Developing Fish Trophic Interaction Indicators of Climate Change for the Great Lakes

Final Report to:
The Department of the Interior Northeast Climate Science Center
and the
Upper Midwest and Great Lakes Landscape Conservation Cooperative

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*including FY11 carry-over.
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Public Summary

This project addressed regional climate change effects on aquatic food webs in the Great Lakes. We sought insights by examining Lake Erie as a representative system with a high level of anthropogenic impacts, strong nutrient gradients, seasonal hypoxia, and spatial overlap of cold- and cool-water fish guilds. In Lake Erie and in large embayments throughout the Great Lakes basin, this situation is a concern for fishery managers, as climate change may exacerbate hypoxia and reduce habitat volume for some species. We examined fish community composition, fine-scale distribution, prey availability, diets, and biochemical tracers for dominant fishes from study areas with medium-high nutrient levels (mesotrophic, Fairport study area), and low nutrient levels (oligotrophic, Erie study area). This multi-year database (2011-2013) provides the ability to contrast years with wide variation in rainfall, winter ice-cover, and thermal stratification. In addition, multiple indicators of dietary and distributional responses to environmental variability will allow resource managers to select the most informative approach for addressing specific climate change questions. Our results support the incorporation of some relatively simple and cost-efficient approaches into existing agency monitoring programs to track the near-term condition status of fish and fish community composition by functional groupings. Other metrics appear better suited for understanding longer-term changes, and may take more resources to implement on an ongoing basis. Although we hypothesized that dietary overlap and similarity in selected species would be sharply different during thermal stratification and hypoxic episodes, we found little evidence of this. Instead, to our surprise, this study found that fish tended to aggregate at the edges of hypoxia, highlighting potential spatial changes in catch efficiency of the fishery. This work has had several positive impacts on a wide range of resource management and stakeholder activities, most notably in Lake Erie. The results were instrumental in the development of an interim decision rule for dealing with data collected during hypoxic events to improve stock assessment of Yellow Perch. In addition, novel findings from this study regarding spatial and temporal variability in hypoxia have aided US-Environmental Protection Agency in the development of a modified sampling protocol to more accurately quantify the central basin hypoxic zone, and this directly addressed a goal of the Great Lakes Water Quality Agreement of 2012 to reduce the extent and severity of hypoxia. Finally, the study areas developed in this project formed the basis for food web sampling in the 2014 bi-national Coordinated Science and Monitoring Initiative work in Lake Erie.

Data Management

Data sets collected during the execution of this study will be made publically available in a permanent repository at www.sciencebase.gov.
Technical Summary

Climate driven changes in temperature, freshwater inputs, and nutrients in aquatic systems are predicted to result in a northward expansion of cool- and warm-water fish populations and a reduction in habitat for coldwater species. As suitable aquatic habitats change in volume and extent, individual fish species will experience increased or reduced spatial overlap with competitors, and the composition of prey resources may change dramatically. This will be especially challenging in the Great Lakes where altered food webs may affect the sustainability of fisheries valued at several billion dollars. Across three years, we examined interannual and seasonal changes in fishery food webs from Lake Erie as a representative system in which trophic interactions are influenced by temperature trends, thermal stratification, and hypoxia. We contrasted study areas along a production gradient from mesotrophic habitats of the central basin to oligotrophic habitats of the eastern basin. Our objectives were four-fold:

1. Quantify seasonal changes in the vertical and horizontal distributions of fishes.
2. Characterize spatial and temporal variability in diet and trophic position.
3. Develop synoptic trophic interaction indicators related to climate change.
4. Examine fine-scale distribution of fish near hypoxia to inform the development of an interim decision rule on data inclusion thresholds from management surveys affected by Lake Erie’s dead zone.

