Erie food web since their introduction into the system. Round goby now serve as a critical forage species in the diets of many piscivorous fishes (Steinhart et al. 2004; Johnson et al. 2005; Campbell et al. 2009; Madenjian et al. 2011). Round goby are one

of the few species within the lake that will primarily feed upon the invasive mussels, with measurable impacts on nutrient cycling and trophic energy transfer (Barton et al. 2005; Bunnell et al. 2005; Andraso et al. 2011). Yellow perch (*Perca flavescens*) are benthic-pelagic mesopredators that predate on a wide variety of organisms within Lake Erie. They serve as a dominant component of the food web (Parrish and Margraf 1994; Hrycik et al. 2018) and support commercial and recreational fisheries. White perch (*Morone americana*) are introduced pelagic generalists that overlap with yellow perch for similar prey (Schaeffer and Margraf 1986) but generally display higher pelagic resource utilization (Parrish and Margraf 1994).

3.2.2 Sample collection

Fishes were collected from August to October during 2017 and 2019 within two broad regions of the central basin of Lake Erie (Figure 1). The northern region covered the distance from approximately 82.376° W and 41.787° N to 81.205° W and 42.530° N. The southern region covered the distance from approximately 82.142° W and 41.548° N to 81.011° W and 42.082° N. Samples from within the southern region were collected by the United States Geological Survey and Ohio Department of Natural Resources. Samples from within the northern region were collected by the United States Geological Survey and the Ontario Ministry of Natural Resources and Forestry. All fishes were collected using benthic trawls as part of long-term monitoring programs conducted by the respective agencies. Trawling took place between 12 and 22 meters below the surface, depending on the maximum depth at each sample site. Exact sampling locations and specifications for tow duration, net size, trawl speed, and number of replicate samples per site varied slightly among agencies. Full descriptions of trawling procedures can be found within the status reports associated with each monitoring effort (USGS 2018; OMNRF 2019; ODNR 2020). Lower trophic prey samples were collected only during the 2019 season in the same regions previously described.

Benthic invertebrates were collected using a small PONAR grab sampler with an open-jaw area of 0.023 m². Raw benthic grabs were rinsed over a strainer to remove fine sediment. Zooplankton were collected by performing vertical daytime tows with a 150 µm, 0.3-m diameter zooplankton net. All samples were frozen immediately upon collection and transported to Purdue University for later processing.

3.2.3 Sample processing

Samples were stored at -20°C until thawed for processing. Zooplankton samples were separated into 1/8th sample fractions using a splitter, then fraction contents were identified to one of four major taxonomic groupings (Calanoid copepods, Cyclopoid copepods, herbivorous Cladocerans, predatory Cladocerans) and separated, according to a standard protocol (EPA 2003). Benthic invertebrates were hand-picked from PONAR grabs, identified, and separated to the lowest possible taxonomic grouping. Invertebrate field collections resulted in fewer viable organism for analyses than anticipated. To bolster sample sizes, gut contents were removed from all fish samples and five zooplankton and ten benthic invertebrate samples were extracted from the diet contents of fishes and included in invertebrate sample processing. Individual fish wet mass (to 0.1 mg) and total length (to 1 mm) were recorded prior to processing. Fish ≤ 120 mm total length were dried whole following the removal of the cranium, caudal fin, and gut contents, according to standard practice (e.g., Keough et al., 1996; O'Reilly et al., 2002). Fish >120 mm total length had a section of dorsal white muscle tissue removed and dried for stable isotope analysis. Lower trophic samples were dried whole. In the case of small taxa (e.g., Calanoid copepods), multiple individuals from the same sample (i.e., zooplankton tow or PONAR grab) were pooled in order to produce sufficient dry mass for analysis. All samples were dried at 40°C for 72 hours.

Dry samples were ground into a fine homogenous powder using XXX between a sheet of wax paper. For each sample, ~1 mg of dry material was sealed into a 3.5 x 5 mm tin capsule. Individual tin capsules were placed into labeled 96-well plate and shipped to the Cornell University Stable Isotope Laboratory (COIL) for isotopic analysis. Sample values of carbon and nitrogen isotopes were measured using a Thermo Scientific Delta V Advantage Isotope Ratio Mass Spectrometer (IRMS). Percent carbon and nitrogen were measured by combustion analysis within a Carlo Erba NC2500 elemental analyzer. For quality control and measuring precision of sample values, COIL uses in-house standards that are routinely calibrated against the international reference materials provided by the International Atomic Energy Association (IAEA) for carbon (Vienna Pee Dee Belemnite, $\delta^{13}\text{C}_{\text{VPDB}}$) and nitrogen (atmospheric air, $\delta^{15}\text{N}_{\text{AIR}}$). The in-house standard used for animal samples ('Deer') was analyzed after every ten samples to ensure accuracy and precision, and to measure error. Our samples were measured over three separate runs between April and December of 2020. Among these three runs, analysis of the in-house animal standard indicated a standard deviation that varied between $\pm 0.07\text{‰}$ and $\pm 0.11\text{‰}$ for $\delta^{13}\text{C}$ values and between $\pm 0.03\text{‰}$ and $\pm 0.04\text{‰}$ for $\delta^{15}\text{N}$ values. Following raw isotopic analysis, preliminary isotope corrections were performed by COIL via a two-point normalization of all $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ data using two additional in-house standards ('KCRN' – corn, and 'CBT' – trout). Final delta values were calculated as:

$$\delta^{13}\text{C} = \frac{\frac{^{13}\text{C}_{\text{sample}}}{^{12}\text{C}_{\text{sample}}}}{\frac{^{13}\text{C}_{\text{VPDB}}}{^{12}\text{C}_{\text{VPDB}}}} - 1 \quad \text{and} \quad \delta^{15}\text{N} = \frac{\frac{^{15}\text{N}_{\text{sample}}}{^{14}\text{N}_{\text{sample}}}}{\frac{^{15}\text{N}_{\text{AIR}}}{^{14}\text{N}_{\text{AIR}}}} - 1$$

Ratios of carbon stable isotopes, especially those constituted from whole-body samples, are affected by the presence of lipids within tissues (Logan et al. 2008; Mateo et al. 2008; Cloyed et al. 2020). To account for lipid compositional effects, quantitative lipid correction is typically

preferred over lipid extraction with chemical solvents when analyzing entire communities because chemical extraction carries the risk of introducing bias to $\delta^{15}\text{N}$ values (Carabel et al. 2006; Murray et al. 2006). Post-hoc lipid corrections using mass-balance equations based on proportional carbon composition were conducted for the $\delta^{13}\text{C}$ values of all samples. Separate equations were used for fishes (Hoffman et al. 2015), zooplankton (Smyntek et al. 2007), and benthic invertebrates (Logan et al. 2008).

