# Yellow Perch Distributions and Feeding Ecology in Response to Hypoxia in Lake Erie's Central Basin

Thesis

Presented in Partial Fulfillment of the Requirements for the Degree Master of Science in

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By

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#### Abstract

Hypoxia, or low concentration of dissolved oxygen in the water, is becoming a more frequent and extensive phenomenon in many aquatic ecosystems around the world, impacting the ecology of lakes, estuaries, and marine fishes. This often-recurring state of low oxygen degrades habitat quality, affects fish physiology, and can lead to changes in the behavior and distribution of species. Hypoxia can alter predator-prey dynamics through species-specific responses to low oxygen and changes spatiotemporal distributions of populations. The central basin of Lake Erie experiences seasonal hypolimnetic hypoxia every year due to a combination of natural thermal stratification and human practices. Lake Erie supports ecologically important and lucrative recreational and commercial fisheries, so considerable research has gone into understanding the impacts of hypoxia on the Lake Erie ecosystem. In the last decade, adult yellow perch (Perca flavescens) catch in the central basin of Lake Erie has significantly declined, raising questions about the drivers of decreases in yellow perch catch. The goal of this research was to gain better understanding about how hypoxia and other environmental variables associated with the hypoxic season (i.e. higher temperatures) influence adult (2+) yellow perch distributions and overall abundance as well as their diets and foraging behavior. Towards this goal, we conducted hydroacoustic surveys, analyzed data from 2021 annual Ohio Department of Natural Resources – Division of Wildlife trawl surveys,

collected data on environmental variables, quantified adult yellow perch stomach contents, and collected data on zooplankton and benthic macroinvertebrates. In the first chapter, we used paired bottom trawl-hydroacoustic surveys to investigate the effects of hypoxia on adult yellow perch distributions. We compared where yellow perch were located in the water column (both fish and site depth) and yellow perch densities between sampling months. The second chapter further explores behavioral responses to hypoxia through a diet study. In this thesis, I show that hypoxia influences adult yellow perch in various ways. First, I show evidence that during hypoxia, fish are higher in the water column, often above the thermocline, where dissolved oxygen levels are higher. We also found that yellow perch not only moved vertically, but they also shifted their general horizontal location and formed aggregations at shallower site depths during hypoxia. Our data also suggest that yellow perch most likely inhabited hypolimnetic waters during hypoxia. Hydroacoustic targets consistent with adult yellow perch were detected in hypoxic waters and we found evidence that yellow perch consumed benthic prey during hypoxic months. This research supports previous findings suggesting yellow perch conduct hypoxic foraging forays and aggregate in waters adjacent to hypoxia that contain higher dissolved oxygen. We demonstrate that hydroacoustics can successfully be used to study the effects of hypoxia on yellow perch populations in Lake Erie. Using in situ target strength information gained from hydroacoustics along with fish catch data will help researchers better understand how changing environmental conditions impact the Lake Erie fish population. Understanding how yellow perch and their predators and prey

respond to novel conditions is important for properly managing the fisheries and protecting the lake's resources.

# Dedication

To Giovanni Aletto, for always showing enthusiasm about "Bintotrephies", but most importantly, for your support, encouragement, and unwavering love.

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## Publications

Hoch, J. M., Cabanelas Bermudez, A., Coury, O. S., Donahou, A. S., Jeffers, C. N.,
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# Fields of Study

Major Field: Evolution, Ecology & Organismal Biology Specialization: Aquatic Ecology

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## Chapter 1. Exploring the Influence of Seasonal Hypoxia on Distributions of Adult Yellow Perch in Lake Erie's Central Basin

## Introduction

Globally, eutrophication-driven hypoxia (dissolved oxygen (DO)  $\leq 2 \text{ mg L}^{-1}$ ) has increased in magnitude, duration, and frequency in many freshwater, marine, and estuarine environments (Caddy 1993; Nixon 1995; Carpenter et al. 1998; Cloern 2001; Diaz 2001; Diaz and Rosenberg 2008); the consequences of these changes to fish communities and catch remain uncertain. Chronic seasonal hypoxic events are becoming more prevalent (Breitburg et al. 2018) in the Gulf of Mexico (Rabalais et al. 2002; Turner et al. 2008; Hazen et al. 2009; Zhang et al. 2009, 2014), Chesapeake Bay (Boynton et al. 1995; Boesch et al. 2001; Hagy et al. 2004; Costantini et al. 2008; Ludsin et al. 2009; Kraus et al. 2015b), the Neuse River Estuary (North Carolina) (Eby and Crowder 2002; Taylor and Rand 2003; Taylor et al. 2007), and the Laurentian Great Lakes (Blumberg and Di Toro 1990; Vanderploeg et al. 2009b; Scavia et al. 2014), often resulting in altered fish behavior and ecosystem function (Craig 2012; Chamberlin et al. 2020). Hypoxic events are expected to worsen in lakes owing to higher water temperatures resulting from anthropogenic climate change that leads to earlier and longer stratification in the summer and later fall turnover (Scavia et al. 2014; Watson et al. 2016).

Understanding how fish abundance and distribution in the water column is influenced by

seasonal hypoxic events will allow us to better understand the consequences of changing environmental conditions on fish communities and the influence this has on the fisheries.

Hypoxia is a stressor for many fish and aquatic species, eliciting physiological responses that can alter the behavior of individuals (Breitburg et al. 1997, 2002). Although direct mortality of fish can occur as a result of hypoxia exposure (Rao et al. 2014), these events are rare and sublethal effects are much more common (Breitburg 2002; Shimps et al. 2005) but poorly understood (Marcus et al. 2004; Zhang et al. 2009; Hrycik et al. 2017). Sublethal effects of hypoxia exposure can lead to physiological responses (Wu 2002; Fitzgibbon et al. 2007; Taylor et al. 2007) such as reduced feeding, slower growth (Priede 1985; Chabot and Dutil 1999; Petersen and Phil 1995; Pichavant et al. 2000; Breitburg 2002; Eby et al. 2005; Stierhoff et al. 2006; Hrycik et al. 2017; Stone et al. 2020), and reduced reproductive potential (Wu et al. 2003; Thomas et al. 2007; Thomas and Rahman 2009; Wu 2009; Arend et al. 2011). Fish reproductive success may be impacted due to changes in courtship behaviors, mate choice, reduced reproductive efforts, and retarded gonad, embryonic, and larval development (Zhou 2001; Breitburg et al. 2003; Wu et al. 2003; Shang and Wu 2004). These physiological responses to reduced habitat quality can displace fish into marginal habitats (Coutant 1985; Hrycik et al. 2017). Mobile aquatic species, such as fish, can often detect low DO and behaviorally respond to these changes in habitat quality. In contrast to non-mobile species, fish can adjust their position in the water column to avoid hypoxic waters (Magnuson et al. 1985; Suthers and Gee 1986; Pihl et al. 1991; Eby and Crowder 2002; Bell and Eggleston 2005; Craig and Crowder 2005; Stierhoff et al. 2006; Hazen et al. 2009) making it more challenging to

understand how seasonal hypoxia influences fish behavior and the effects this has on the food web.

Behavioral responses to hypoxia include complete avoidance of hypoxic areas (Aku et al. 1997; Ludsin et al. 2009; Zhang et al. 2009; Craig 2012; Chamberlin et al. 2020; Stone et al. 2020), foraging forays into hypoxic zones to feed on the benthos (Rahel and Nutzman 1994; Taylor et al. 2007; Roberts et al. 2009, 2012), and use of hypoxic areas as a refuge from predators (Stierhoff et al. 2006; Hedges and Abrahams 2015; Vejrík et al. 2016). These physiological and behavioral responses of fish to hypoxia can ultimately lead to changes in the spatial (Craig et al. 2005; Craig and Bosman 2013) and temporal distribution of individuals and populations (Craig and Crowder 2005; Zhang et al. 2009; Campbell and Rice 2014). Changes in fish behavior as a result of hypoxia can potentially result in altered predator-prey interactions (Pihl et al. 1992; Kolar and Rahel 1993; Breitburg et al. 1997; Nestlerode and Diaz 1998; Aku and Tonn 1999; Shoji et al. 2005; Costantini et al. 2008), habitat use (Ludsin et al. 2009; Stone et al. 2020), community composition (Smale and Rabeni 1995; Killgore and Hoover 2001), and food web structure and function (Breitburg et al. 1997; Breitburg 2002; Eby and Crowder 2002; Pothoven et al. 2012). Avoidance of hypoxic areas can result in higher fish densities near the edges of hypoxia. Some species aggregate at the horizontal edge of hypoxic zones (Craig, 2012) and move vertically to the normoxic mixed layer (Magnuson et al. 1985; Aku et al. 1997; Taylor and Rand 2003; Bell and Eggleston 2005; Taylor et al. 2007; Hazen et al. 2009; Ludsin et al. 2009; Roberts et al. 2009; Vanderploeg et al. 2009a, 2009b; Zhang et al. 2009; Stone et al. 2020).

Aggregations of fish along the hypoxic edge can increase their susceptibility to catch from both commercial and recreational fishers (Kraus et al. 2015a; Chamberlin et al. 2020; Stone et al. 2020). These changes in habitat use and fish distributions can result in higher catches depending on conditions (Coutant 1985; Craig and Crowder 2005), raising concern over population estimates since surveys conducted during hypoxia can result in overestimates of abundance (Rose and Kulka 1999; Kraus et al. 2015a; Chamberlin et al. 2020). How these organismal responses influence catches in the commercial and recreational fisheries are not fully understood (Kraus et al. 2015a). Higher fishery catches and erroneous fishery-independent recruitment estimates during hypoxic events can potentially lead to overfishing and mismanagement of the fisheries.

While the causes of increases in hypoxia in freshwater and coastal systems are well studied, their consequences to the behavior of Lake Erie yellow perch (*Perca flavescens*) and the resulting effects on the fisheries are still poorly understood. In Lake Erie, hypoxia is known to affect the spatial distribution of yellow perch (Roberts et al. 2009, 2011, 2012; Chamberlin et al. 2020), which supports one of the largest commercial fisheries and the second largest recreational fishery in the lake (ODNR-DOW 2022; Francis et al. 2020). Changes in the spatial distribution of yellow perch in response to hypoxic events may affect catch rates in these fisheries. Previous researchers and management groups, such as the Lake Erie Yellow Perch Task Group, have used a combination of fishery-independent surveys (trawl and gill net), commercial harvest, and recreational angler catch rates to effectively assess populations in the Great Lakes. In recent years, however, the agreement among these indicators of yellow perch abundance in the central basin of Lake Erie has decreased (Yellow Perch Task Group 2022). Yellow perch populations have been on a downward trajectory in the central basin of Lake Erie since approximately 2012 (Chamberlin et al. 2020; Figure 1.1). Commercial yellow perch harvest in the central basin has been steadily decreasing since 2013, after reaching historical highs in previous years (Figure 1.1). Recreational catch of yellow perch has been decreasing since 2014, reaching an all-time low in 2017 and continuing to decline. The conditions driving these changes in harvest are poorly understood, raising concerns about the continued effectiveness of current monitoring protocols (Rose and Kulka 1999; Hosack et al. 2014). If anglers are targeting yellow perch in areas and at depths in which perch have historically been feeding, recent habitat and diet shifts may be causing a mismatch between angler effort and yellow perch presence. A better understanding of spatiotemporal distributions and habitat use of yellow perch as a function of hypoxia and temperature is important to understanding recent trends in the sport fishery. The overarching goal of this research is to shed light on how hypoxia affects yellow perch distribution and abundance in the central basin of Lake Erie. To meet these objectives, we investigated and quantified how adult yellow perch populations respond to changing DO and temperatures using coupled hydroacoustics surveys and bottom trawling. I hypothesized that adult yellow perch would respond to hypoxia by changing their distributions in the water column, moving away from hypoxic water, with distinct fish aggregations detected during our hydroacoustic surveys.

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#### Methods

#### Study design

Acoustic surveys were conducted from the *R/V Carmen* during the daytime<sup>1</sup> in the central basin of Lake Erie at two areas (Chagrin-Fairport and Perry, OH) in July (mild-hypoxia), August (peak hypoxia), and November (post-hypoxia, after fall turnover) 2021 (Figure 1.2). We were specifically interested in the mid-summer to mid-fall months, as these are the months in which recreational fishing for yellow perch and hypoxia-driven habitat shifts are most likely to conflict. Due to weather-driven limitations in sampling, we were unable to survey during the daytime in September and October. The survey design included 12 sites at each location across four 5-m depth strata (5-10, 10-15, 15-20, >20 m), with 3 transects per depth stratum. Surveying during various conditions throughout the field season (from late summer through late fall) and at different depths (offshore vs. inshore) allowed us to examine how yellow perch distributions and relative abundance are influenced by hypoxia at multiple sites. Shallower sites closer to shore exhibited more mixing whereas deeper offshore sites had relatively more stratification and a more distinct thermocline and hypoxic hypolimnion.