We used multiple field-based sampling approaches combined with laboratory-derived measurements to understand variation in fish community composition, prey, water quality, trophic interactions, and somatic condition of selected species. Study areas contrasted sharply with higher fish densities, lower diversity, and lower fraction of coldwater species in the mesotrophic study area. To our surprise, analysis of fine-scale distribution patterns revealed aggregation of fish near hypoxia, as opposed to avoidance. Mean trophic level of the fish community and the composition of functional groups were highly variable across seasons and years. Diets of selected species exhibited broad variation in similarity and overlap indices. Further, we observed no pattern in diet overlap with respect to hypoxic events, when we expected diet overlap to increase. We examined three different stable isotopes as longer-term integrated measures of diet, and found approximately equal contributions of benthic, pelagic, and terrestrial sources of primary production for most taxa. We could not distinguish study areas or years with stable isotopes, but we did find significant variation in somatic condition indices with unique patterns by species and study area.

These novel data on Lake Erie ecosystems have already informed important decisions by State, Federal, and provincial managers in the Great Lakes. Specifically, our analysis of fish distribution with respect to hypoxia has informed a decision rule on the inclusion of stock assessment data for annual development of fishery quotas. This work also aided US-EPA in the development of a robust bi-national food web investigation through the Coordinated Science and Monitoring Initiative annex of the Great Lakes Water Quality Agreement. Finally, our results
support incorporation of foodweb metrics into resource management, and selection of informative variables over those that lack sufficient contrast for tracking progress in achieving policy goals.

List of Common and Scientific Names

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<thead>
<tr>
<th>Common name</th>
<th>Scientific name</th>
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<tr>
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**Purpose and Objectives**

Great Lakes’ fisheries are a multinational resource valued at several billion dollars annually (Allen and Southwick 2007). Great Lakes fishery managers strive to maintain food web structures that provide optimum production of exploited fish species (Ryan et al. 2003), but rapidly changing climate is predicted to alter food web dynamics and consequently the sustainability of fish resources. Thus, there is a need to understand how climate driven changes influence food webs before such changes are realized.

Over the past century, dramatic changes in Great Lakes fishery resources have occurred with many resulting in undesirable consequences for the resource stakeholders. In most cases, the causes have been due to overfishing, invasive species, mineral nutrient input increases, and habitat alteration (Ludsin et al. 2001). These changes are often associated with dramatic shifts in food web structure that have consequences to the sustainability of fishery resources and regional economies that depend on the resources (Munawar et al. 2005). Changes in trophic interactions often occur in concert at multiple trophic levels; therefore, synoptic measures of the trophic structure of fisheries are key to informing and adapting management strategies in the face of a changing climate.

In the Great Lakes and elsewhere, increases in temperature, freshwater inputs, and eutrophication are predicted to result in a northward expansion of cool- and warm-water fish populations and a reduction in habitat for coldwater species (Magnuson et al. 1990). The most important environmental variables that determine large scale distribution and primary niche space of fishes in freshwater ecosystems are temperature and dissolved oxygen, which are the predominate factors that regulate physiological processes of development, growth, and reproduction of individual fish. As fish seek out preferred temperatures or thermal refuges (depending on the range of available temperatures), zoogeographic ranges shift and expand or contract on seasonal and long-term scales. This phenomenon can shift the phenology of life histories and alter the outcome of competition and predation interactions via changes in community structure (Winder and Schindler 2004). Also contributing to changes in community structure, long-term variability in temperature can allow the proliferation and range expansion of invasive species (Johnson and Evans 1990). Further, warmer temperatures, and increases in nutrients and pulses of water from tributaries may contribute to oxygen availability limitations for fishes in the hypolimnion during stratified conditions, and possibly at the start of ice-on in winter (Magnuson et al. 1997). Low oxygen conditions can change food web dynamics both directly, by restricting access of fish to habitats with preferred temperatures and prey, and indirectly, by reducing the productivity of oxygen-sensitive species (Arend et al. 2011).