3.2.4 Data analysis

Sampling occurred over two separate years (2017 and 2019) with potentially different physiochemical conditions and realized differences in species-specific sample sizes by year. Thus, data were separately analyzed by year, in part to evaluate if any observed patterns were temporally consistent. Isotopic values were initially visualized using $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ biplots. A series of analysis of covariance (ANCOVA) models were used to evaluate the effects of spatial location on species-specific differences in isotopic ratios of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Isotopic ratios of fishes often change through ontogeny due to shifts in prey selection (e.g., Johnson et al. 2004; Heuvel et al. 2019; Dixon et al 2012; Pennock et al. 2019). To account for such effects, first, the interquartile range rule was used to identify sample outliers for total length in each species and year dataset, so that only samples of comparable size ranges were included. Second, individual length was included as a covariate in the ANCOVA models. Region (north versus south) was evaluated as a factor in the ANCOVA models. Longitude of sample collection site was included as a covariate to potentially capture any variation in stable isotope ratios along the east-west gradient of the central basin. Separate ANCOVA models to describe spatial variation in $\delta^{13}\text{C}$ or $\delta^{15}\text{N}$ were produced for each of the four study species (yellow perch, white perch, rainbow smelt, round goby) and for each year, i.e., 12 total ANCOVA models were produced (data were insufficient for yellow perch in

2019 and white perch in 2017). Region (north or south), longitude of collection site, total length, and all two-way interactions were considered as explanatory variables. Non-significant ($\alpha = 0.05$) interaction terms were not included in the final models. Welch's two-sample t-tests were conducted during a supplemental analysis of lower trophic organisms (See Appendix). All graphical and statistical analyses were conducted in R Version 3.6.3 (R Core Team 2020) using RStudio Version 1.1.456 (Rstudio Team 2016).

3.3 Results

3.3.1 Collection of isotopic samples

In total, isotopic ratios of carbon and nitrogen were calculated for 310 individual fishes, 14 zooplankton samples (10 predatory Cladocerans and 4 Calanoid copepods), and 43 benthic invertebrates (33 Chironomidae, 3 dreissenid soft tissue samples, 5 Oligochaeta, 2 Amphipoda) across both regions and years. Samples sizes were generally comparable between the northern and southern regions for all four fish species (Table 1). White perch and lower trophic samples were only collected in 2019 due to constraints on sampling durations and equipment. In addition, insufficient numbers of yellow perch were collected in 2017 to allow for statistical analyses. Mean total lengths of all fishes (mm \pm SD) were 59.3 ± 15.7 , 48.6 ± 11.3 , 139.6 ± 45.9 , and 218.2 ± 51.0 for rainbow smelt, round goby, yellow perch, and white perch, respectively.

3.3.2 Summary statistics and graphical analysis

Mean $\delta^{13}\text{C}$ of invertebrate samples ranged from -23.2 ± 0.9 ‰ (mean \pm 1 SD, $n = 33$) for chironomids to -26.5 ± 0.2 ‰ ($n = 4$) in Calanoid copepods. Across all individual fishes sampled, $\delta^{13}\text{C}$ values ranged from -24.7 to -21.6 , but mean values among species were less variable: from -23.0 ± 0.6 ‰ ($n = 29$) for white perch to -23.5 ± 0.5 ‰ for round goby ($n = 121$; Figure 2). Small

samples sizes precluded the spatial analysis of most lower trophic taxa beyond simple baseline context for fish species. When accounting for the fact that ^{13}C is slightly enriched with increasing trophic position (Vander Zanden et al. 1999; Post 2002), isotopic ratios of carbon from invertebrate samples matched the range of relative isotopic ratios of carbon reported for fish species. ^{13}C was depleted in zooplankton samples ($-25.4 \pm 0.8 \text{ ‰}$, $n=14$) relative to benthic invertebrates ($-23.3 \pm 0.9 \text{ ‰}$, $n = 43$). ^{13}C was also generally more depleted for dreissenids ($-24.4 \pm 1.2 \text{ ‰}$, $n = 3$) than other benthic invertebrates (Figure 3). ^{15}N was enriched in predatory cladocerans ($+14.6 \pm 0.8 \text{ ‰}$, $n=10$) relative to calanoid copepods ($+11.6 \pm 1.5 \text{ ‰}$, $n=4$) (Figure 3). Chironomids were the only lower trophic taxa with a large enough sample size to conduct dedicated statistical comparisons of isotopic ratios. Welch's two-sample t-tests were conducted to test for significant difference between the northern and southern groups, both with and without the inclusion of the 11 (11 North, 0 South) chironomids retrieved and processed from stomach contents. Chironomid $\delta^{13}\text{C}$ values did not significantly differ between individuals collected in the northern and southern regions when stomach content individuals were included ($p = 0.3902$, $t = 0.874$, north mean = -23.1‰ , south mean = -23.4‰) but did significantly differ when stomach content individuals were excluded ($p < 0.01$, $t = 3.274$, north mean = -22.5‰ , south mean = -23.4‰) (Figure A1). Most zooplankton and benthic invertebrate samples were more depleted in ^{15}N axis relative to fishes. Mean $\delta^{15}\text{N}$ values among lower trophic organisms ($+12.7 \pm 1.5 \text{ ‰}$, $n = 57$) were, on average, 2.5 ‰ lower than those reported for fishes ($+15.2 \pm 1.0 \text{ ‰}$, $n = 310$). Among fish species, white perch exhibited the most enriched ^{13}C values ($-23.0 \pm 0.6 \text{ ‰}$, $n = 29$), followed by yellow perch ($-23.1 \pm 0.4 \text{ ‰}$, $n = 39$), rainbow smelt ($-23.5 \pm 0.3 \text{ ‰}$, $n = 121$), and round goby ($-23.5 \pm 0.5 \text{ ‰}$, $n = 121$). Conversely, rainbow smelt exhibited the most enriched ^{15}N values ($+15.8 \pm 0.8 \text{ ‰}$, $n = 121$), followed by white

perch ($+15.3 \pm 0.6$ ‰, $n = 29$), yellow perch ($+15.3 \pm 0.6$ ‰, $n = 39$), and round goby ($+14.4 \pm 0.7$ ‰, $n = 121$).

3.3.3 ANCOVA models

All six ANCOVA models significantly explained $\delta^{13}\text{C}$ variation (Figure 4; Table A1). The proportional variation explained by the significant models varied from 0.10 (2019 rainbow smelt) to 0.50 (2017 rainbow smelt). Region of capture was a significant explanatory variable in two of the models (2017 rainbow smelt, 2019 round goby), and both of these models indicated that ^{13}C was significantly more enriched in the southern region relative to the northern region. Longitude was significant in two of the models (2017 and 2019 round goby), and both of these models indicated that ^{13}C became more depleted the further eastward that a goby was collected. Total length was a significant explanatory variable in two of the models (2019 rainbow smelt, 2017 yellow perch; Figure A2). None of the final models for carbon contained any significant interaction terms among explanatory variables.

Five of six ANCOVA models significantly explained $\delta^{15}\text{N}$ variation (Figure 5; Table A2). The proportional variation explained by the significant models varied from 0.18 (2019 round goby) to 0.86 (2017 rainbow smelt). Concerning the five significant models, region of capture was a significant explanatory variable without any interactive effects in two of the models (2017 round goby and rainbow smelt), and both of these models indicated that ^{15}N was significantly more depleted for individuals in the southern region relative to the northern region. Two models included a significant interactive effect of region with either longitude (2019 rainbow smelt) or total length (2019 white perch). Longitude was a significant explanatory variable in three of the models (2017 and 2019 rainbow smelt, 2019 white perch). However, the directionality of the effect of longitude was not consistent among species or years and two of the models included significant interactive

effect with longitude, confounding interpretation. Total length was a significant explanatory variable in three of the models (2017 round goby, 2019 rainbow smelt, 2019 white perch; Figure A3). Length had a negative effect in goby models and a positive effect in all other models. For 2017 round goby, ^{15}N became more depleted as total length increased. For 2019 rainbow smelt and white perch, ^{15}N became more enriched as total length increased.