#### Environmental data

Vertical profiles of depth (m), water temperature (°C) and DO (mg/L) were recorded at the beginning and end of each acoustic transect using a YSI EXO2 multiparameter sonde (YSI Inc., Yellow Springs, Ohio), deployed from the water surface

<sup>&</sup>lt;sup>1</sup> Additional nighttime surveys were completed in September and October, but not included here. Those data are available upon request.

to the bottom. Temperature and DO were recorded every second and then averaged to 1m depth intervals for data analyses. Secchi readings were recorded, to the nearest 0.5 m, at the beginning of every transect to measure water transparency. Thermocline depths and mean epilimnion, metalimnion, and hypolimnion temperatures were calculated using the R package rLakeAnalyzer (v1.11.4.1; Winslow et al. 2019). This package calculates volumetrically weighted averaged epilimnion, metalimnion, and hypolimnion temperatures. When the lake was not stratified, the epilimnion depth was set to the deepest measured depth at that transect. Recorded field temperatures at each transect location were used to calculate speed of sound and absorption coefficients needed for hydroacoustic data processing.

#### Hydroacoustic data collection

Acoustic data were collected using a BioSonics DTX split-beam echosounder (BioSonics Inc., Seattle, Washington) with a 208 kHz transducer (beamwidth =  $6.8^{\circ}$ )<sup>2</sup>. Acoustic data collection settings included a pulse duration of 0.4 ms, a ping rate of 8 pings s<sup>-1</sup>, a -130 decibels (dB) collection threshold, -10 dB reduced power output (re 1 µPa at 1m depth), and with a time-varied-gain (TVG) of 40 log R. This down-looking transducer was mounted on the starboard side of the vessel and towed 1.4 m below the water surface.

<sup>&</sup>lt;sup>2</sup> Transducers with 70 kHz and 129 kHz were also used, though limitations on equipment availability did not allow us to use either one of those on all sample dates. The 208 kHz transducer was used on all sample dates and sites. The data from the other transducers are available from the Ohio Department of Natural Resources – Division of Wildlife.

Acoustic sampling was conducted at the same sites as the bottom trawls conducted by Ohio Department of Natural Resources – Division of Wildlife (ODNR-DOW) for a total of 10 min at each site at a speed of ~ 7.5 km/h. Acoustic data were georeferenced with an integrated Garmin GPS. The echosounder was calibrated three times throughout the field season in waters deeper than 15 m using a 36 mm tungstencarbide calibration sphere of known target strength (TS; TS = - 39.6 dB at 1480 m/s sound speed in ~ 20 °C freshwater), following the standard calibration methods of Foote et al. (1987).

#### Species Composition

We paired acoustic surveys with ODNR-DOW bottom trawling to validate species identities and fish size. Acoustic and trawl surveys were conducted the same day or within a few days of each other (Table 1.1). Coupling acoustic surveys with validation bottom trawls to explore the fine-scale distribution of fish has been successfully accomplished in previous studies (Roberts et al. 2009; Vanderploeg et al. 2009b) and the ODNR-DOW has completed a proof-of-concept study for age-2+ yellow perch in the central basin of Lake Erie (Mark DuFour, Great Lakes Science Center, USGS, unpublished data). We used trawl catch data and temperature profiles to inform our allocation of acoustic data to different fish species and sizes.

ODNR-DOW bottom trawls were conducted from the *R/V Grandon* and consisted of 10-min tows in waters deeper than 10 m and 5-min tows in depths less than 10 m at a cruising speed of 3.2 km/h, with a Yankee-style two-seam bottom trawl with a 1.7-m vertical opening, 10.4-m head rope, 25-mm bar mesh in the cod end, 13-mm stretched mesh liner, and 25.4-cm roller gear (ODNR-DOW 2022). Fish caught in trawls were counted, identified to species, and measured (TL) to the nearest mm. Trawl surveys provided valuable information about size composition and species abundance estimates allowing us to estimate hydroacoustic species abundance. Raw trawl catches were converted into catch per hectare by species to compare with hydroacoustic abundance estimates. Densities of adult yellow perch in each hydroacoustic sample were estimated by b multiplying the proportion of adult yellow perch in the trawl sample associated with each hydroacoustic survey. It is not possible to identify species with hydroacoustics alone; pairing hydroacoustic and trawl surveys allowed us to apportion fish to species based on TS to total length (TL) relationships and provided information on the fine-scale distributions of yellow perch in the central basin of Lake Erie.

#### Hydroacoustic data processing

Acoustic data were collected with the BioSonics software Visual Acquisition 6 (DTX, BioSonics Inc., Seattle, Washington) as .DT4 files. These data were then processed using Echoview® 12.0.304 (EV; Echoview Software Pty Ltd, Hobart, Australia) following the Standard Operating Procedures for Fisheries Acoustic Surveys in the Great Lakes (Parker-Stetter et al. 2009). Hydroacoustic surveys allowed us to quantify yellow perch densities and distributions throughout the water column in targeted sampling areas and provided abundance estimates during normoxic and hypoxic conditions using the Echo Integration method, which relates fish density to the backscattered energy to obtain fish biomass estimates (Simmonds and MacLennan 2005). M. DuFour (unpublished data) provided an analysis in support of the feasibility of identifying Lake Erie yellow perch based on TS in hydroacoustic samples.

In EV, the lake bottom was automatically detected using the bottom detection algorithm, and a backstep of 0.5 m above the detected bottom was applied. The top 2.4 m of the water column, including 1.4 m tow depth and transducer near field range (~1 m) was excluded. All surface and bottom lines were inspected and corrected manually when necessary. Data below the backstep bottom line and above the surface exclusion line were excluded during analyses. An epilimnion line was applied to each echogram automatically in EV. Each line was manually checked and edited based on calculated mean thermocline depths from our field water column profiles. After the epilimnion line was defined, regions were identified and classified as epilimnion (above the epilimnion line) and hypolimnion (below epilimnion line). When no thermocline was present, the entire transect was defined as an epilimnion region.

Fish abundance and size were estimated through TS analysis and echo integration. Single targets were detected using the split beam (method 2) algorithm in EV. To ensure only single targets were identified and exclude small targets we used the following single echo detection (SED) parameters: a TS threshold of -64 dB (re 1 m<sup>2</sup>), a volume backscattering strength ( $S_v$ ) threshold of -70 dB, a pulse length determination level of 6 dB, a minimum normalized pulse length of 0.6, a maximum normalized pulse length of 1.5, an angular standard deviation of 0.6, and a maximum beam compensation of 6 dB. To interpret the observed echoes, we used in situ TS values to calculate average backscattering cross sections ( $\sigma_{bs} = 10^{\frac{TS}{10}}$ ), which were then used to scale area backscattering coefficients (ABC) into fish abundance. Our EV dataflow also included a Sawada index (fish per acoustic sampling volume [N<sub>v</sub>]) filter criteria, where only cells with Nv < 0.1 (Sawada et al. 1993; Warner et al. 2002; Rudstam et al. 2003, 2009) and a ratio of multiple echoes (M) < 70 (Sawada et al. 1993) were kept, to avoid classifying multiple targets as single targets and remove biased in situ TS.

In situ TS was used for separating fish targets into size groups (allowing us to distinguish young vs adult fish), which was validated through bottom trawling. To determine an appropriate TS threshold for adult yellow perch ( $\sim > 107 \text{ mm TL}$ ), we compared trawl catch length histograms (Figure 1.3) with hydroacoustic TS histograms (Figure 1.4) to apportion fish species and sizes observed in the acoustic surveys (Rudstam et al. 2009; DuFour et al. 2018). A distinct hump in TS count frequencies from approximately -48 dB to -37 dB and similar pattern in yellow perch size, with a drop in frequency in > 200 mm TL fish, matches previous work (M. DuFour, unpublished data; DuFour et al. 2018). To verify that -48 dB most likely represents adult yellow perch and is an appropriate TS threshold for our analyses, we converted in situ TS data to fish size (TL) (Figure 1.5; Hrabik et al. 2006). Due to lack of a published empirical TS-to-TL equation for Lake Erie yellow perch and Love's (1977) generic dorsal-aspect TS-TL equation being unsuitable for our species of interest, we used a modified version of Love's (1977) generic equation and Mehner's (2006) equation based on Lake Erie yellow perch information (MacLennan and Menz 1996; DuFour et al. 2021). To estimate target

length of fish based on TS, we regressed compensated TS to TL using a function derived from Lake Erie yellow perch (M. DuFour, unpublished data),

 $TS = 37.22 \log_{10} (TL) - 94.41$ 

We back-calculated TL from our TS data

TL (cm) =  $10^{((TS + 94.41)/37.22)}$ 

We found agreement between the TL histogram derived from in situ Lake Erie TS data (Figure 1.5) and the TL histogram derived from the trawl sample (Figure 1.3), with similar patterns in distributions. This comparison of in situ TS with trawl catches suggested that a TS < -48 dB most likely represents adult yellow perch in the 147 – 307 mm size range. Following this approach, we changed our thresholds in EV to -48 dB and -54 dB for TS and S<sub>v</sub>, respectively. S<sub>v</sub> was then used to calculate relative fish biomass (Vanderploeg et al. 2009b; Egerton et al. 2018), where higher S<sub>v</sub> values correspond to higher fish biomass (Simmonds and MacLennan 2005; Taylor et al. 2007; Vanderploeg et al. 2009b). The S<sub>v</sub> in conjunction with mean TS and ABC values allowed us to determine the spatial distribution of fish in the transects. We compared acoustic and trawl density and apportioned acoustic data based on trawl catches (multiplying acoustic density by proportion of adult yellow perch in trawls). After echograms were processed in Echoview, data were exported and statistical analyses were conducted in R Statistical Software (v4.2.1; R Core Team 2022).

#### Results

#### Hypoxia

We conducted surveys before, during, and after hypoxia to compare fish abundance and distributions during different environmental conditions. July represented our pre-hypoxic sampling conditions with some mild hypoxia detected. In July, we detected mild hypoxia (2 < DO < 4 mg/L) at two trawl locations and four hydroacoustic sites. As the summer progressed and water temperatures increased, accompanied by calmer conditions, the lake became more stratified and hypoxic conditions intensified. DO readings below 2 mg/L were frequently detected in trawls conducted during August, our peak-hypoxic season. During peak hypoxia, 46% of the hydroacoustic sites had a hypolimnion mean DO  $\leq 2$  mg/L, with a minimum detected value of 0.33 mg/L in August. We assumed that, during hypoxia, most of the water was hypoxic below the thermocline. The maximum thickness of the bottom hypoxic layer was 4.1 m. In November, the lowest DO value was 8.8 mg/L and most of the water column had mean DO > 10 mg/L, confirming post-stratification conditions. Water column temperature profiles and, in particular, mean temperatures in July and August were similar but August had a more pronounced thermocline (Figure 1.6). After the fall turnover, waters were well mixed and no thermocline was detected. In November, mean surface temperatures were ~10 °C colder than in July and August.

#### Bottom trawl catches

Bottom trawl catches were used to gain information about species composition, total lengths, and fish ages necessary for hydroacoustic species apportionment. The catch results discussed here represent trawls that had an associated hydroacoustic transect. More comprehensive information about 2021 ODNR-DOW bottom-trawl surveys can be found in ODNR-DOW (2022). The ODNR-DOW trawl samples used in this study included 22,330 individual fish encompassing 20 species, with the post-hypoxic month (November) having the highest species diversity. The most abundant species in trawl catches were rainbow smelt (Osmerus mordax), round goby (Neogobius melanostomus), walleye (Sander vitreus), white perch (Morone americana), and yellow perch (Figure 1.7). Smallmouth bass (*Micropterus dolomieu*) were present only in July catches; sea lamprey (*Petromyzon marinus*), lake trout (*Salvelinus namaycush*), and golden redhorse (Moxostoma erythrurum) were unique to August trawls; and gizzard shad (Dorosoma *cepedianum*), carp (*Carassius auratus*), brown bullhead (*Ameiurus nebulosus*), alewife (Alosa pseudoharengus), and emerald shiners (Notropis atherinoides) were caught only in November. Trawl catch rates were highest during August (Figure 1.8), including yellow perch whose relative abundance peaked during the peak-hypoxic month, with 14% of the August catch being yellow perch.

A total of 1,912 yellow perch (all ages) were caught in trawls: 372 in July, 1,336 in August, and 204 in November. A subsample of 787 (41%) yellow perch were measured to inform length distributions. Mean bottom-trawl catch per hectare of yellow perch of all ages was 34, 132, and 16 for July, August, and November. The mean TL of adult (age 2+) yellow perch was 213 mm. The largest (330 mm) and smallest (108 mm) adult yellow perch were caught in November. Information about catch length frequency distributions of all species is important for apportioning hydroacoustic observations. Walleye, white perch, and rainbow smelt had the most overlap in TL with yellow perch, with the most overlap in sizes occurring in November. During all months, rainbow smelt were most abundant at the deeper sites (> 15 m), spatially overlapping less with yellow perch. White perch appeared to overlap the most with yellow perch in TL and also in habitats occupied (Figure 1.8). Due to similar sizes, body shapes (which influences hydroacoustic backscattering strength), and habitats occupied between white and yellow perch, these species are most likely to return similar signals.