Lake Erie represents a window to these future trophic interactions, which are occurring in small lakes and reservoirs throughout the region, and in large embayments of other Laurentian Great Lakes, such as Saginaw Bay in Lake Huron, Green Bay in Lake Michigan, and the Bay of Quinte in Lake Ontario. Lake Erie is the southernmost and shallowest of the Laurentian Great
Lakes, and as a consequence it has the most extreme water temperatures. Lake Erie is also the most productive of the Great Lakes, and on average the amount of fish harvested from Erie equals or exceeds all the other Great Lakes combined (http://www.glsc.usgs.gov/commercial-fishing-reports). Erie has three significant sub-basins with contrasting depths, nutrient levels, and temperature distributions, but all three are strongly hydrologically connected through prevailing currents and circulation patterns (Figure 1). The western and central basins are relatively shallow and have varied historically between eutrophic and mesotrophic with a combination of productive cool- and warmwater species, dominated by percids (yellow perch and walleye). By comparison the eastern basin is much deeper and represents a refuge for coldwater species, such as stocked salmonids and native lake whitefish. The transition between Erie’s mesotrophic central basin and the deeper, oligotrophic eastern basin provides a unique natural laboratory for examining food web dynamics that are driven by environmental and behavioral changes of different fish guilds. On a seasonal basis, cool- and coldwater fish guilds in the central basin are squeezed vertically into the metalimnion and horizontally towards the eastern basin and shallower depths by increasing surface temperature and developing hypoxia in the hypolimnion. This phenomenon produces intense spatial overlap of species and cohorts that would otherwise segregate in the absence of hypoxia, and it occurs at a critical period when 1) metabolic needs are high owing to warm water temperatures, and 2) many species are building up energy reserves for overwintering and gonad maturation for spring reproduction. Due to climate driven processes, these effects are projected to intensify and increase in duration. Like most other lakes throughout the region, Lake Erie has been gradually warming since the 1960s (Figure 2), and this phenomenon has had mixed effects (positive, neutral, or negative) dependent upon the thermal preferences of a particular species. In general, summer refuge habitats for coldwater species have become more limited in extent and the time spent in marginal habitats has tended to increase. In addition, favorable conditions for early life stages of several of these species (including some coolwater species) have diminished with warmer winters and less ice cover.
Habitats and refuges for fishes in Lake Erie are also limited seasonally by low dissolved oxygen in the hypolimnion, most notably in the central basin, where nearly all of the hypolimnion may become hypoxic in years with high temperature and strong vertical stratification. This situation not only blocks access to a potential cold water refuge, but it is also devastating to the benthic macroinvertebrate community, especially indicator species, such as mayflies (*Hexagenia* spp.), that provide a critical food resource for fishes (Edsall et al. 2005). Previous research in the central basin of Lake Erie has demonstrated that hypoxia-driven changes in vertical and horizontal distributions of organisms may have profound effects on predator-prey interactions at lower trophic levels, i.e., phytoplankton, zooplankton, and planktivorous fishes (Vanderploeg et al. 2009). Hypoxia-driven changes also influence higher trophic levels; for example, changes in vertical distribution of yellow perch result in a shift in the consumption of high energy benthic invertebrates to pelagic invertebrates with lower caloric value (Roberts et al. 2009). Recent studies have shown that Lake Erie fish communities can have high spatial variability in trophic position of a particular species that may reflect differences in local primary production (Guzzo et al. 2011), but the food web structure as influenced by abiotic variables and water column stratification has yet to be examined in sufficient detail. Moreover, the extent and severity of low oxygen in the hypolimnion has increased in the most recent decade, and the resultant spatial distribution of fishes is related to anomalous high survey catches in lake-wide assessments of perch recruitment. The mechanism for this is not entirely clear, but preliminary results demonstrate that clustering of fishes both vertically and laterally to avoid hypoxia may explain anomalous high survey catch rates at normoxic sites that are adjacent to hypoxic hypolimnetic conditions (Kraus et al. 2015). Our understanding of how the food web structure changes in response to this redistribution of fish and how it may affect the long-term outcome of species interactions and community structure is vague at best.

This study aimed to build upon previous findings (Hawley et al. 2006) addressing three key questions: 1) how do predator-prey interactions between cool- and coldwater fish guilds change as environmental conditions increase spatial overlap; 2) does prey choice become more selective, leading to segregation of diets across species within a trophic level or does diet overlap increase between potentially competing species as a result of environmental change; and 3) how do the length and structure of the food web and trophic level of secondary consumers change with environmentally driven changes in vertical and horizontal distribution? Our ultimate goal is to provide managers with a better understanding of food web changes that may occur as different fish guilds compete for habitat and prey resources under forecasted climate conditions, and also to provide information for management in the form of indicator variables based on diet and natural tracers of food web structure.