3.4 Discussion

Variation in isotopic ratios were significantly explained by region (i.e., north or south) and longitude (i.e., an east-west gradient) for several study species, indicating apparent intraspecific spatial differences in resource utilization. Results indicated that ^{13}C was significantly more depleted in the southern region relative to the northern region for round goby in 2017 and rainbow smelt in 2019, and that ^{15}N was significantly more depleted in the southern region relative to the northern region for three of the six groups. The two groups with the strongest effect (2017 round goby, 2017 rainbow smelt) were both collected in 2017, perhaps also indicating interannual differences in isotopic spatial structuring. Longitude was a significant explanatory variable of δ ^{13}C values for round goby in both 2017 and 2019, however the directionality of this relationship was not consistent across years. In 2017, round goby became significantly more depleted in ^{13}C as longitude increased (i.e., traveling eastward). This relationship was reversed in 2019, when round goby became significantly more enriched in ^{13}C as longitude increased. Longitude was also a significant explanatory variable of δ ^{15}N values for rainbow smelt. In both 2017 and 2019, rainbow smelt became significantly more depleted in ^{15}N as longitude increased (i.e., traveling eastward). Total length significantly explained δ ^{15}N variation in three of six models. ^{15}N became significantly more enriched as total length increased for rainbow smelt and white perch in 2019. Most species experience an enrichment in ^{15}N with length, commonly considered to reflect the fact that fishes

feed at higher trophic levels as they grow and transition among life stages. However, 2017 round goby showed the opposite relationship, with ^{15}N becoming significantly more depleted as total length increased. This is reflective of the fact that gape limitations prohibit round goby from feeding on dreissenids (which are characteristically depleted in ^{15}N) at very small sizes, but then begin feeding on dreissenids once they are large enough to consume the shells of the entire organisms (Andraso et al., 2011).

Results vary in terms of agreement with prior studies investigating spatial differences in isotopic ratios. Guzzo et al. (2011) found that nutrient loading and discharge from the Detroit and Maumee River plumes directly influences the isotopic ratios of fish populations in the northern and southern regions of the western basin of Lake Erie, with ^{13}C depleted and ^{15}N enriched in the Maumee (south) relative to the Detroit River (north) plume. In contrast, our models indicated that ^{13}C was enriched and ^{15}N depleted in the southern relative to the northern central basin for two study species (round goby and rainbow smelt). This may indicate that the influence of the western basin river plumes on isotopic values of consumers does not extend into the central basin. An inter-basin ridge separates the western basin from the central basin near Pelee Island (Holcombe et al., 1997), causing the river plumes to mix before flowing eastward into the central basin and likely negating any congruity in spatially distinct isotopic patterns between basins. Moreover, prior studies have found that natural fertilizer use (e.g., manure) in surrounding catchments decreases ^{13}C and increases ^{15}N relative to artificial chemical fertilizer use (Choi et al., 2017; Guiry, 2019). Widespread use of artificial fertilizers results in negative shifts in $\delta^{15}\text{N}$ because over-abundant dissolved inorganic nitrogen allows for greater discrimination against ^{15}N during assimilation by primary producers (Fogel and Cifuentes, 1993; Needoba et al., 2004). Our results align with these expectations given agricultural practices in the surrounding watersheds. ^{13}C was depleted and ^{15}N

was elevated in the northern region, where manure is widely used as fertilizer on Canadian farms, relative to the southern region, where artificial fertilizer use is the dominant practice among U.S. farms (Limnotech, 2017).

Results revealed complex patterns in carbon and nitrogen isotopic composition within and among species. All fish species overlapped heavily in reported values of $\delta^{13}\text{C}$, which may indicate resource use overlap. Prior studies in Lake Erie have indicated diet and trophic overlap between juvenile yellow perch and round goby (Duncan et al., 2011), and yellow perch and white perch (Guzzo et al., 2013, Parrish and Margraf, 1990; Schaeffer and Margraf, 1986) that are consistent with our findings. Moreover, mean isotopic ratios of carbon for zooplankton (-25.86 ‰), benthic invertebrates (-23.26 ‰), dreissenids (-24.39 ‰), and among all fish species (-23.41 ‰) suggest that consumers may be deriving more of their energy from benthic, rather than pelagic, pathways within the central basin. Results indicating that fishes, especially young fishes, are relying primarily on benthic production pathways is unexpected considering the increased reliance on planktonic resources at early life stages, relatively high pelagic production within Lake Erie (e.g., Munawar and Burns, 1976), and the aforementioned offshore hypolimnetic hypoxia that seasonally restricts access to large areas of benthic habitat. Hypoxia may force fishes within the central basin to rely more on nearshore benthic production, which would be more accessible to forage on in shallower waters. Furthermore, dreissenids (which are prolific in Lake Erie outside of the hypoxic zone) redirect sestonic material to benthic production pathways and directly compete with zooplankton for pelagic food sources (Garton et al. 2005; Ozersky et al. 2012). Trophic structure and diet shifts revealed an increased dependence among consumers on nearshore benthic resources following the invasion of dreissenid mussels in Lake Michigan (Turschak et al., 2014) and Lake Simcoe (Rennie et al., 2013). Dreissenids are

intolerant of low dissolved oxygen and are largely absent from hypoxic offshore regions (Karatayev et al., 2018), highlighting the complex interplay between biotic and abiotic drivers of food web production.

Other land use and watershed characteristics may also influence isotopic values of consumers. ^{15}N is often elevated in urban catchments or those with widespread industrial activity (e.g., Cole et al., 2006; Dillon and Chanton, 2008; Pierce et al., 2019). However, our results found that ^{15}N was elevated in the northern region relative to the southern region despite the abundance of urban and industrial centers along the southern coastline of the central basin. It is possible that the influence of extensive agricultural land use surrounding Lake Erie masks and overwhelms any contribution of allochthonous urban nitrogen loading. Excess nutrients from agricultural runoff also contribute to the widespread eutrophication issues afflicting Lake Erie. Eutrophication is associated with elevated baseline levels of ^{15}N in aquatic systems (Camilleri and Ozersky, 2019; Wang et al., 2015; Zheng et al., 2019). Longitudinal trends in rainbow smelt $\delta^{15}\text{N}$ variation in the present study are consistent with the distinctive east-west trophic gradient that exists within the lake. Relative eutrophic intensity decreases from west to east, and smelt tissues experienced a significant decrease in $\delta^{15}\text{N}$ with increasing longitude.

In contrast to diet analysis, which only reveals the resources consumed by an organism within a brief timeframe before collection, isotopic ratios of adult fishes generally represent assimilation of resources over a timespan of several months (Post, 2002). However, juvenile fishes experience more rapid tissue turnover than adults due to accelerated growth, so isotopic ratios of juveniles may only represent resource use over a timespan of several weeks to one month (e.g., Busst et al., 2018; Hertz et al., 2016). Most of the individuals collected and analyzed during the present study were juvenile or sub-adult (based on length-at-age estimates for each species), which

has implications for the interpretation of results. Samples were collected during the hypoxic season, so isotopic ratios would be reflective of a timeframe in which access to offshore benthic resources is greatly reduced or altogether prohibited. Moreover, many species within the central basin have evolved to take advantage of seasonally abundant prey resources (e.g., Brush et al., 2012; Heuvel et al., 2019; Hrycik et al., 2018) and experience resultant seasonal variation in isotopic ratios.