#### Hydroacoustic density

Determining appropriate TS-TL relationships for species of interest and apportioning acoustic data accordingly is challenging. Although we did not find a 1:1 relationship between trawl-catch densities and hydroacoustic density estimates, the patterns in density by month followed similar trends between the two sampling methods. By apportioning hydroacoustic signals to adult yellow perch catches and comparing estimates of yellow perch density from trawls and hydroacoustics, we found good agreement between the two sampling methods (Figure 1.9), supporting the validity of the TS-TL relationships we used to identify yellow perch in hydroacoustic targets in the rest of the analysis. Both trawl-based and hydroacoustic-based estimates of densities of yellow perch were highest during August. To assess where agreement between the two sample methods was weakest, we plotted the difference in estimates of density between trawl and hydroacoustic samples (Figure 1.10). Estimates of density were in close agreement between the two methods at deeper sites (site depth > 15 m) and during November. At shallower sites, density estimates based on trawls tended to be higher than those based on hydroacoustics in July, with less consistency in pattern in August. (In this analysis, hydroacoustic density was calculated only from the bottom ~ 1.7 m of hydroacoustic data, to be comparable to the bottom trawl height.) Despite its limitations, histogram matching (see Methods) and comparison of yellow perch catches and apportioned acoustic estimates, resulted in comparable estimates of density, using a TS threshold of < -48 dB as representative of our species of interest: adult yellow perch.

To assess where yellow perch are in the water column during a given season and examine how hypoxia might influence their spatial distribution (horizontal and vertical), we visualized hydroacoustic targets by depth across month and site-depth strata (Figure 1.11). Distributions of single targets estimated to be in the size range of adult yellow perch suggest that during July and November (i.e., when hypoxia is not present), yellow perch are mainly in deeper waters, whereas during August, they also occur in shallower sites (Figure 1.11). During August (peak hypoxia), most targets were located around or above the thermocline in the two shallowest site-depth strata; in the two deeper site-depth strata (depths > 15 m), targets also appeared in the hypolimnion, near the bottom. Fish appeared to have been concentrated in the offshore sites before hypoxia then moved to shallower, more inshore sites during hypoxia and then moved to deeper offshore sites after the fall turnover.

Determining whether an individual fish was directly experiencing DO < 2.0 mg/L is challenging due to fluctuations in hypolimnetic DO within a single transect. To examine whether targets were occupying waters with low DO, we matched vertical oxygen profile values by depth to target depth for each transect (Figure 1.12). In July,

targets were predominantly found in parts of the water column with high DO levels, but during this month we only detected hypoxia in a handful of sites and only one target had an associated DO value < 2.0 mg/L (at 15 m). In August, despite targets detected near the bottom at deep sites (site depth > 15 m; Figure 1.11), when we considered the site-, date-, and position in the water column- specific DO, we found that all of these fish were in water with DO > 2.0 mg/L. At the shallower sites (< 15 m) in August, some fish were detected in hypoxic waters. During this month, at site depths of 5 and 20 m, there were aggregations right above the 2.0 DO threshold, experiencing conditions of DO 2-3 mg/L. In November, DO values were high at all our sites.

Similarly, understanding whether fish are located above or below the thermocline can inform us about their habitat and thermal preferences (Figure 1.13). In July, many targets were located well below the thermocline. While a considerable number of targets were detected below the thermocline in August, they were closer to the thermocline than in July, most likely avoiding the hypoxia layer (Figure 1.12) at those depths. More generally during August, targets were aggregated near the thermocline.

#### Discussion

Hypoxia influenced adult yellow perch spatiotemporal distributions and abundance in the central basin of Lake Erie in 2021. We found that fish occupied and aggregated in different depths before, during, and after hypoxia. The onset of hypoxia appeared to influence fish horizontal and vertical distributions, with yellow perch moving closer to the surface and inshore during the peak of hypoxia. These changes in distributions suggest that adult perch were actively avoiding the hypoxic hypolimnion. Hydroacoustic and ODNR-DOW trawl-based estimates of densities were both highest during August, when we recorded peak-hypoxic conditions. These observations support our hypothesis that hypoxia and associated environmental changes (i.e. warmer temperatures) influence fish behavior and alter their distributions, forcing fish to habitats with higher DO levels. Avoidance of hypoxic waters by fishes has been widely investigated in different ecosystems, and our results are consistent with prior research showing that fish often respond to hypoxia by moving to shallower waters (horizontally away from hypoxic waters) closer to the surface (above hypoxic layers) where DO levels are higher (Roberts et al. 2009; Vanderploeg et al. 2009a; Brandt et al. 2011). This behavioral response to hypoxia by fish in search of higher DO levels have physiological and ecological consequences that we are only beginning to understand, especially for demersal species such as yellow perch.

In Lake Erie, hypoxia tends to be most persistent during the warm summer months, with species experiencing the combined effects of declining DO and increasing temperature. As a cool-water demersal species, yellow perch must navigate the tradeoff between remaining at deeper, colder waters where DO is most likely to be depleted or moving to the warm epilimnion with likely suboptimal thermal conditions (Scavia et al. 2014; Chamberlin et al. 2020). Balancing thermal preferences while searching for higher DO can lead to habitat compression, often referred to as the "temperature-oxygen squeeze" (Coutant 1985; Coutant and Benson 1990; Arend et al. 2011; Kraus et al. 2015b). The hypoxic hypolimnion forces fish to shallower water but the surface temperatures are too warm, so fish are "squeezed" into intermediate depths. If different
species are squeezed to the same general areas, predation and competition will most likely be intensified during periods of hypoxia. Our findings further support the idea of hypoxia leading to a temperature-oxygen squeeze with yellow perch aggregating at or near the thermocline.

In addition to detecting changes in yellow perch distributions between months, we detected aggregations of yellow perch in areas suspected to have higher DO compared to the hypolimnion. Aggregations of fish bordering the hypoxic regions have been previously observed for Lake Erie yellow perch (Kraus et al. 2015a; Chamberlin et al. 2020), raising concerns about the consequences this behavioral response may have on population dynamics and catch rates. Fish aggregations on the periphery of hypoxia have been shown to influence fishery-dependent and -independent catches (Chamberlin et al. 2020), with hypoxia leading to higher or lower catches (context-dependent). Higher catches have been observed in commercial fisheries in Lake Erie due to operators being able to target these aggregations. High catches could destabilize the population if these harvested aggregations represent a large portion of the total population (Kraus et al. 2015a). Conversely, if recreational anglers maintain a consistent fishing behavior between months and fail to target perch in the areas they move to during hypoxia, their catch rates could decline. Population estimates and, consequently, catch quotas are based on ODNR-DOW's surveys that span hypoxic and non-hypoxic periods (~June-November). During our study in 2021, ODNR-DOW yellow perch catches were highest during the hypoxic month of August. Kraus et al. (2015a) and Chamberlin et al. (2020) also reported that yellow perch catch in the central basin of Lake Erie was highest during

hypoxia, raising concern about population estimates and catch quotas based on surveys conducted during these months when aggregations of fish might influence catch (Campbell and Rice 2014; Craig 2012; Selberg et al. 2001; Roberts et al. 2009). Similar patterns of higher susceptibility to catches as a result of fish behavioral response to hypoxia have been documented for Lake Erie rainbow smelt (Stone et al. 2020). Higher catches during hypoxia may lead to overfishing by some gears, underfishing by others and, ultimately, to equivocal management of the fisheries.

Although August represented our peak-hypoxic sampling conditions, hypoxia is known to be patchy and highly variable in the central basin. Kraus et al. (2015b) detected this patchiness of hypoxia and thermocline variability in Lake Erie by deploying temperature and DO loggers for long periods of time (~1 month), providing finer-scale information about environmental conditions and further support that DO levels change often and rapidly in this area. The dynamic nature of DO, due to internal waves and other physical mixing processes, leads to changes in the thickness (Kraus et al. 2015b; Chamberlin et al. 2020) and areal extent of hypoxia. Classifying individual trawl or hydroacoustic transects as fully hypoxic is challenging (ODNR-DOW 2022) since there might be pockets of higher DO where fish could be aggregating. To gain the most comprehensive understanding of DO and temperature conditions during our surveys, we collected water column information before and after every hydroacoustic transect and complemented these with DOW's bottom trawl water profiles. To overcome the confounding possibility of hypoxia patchiness, we matched associated water column profiles readings by depth to individual target depths by transect. This allowed us to

determine whether individual fish were occupying hypoxic waters. Not surprisingly, we did observe some fish in hypoxic regions, but most were right outside our defined hypoxic threshold. Dynamic environmental conditions in the lake are therefore likely to lead to dynamic responses from individuals.

In this research, we defined hypoxia as DO < 2 mg/L, which is the most widely used definition. However, various studies have shown that fish demonstrate effects even at higher DO concentrations (up to  $DO \sim 4.5 \text{ mg/L}$ ) (Eby and Crowder 2002; Hrycik et al. 2017). Due to species-specific effects, not every species will respond to hypoxia equally. It is important to keep in mind that the 2 mg/L threshold could potentially be too conservative, with studies showing that higher levels lead to altered behavior and physiology of aquatic species (Zhang et al. 2014; Chamberlin et al. 2020). Additionally, other environmental variables influence fish behavior and distributions. Light levels have been reported to influence yellow perch and other species' foraging (Brandt et al. 2011). Chamberlin et al. (2020) suggested that hypolimnion thickness and temperature also play a big role in yellow perch behavior.

Identifying species based on hydroacoustics echoes is challenging (McClatchie et al. 2000; Simmonds and MacLennan 2005; Mann et al. 2008; DuFour et al. 2021) but with our comprehensive approach and examination of trawl catches we are confident that targets observed and reported in this study mainly represent adult yellow perch. Matching bottom trawls to validate acoustic backscattering and incorporating life history and species information allowed us to classify our targets as yellow perch. For example, round gobies which were relatively abundant in bottom trawls are bottom-dwelling fish

and lack a swim bladder, therefore they are most likely to be missed in hydroacoustic surveys due to the bottom dead zone and also return a different signal due to their lack of swim bladder. Rainbow smelt can potentially confound interpretation of hydroacoustic signals since they were very abundant in trawls and have been observed to stay in the cold hypolimnion even during hypoxia (Stone et al. 2020); however, during our surveys they tended to be more abundant in sites where yellow perch were not as abundant. White perch, which has the most overlap in size and shape to yellow perch, are most likely to be mistaken for yellow perch. During our study, white perch and yellow perch were found in similar habitats and, during hypoxia, both species were most abundant at shallower sites. The limited studies available comparing white and yellow perch behavior in Lake Erie show that these two species have significant trophic overlap (Parrish and Margraf 1990; Tellier et al. 2023), often feeding on similar prey in similar habitats (Schaeffer and Margraf 1986), but published TS-TL relationships for white perch (Hartman and Nagy 2004; Hoffman et al. 2009) are different than what we found to represent yellow perch. Thermal preferences between these species also seem to differ, with white perch favoring warmer waters (Dippold et al. 2020). Targeted hydroacoustic studies on white perch populations and a better understanding on how they interact with yellow perch will help in differentiating between both species. Besides proper species identification being difficult with hydroacoustics, especially in less studied fish, a limitation with this approach is that the top- and bottom-most layers of the water column are lost. Due to the surface exclusion to reduce bubble noise and bottom exclusion to reduce the chance of including bottom features in calculations, fishes in those regions will not be detected.

This was not a big concern in this study because, although yellow perch are demersal, they tend to occur a few meters above the bottom.

We show that hydroacoustics methods can be used as a tool to quantify yellow perch habitat use in Lake Erie, especially when validated with trawl catches and incorporating knowledge about the behavior and ecology of other fish. Hydroacoustic surveys also provide information on fish locations in layers of the water column not targeted by bottom trawls as well as locations of individual fish. Hydroacoustics provides density estimates and information about where in the water column fish are located, while trawling provides data on size, age, and species composition. An advantage of hydroacoustics is that large areas can be covered with relatively lower effort in the field in comparison to trawling. Despite the limitations associated with hydroacoustics, here we show how this approach can be used to study yellow perch populations in the central basin of Lake Erie to quantify the behavioral effects of changing environmental conditions.

The goal of this research was to investigate how hypoxia influences distributions of adult yellow perch in the central basin of Lake Erie in an effort to understand how this recurring phenomenon is impacting the fisheries supported by this population. We show that yellow perch 1) respond to hypoxia by moving to shallower sites with higher DO levels and shifting higher in the water column (i.e. moving vertically), 2) aggregate at these zones of higher DO, and 3) some continue to be detected in the hypoxic hypolimnion. Understanding how hypoxia affects the physiology, behavior, and catches of yellow perch will lead to more informed fisheries management. Climate change and associated increases in temperatures is expected to lead to more frequent and longer hypoxia in Lake Erie and other systems, potentially negatively impacting many aquatic organisms. Ultimately, because hypoxia is becoming a problem in many ecosystems, information learned about Lake Erie fish populations can help inform and understand the effects of hypoxia on other species in various ecosystems.

Acoustic Survey Date	Bottom Trawl Date	Area	Acoustic
7/20/2021	7/19/2021	Chagrin -Fairport	7/28/2021
7/27/2021	7/20/2021	Perry	7/28/2021
7/27/2021	7/19/2021	Chagrin-Fairport	7/28/2021
7/28/2021	7/20/2021	Perry	7/28/2021
8/16/2021	8/16/2021	Chagrin-Fairport	8/16/2021
8/17/2021	8/18/2021	Perry	8/16/2021
8/18/2021	8/16/2021	Chagrin-Fairport	8/16/2021
11/4/2021	11/4/2021	Chagrin-Fairport	9/15/2021
11/5/2021	11/5/2021	Chagrin-Fairport	9/15/2021

Table 1.1. Acoustic and ODNR-DOW bottom trawl survey dates. Acoustic surveys were conducted on the same day or within a few days of bottom trawls. The best three acoustic calibrations were applied to the closest acoustic survey date.