This project directly addresses the Fish Community Goals and Objectives for Lake Erie defined in the Great Lakes Fishery Commission (GLFC) special publication 03-02 (2003), which states in its food web structure goal: “…manage the food web structure of Lake Erie to optimize production of highly valued fish species…” More broadly, this supports the Great Lakes
Fishery Commission’s Strategic Vision for ecosystem approaches for fisheries management (GLFC 2001; http://www.glfc.org/pubs/SpecialPubs/StrategicVision2001.pdf). Recently, our results were used to support urgent efforts by Council of Lake Committees fishery management partners to develop an interim decision rule for handling anomalously large survey catches associated with hypoxia in Lake Erie’s seasonal “dead zone”. Our objectives were four-fold:

1. Quantify vertical and horizontal distributions of dominant prey and predator fishes during spring, summer stratification, and after fall turnover in the central basin and eastern basin of Lake Erie.
2. Characterize spatial and temporal variability in diet and trophic position of fishes in response to seasonally-driven habitat changes.
3. Develop synoptic trophic interaction indicator variables (e.g., trophic position, diet composition, percent of benthic versus pelagic prey, percent contribution of allochthonous versus autochthonous primary production, etc.) that capture seasonal environmental variability as related to long-term climate change.
4. Examine proposed dissolved oxygen thresholds for excluding data from bottom-trawl surveys used in fisheries management in light of fine-scale depth stratified spatial analysis of fish distribution obtained from this study.

This report provides a description of the field and laboratory methods as well as summary analyses of the resulting data sets. In addition, the first publication from this project (Kraus et al. 2015) is appended to the report.

**Organization and Approach**

*Sampling Design*

We examined two sub-basins of Lake Erie with contrasting trophic and physical conditions: in the central basin near Fairport Harbor, Ohio, and in the eastern basin near Erie, Pennsylvania in the vicinity of a zoogeographic feature, the Pennsylvania Ridge (Figure 3). Throughout this report, we refer to these as the Fairport and Erie study areas, respectively. Depths sampled ranged from 10 to 35m; therefore, these areas represented offshore lake ecosystems. The Fairport area was chosen based upon the regular seasonal occurrence of hypoxia and mesotrophic conditions. In contrast, sites in Pennsylvania waters were chosen as oligotrophic ecotones where hypoxia does not typically occur. One of the main strengths of our approach was that widely separated areas with contrasting conditions were compared both within and between sub-basins of Lake Erie in each of the three seasonal periods. Previous work has tended to examine seasonal differences within a sub-basin, and this has limited broader application of the results. We surveyed each study area at three times: i) prior to stratification in late-May or early-June, ii) during stratification in August when hypoxia was expected at the Fairport study area, and iii) in September targeting the period immediately following lake turnover (post-stratification). We repeated this seasonal sampling scheme in each of three years,
2011 to 2013, with the exception that no sampling was conducted in June of 2011 due to unavailability of funding. On each sampling round, the effort varied according to the type of sample as described below.

Sampling was defined by transects, prescribed for each study area. At the Fairport study area, four North-South transects, approximately 8 km long and spaced 4 km apart, were sampled on each trip (Figure 3). During the first sampling trip in August 2011, we discovered several obstacles to trawling on the western most transect; therefore, the array was shifted east for all subsequent sampling trips. At the Erie study area, three transects, approximately 10 km long, were sampled on each trip. The Erie transects represented three prominent features of the oligotrophic eastern basin of Lake Erie: i) an East-West transect across the Pennsylvania Ridge, ii) the transition from the central basin to the eastern basin, and iii) the deep offshore waters of the eastern basin (Figure 3).