Recent studies have brought to light the importance of considering isotopic baselines when drawing inference from the results of stable isotope analysis (Graham et al., 2010; Guiry, 2019; Kjeldgaard et al., 2021). External factors (i.e., fertilizer use, excess nutrient input, urbanization, etc.) influence isotopic ratios by altering the relative availability and proportions of heavy and light isotopes in the ambient aquatic environment. This, in turn, sets the baseline for the isotopic ratios that are assimilated by producers and consumers in a localized area. The present study did not have access to isotopic ratios of primary producers, so it is impossible to definitively determine whether the isotopic differences seen within the Lake Erie central basin are reflective of ambient baseline isotopic ratios being spatially conserved, or true spatial differences in resource utilization among consumers. Importantly, baselines are known to vary among (e.g., Belle et al., 2017; Caban and Rasmussen, 1996) and within systems (e.g., Mbabazi et al., 2010; Smyntek et al., 2012; Syvaranta et al., 2006) on spatial and temporal scales. Our findings are generally consistent with known patterns of land use and baseline variation, so it is likely that spatially distinct isotopic baselines contribute to the apparent trends in resource use detected within the central basin.

The Great Lakes ecosystem has been heavily altered from a natural state by anthropogenic actions, and such changes are likely to continue well into the future. Agricultural practices have been at the frontier of research concerning nutrient loading and eutrophication of the Laurentian Great Lakes. Changes in agricultural best management practices (Bosch et al., 2013; Scavia et al.,

2017) may alter nutrient loading characteristics and consequently baseline isotopic values and production pathways of aquatic systems. Furthermore, inherent differences in baseline isotopic ratios exist within Great Lakes primary producers (Camilleri and Ozersky, 2019), but are largely overlooked and under-studied. As such, our current understanding of the patterns and relationships within Great Lakes food webs is likely incomplete. The present study reports the broad occurrence of spatiotemporal variation in isotopic signatures of consumers within the Lake Erie central basin. However, given the complex chemistry of isotopic fractionation, more work is necessary to elucidate the drivers of this variation within and among species. Investigating the dynamic patterns of resource use present within aquatic food webs may help resource managers to more accurately characterize aquatic food webs and predict the effect allochthonous nutrient loading on interpretations of isotopic food web studies.

3.5 Tables and Figures

Table 3.1. Samples collected in 2017 and 2019 and submitted for isotopic analysis from spatially distinct regions of the Lake Erie central basin.

<i>Species/ Functional Group</i>	<i>North region (2017; 2019)</i>	<i>South region (2017; 2019)</i>
<i>Rainbow smelt</i>	62 (32; 30)	59 (30; 29)
<i>Round goby</i>	60 (30; 30)	61 (31; 30)
<i>Yellow perch</i>	21 (15; 6)	18 (15; 3)
<i>White perch</i>	15 (0; 15)	14 (0; 14)
<i>Zooplankton</i>	4 (0; 4)	10 (0; 10)
<i>Benthic Invertebrates</i>	31 (0; 31)	12 (0; 12)

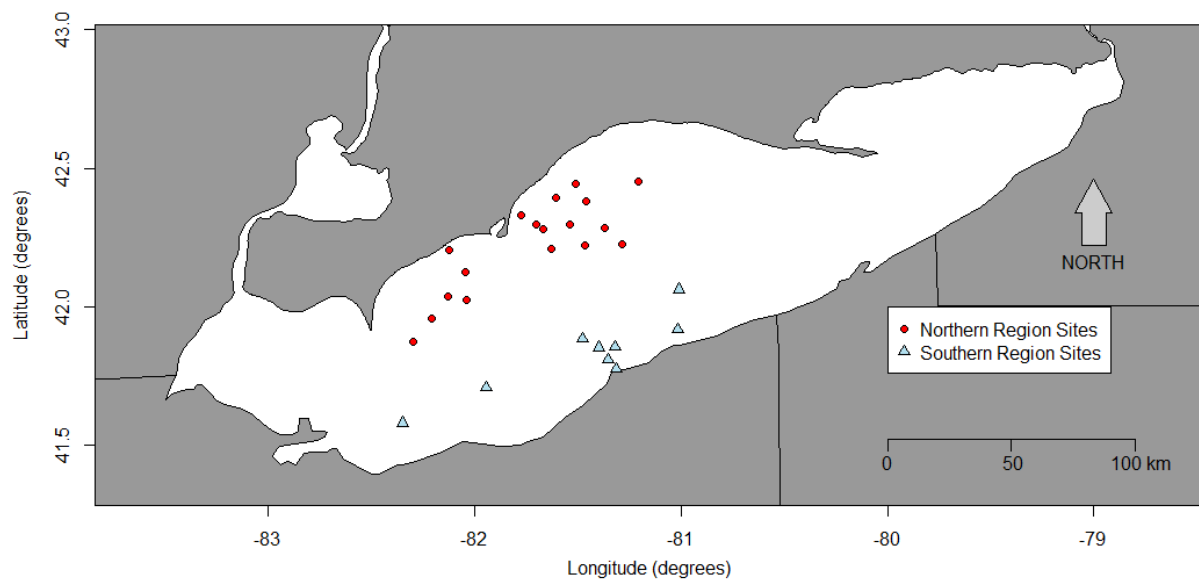


Figure 3.1. Sampling locations from which fishes, zooplankton, and benthic invertebrates were collected as part of long-term monitoring programs. Red circles indicate sites that were considered within the northern region. Blue triangles indicate sites that were considered within the southern region. Sampling at northern sites was conducted by the Ontario Ministry of Natural Resources and Forestry and the United States Geological Survey. Sampling at southern sites was conducted by the Ohio Department of Natural Resources and the United States Geological Survey.