Figure 1.1. Yellow perch commercial (dashed line) and sport (solid line) harvest (in pounds) in Lake Erie's central basin by year (1981-2021). Data are from Tables 1.3 & 1.4 in 2022 Report of the Lake Erie Yellow Perch Task Group.



Figure 1.2. Survey sites in Lake Erie's central basin at each location (Chagrin-Fairport and Perry, OH) across the four 5-m depth strata. Hydroacoustic surveys consisted of 10-min transects, at each site (red circle), parallel to shore. This map was created using ArcGIS Desktop Release 10.8.



Figure 1.3. Trawl catch length frequency histogram with fish total length binned into 10mm intervals. Includes data from July, August, and November 2021 ODNR-DOW bottom trawls that had a matching hydroacoustic survey. Black bars represent yellow perch and gray bars represent other species. Bars are not stacked; black bars representing yellow perch bars are overlaid on the gray bars.



Figure 1.4. Hydroacoustic frequency histogram of fish compensated target strength (TS) for entire survey period. Valley in TS at -48 dB and -37 dB matches with previous work on Lake Erie yellow perch.



Figure 1.5. Histograms of lengths (TL) back-calculated from linear regression between TS and TL. TS = TS =  $37.22 \log_{10} (TL) - 94.41$ . The distinct change in count frequency at 147-mm matches the change on count frequency in the length-frequency histogram of yellow perch measured from the trawl samples (Figure 1.3).



Figure 1.6. Water column profiles of mean A) dissolved oxygen (mg/L) and B) temperature (°C) for July (light gray, two-dash line), August (black, solid line), and November (dark gray, dashed line). Red stars indicate mean thermocline depth, as estimated from R package rLakeAnalyzer (v1.11.4.1; Winslow et al. 2019), for each month (note: no thermocline was present in November).



Figure 1.7. Relative abundance (% of individuals) of ODNR-DOW bottom trawl catches by month. Legend includes all species identified in trawls; however, some species exhibited very low abundances, making them challenging to visualize on the bar plot. The most abundant species are labeled on the bars for ease of visualization.



Figure 1.8. Total trawl density (catch/ha) by month and site depth (m). Showing the five most abundant species caught in trawls: rainbow smelt, round goby, walleye, yellow perch, and white perch. Left panel contains July density, middle panel has August density, and the right panel shows fish density in November.



Figure 1.9. Comparison of estimates of adult yellow perch densities based on bottom trawl samples (left panel) and hydroacoustic sampling (right panel) in fish per hectare. Hydroacoustic density was calculated from the bottom  $\sim 1.7$  m of hydroacoustic data and apportioned by multiplying by the proportion of adult yellow perch caught in trawls by month, to be comparable to the bottom trawl height.



Figure 1.10. Difference between adult yellow perch bottom densities as estimated from trawls and hydroacoustics, for each sample month (*x*-axis) for each site-depth stratum (panels: 5-10, 10-15, 15-20, >20 m). Estimates of density were in close agreement between the two methods at deeper sites (site depth > 15 m) and during November. At shallower sites, density estimates based on trawls tended to be higher than those based on hydroacoustics in July, with less consistency in pattern in August. Hydroacoustic density was calculated only from the bottom ~ 1.7 m of hydroacoustic data and apportioned by multiplying by the proportion of adult yellow perch caught in trawls by month, to be comparable to the bottom trawl height.



Figure 1.11. Individual adult yellow perch fish targets by target depth (m) grouped by month (columns) and site-depth (rows: 5-10, 10-15, 15-20, >20 m). Values on each panel show the total density (fish/ha) estimated with hydroacoustics for each month and site depth. The horizontal red line represents the average thermocline by site depth during each month (note: no thermocline was present in November). Black rectangle depicts the lake bottom.



Figure 1.12. Dissolved oxygen (mg/L) values for each hydroacoustic yellow perch single target by target strength (dB) grouped by month (columns) and site-depth (rows: 5-10, 10-15, 15-20, >20 m). The horizontal dashed line denotes hypoxia (DO = 2 mg/L). This was calculated by matching water column profile values by depth to target depth.



Figure 1.13. Target depth (m) minus thermocline depth (m) by target strength (dB) grouped by month (columns) and site-depth (rows: 5-10, 10-15, 15-20, >20 m). Dots represent adult yellow perch single targets. The horizontal red lines (at y = 0) represent the thermocline. This figure shows the vertical distance of each single target from the thermocline, with targets above the red line (negative values) being above the thermocline while targets below the red lines (positive values) being below the thermocline. For each month and site, a thermocline depth value was assigned to each target based on the mean thermocline of readings collected at the start and end of each individual transect. No thermocline was detected in November, so points represent target depths minus site depth.

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# Chapter 2. The Influence of Seasonal Hypoxia on the Feeding Ecology of Yellow Perch (*Perca flavescens*)

# Introduction

Eutrophication-driven hypoxic events have increased in extent, duration, and frequency in many coastal (Diaz and Rosenberg 1995; Vollenweider et al. 1992; Justic et al. 1993; Diaz 2001; Diaz and Rosenberg 2008) and freshwater ecosystems (Caddy 1993; Nixon 1995; Carpenter et al. 1998), with implications for predator-prey interactions and aquatic food webs (Turner and Rabalais 1994; Breitburg et al. 1997; Breitburg 2002; Wu 2002). Fishes and other mobile aquatic organisms, such as zooplankton (Marcus 2001; Klumb et al. 2004) and benthic macroinvertebrates (Kolar and Rahel 1993; Reynoldson and Hamilton 1993; Diaz and Rosenberg 1995), are stressed by hypoxia (dissolved oxygen (DO)  $\leq 2.0 \text{ mg/L}$ ) in several ways. Hypoxia can lead to changes in behavior (Aku et al. 1997), feeding patterns (Pihl et al. 1992; Aku and Tonn 1999), and physiology (Wu et al. 2003; Pollock et al. 2007; Wu 2009). Altered behavioral patterns, such as shifting location in the water column to escape hypoxic areas (Aku et al. 1997; Aku and Tonn 1999; Breitburg 2002; Ludsin et al. 2009; Zhang et al. 2009; Craig 2012; Chamberlin et al. 2020), can lead to changes in diet and feeding patterns of many species, particularly for benthivorous fishes. Understanding trophic interactions between predators and prey under hypoxic conditions is needed to understand the consequences of hypoxia on population dynamics.

Species-specific tolerance and avoidance responses to hypoxia can alter community structure and disrupt ecosystem function, potentially decoupling the

benthopelagic food web (Diaz and Rosenberg 1995; Goto et al. 2017). Fishes are generally more sensitive to low oxygen concentrations in the water column compared to zooplankton (Stalder and Marcus 1997; Lass et al. 2000; Vanderploeg et al. 2009b) and benthic macroinvertebrates, which tend to have a higher tolerance to hypoxia and can remain in the hypoxic hypolimnion for longer periods (Diaz and Rosenberg 1995). When hypoxia results in increased overlap of predators and prey, vulnerability to predators can be heightened for certain prey species (Costantini et al. 2008; Brandt et al. 2011; Zhang et al. 2014). On the other hand, spatial mismatch between predators and prey can decrease access to prey (Ludsin et al. 2009; Stone et al. 2020), particularly benthic prey that inhabit bottom hypoxic waters and are able to use the hypoxic hypolimnion as a refuge (Klumb et al. 2004; Taylor et al. 2007; Vanderploeg et al. 2009a; Hedges and Abrahams 2015). The compounding effects of hypoxia and warm temperatures during the summer can also result in habitat compression (Eby and Crowder 2002; Prince and Goodyear 2006; Vanderploeg et al. 2009a, 2009b; Campbell and Rice 2014; Zhang et al. 2014), with hypoxia at the bottom of the water column forcing fish into the epilimnion where temperatures are too warm in the summer (Pothoven et al. 2009), resulting in an oxygen-temperature squeeze (Coutant 1985; Aku and Tonn 1999). Distributional changes of predators and prey during seasonal hypoxia may therefore lead to changes in diets of some fish species (Pihl 1994; Aku and Tonn 1999).

In Lake Erie, seasonal hypolimnetic hypoxia occurs annually from late summer through early fall due to thermally induced stratification combined with cultural eutrophication (Boyce et al. 1987; Bertram 1993; Burns et al. 2005; Hawley et al. 2006). Hypoxia is most persistent in Lake Erie's large central basin but has been increasing in frequency and spatial extent since the mid-1990s (Scavia et al. 2014). The consequences of recurring hypoxia on predator-prey interactions and community structure are of concern because Lake Erie provides habitat for many ecologically and economically important species, which can be affected by the degradation of habitats as a result of hypoxia. Yellow perch (Perca flavescens) supports one of the most important fisheries in Lake Erie, providing ample recreational and commercial fishing opportunities. However, compared to the last 40 years, yellow perch harvest in the central basin of Lake Erie reached an all-time low in 2018 and continues to decline. Specifically, recreational catch of yellow perch in the central basin of Lake Erie has been steadily declining since 2014 (Yellow Perch Task Group 2022). In addition to supporting an important fishery, yellow perch are important ecologically because they consume primary consumers such as zooplankton and macroinvertebrates and are also prey for larger piscivores in the lake. The significant decrease in recreational yellow perch catch in the central basin has sparked an interest in better understanding how hypoxia is affecting this important fishery.

Yellow perch are bottom-oriented omnivores that prefer deep cold waters and prey items such as small fishes (emerald shiners and round gobies) and benthic invertebrates (chironomid larvae and pupae) (Hayward and Margraf 1987). Seasonal diet analyses have shown shifts in Lake Erie's central basin yellow perch diets, with decreasing consumption of fish and benthic prey to increased consumption of zooplankton prey (Roberts et al. 2009), specifically the abundant invasive cladocerans,

Bythotrephes longimanus (hereafter "Bythotrephes"; Joseph Schmitt, Great Lakes Science Center, USGS, unpublished data). Since 2016, prey fish have made up less than 10% of yellow perch diets in the lake (Yellow Perch Task Group 2022). During normoxic conditions, yellow perch diets are dominated by energy-rich benthic chironomids (Roberts et al. 2009). On the other hand, during hypoxic events, yellow perch shifted from consuming benthic chironomids to increased foraging on pelagic cladocerans (Roberts et al. 2009, 2012; Vanderploeg et al. 2009a). However, recent studies have shown that yellow perch maintain some benthic prey (chironomid larvae) in their diets, even during hypoxic events (Pollock et al. 2007; Roberts et al. 2012), suggesting that yellow perch undergo foraging forays into hypoxic waters. The exact mechanisms and how yellow perch diets and foraging behaviors are changing as a result of hypoxia and other environmental conditions are not clearly understood. The location in the water column of yellow perch differs greatly depending on whether they are feeding below or at the thermocline on chironomid larvae, near and above the thermocline on fish prey, or higher in the water column on Bythotrephes; therefore, an understanding of the patterns in yellow perch diet is essential to understanding patterns in catch rates by recreational fishers relative to commercial catch and fishery-independent surveys.

This study focuses on understanding how adult (age 2+) yellow perch diets are influenced by seasonal hypoxia in the central basin of Lake Erie. We collected diet samples in the central basin of Lake Erie and used information about yellow perch diets to infer depths at which yellow perch are feeding under different habitat conditions (DO, water temperature, and depths). This includes not only the differences between feeding on benthic and zooplankton prey, but also the idea that feeding on chironomid larvae when a bottom hypoxic layer is present suggests that yellow perch make feeding forays into the hypoxic zone, whereas feeding on chironomid pupae in these same conditions may allow yellow perch to remain above hypoxic waters and feed on insects rising in the water column. We hypothesized that adult yellow perch would decrease consumption of benthic prey during the peak hypoxic season but still maintain some benthic prey as suggested in other studies in which they have been recorded to undergo hypolimnetic foraging forays (Roberts et al. 2012). Analyses were focused on individual taxonomic groups that are shown to be important in this study and in historical diet data, such as *Bythotrephes* and chironomids. Understanding how hypoxia impacts the Lake Erie food web is important for effectively managing the fisheries and elucidating why yellow perch catch has substantially declined in the past decade.

## Methods

#### Study Area

Lake Erie, the shallowest (maximum depth of 64 m) and warmest of the five Laurentian Great Lakes has three main basins which vary in depth and hypoxic extent during the summer and fall (Bolsenga and Herdendorf 1993). The combination of intermediate depths and warmer water temperatures results in thermal stratification during the summer, which leads to hypoxia, particularly in the central basin of the lake. Although Lake Erie has a long history of seasonal hypolimnetic hypoxia, there is a trend of increasing frequency and duration of hypoxic events. Hypoxia has been a focus of
research in the lake; however, questions remain about how increases in the spatial and temporal extent of hypoxia influence the Lake Erie food web.