**Trawl Sampling**

To obtain aggregate catches of fishes for community analyses and laboratory processing, we used three different vessels and four different trawl nets. Trawl samples were distributed at the ends and the middle of prescribed transects in each study area, with supplementary sampling at adjacent locations (Figure 3). In general, three daytime bottom trawls were conducted on 2 to 4 transects, depending on availability of research vessels and configuration of the study area. Due to various factors, including the decommissioning of a USGS research vessel, changes in gear types were unavoidable. Effects of gear differences were quantified with comparative experiments conducted in 2012 (LEBS, 2013). On average the bottom trawl introduced in September 2012 was more efficient at catching pelagic species (Emerald Shiner and Gizzard Shad) and less efficient at catching some demersal species (White Perch, Trout-perch, and Freshwater Drum), but analyses also showed that fishing power correction factors would introduce variance for these species and should not be applied to correct for gear differences. Technical details of the vessels, gear and net geometry are provided in the appendix. Field collections were carried out in accordance with guidelines for the care and use of fishes by the American Fisheries Society (http://fisheries.org/docs/wp/Guidelines-for-Use-of-Fishes.pdf).
We analyzed the catch data for the eight most abundant species (Alewife, Emerald Shiner, Freshwater Drum, Rainbow Smelt, Round Goby, Trout-perch, White Bass, White Perch, and Yellow Perch) to understand interannual and seasonal changes in species composition at each study area. Other species made comparatively small contributions numerically to the overall catch, and were included in the analysis as a single pooled category.

To understand changes in piscivore-prey balance, we classified all species as either predator or forage, and either pelagic or demersal. The forage category included all age-classes of Alewife, Emerald Shiner, Gizzard Shad, Rainbow Smelt, Round Goby, Silver Chub, and Trout-perch, but only young-of-year ages of Freshwater Drum, Lake Trout, White Bass, White Perch, and Yellow Perch. The predator category included all piscivores: Burbot, Channel Catfish, adult Freshwater Drum, adult Lake Trout, Smallmouth Bass, Walleye, adult White Bass, adult White Perch, and adult Yellow Perch. Pelagic species included Alewife, Emerald Shiner, Gizzard Shad, and Rainbow Smelt. Other species were classified as demersal. Ratios, predators:forage and pelagic:demersal, were calculated based upon catch per hectare in each sample and examined in box-and-whisker plots.

We examined the overlap of cold- and coolwater species in trawl catches by estimating this fraction of the total catch. Coldwater species were: Burbot, Lake Trout, Lake Whitefish, and Rainbow Smelt. Other species were classified as coolwater.

To track changes in trophic status of the fish community, we estimated weighted mean trophic level of each catch by assigning trophic levels for each species (www.fishbase.org, by age-group if data were available) and using catches per hectare as weights in the averaging. We used trophic level values reported in the literature instead from our own samples, because diet and stable isotope measurements were only made on a subset of species (n=5). These results were also examined in box-and-whisker plots by year, season, and study area.

Finally, for the catch data, we examined similarity in the species composition of the fish community between mesotrophic (Fairport) and oligotrophic (Erie) study areas. This was accomplished by calculating Shannon’s Diversity index for each sample, and via non-metric multi-dimensional scaling (or NMDS) to understand how much overlap was present across cool- and coldwater fish guilds. For the NMDS, we evaluated multivariate distances in k=2 dimensions with Bray-Curtis similarity and the Wisconsin square root transformation to achieve acceptable stress levels (<0.3, an indication of model fit) for 2-dimensional plotting. In addition, species with very low catch rates (<9 total captured) were not included in the NMDS analysis (Common Carp, Lake Trout, Lake Whitefish, Quillback, Sea Lamprey, Shorthead Redhorse, Silver Chub, Smallmouth Bass).
**Water Quality**

We measured temperature and dissolved oxygen in surface (<2m) and bottom (the deepest 2 meters) waters at each trawl sampling site. Dissolved oxygen was measured with an optical sensor using various YSI® instruments (sondes and handheld devices). Temperature sensors were calibrated by the manufacturer, and dissolved oxygen was calibrated prior to each sampling trip. Once temperature stabilized (by holding the sensor at a constant depth), a minimum of 3 readings averaged over 60s were used to characterize dissolved oxygen (mg/L) and temperature (°C) for each depth stratum at each site. Supplementary water quality sampling at the Fairport study area was conducted in August at ancillary sites to better map the distribution of hypoxia. These supplementary samples were collected as water column profiles of temperature and dissolved oxygen at 1m depth intervals. These data were modeled with 3-dimensional anisotropic interpolation techniques (in Voxler ®) to visualize the hypoxia phenomenon. Additionally, we measured Secchi depth (m) to the nearest 0.1 m with a 0.5 m diameter Secchi disc at each site that was sampled during day time.