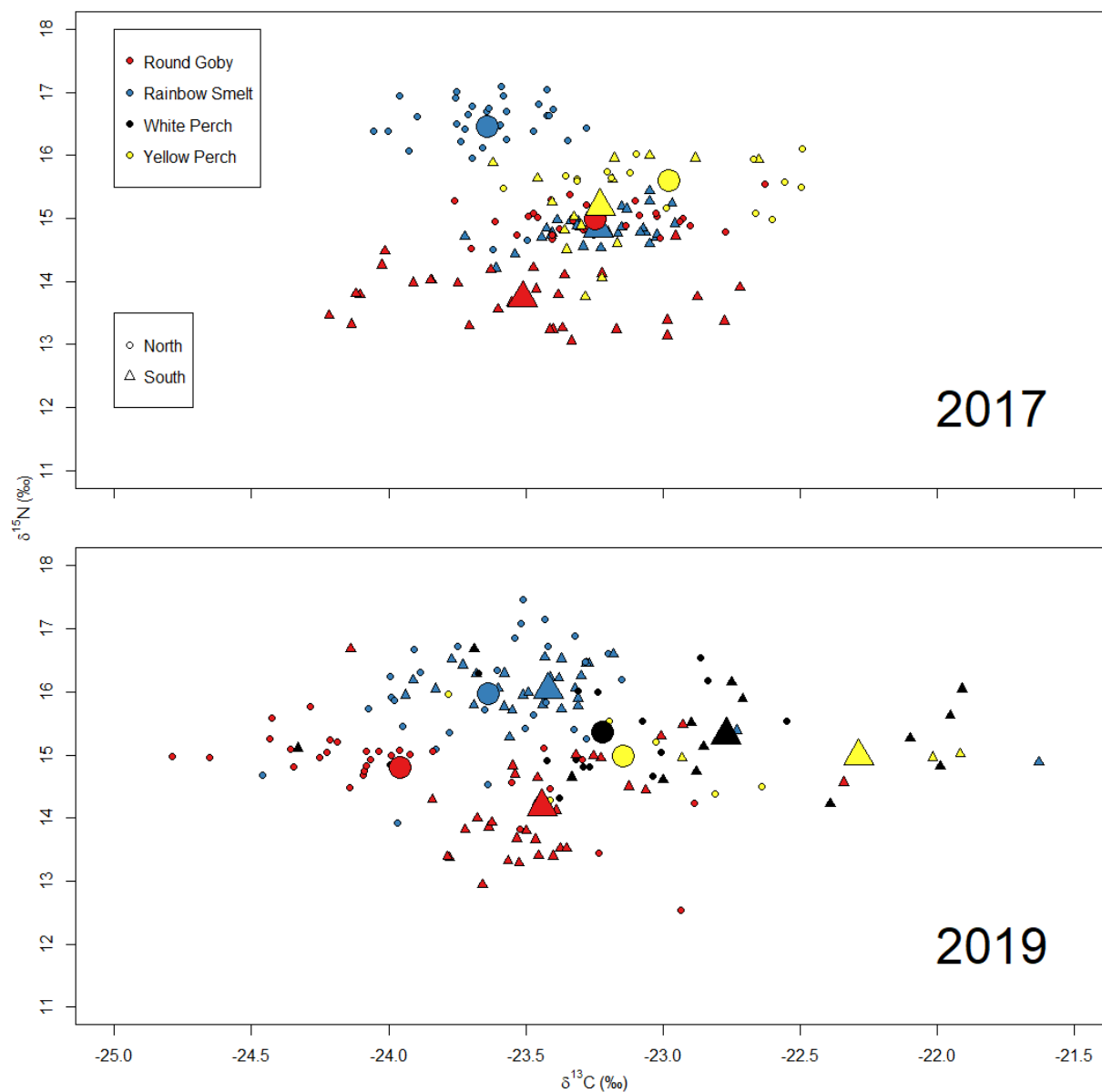


Figure 3.2. Carbon-nitrogen biplot for four fish species collected from spatially distinct regions of the central basin of Lake Erie during the summers of 2017 and 2019. Filled circles represent samples originating from the southern region. Filled triangles represent samples originating from the northern region. Large shapes denote group means.

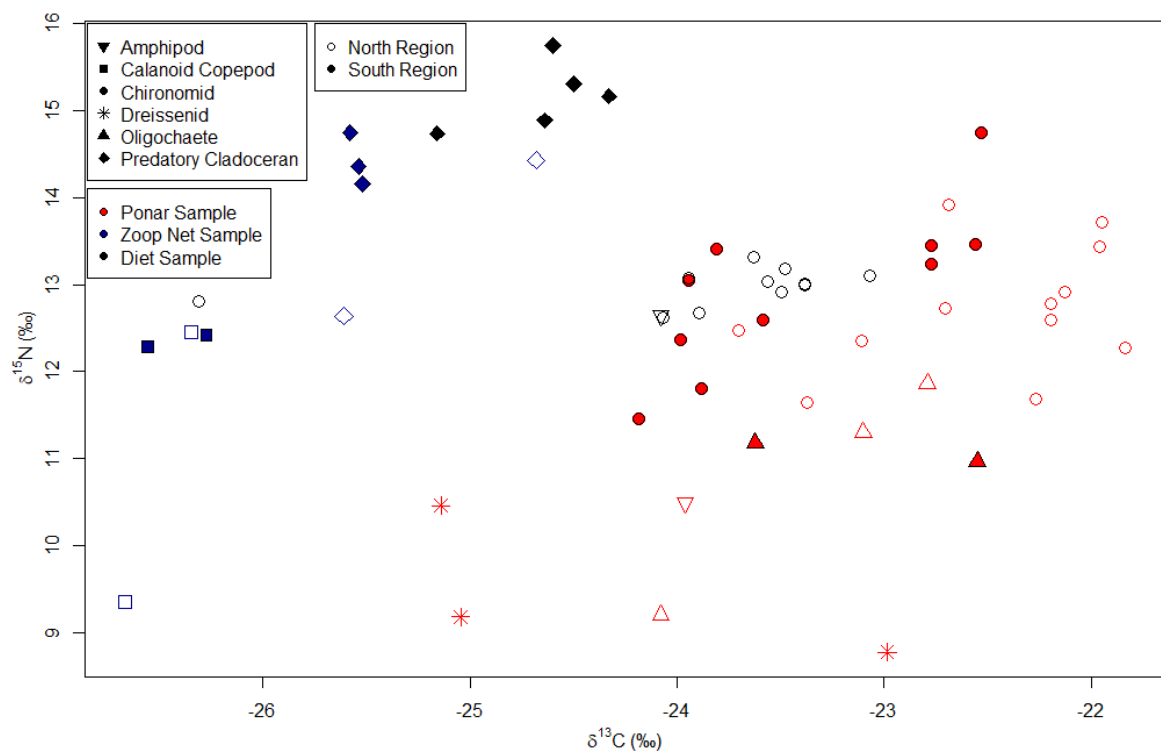


Figure 3.3. Carbon and nitrogen stable isotope ratios for lower trophic (benthic invertebrate and zooplankton) samples collected in distinct regions of the Lake Erie central basin during the summer of 2019. Symbol type indicates taxa. Symbol color indicates collection method. Open and closed symbols denote samples collected from the northern and southern regions, respectively. Note: All three dreissenid samples were collected in the northern region.