# Field Collections

Yellow perch were collected via bottom trawling by the Ohio Department of Natural Resources – Division of Wildlife (ODNR-DOW) in the central basin of Lake Erie at five areas (Ashtabula, Cleveland, Lorain, Chagrin-Fairport, and Perry, OH) during the day in June, July, August, and November 2021. In July and August, trawls were conducted only in Chagrin-Fairport and Perry (Table 2.1). During 2021, these sampling months represented pre-hypoxic (June and July), peak-hypoxic (August), and posthypoxic (November) conditions. Yellow perch were collected at 12 sites in each area along four depth strata (5-10, 10-15, 15-20, >20 m), with a total of three transects per 5-m depth strata. Ten-minute tows were conducted in waters deeper than 10 m and fiveminute tows in waters less than 10 m with a two-seam Yankee bottom trawl (10.4-m head rope, 25-mm bar mesh in the cod end, 13-mm stretched mesh liner, and 25.4-cm roller gear), at a cruising speed of 3.2 km/h aboard the R/V Grandon. Trawl catches were identified to species, counted, weighed, and measured. Other biologically relevant information such as age, sex, and maturity were also recorded. A sub-sample (20 fish per trawl) of adult (age 2+) yellow perch collected in the trawls were stored in ice and brought back to the laboratory for stomach content examination.

#### *Physical variables*

To assess how yellow perch diets varied under different environmental conditions, vertical profiles of depth (m), water temperature (°C), and DO (mg/L) were

recorded at the start and end of each trawl transect using a YSI EXO2 multiparameter sonde (YSI Inc., Yellow Springs, Ohio). Temperature and DO were averaged to 1-m depth intervals for data analyses. We used a Secchi disk to measure water transparency to the nearest 0.5 m at the starting point of every transect.

#### Fish diets

The stomach contents of adult (age 2+) yellow perch collected in Lake Erie trawls were processed by personnel from ODNR-DOW and at The Ohio State University's Aquatic Ecology Laboratory to examine diet patterns and composition. In the laboratory, we measured and weighed thawed yellow perch and recorded wet stomach weights for each fish. We then placed stomach contents on a divided Petri dish by rinsing the stomach lining with distilled water. Using a dissecting microscope, we identified and counted prey items to the lowest possible taxonomic level. Due to high densities of zooplankton in stomachs, we subsampled zooplankton by counting prey items in two or more of the sections of the divided Petri dish, averaging counts over the number of areas counted, and multiplying the average number of organisms per area by the number of areas in the Petri dish. The counts of the identified prey were used to estimate the wet and dry weights of prey consumed. When the diet included fish, the fish prey items were measured and weighed. When fish prey items were partially digested, meristic characters were used to identify fish; when species identification was not possible, fish prey items were classified as "unknown fish".

We separated chironomid prey into four categories: chironomid adults, chironomid larvae, chironomid pupae, and chironomids (when the life stage was not distinguishable). The different life stages of chironomids inhabit different areas of the water column, potentially informing where in the water column yellow perch might be feeding. Chironomid pupae ascend to the surface to emerge whereas chironomid larvae are benthic.

#### Statistical analyses

The goal of this research was to investigate how adult yellow perch diets are influenced by hypoxia in the central basin of Lake Erie by analyzing stomach contents of fish collected in 2021. We tested for the influence of environmental conditions, including hypoxia, on occurrence and biomass of specific prey taxa in adult yellow perch diets. To examine how hypoxia and other environmental variables influenced adult yellow perch diets in the central basin of Lake Erie, we used generalized linear models (GLMs) to analyze the most abundant prey taxa in yellow perch stomachs, which included *Bythotrephes*, chironomid pupae, chironomid larvae, amphipods, and *Daphnia*. These five most prominent prey types in the stomachs examined made up 75% of the biomass in yellow perch diets. The next most common prey type, dreissenids, added only 6% more biomass. The remaining prey made up 19% of prey biomass in stomachs. Thus, we focused our analysis on the five most common prey items in the diet, i.e., those that had a frequency of occurrence of at least 10 % across all stomachs (Figure 2.1).

We analyzed *Bythotrephes* count data in yellow perch stomachs using a two-part Zero-Altered Negative Binomial (ZANB) hurdle model. Due to lower abundance of the remaining prey, chironomid pupae, chironomid larvae, *Daphnia*, and amphipods were modeled with binomial GLM models with a logit link function using presence (1) absence (0) metrics. We tested whether the prevalence of empty stomachs is influenced by season using a Pearson's Chi Squared test. Prey taxa were modeled separately because individual prey taxa respond differently to environmental predictors and they also inhabit different parts of the water column.

Hypoxia is broadly defined as low dissolved oxygen in the water (Davis 1975), but the exact cutoff of what dissolved oxygen concentration is considered hypoxic varies by study, species of interest, and ecosystem. The most widely used cutoff for a water body to be considered hypoxic is DO < 2 mg/L, but other researchers have reported 2.5 mg/L (Taylor et al. 2007), 4 mg/L (Stone et al. 2020), and 4.5 mg/L as the threshold (Hrycik et al. 2017) due to differences in species tolerances to low dissolved oxygen. In our analyses, we included two of these cutoffs (hypoxic when DO < 2 mg/L and hypoxic when DO < 4 mg/L) separately in our models to explore whether there were any differences (Figure 2.2).

We were most interested in how hypoxia, depth, and their interaction influenced adult yellow perch diet, but also considered the potential influence of yellow perch size and water temperature on the effect of season and site depth. Hypoxia was represented in models with a categorical variable "season", with three levels: pre-hypoxic, peakhypoxic, and post-hypoxic. Depth was site depth, the maximum depth recorded during a trawl sample. Because yellow perch are known to sit at or above the hypoxic layer when it is present, we considered the mean temperature above the hypoxic layer (with two definitions of hypoxia: DO < 2 mg/L and DO < 4 mg/L). Temperature of the hypoxic water may influence prey availability and yellow perch foraging forays; therefore, we also considered the temperature of hypoxic layer (again, with two definitions of hypoxia). When there was no hypoxic layer, all temperature variables were just the mean temperature for the entire water column. Fish length is known to influence diet, so yellow perch length (linear and quadratic terms) was included as well. The candidate model set included a combination of models that allowed us to test for the effects of season and depth as well as the influence of temperature and fish length on adult yellow perch diet, including a null (intercept only) model (Table 2.2). The response variables were *Bythotrephes* numerical counts in the hurdle model and presence-absence of chironomid pupae, chironomid larvae, amphipods, *Daphnia*, and empty stomachs in the binomial model. Fish with empty stomachs were not used in the analyses of the five individual prey taxa. We used corrected Akaike Information Criteria (AICc) model selection to evaluate the candidate models, considering models with AICc differing by less than 2 as being equally likely.

All statistical analyses were performed using R Statistical Software (v4.2.1; R Core Team 2022). We used the hurdle function from the pscl package in R to fit the hurdle models (Zeileis et al. 2008). To examine model performance, we plotted rootograms (Kleiber and Zeileis 2016), examined deviance, and plotted scaled quantile residuals using the package DHARMa (v0.4.6; Hartig 2022), which was specifically developed to create appropriate visualizations for examining GLMs performance. Data exploration was carried out following the protocol described in Zuur et al. (2010).

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## Results

### Hypoxia

In 2021, hypoxia was most pronounced during the month of August (our peakhypoxic month), with monthly mean DO values < 4 mg/L in waters deeper than ~ 15 m (Figure 2.3). Sites sampled in June, July, and November were not hypoxic. In November (post-hypoxic season) the water column was well mixed which was evident in the vertical column profiles showing almost unchanging DO and temperature values from surface to the bottom.

## Diets of Adult Yellow Perch

Out of the 472 adult (age 2+) yellow perch caught in the central basin of Lake Erie via ODNR-DOW bottom trawling in 2021, a subsample of 185 were brought back to the laboratory for stomach content examination: 97, 66, and 22 from the pre-hypoxic, peak-hypoxic, and post-hypoxic seasons, respectively. The likelihood of empty stomachs was greater during the peak-hypoxic and post-hypoxic seasons than during pre-hypoxia ( $\chi^2$  test = 7.33, *p* = 0.026; Figure 2.4). Ultimately, we analyzed diets for the 59, 27, and 9 fish (from the pre-hypoxic, peak-hypoxic, and post-hypoxic seasons, respectively) with prey in their stomachs.

*Bythotrephes* comprised a large proportion of prey biomass across seasons (Figure 2.5) as well as having the highest percent occurrence in diets across seasons (Figure 2.6). While chironomid larvae and pupae also contributed a large proportion of prey biomass during the pre- and peak-hypoxic seasons, with little contribution from fish prey, diet biomass during post-hypoxic included a large proportion of round gobies (Figure 2.6).

Round gobies were the only fish identified in stomachs, though there also was a small proportion of biomass (<1%) consisting of unidentifiable fish.

### Bythotrephes in yellow perch diets

Over half of the yellow perch with prey in their diets consumed *Bythotrephes*, with spine counts per fish ranging from 6 to 960. Exploratory data analysis revealed that the *Bythotrephes* count data were zero-inflated and overdispersed (mean = 90, standard deviation = 170); thus, we used a zero-altered negative binomial hurdle model (see Appendix A) for consideration of other models) to test for the effects of environmental variables on *Bythotrephes* in yellow perch diets.

Three models (models 3, 4, and 5; Table 2.2) were indistinguishable in terms of fit, each with a delta AICc < 2.0 (Table 2.3). Each of these three models contained depth and season (pre-, peak-, and post-hypoxic) as predictor variables and one included yellow perch fish size. Because the response of *Bythotrephes* consumption to yellow perch total length was very weak, we further explored only the responses to depth and season, using model 5 (which included depth, season, and their interaction) to illustrate the results (Table 2.2).

The zero part of the hurdle model explains the proportion of yellow perch consuming *Bythotrephes*, in other words, the probability of presence or absence of *Bythotrephes* in stomachs. The probability of *Bythotrephes* consumption declined with increasing site depth, with a much more pronounced decline during pre-hypoxia than during later months (Figure 2.7). Although depth contributed to explaining presence/absence of *Bythotrephes* in yellow perch stomachs (p < 0.005), the effect of this predictor is mediated by month (Table 2.4). The count part of the hurdle model revealed that during the peak- and post-hypoxic seasons, yellow perch were more likely to consume more *Bythotrephes* with increasing depth (though the sample size was quite low for the post-hypoxia season). While during the pre-hypoxic season, the trend was less marked (Figure 2.7).

# Model selection for other prey types

Occurrence of chironomid pupae, amphipods, chironomid larvae, and *Daphnia* were each modeled using a binomial GLM with its canonical logit link. Candidate model explanatory variables for these analyses were the same as for the analyses of *Bythotrephes* (Table 2.2).

## *Chironomid pupae*

A quarter of yellow perch with food in their stomachs consumed chironomid pupae. Model 12, which included depth, season, and average temperature above and below the hypolimnion (with hypoxia defined as DO < 4 mg/L) as predictor variables (Table 2.5), was the most likely model for occurrence of chironomid pupae. Due to the low number of chironomid pupae found in stomachs from peak- and post-hypoxic seasons, the results for this prey are focused on pre-hypoxic season data. Our most-likely model indicated that the probability of yellow perch consuming chironomid pupae was 1.33 times more likely for every 1 m increase in depth (Table 2.6; Figure 2.8). The probability of presence of chironomid pupae in stomachs decreased as temperatures increased (Figure 2.8).

# *Amphipods*

Eighteen percent of the 95 adult yellow perch with food in their stomachs consumed amphipods. Depth and season were strong predictors of occurrence of amphipods in yellow perch diets, with depth occurring in three and season occurring in two of the three top models (models 3, 4, and 8; Table 2.5). Fish size also occurred in one of these models, but did not exhibit any obvious relationship with amphipod occurrence. To illustrate the patterns of amphipod occurrence in response to environmental conditions, we used model 4, containing both depth and season (Figure 2.9, Table 2.6). For both pre-hypoxic and peak-hypoxic seasons, the probability of presence of amphipods in stomachs increased with increasing depth (m).

### Chironomid Larvae

Chironomid larvae, a benthic chironomid life-stage, were found in 16% of yellow perch that had prey in their stomachs. No model of chironomid larvae occurrence in yellow perch diets was more likely than the null model.

### Daphnia

*Daphnia* were consumed by 18% of the yellow perch that had prey in their stomachs. The top three models of *Daphnia* occurrence in yellow perch diets included depth, season, and yellow perch total length (Models 3, 6, and 7; Table 2.5). The top models differed in whether they included a depth x season interaction term and a quadratic term for fish size. Neither of these terms had strong effects, so we illustrate the relationships using model 3. The pre-hypoxic season was significant in the model because *Daphnia* were mainly only found in stomachs from fish collected during the prehypoxic season (Table 2.6). During the pre-hypoxic season, the probability of finding *Daphnia* prey in yellow perch stomachs decreases with increasing site depth and increasing fish size (Figure 2.10).

# Discussion

Overall, our results show that adult yellow perch are consuming more zooplankton (*Bythotrephes*) and invertebrate (chironomids) biomass than fish biomass and that they undergo diet shifts with changes in hypoxia presence. We found that yellow perch diets differ across pre-, peak-, and post-hypoxia seasons, but there is insufficient evidence to support that hypoxia alters yellow perch foraging behavior for consuming benthic versus pelagic prey. We cannot conclude that pelagic foraging increased during the peak-hypoxic season, as yellow perch still maintained a significant amount of benthic prey during hypoxia. Environmental variables other than season (i.e., hypoxia) influenced yellow perch diets. In general, our results support relationships between yellow perch diets and season, site depth, and fish size (TL).