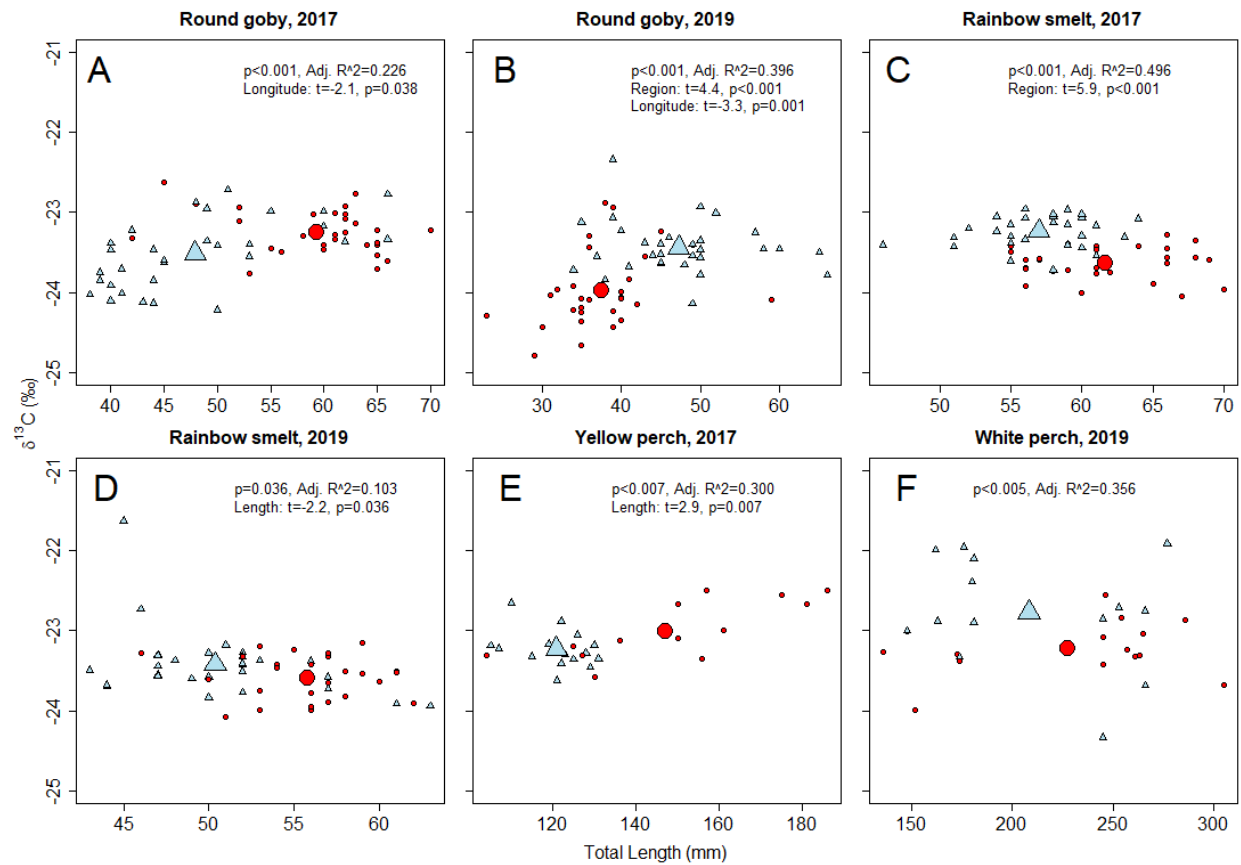


Figure 3.4. $\delta^{13}\text{C}$ by total length for each of six groups that were subjected to analysis of covariance. Red circles indicate samples from the northern region. Blue triangles indicate samples from the southern region. Statistics displayed on each subplot describe overall model statistics (first line) and significant explanatory variables (any subsequent lines). Interaction term only included in final models if significant. Large symbols denote group means.

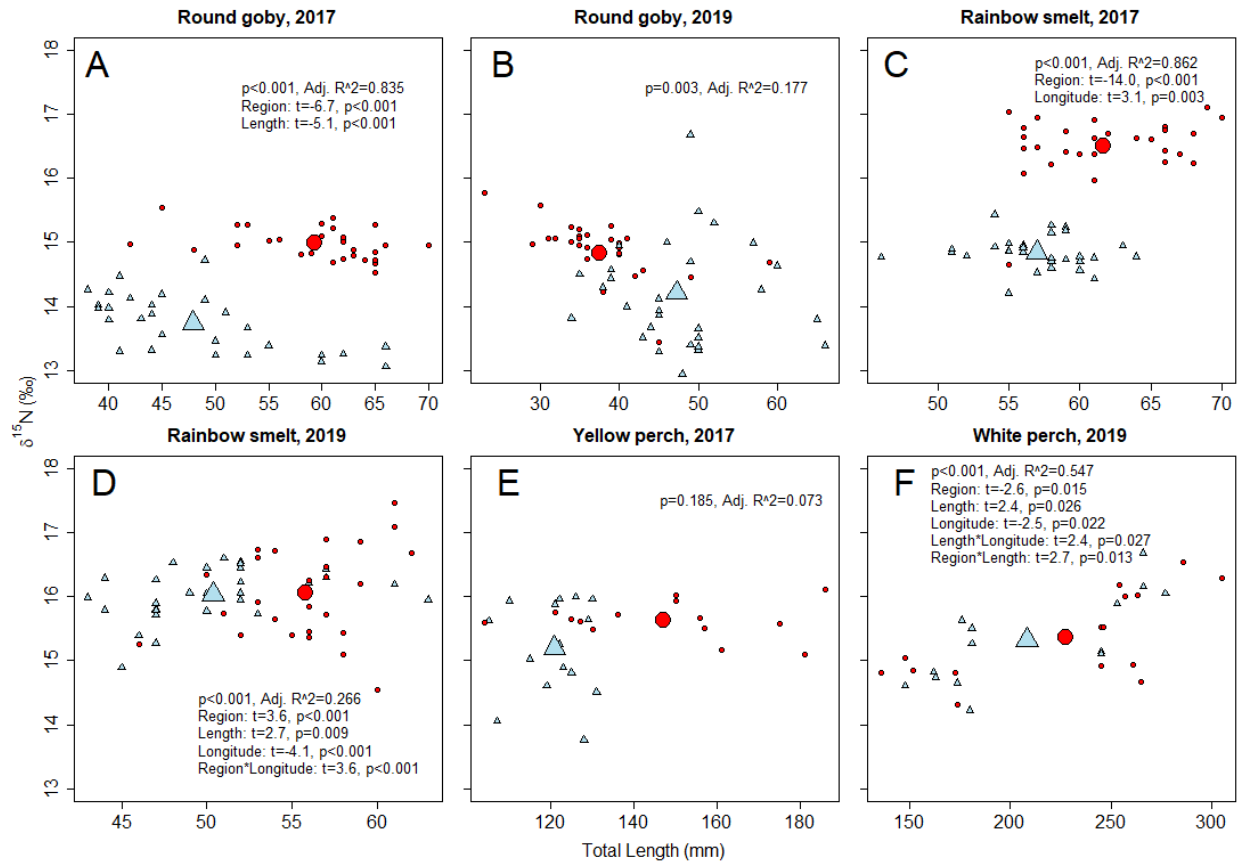


Figure 3.5. $\delta^{15}\text{N}$ by total length for each of six groups that were subjected to analysis of covariance. Red circles indicate samples from the northern region. Blue triangles indicate samples from the southern region. Statistics displayed on each subplot describe overall model statistics (first line) and significant explanatory variables (any subsequent lines). Interaction term only included in final models if significant. Large symbols denote group means.

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APPENDIX

Chironomids were the only lower trophic taxa with a large enough sample size to conduct dedicated statistical comparisons of isotopic ratios. All 33 chironomids (23 North, 10 South) were collected in 2019. Welch's two-sample t-tests were conducted to test for significant difference between the northern and southern groups, both with and without the inclusion of the 11 (11 North, 0 South) chironomids retrieved and processed from stomach contents. Values of $\delta^{13}\text{C}$ did not significantly differ between the northern and southern populations when stomach content individuals were included ($p = 0.3902$, $t = 0.874$, north mean = -23.1‰ , south mean = -23.4‰) but did significantly differ when stomach content individuals were excluded ($p < 0.01$, $t = 3.274$, north mean = -22.5‰ , south mean = -23.4‰) (Figure A1). Values of $\delta^{15}\text{N}$ did not significantly differ between the northern and southern populations when stomach content individuals were included ($p = 0.714$, $t = -0.376$, north mean = 12.8‰ , south mean = 13.0‰) or excluded ($p = 0.508$, $t = 0.677$, north mean = 12.7‰ , south mean = 13.0‰) (Figure A1). Results may indicate that using samples collected from the stomach contents of consumers could introduce bias to the measured isotopic ratios of carbon.

$\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were also plotted against longitude (similar to how they were plotted against total length in Figures 4 and 5). Model statistics are not displayed as they are identical to those in Figures 4 and 5; this is simply another way to visualize the same ANCOVA output.

Table A.1. Complete model statistics for all six $\delta^{13}\text{C}$ ANCOVA models. Directionality of the effect for “Region” is relative to the southern region (i.e., a negative estimate for region indicates that the southern region displayed more depleted values of $\delta^{13}\text{C}$). Only significant interaction terms displayed in tables.

VARIABLE	ESTIMATE	STD. ERROR	T VALUE	P
ROUND GOBY, 2017				
F = 6.742_{3,56}, P < 0.001, ADJ. R² = 0.226				
Region	0.338	0.231	1.463	0.149
Total length	0.009	0.006	1.509	0.137
Longitude	-2.077	0.098	-2.124	0.038
ROUND GOBY, 2019				
F = 13.67_{3,55}, P < 0.001, ADJ. R² = 0.396				
Region	1.682	0.381	4.42	<0.001
Total length	0.002	0.007	0.339	0.736
Longitude	-1.082	0.352	-3.328	0.002
RAINBOW SMELT, 2017				
F = 20.04_{3,55}, P < 0.001, ADJ. R² = 0.496				
Region	0.463	0.078	5.915	<0.001
Total length	0.004	0.006	0.652	0.517
Longitude	-0.273	0.291	-0.937	0.353
RAINBOW SMELT, 2019				
F = 3.064_{3,51}, P = 0.036, ADJ. R² = 0.103				
Region	0.029	0.111	0.265	0.792
Total length	-0.024	0.011	-2.157	0.036
Longitude	-0.113	0.126	-0.902	0.371
YELLOW PERCH, 2017				
F = 5.0_{3,25}, P = 0.007, ADJ. R² = 0.3				
Region	-0.026	0.427	-0.061	0.952
Total length	0.009	0.003	2.959	0.007
Longitude	0.058	0.675	0.087	0.932
WHITE PERCH, 2019				
F = 7.762_{5,23}, P < 0.001, ADJ. R² = 0.547				
Region	-97.606	49.037	-1.99	0.058
Total length	0.003	0.002	1.209	0.238
Longitude	0.29	0.601	0.485	0.632

Table A.2. Complete model statistics for all six $\delta^{15}\text{N}$ ANCOVA models. Directionality of the effect for “Region” is relative to the southern region (i.e., a negative estimate for region indicates that the southern region displayed more depleted values of $\delta^{15}\text{N}$). Only significant interaction terms displayed in tables.

VARIABLE		ESTIMATE	STD. ERROR	T VALUE	P
ROUND GOBY, 2017					
F = 100.8_{3,56}, P < 0.001, ADJ. R² = 0.835					
	Region	-1.339	0.2	-6.676	<0.001
	Total length	-0.028	0.005	-5.125	<0.001
	Longitude	-0.97	0.848	-1.143	0.258
ROUND GOBY, 2019					
F = 5.17_{3,55}, P = 0.003, ADJ. R² = 0.177					
	Region	-1.25	0.711	-1.758	0.084
	Total length	-0.018	0.013	-1.419	0.162
	Longitude	0.743	0.607	1.224	0.226
RAINBOW SMELT, 2017					
F = 122.2_{3,55}, P < 0.001, ADJ. R² = 0.862					
	Region	-1.878	0.134	-14.058	<0.001
	Total length	0.011	0.011	1.024	0.31
	Longitude	1.538	0.496	3.099	0.003
RAINBOW SMELT, 2019					
F = 5.88_{4,50}, P < 0.001, ADJ. R² = 0.266					
	Region	104.783	29.451	3.558	<0.001
	Total length	0.041	0.015	2.693	0.009
	Longitude	-1.178	0.286	-4.113	<0.001
	Region: Longitude	1.28	0.36	3.552	<0.001
YELLOW PERCH, 2017					
F = 1.735_{3,25}, P = 0.185, ADJ. R² = 0.073					
	Region	-1.344	0.927	-1.45	0.16
	Total length	0.002	0.007	0.233	0.818
	Longitude	1.457	1.464	0.996	0.329
WHITE PERCH, 2019					
F = 7.762_{5,23}, P < 0.001, ADJ. R² = 0.547					
	Region	-6.994	2.659	-2.631	0.015
	Total length	3.026	1.275	2.373	0.026
	Longitude	-9.553	3.895	-2.453	0.022
	Total length: Longitude	0.037	0.016	2.366	0.027
	Region: Total Length	0.028	0.011	2.683	0.013

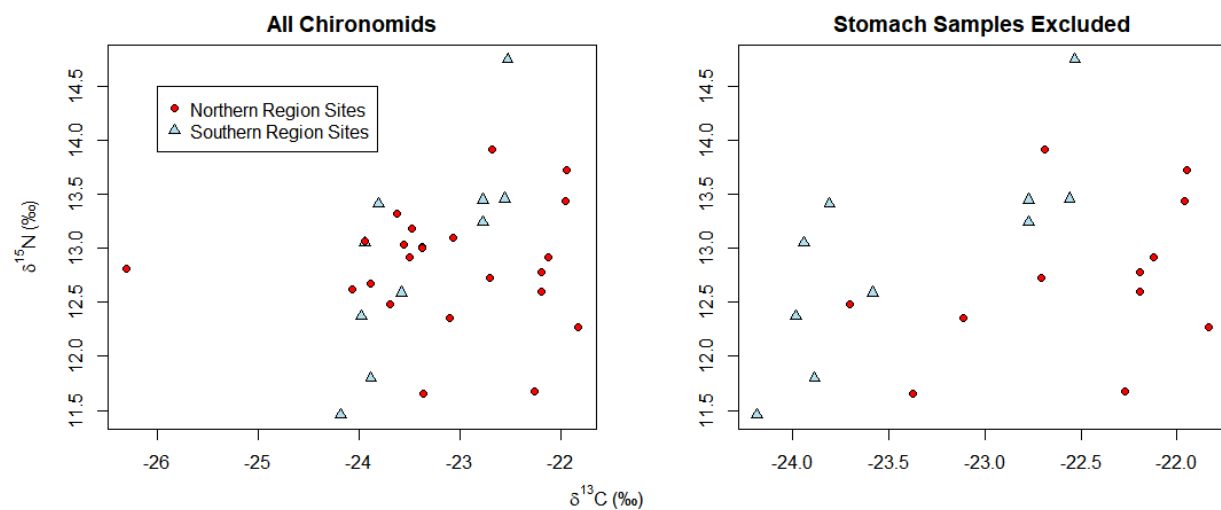


Figure A.1. Carbon-nitrogen biplot for chironomid larvae collected from the central basin of Lake Erie in summer 2019. Samples were collected either by benthic PONAR grabs or by processing undigested chironomids found in the stomachs of predatory fishes (e.g., white perch, round goby). Left panel shows the plot for all individual chironomids collected and processed from both methods. Right panel shows the plot for only individuals collected from benthic substrate using the Ponar grab.