### Feeding in hypoxic hypolimnion

Adult yellow perch consumed benthic prey even during the peak-hypoxic season, suggesting that they are conducting foraging forays into the hypoxic hypolimnion to feed as has been suggested before for Lake Erie yellow perch (Roberts et al. 2009, 2012). Other species such as spot (*Leiostomus xanthurus*) (Pihl et al. 1992) and central mudminnows (*Umbra limi*) (Rahel and Nutzman 1994) have been reported to feed in the hypoxic benthos as well. Yellow perch consumed the most chironomid larvae biomass, a benthic chironomid life-stage, during the peak-hypoxic season. Similarly, the highest

biomass and frequency of occurrence of amphipods, another benthic prey, in yellow perch stomachs was observed during the peak-hypoxic season. However, we also found that adult perch had the highest occurrence of and consumed the most biomass of *Bythotrephes*, a pelagic invasive cladoceran, during the peak-hypoxic season. Although our results support benthic feeding during the hypoxic season, hypoxia is known to be patchy in certain areas of the lake, resulting in bottom areas with higher DO than surrounding waters. We cannot rule out the possibility that some of the benthic prey in yellow perch diets resulted from exploitation of localized patches of higher DO, though, the prevalence of benthic prey in yellow perch diets during July is unlikely to be explained entirely by foraging in small patches of high-DO water.

### Environmental variables

Season and depth were important in explaining occurrence and counts of a variety of prey items in yellow perch stomachs. Before hypoxia sets in, yellow perch are more likely to consume *Bythotrephes* and *Daphnia*, both pelagic prey, in shallow water than deep water and more likely to consume amphipods, a benthic prey, in deep water than shallow water. This difference in consumption patterns with depth between benthic and pelagic prey may reflect prey distributions (e.g., in Lake Erie, Burlakova et al. 2018 found the highest density of benthic organisms in the deepest basin of Lake Erie) or prey vertical overlap with yellow perch. *Bythotrephes* reside in warm epilimnetic waters (Marino et al. 2020), so at greater depths, there will be less vertical overlap between benthic (or thermocline-associated) yellow perch and epilimnetic *Bythotrephes*. The

decrease in pelagic prey in the diets In deeper water may be a result of the benthic habitat preferred by yellow perch or changes in prey abundance with depth.

## Stomach content approach

Although informative, quantifying fish diets by examining stomach contents provides only a snapshot of a fish's diet. Stomach content analysis allows researchers to gain insight about short-term diet trends or immediate responses to environmental stress with the caveat of potentially underestimating or overestimating certain prey (Zorica et al. 2021). This approach has challenges and limitations, most notably varying digestion rates and difficulties in identifying certain prey items. Round gobies were the only fish species identified in yellow perch stomachs; however, prey condition (i.e., rate of digestion) makes it challenging and sometimes impossible to identify fish prey. Different prey items and body parts have different digestion rates (Hyslop 1980; Manko 2016). For example, *Daphnia* are known to be digested quickly and tend to be underestimated in diets (Gannon 1976). Bythotrephes were the most frequent prey in stomachs; however, Bythotrephes spines might be retained longer and digested slower than other prey items such as fish (Parker-Stetter et al. 2005). Due to spine-body breakage, we counted Bythotrephes spines only (not heads) to avoid double counting individuals. If spines are retained for longer periods than other prey, it can potentially inflate estimated yellow perch consumption of Bythotrephes. Parker et al. (2001) demonstrated that Bythotrephes spines, which are made up of chitinous material, were retained in rainbow smelt stomachs. Conversely, Pothoven et al. (2009) did not find that Bythotrephes spines were retained by emerald shiners nor rainbow smelt. The rate of digestion and spine retention

seems to vary between species and is also influenced by how fish are handled and preserved. Using stomach contents to determine fish diets is a simple yet incomplete method of assessing foraging and food web interactions. This approach allows researchers to get a glimpse of what fish have recently eaten whereas other methods including stable isotope analyses and fatty acid profiles can provide long-term information on food consumption, give insight into seasonal changes, and reveal ontogenetic shifts. A combination of these techniques could be used in future studies to complement information obtained from stomach contents.

### Forage fish

Regardless of whether predators such as yellow perch continue foraging in the benthos during hypoxia, if their benthic prey are also responding to hypoxia, we would expect to see shifts in yellow perch diets during hypoxia. The seasonal dietary patterns observed could reflect a change in the prey fish, zooplankton, and benthic invertebrate community available to yellow perch to forage on. Stone et al. (2020) revealed that abundance of emerald shiner and rainbow smelt, two abundant planktivores in Lake Erie known to be sensitive to low DO (Arend et al. 2011), decreased with increased hypoxic severity. They also reported that low oxygen excluded these two fishes from the hypoxic hypolimnion and caused shifts in their diets. Although consumption of prey fish such as round gobies was overall low throughout the seasons, yellow perch consumed the most biomass of round gobies during the post-hypoxic season. This could be as a result of hypoxia limiting access to this benthic prey, but could also reflect changes in round goby distributions and abundances. Species-specific tolerances to low DO and consequent responses to hypoxia might lead to prey behavioral changes and affect foraging ecology and diet of yellow perch. As opportunistic feeders in Lake Erie, yellow perch have been deemed more resilient to decreases in forage fish abundance due to being able to switch their diet and depend on zooplankton and invertebrate prey (knight et al. 1984). They are also known to have a higher tolerance to depleted DO levels compared to other fishes (Arend et al. 2011), which could explain why more sensitive species such as rainbow smelt have been found to be excluded from hypoxic waters while yellow perch can continue foraging in hypoxia. To understand how hypoxia and other environmental conditions influence food web dynamics in Lake Erie it is important to understand the diet and behavior of prey fish including round goby, gizzard shad, rainbow smelt, and emerald shiners. Additional research on the prey communities in Lake Erie will aid in our understanding of how hypoxia might affect recreational catches in the central basin.

This study focused on addressing how seasonal hypoxia in the central basin of Lake Erie influences adult (age 2+) yellow perch diets. Our study confirmed that even though yellow perch diets change between seasons, the presence of hypoxia did not restrict yellow perch from feeding on benthic prey. Our study suggests that yellow perch feed on benthic prey during hypoxic conditions. Hypolimnetic hypoxia in Lake Erie and other aquatic ecosystems (i.e. coastal areas, estuaries, lakes) is expected to increase in both severity and extent as a result of climate change and land use, leading to unknown implications for food webs and predator-prey interactions. Understanding how hypoxia influences foraging behavior and distribution of zooplankton, fish, and other important aquatic species will result in better understanding of how hypoxia can affect food web dynamics and aquatic ecosystems.

Month	Area	Number of Trawls	
June	Ashtabula	12	
June	Cleveland	12	
June	Chagrin-Fairport	12	
June	Lorain	7	
June	Perry	9	
July	Chagrin-Fairport	12	
July	Perry	12	
August	Chagrin-Fairport	12	
August	Perry	12	
November	Cleveland	9	
November	Chagrin-Fairport	11	
November	Perry	12	

Table 2.1. Number of Bottom Trawls Conducted by Month and Area

Table 2.2. Variables used in candidate models for explaining *Bythotrephes*, Chironomid pupae, amphipods, Chironomid larvae, and *Daphnia* in adult yellow perch stomachs, where depth is the maximum depth of the trawl transect where fish were collected, Season is a categorical variable (pre-hypoxic, peak-hypoxic, and post-hypoxic), yellow perch total length (TL) with both a linear and squared term, EpiTDO2 and EpiTDO4 are the average temperatures above the thermocline when hypoxia was defined as either DO < 2 mg/L or DO < 4 mg/L, and HypoTDO2 and HypoTDO4 are the average temperatures below the thermocline when hypoxia was defined as DO < 2 mg/L or DO < 4 mg/L. When no hypoxia was present, the average temperatures of the entire water column were used.

Model	Depth	Season	Depth	Total	Total	ЕріТ	ЕріТ	НуроТ	НуроТ
			X	Length	Length <sup>2</sup>	DO2	DO4	DO2	DO4
			Season						
1	Х	Х		Х		Х		Х	
2	Х	Х				Х		Х	
3	Х	Х		Х					
4	Х	Х							
5	Х	Х	Х						
6	Х	Х	Х	Х					
7	Х	Х	Х	Х	Х				
8	Х								
9						Х			
10		Х							
11	Х	Х		Х			Х		Х
12	Х	Х					Х		Х
13							Х		
Null									

Model <sup>1</sup>	K	Delta AICc	AICc Weight
Model 5	13	0.00	0.34
Model 3	11	0.69	0.24
Model 4	9	1.53	0.16
Model 6	15	2.08	0.12
Model 7	17	2.23	0.11
Null	3	20.67	0.00

Table 2.3. Candidate zero-altered negative binomial hurdle models for *Bythotrephes* presence/absence and count data, number of estimated parameters (*K*), delta AICc, and AICc weight.

<sup>1</sup>Only models with a delta AICc between 0 and 4 and the null model are included

Table 2.4. Estimated coefficients, rate ratios (RR), odds ratios (OR) from the Zero-Altered Negative Binomial hurdle model for model 5 explaining numbers (count part) and occurrence (zero part) of *Bythotrephes* in yellow perch diets. \* p < 0.05, \*\*\* p <0.001. RR are the exponentiated coefficients of the count part of the hurdle model and represent the multiplicative effect of the independent variable on the response variable (i.e. consumption of *Bythotrephes*). RR values greater than 1 suggest an increase in the count rate for each predictor compared to the control group (in this case, the pre-hypoxic season) while values less than 1 indicate a decrease. OR are the exponentiated coefficients of the zero part of the hurdle model and explain the probability of occurrence (i.e. fish consuming *Bythotrephes*) for each independent variable. OR with values greater than 1 suggest an increase in *Bythotrephes* occurrences whereas OR values less than 1 indicate a decrease in the odds of finding *Bythotrephes* in yellow perch stomachs.

	Coefficient	RR (95% CI)	Coefficient	OR (95% CI)
	Count part		Zero part	
Intercept	5.89***	$3.60 \times 10^{2}$	4.02***	55.84
		$(1.05 \times 10^2 - 1.24 \times 10^3)$		(6.35 - 491.08)
Depth	-0.05	0.95 (0.85 - 1.06)	-0.32***	$0.73 \ (0.62 - 0.85)$
SeasonPeak	-3.03***	0.05 (0.01 - 0.26)	-2.55	0.08 (0.003 - 1.99)
SeasonPost	-2.74	0.06 (0.001 - 2.98)	-3.95	0.02
				$(3.0 \times 10^{-5} - 13.77)$
Depth x	0.17*	1.19 (1.03 – 1.36)	0.27*	1.31 (1.04 – 1.67)
SeasonPeak				
Depth x	0.21	1.23 (0.95 – 1.60)	0.30	1.35 (0.88 - 2.08)
SeasonPost				
Log(theta)	0.14			
Log-likelihood	-344.60			
Ν	95			

Response	Model <sup>3</sup>	K	Delta AICc	AICc Weight
Chironomid pupae	Model 12	6	0.00	0.52
	Model 11	7	2.33	0.16
	Model 4	4	2.83	0.13
	Null	1	23.17	0.00
Amphipods	Model 4	4	0.00	0.24
1 1	Model 3	5	0.39	0.20
	Model 8	2	1.65	0.10
	Model 2	6	2.47	0.07
	Model 5	6	2.66	0.06
	Model 1	7	2.86	0.06
	Model 9	2	2.95	0.05
	Model 6	7	3.19	0.05
	Null	1	4.88	0.02
Daphnia	Model 6	7	0.00	0.37
	Model 7	8	0.14	0.34
	Model 3	5	1.14	0.21
	Null	1	12.35	0.00

Table 2.5. Candidate binomial models for Chironomid pupae, amphipods, and *Daphnia* occurrence in yellow perch diets, with number of estimated parameters (K), delta AICc, and AICc weight.

<sup>&</sup>lt;sup>3</sup>Only models with a delta AICc between 0 and 4 and the null model are included here.

Table 2.6. Estimated coefficients and odds ratios (OR) for top binomial models for occurrence of Chironomid pupae, amphipods, and *Daphnia* in yellow perch diets. Confidence intervals are included in parentheses. Depth is the maximum depth of the trawl transect where fish were collected, Season is a categorical variable (pre-hypoxic, peak-hypoxic, and post-hypoxic), EpiTDO4 represents the averaged epilimnion temperatures (i.e. above the hypolimnion) when hypoxia = DO < 4 mg/L, HypoTDO4 is the average temperature below the hypolimnion when hypoxia = DO < 4 mg/L, fish size used was the total length (TL). \* p < 0.05, \*\*\* p < 0.001.

		Coefficient	OR (95% CI)
Chironomid pupae	Intercept	6.35	570.73 (0.04 – 1.9× 10 <sup>8</sup> )
Model 12	Depth	0.28***	1.33 (1.16 – 1.56)
	SeasonPost	-6.70*	$1.20  imes 10^{-3} (1.00  imes 10^{-6} - 0.29)$
	SeasonPre	-1.77	$0.17 (4.10 \times 10^{-3} - 3.70)$
	EpiTDO4	-0.64*	0.52 (0.27 – 0.86)
	HypoTDO4	0.18	1.19 (0.95 – 1.54)
Amphipods	Intercept	-3.13	$0.044~(5.0  imes 10^{-3} - 0.27)$
Model 4	Depth	0.15*	1.17 (1.04 – 1.33)
	SeasonPost	-16.84	$0 (NA - 1.91 \times 10^{28})$
	SeasonPre	-0.75	0.47 (0.15 – 1.55)
Daphnia	Intercept	-1.61	$0.20 (3.85 \times 10^{-8} - 128.89)$
Model 6	Depth	0.25	1.28(0.85 - 2.77)
	SeasonPost	-11.31	$1.22 \times 10^{-5} (NA - Inf)$
	SeasonPre	10.43*	$3.39  imes 10^4 \left( 37.31 - 1.43  imes 10^{11}  ight)$
	Fish size	-0.026*	0.97 (0.95 - 0.99)
	Depth:SeasonPost	-0.32	$0.72 (1.87 \times 10^{-8} - \text{NA})$
	Depth:SeasonPre	-0.62*	0.54 (0.24 - 0.89)



Figure 2.1. (A) Frequency of occurrence of prey in adult yellow perch stomachs for all seasons combined. (B) Prey biomass in adult yellow perch stomachs (excluding prey making up less than 1% of total biomass). We formally analyzed the five most common prey types, i.e. those that occurred in at least 10% of the stomachs.



Figure 2.2. Proportion of hypoxic sites by season and by hypoxia cutoff used in models (DO < 2 mg/L and DO < 4 mg/L). Light gray areas indicate proportion of hypoxic sites whereas black areas indicate that hypoxia was not detected.



Figure 2.3. Water column profiles of mean dissolved oxygen (mg/L) (left panel) and temperature (°C) (right panel) for June (blue), July (yellow), August (green), and November (purple). This figure includes vertical profiles conducted by ODNR-DOW prior to trawling at a station of each depth stratum.



Figure 2.4. Proportion of empty adult yellow perch stomachs by season with sample size (*n*) above the bars. Pearson's  $\chi^2$  test ( $\chi^2 = 7.33$ , p = 0.026) indicated that season significantly influenced the proportion of empty stomachs.



Figure 2.5. Proportion of prey biomass (%) in adult yellow perch stomachs by taxon and season. The pre-hypoxic season represents fish caught in June & July; peak-hypoxic, August; and post-hypoxic, November. Printed prey name labels (in yellow text) on the bars represent prey items that contributed to > 3% of biomass in stomachs by season. Data representing pelagic prey are shaded with dots; data representing benthic prey are shaded with diagonal lines. Other, which include prey that could not be characterized as benthic or pelagic (chironomid adult, chironomid, egg mass, fish eggs, and unidentified prey), are represented by solid color bars (no shading). The "Chironomid" prey group consists of chironomids whose life stage could not be determined in the diet samples.



Figure 2.6. Frequency of occurrence (%) of each taxon found in yellow perch stomachs by season. Frequency of occurrence was calculated by dividing the number of stomachs containing a particular prey items by the total number of (non-empty stomachs by season. Top panel shows data for the pre-hypoxic season, middle panel shows peak-hypoxic, and bottom panel shows post-hypoxic season.



Figure 2.7. Hurdle model results for *Bythotrephes* prey in yellow perch stomachs by season. (A) Zero part of the hurdle model showing probability of presence (1) or absence (0) of *Bythotrephes* in adult yellow perch stomachs by season, and (2) Count part of the hurdle model showing predicted counts by season.



Figure 2.8. Binomial GLM model results for chironomid pupae. Probability of presence of Chironomid Pupae in adult yellow perch stomachs by (A) average water temperature (°C) above the hypolimnion when DO < 4 mg/L and (B) site depth (m).



Figure 2.9. Binomial GLM model results for amphipods. Probability of amphipod presence in adult yellow perch stomachs against trawl depth (m). Left panel shows prehypoxic season and right panel shows peak-hypoxic season. Amphipods were not recorded in fish stomachs collected during the post-hypoxic season.



Figure 2.10. Binomial GLM model results for *Daphnia* for the pre-hypoxic season. Probability of *Daphnia* presence against depth (m) (left panel) and fish total length (mm) (right panel) as predicted by model 6.

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Appendix A. Chapter 2 Choosing appropriate data distributions for statistical analysis

We used generalized linear models (GLMs) to model *Bythotrephes*, Chironomidae pupae, Chironomidae larvae, amphipods, and *Daphnia* in adult yellow perch stomachs because those prey were the most abundant in stomachs. Poisson regression is often used to model count data, but this method is only valid when data are equidispersed (variance = mean). Our data were zero-inflated and overdispersed (Figure A.1) making the Poisson model an unsuitable choice since the variance was much greater than the mean. To model the number of prey consumed by adult yellow perch before, during, and after the hypoxic season, we explored other GLMs that can better model zero-inflated and overdispersed count data. We examined and compared the fit of six models on the Bythotrephes prey data: Quasi-Poisson GLM, Negative Binomial, Zeroinflated Poisson (ZIP), Zero-Inflated Negative Binomial (ZINB), Zero-Altered Poisson (ZAP) hurdle, and Zero-Altered Negative Binomial (ZANB) hurdle models. Various model diagnostic tools such as rootograms, residual plots, and AICc, indicated that the zero-inflated negative binomial and zero-altered negative binomial (hurdle model) were the best performing models for the *Bythotrephes* count data (Kleiber and Zeileis 2016). We used a Vuong test to compare the ZINB and ZANB models and a likelihood ratio test to determine which distribution fit the data best for both the zero-inflated and zero-altered models, which confirmed that the negative binomial distribution was more appropriate.

We decided to use the two-part zero altered negative binomial (hurdle) model for the Bythotrephes data due to the nature of zeros in our data and since it is more straightforward to implement and interpret (Potts and Elith 2006). Due to quasi-complete separation of data (i.e., specific taxa being completely absent in stomachs in at least one of the seasons), chironomid pupae, amphipod, chironomid larvae, and Daphnia were modeled as binomial presence-absence data, instead of using a hurdle model to interpret their numerical counts. For these taxa, we used a binomial GLM with a logit link function. The response variable was coded as a value from 0 (absent) to 1 (present). A total of 13 candidate models were investigated for all prey taxa analyzed and these were compared using AICc to select the most likely model (Burnham and Anderson 2002). Due to relatively low frequency of the remaining prey taxa in stomachs, the rest of the taxa were not formally analyzed, instead, their occurrence and biomass in stomachs were graphically examined and described. We fit all models using R Statistical Software (v4.2.1; R Core Team 2022): quasi-Poisson model using the function glm from the stats package, negative binomial models using the function glm.nb from the MASS package (v7.3.57; Venables and Ripley 2002), zero inflated models using the zeroinfl function from the pscl package (v1.5.5; Jackman 2020), and hurdle models with the pscl package (Zeileis et al. 2008).



Figure A.1. Comparison of A) empirical density histogram with theoretical density curve (dashed line) and B) cumulative distribution function of zero-inflated and overdispersed count *Bythotrephes* data.

Appendix B. Zooplankton and Benthic Invertebrate Prey Community Composition

Gaining a complete picture of yellow perch diets and food web dynamics requires information about the prey community available to yellow perch. We sampled zooplankton and benthic macroinvertebrates during additional field surveys aboard the *R/V Carmen*. Due to low sample numbers, lack of suitable temporal correlation with DNR-DOW trawls, inability to sample all substrate types, and low taxonomic overlap with yellow perch diets, these results were not included with the diet analysis, but presented here. Here, we characterized the zooplankton and benthic prey community and explored relationships between environmental variables and zooplankton abundance.

# Methods

#### Field collections

Zooplankton and benthic macroinvertebrates were collected aboard the R/V*Carmen* at the start and end of every ONDNR-DOW bottom trawl transect in July, August, and November 2021 (no prey were collected in June). Prey were collected at bottom trawls conducted in Chagrin-Fairport and Perry, OH. For each sample (start or end of transect) for each prey type (zooplankton or benthos), we combined collections from two hauls. We collected zooplankton via whole water column vertical hauls using a weighted 64 µm-mesh conical zooplankton net (0.5-m net diameter) with a calibrated flow meter (Sea-Gear MF315) mounted in the center of the net and a 500-ml collection jar. The zooplankton net was washed after each collection and flow meter numbers were recorded before and after each vertical tow to calculate volume sampled. We calculated volume sampled by multiplying distance sampled by the net opening area (0.183 m<sup>2</sup>). We used a Standard size (box size: 15 x 15 x 15 cm; sample area: 232 cm<sup>2</sup>) Wildco Standard Ekman Grab (Wildco, Yulee, FL, USA) to collect benthic invertebrates and washed collections through a Wildco 504-µm mesh bucket. Retained prey samples were preserved in a 10% sugar formalin solution and brought back to the laboratory for processing. The Ekman Grab was ineffective at sampling on rocky substrates, so we were unable to collect benthic macroinvertebrates at every site. Benthic samples were collected only in August and November. Zooplankton were collected off the starboard side of the boat while benthic macroinvertebrates were collected simultaneously off the stern. We aimed to temporally and spatially pair ODNR-DOW trawl samples with prey collections, but logistical challenges did not always allow exact pairing.

# Prey sample processing

Preserved zooplankton samples were transported back to the laboratory, rinsed through a 64-µm sieve, and diluted with distilled water to a known volume, from 50 to 200 ml. After samples were well-mixed, a pipette was used to take an aliquot from a known sample volume. Each zooplankton sample was processed by counting two subsamples of at least 3 ml each (no more than 10 ml), resulting in a minimum total subsampled volume of 6 ml. After the subsample was extracted using a pipette, it was transferred to a zooplankton counting wheel. We used a dissecting microscope to count and identify individual zooplankton. We identified zooplankton to broad taxonomic

groups: Cladocerans included *Leptodora*, *Bythotrephes*, *Daphnia*, *Diaphanasoma*, *Bosmina/Eubosmina*, and *Chydorids*; copepods were classified as calanoid, cyclopoid, or hapacticoid; and *Mysidae* were identified as belonging to *Mysis* or *Hemimysis*. Benthic invertebrate samples were rinsed with distilled water through a 500-µm sieve to remove sugar formalin, and contents were then transferred to a counting tray. Similar to processing zooplankton, we identified and counted benthic invertebrates using a dissection microscope. We identified invertebrates into the following groups: *Amphipoda*, *Isopoda*, *Chironomidae*, *Annelida*, *Nematoda*, *Turbellaria*, *Hirudinea*, *Dreissena*, *Gastropoda*, *Sphaeriidae*, *Pelecypoda* (*Bivalvia*), *Ostracoda*, *Hydrachnidia*, and *Daphnia* eggs. In contrast to zooplankton processing, we processed whole benthic invertebrate samples (no subsampling). All prey items were recorded as numerical counts of individuals (not mass). As with the yellow perch diet data, we separated chironomid prey into four categories: chironomid adults, chironomid larvae, chironomid pupae, and chironomids (when the life stage was not distinguishable).

## Statistical Analyses

#### Zooplankton: Constrained Ordination – Redundancy Analysis

To explore zooplankton community composition and the relationships between zooplankton abundance and environmental variables, we applied one constrained and one unconstrained ordination method. We first applied a detrended correspondence analysis (DCA) to determine whether linear or unimodal ordination methods were appropriate for the data (Hill and Gauch 1980; Leps and Smilauer 2003). The length of the gradient (SD = 1.9) indicated a homogeneous dataset; therefore, we used redundancy analysis (RDA), a linear constrained ordination technique (Legendre and Legendre 2012), to examine how environmental variables influence zooplankton community. Species data were Hellinger transformed and log transformed (log[X+1]) to minimize the effects rare or very common species have on the data (Legendre and Gallagher 2001). Very rare taxa, *Hemimysis* and harpacticoids, were removed for the ordination analyses. Cladoceran and copepod eggs were also removed. Environmental variables were centered and scaled. Sample replicates, collected at the start and end of each trawl transect, were combined into one sample for each trawl transect per sampling date.

The full RDA model included maximum site depth, water temperature (mean whole water column temperature, mean hypolimnion temperature, and mean epilimnion temperature), thermocline depth, dissolved oxygen, and water transparency (Secchi reading) as the explanatory variables. To test whether zooplankton communities differed between season, sites sampled were grouped by season. To simplify the RDA model, we used a stepwise forward selection to determine which explanatory variables best explained the variation in the zooplankton species data (response variables) (Leps and Smilauer 2003). Forward selection indicated temperature, hypolimnion temperature, depth, epilimnion temperature, and dissolved oxygen as important variables. Temperature and epilimnion temperature, depth, and dissolved oxygen in the RDA. Variance inflation factors (VIFs) of the predictor variables included in the model were examined to ensure that multicollinearity among these predictors were not a problem (Borcard et al. 2011). All VIFs for variables included in the final model were < 10. We assessed the significance of the RDA by applying a post hoc one-way analysis of variance (ANOVA) with up to 999 permutations to examine if there was a significant difference in the community composition of zooplankton between the seasons. The variation explained by each variable was estimated using adjusted  $R^2$ , which provided unbiased estimates of the explained variation (Legendre and Legendre 2012).