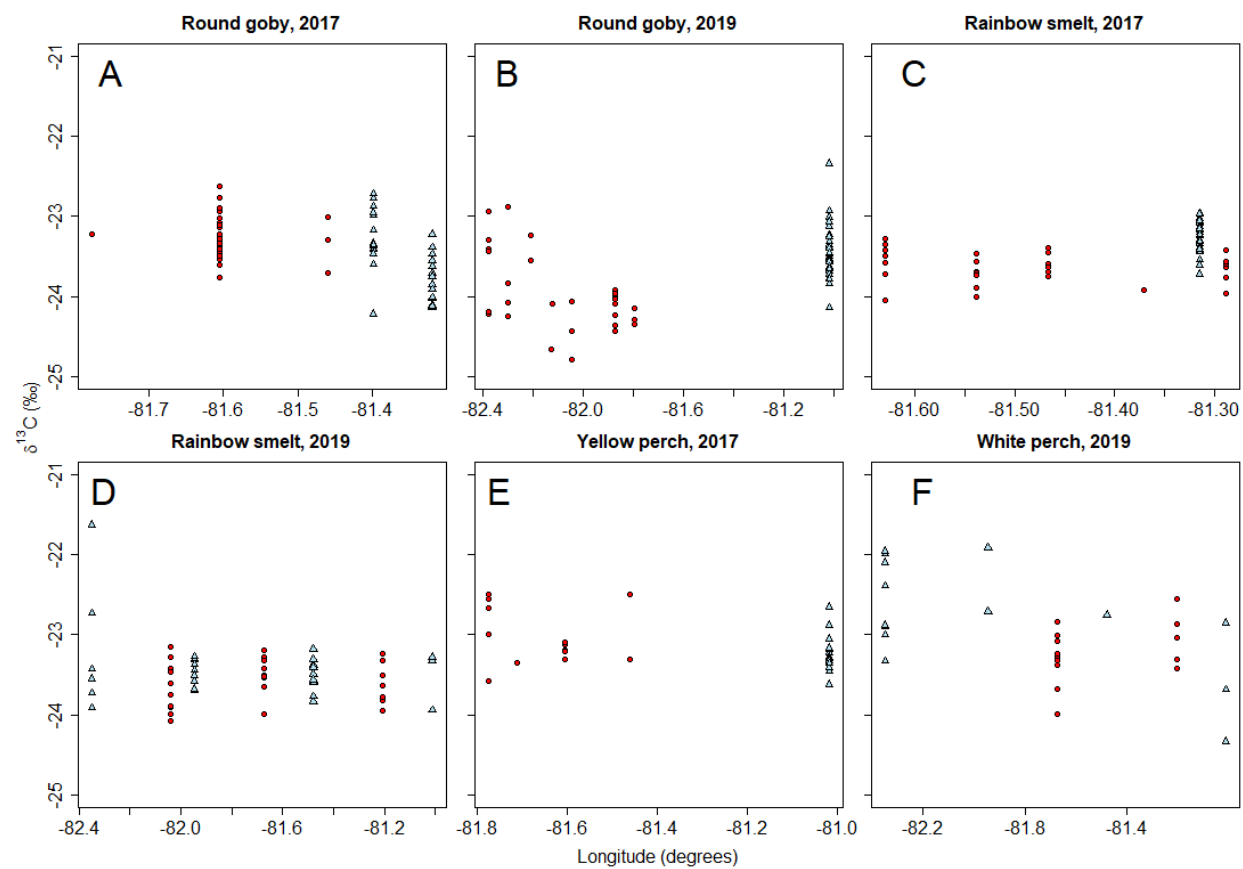


Figure A.2. $\delta^{13}\text{C}$ by longitude for each of six groups that were subjected to analysis of covariance. Red circles indicate samples from the northern region. Blue triangles indicate samples from the southern region.

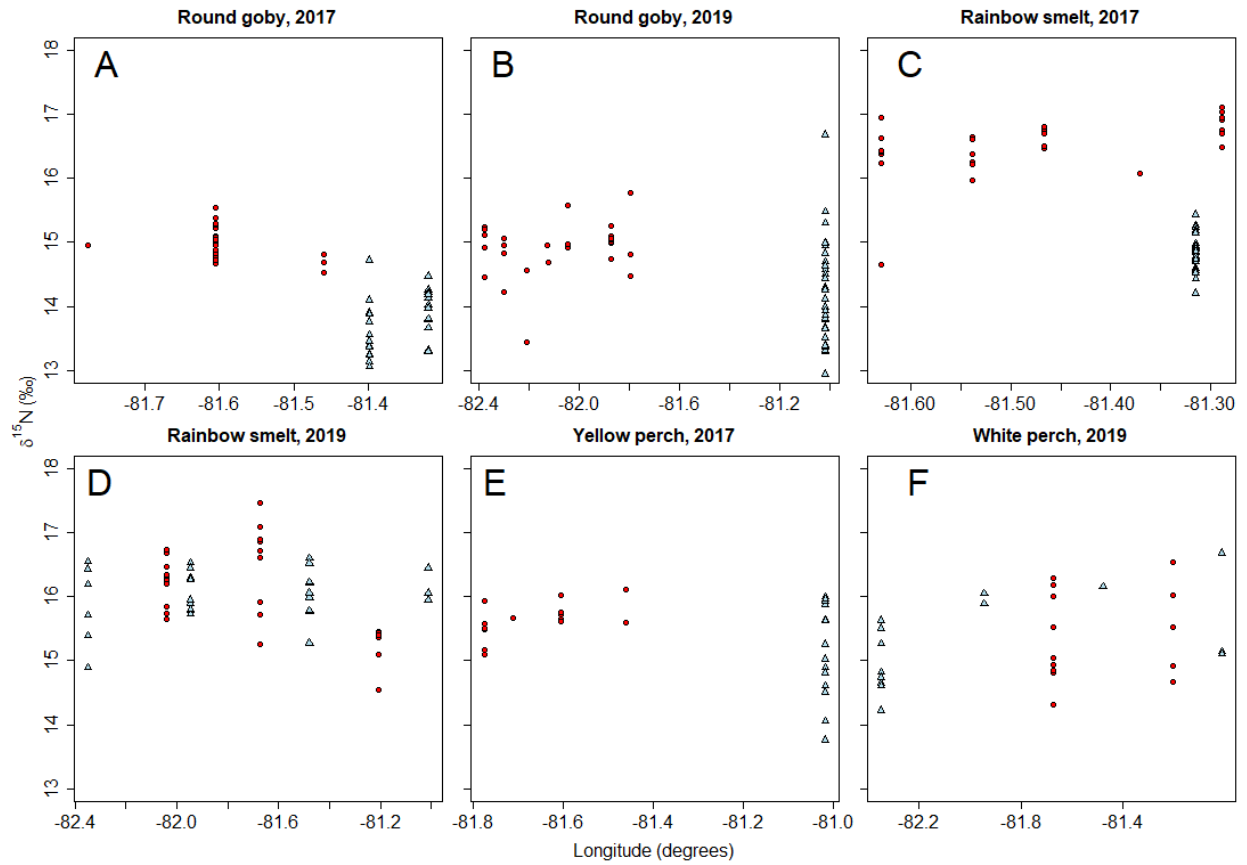


Figure A.3. $\delta^{15}\text{N}$ by longitude for each of six groups that were subjected to analysis of covariance. Red circles indicate samples from the northern region. Blue triangles indicate samples from the southern region.