#### Unconstrained Ordination – Non-metric Multidimensional Scaling

For the unconstrained ordination, we conducted non-metric multidimensional scaling (nMDS) to examine similarities and patterns in the zooplankton community across seasons. NMDS was applied with Bray-Curtis dissimilarity index and species data were Wisconsin double standardized. Two axes (k = 2) were specified for the nMDS ordination with 100 random starts. Correlations and goodness of fit (stress) in the nMDS were examined to ensure that the ordination results were appropriate for interpretation. Environmental variables were fitted post hoc to the nMDS results using the envfit function from the vegan package (v2.6.2; Oksanen et al. 2022) in R. We also tested whether season significantly influenced dissimilarities in the zooplankton community by conducting a permutational analysis of variance (PERMANOVA) using the function adonis2 from the vegan package. Rare species (< 1% occurrence in samples) including harpacticoid and *Hemimysis* were removed before analysis. Ordination analyses were performed using the rda, metaMDS, and decorana functions in the vegan package (v2.6.2; Oksanen et al. 2022).

# Benthic Macroinvertebrates

Due to equipment and logistical difficulties, benthic prey were collected only in August and November 2021. Due to the low number of benthic macroinvertebrates samples, these were not formally analyzed. Rather, the benthic prey community data are presented graphically using measures such as relative abundance, total individual counts by taxa, and frequency of occurrence of each benthic macroinvertebrate group.

# Results

#### Zooplankton

To characterize the zooplankton community in the central basin of Lake Erie, we quantified zooplankton abundance and frequency of occurrence, and applied two ordination techniques to test how environmental variables influenced the zooplankton community. A total of 10 different zooplankton taxa were identified in our samples (excluding cladoceran and copepod eggs) but only 8 were used in the formal ordination analysis (harpacticoid and *Hemimysis* were excluded because of their rareness). *Bosmina, Leptodora, Daphnia*, calanoids, and cyclopoids were the most abundant groups in our samples (Figure B.1). The community was dominated by calanoids and cyclopoids throughout the pre- and peak-hypoxia seasons and these taxa made up nearly half of the density during the post-hypoxic season (Figure B.1). Calanoid density decreased with season, whereas cyclopoid density was highest in the peak-hypoxic season. *Bosmina* and *Daphnia* abundance were both highest during the post-hypoxic season. Calanoids and cyclopoids were found in every sample processed (Figure B.2). *Bosmina* were found in

all peak-hypoxic and post-hypoxic samples, and in 94% of the pre-hypoxic samples. *Bythotrephes* were not very abundant in the zooplankton samples, in contrast to their commonness in yellow perch stomach contents (Chapter 2). The only zooplankton prey identified in the samples that were also important and relevant to the stomach content analyses were *Bythotrephes* and *Daphnia*.

## Redundancy analysis

To examine the zooplankton community, similarities among taxa and sites, and the influence of environmental variables, we applied one constrained and one unconstrained ordination technique. RDA analyses revealed that the environmental variables included in the model (dissolved oxygen, temperature, hypolimnion temperature, and depth) explained 61% ( $R^2 = 0.61$ ) of the variation in zooplankton abundance across sites (39% unexplained variance). When we corrected for the number of variables in the model, the adjusted  $R^2$  suggested that the 3 selected variables explained 57% of the variance in zooplankton abundances. The first, second, and third axes explained 40%, 12%, and 9% of the variation observed, respectively. We only retained the first two axes since these explained most of the variation in zooplankton abundance. The ANOVA results showed that the model, the first three RDA axes, and environmental variables of depth, temperature, and hypolimnion temperature significantly explained (p < 0.001) the variation in zooplankton abundances.

The RDA demonstrated that the post-hypoxic zooplankton community is distinguishably different from the pre- and peak-hypoxic communities (Figure B.3). The RDA triplot also suggests some overlap in the communities between the pre- and peakhypoxic seasons, with hypolimnion temperature and the presence of *Leptodora* shifting the pre-hypoxic community. The first axis of the RDA shows a positive correlation with water temperature whereas the second axis is negatively related to site depth and positively related to dissolved oxygen and hypolimnion temperature. Calanoids and cyclopoids were positively associated with temperature, whereas *Bosmina*, *Daphnia*, and chydorids were positively related to dissolved oxygen. Chydorid, *Diaphanasoma*, and *Bythotrephes* were more similar to each other compared to the other taxa, most likely due to their overall low abundance in our samples. *Leptodora* seemed to be dissimilar from the other taxa and was most strongly associated with hypolimnion temperature and the sites sampled during the pre-hypoxic season. *Bosmina*, *Leptodora*, calanoids, and cyclopoids influenced more than 60% of the variation observed in zooplankton abundance.

# Non-metric multidimensional scaling

To further explore dissimilarity among the zooplankton community across seasons, we used non-metric multidimensional scale (nMDS) ordination using the Bray-Curtis distance matrix. The nMDS ordination with two dimensions had a stress value of 0.16 (Figure B.4), suggesting that nMDS results are valid for interpretation and no additional dimensions were required.

The nMDS results suggest that cyclopoids and calanoids had similar abundance patterns between months (Figure B.5), agreeing with the RDA results. Consistent with the RDA results, Chydorid, *Bythotrephes*, and *Leptodora* appear to be dissimilar compared to the rest of the zooplankton community. In contrast to the RDA, the nMDS showed that *Diaphanosoma* were dissimilar from chydorid and *Bythotrephes*. Similar to the RDA, the nMDS also demonstrated that there was some overlap in zooplankton community between the pre-hypoxic and peak-hypoxic seasons, while the post-hypoxic zooplankton community more dissimilar compared to the other two seasons (Figure B.5).

Environmental variables were fitted post hoc to the nMDS using the envfit function in the vegan package (v2.6.2; Oksanen et al. 2022) in R (v4.2.1; R Core Team 2022). This function allowed us to assess the significance of environmental predictors in explaining the zooplankton community. Permutation tests suggested that depth, temperature, and hypolimnion temperature were significant. Unlike the RDA, dissolved oxygen was not significant in the nMDS. After fitting environmental variables to the nMDS, we visualized how each environmental predictor was associated with the sites sampled. Temperature and hypolimnion temperature were positively correlated with the pre-hypoxic zooplankton community, whereas depth was associated in driving the peakhypoxic community (Figure B.6).

A permutational analysis of variance (PERMANOVA) was applied to test the effects of season on zooplankton community structure. The PERMANOVA was significant (p < 0.001) showing that the different seasons explain 34% of the variation in zooplankton community structure. Lastly, an analysis of congruence (Procrustes test) was performed to compare the RDA and nMDS ordinations (Figure B.7). The test was conducted by scaling to unit variance which gives a more scale-independent and symmetric statistic (Procrustes  $m^2 = 0.544$ ) with its significance assessed by permutation tests.

Applying these two ordination techniques allows for a deeper interpretation of the zooplankton community structure. Each technique has unique ordination processes that can be complementary to each other. In both the RDA and nMDS, depth and water temperature influenced zooplankton community the most. The zooplankton composition during the peak-hypoxic season was more strongly associated with station depth than during other seasons. Overall, temperature seems to be the environmental variable that shapes zooplankton community the most.

#### Benthic Macroinvertebrates

To better understand the benthic macroinvertebrate community composition in the central basin of Lake Erie, we explored relative abundance and frequency of occurrence of individual taxon in our benthic samples. We conducted 80 individual benthic grabs (including two replicates per sample site) which were combined into one grab per site per date, resulting in 31 combined total samples. Additionally, due to the effectiveness of Ekman Grabs on hard rocky bottoms, some of these grabs were almost empty or only contained rocks and/or mussels. Due to the low number of grouped samples collected (n = 31) and lack of benthic sampling in July, we were unable to make comparisons across seasons.

Annelids, *Daphnia* eggs, and dreissenids were the most abundant taxa in our benthic samples (Figure B.8). Together, these three groups made up 64% and 74% of relative abundance in August and November, respectively. In August, the taxa with the fourth highest relative abundance, after annelids, were ostracods (10.6%). Following dreissenids, ostracods were also the taxa with the next highest (9.5%) relative abundance in November. Benthic prey relative abundance in August and November was very similar with the most notable difference being that August samples had a higher proportion of isopods (9% in August versus 0.5% in November). In August, 16 different types of prey were identified in our samples including three distinct life stages of chironomids (adults, eggs, and larvae) and *Daphnia* eggs; whereas in November, only 10 types of prey were identified with no chironomid eggs or adults recorded. *Hirudinea, Hydrachnidia, Pelecypoda (Bivalves), Turbellaria*, and chironomid adults and eggs were not found in any of the November samples. The highest number of individuals counted in August were *Daphnia* eggs with a total of 4,096 eggs (Figure B.9). In November, the most abundant benthic prey were Annelids, with 709 individuals counted. *Daphnia* eggs occurred in 95% and 100% of the samples processed in August and November, respectively (Figure B.10). Sphaeriids occurred in 89% of the samples in November and in 68% of the August samples. In comparison to prey found in yellow perch stomach contents, only amphipods and chironomid larvae were identified in our benthic samples.

## Discussion

To gain a more complete understanding of yellow perch foraging and food web dynamics, it is necessary to also understand how the prey community is influenced by hypoxia and associated seasonal environmental changes. By quantifying and visualizing density, frequency of occurrence, and relative abundance of pelagic zooplankton and benthic macroinvertebrates we were able to describe the dominant groups and seasonal shifts in community composition and abundance. Ideally, sampling of both predators and prey should incorporate more areas and months. Due to low sample size, these data might not be representative of the whole zooplankton and benthic communities available for yellow perch to prey on.

The prey community results presented in this Appendix do not match well with what was observed in yellow perch stomach contents. *Daphnia* density was highest in samples collected after the fall turnover (post-hypoxic) whereas in yellow perch diets *Daphnia* were not found in stomachs from the post-hypoxic season. This mismatch could be a result of limitations associated with stomach contents and digestion time, limiting the prey available to researchers to examine. As mentioned in Chapter 2, *Daphnia* have been reported to be digested quickly (Gannon 1976). The total density and frequency of occurrence of *Bythotrephes* was low in the zooplankton samples whereas this was the most abundant prey in stomachs. This could be a result of inflated stomach contents values due to *Bythotrephes* spine retention discussed in Chapter 2.

In agreement with the diet results, the zooplankton community during the posthypoxic season was distinctively different from the other seasons. The dissimilarity observed between seasons sampled was expected due to the different temperatures and dissolved oxygen levels associated with each season. A higher sample size would have allowed us to ordinate the data by season separately to look at environmental effects for each season. Similar to yellow perch stomach contents, the ordinations showed that the zooplankton composition is influenced by depth. Both depth and season were important variables in explaining yellow perch diets and zooplankton community composition. In the ordinations, depth was most strongly associated with the peak-hypoxic zooplankton community which could be associated with hypolimnion thickness and degree of water column stratification. There are other variables that we did not consider (e.g. distance from shore; chlorophyll *a*) that might also influence zooplankton and benthic invertebrates. Sampling in this study occurred during the day, and nighttime sampling might reveal different trends. To collect zooplankton, we used whole water column net tows. To gain more detailed understanding on how hypoxia influences zooplankton community and spatiotemporal distributions, it might be helpful to collect samples at specific depths or areas of the water column (e.g., using a MOCNESS net). Additionally, benthic surveys are needed and the benthic community seems to be an understudied aspect in the central basin. The main takeaway from these results is that depth and season play a strong role in both yellow perch diet and zooplankton community composition but limitations of both sets of data do not allow a comparison of diet and prey.



Figure B.1. Proportion of zooplankton abundance (density) in samples collected in the central basin of Lake Erie in 2021 by season with most abundant taxa labeled on the bars.



Figure B.2. Frequency of occurrence of each zooplankton taxon by season. Harpacticoid and *Hemimysis* were not included in the formal analysis. Frequency of occurrence was calculated by dividing the number of samples containing a particular zooplankton taxon by the total number of samples collected by season.





Figure B.3. RDA Triplot of the spatial correlation between zooplankton abundance and environmental variables on the first two axes. Red points represent sites sampled during the pre-hypoxic season; green points, peak-hypoxic season; and blue points, post-hypoxic season. Harpacticoid and *Hemimysis* were excluded from this analysis.


Figure B.4. NMDS stress plot showing that after two dimensions the stress value does not decrease significantly, validating our decision of using two dimensions for our ordination.



Figure B.5. NMDS ordination of zooplankton abundance data grouped by season. Blue squares represent the pre-hypoxic season, red points represent the peak-hypoxic season, and green triangles represent the post-hypoxic season.



Figure B.6. NMDS ordination with significant environmental variables (Depth, Temp, and hypo.temp) and sites distinguished by season. Depth is the maximum site depth, Temp is mean water column temperature, and hypo.temp is the mean hypolimnion temperature. Blue squares represent the pre-hypoxic season, red points represent the peak-hypoxic season, and green triangles represent the post-hypoxic season. Arrows show the correlation between ordination axes and environmental variables.



Figure B.7. Procrustes error plots comparing RDA and nMDS ordinations. The left panel shows how sites have shifted positions from the RDA to the nMDS. The right panel shows the residuals for each sample, horizontal lines from top to bottom show the 75% (top dashed line), 50% (middle solid line), and the 25% (bottom dashed line) quantiles of the residuals.



Figure B.8. Proportion of benthic prey counts identified in samples. Labels of prey names printed are for prey that had > 3% relative abundance.



Figure B.9. Total counts of benthic macroinvertebrate taxa by month. Taxon with counts < 10 were excluded from this figure for visualization purposes.



Figure B.10. Frequency of occurrence (% FO) of each benthic macroinvertebrate taxon identified by month. Frequency of occurrence was calculated by was calculated by dividing the number of samples containing a particular zooplankton taxon by the total number of samples collected by season.