We examined bi-plots of temperature and dissolved oxygen with 95% confidence ellipsoids to understand changes in fish habitat across study areas, years, seasons, and vertical strata (epilimnion v. hypolimnion). Unfortunately, our dissolved oxygen sensor malfunctioned during surveys at the Erie study area in August of 2012; therefore, we do not have oxygen data from this period and location. We also graphically evaluated Secchi depth changes. In addition, we used ancillary water quality data from vertical profiles collected at the Fairport study area to interpolate and map the distribution of hypoxia, which was only present in August of 2011 and 2013. We used a 3-dimensional inverse distance weighted interpolation algorithm with anisotropic search window to account for greater variability with depth than in the latitude-longitude dimensions. We carried out this routine in Voxler ® (ver. 3, Golden Software, Inc, Colorado).

**Zooplankton Sampling**

To characterize zooplanktonic food resources for fish, we conducted vertical tows with 0.5 m diameter plankton nets with 62μm mesh size. This sampling was conducted from the Muskie (at both Fairport and Erie) and small research vessels at Fairport when possible. Whole samples were concentrated into the cod end, transferred to plastic containers, and preserved with 10% neutral buffered formalin. Immediately prior to preservation, we used Alka-Seltzer® to anesthetize zooplankton, ensuring their appendages were not autotomized during preservation. Zooplankton samples were quantified using light microscopy at an external laboratory, following typical Great Lakes protocols. Briefly, each sample was diluted to a known volume (typically between 50 and 2000 mL), and two to three subsamples of 10 mL each were quantified with a plankton wheel. Enumeration continued until a minimum of 100 individuals per taxon or 20% of the total volume was quantified. Zooplankton were identified to the lowest possible taxon and enumerated; however, for purposes of this report the data were pooled by function groupings (defined below). Counts were converted to density by dividing by volume filtered. Volume
filtered was calculated as the product of site depth and the area of the net opening \((\pi^*(0.25m)^2=0.196\ m^2)\). We collected between \(n=3\) and \(n=8\) zooplankton samples per study area on each sampling trip, and this varied depending upon the availability of assistance from collaborators with small research vessels.

We examined zooplankton community structure by functional group, and graphically evaluated the seasonal and spatial variation in density (number per \(m^3\)) and percent composition. Five functional groups were defined: 1) cyclopoid and calanoid copepods, 2) predatory cladocerans (primarily invasive *Bythotrephes longimanus*, and to a lesser degree 3) *Leptodora kindtii*, 4) daphnids, and 5) non-daphnid cladocerans. Other taxa present in low proportions were only considered in estimation of species richness and Shannon species diversity indices for each catch. We compared functional groups with analysis of variance, including all possible interaction effects with year, month, and area, and identified differences using confidence intervals (95%) with Tukey adjustment for multiple comparisons.

**Benthic Sampling**

On each sampling trip in each study area, we collected benthic grab samples with a petite Ponar dredge (sampling area = 0.023 \(m^2\)). Each sample was rinsed through a 250 \(\mu m\) sieve, stained with Phloxin-B to enhance visibility of macroinvertebrates, and frozen at \(-20^\circ C\) for laboratory processing. We used light microscopy to enumerate and identify benthic macroinvertebrates to order or family level classification. Samples were collected from the Musky II, Muskie, or smaller research vessels depending upon availability of assistance from collaborators. We analyzed between \(n=4\) and \(n=12\) benthic samples from each sampling trip per study area. We examined community structure of benthos in terms of numerical percentages of each taxon within each season, year, and study area.

**Hydroacoustics**

To examine vertical distribution of fish within the water column, we conducted hydroacoustic transects in each study area with a BioSonic DT-X echosounder using 120 kHz, 8.2°, split-beam transducers. We followed Great Lakes Standard Operating Procedure for data collection and analysis (Parker-Stetter et al. 2009, Rudstam et al. 2009). At the Fairport study area, we sampled \(n=2\) - 4 transects (Figure 3) during night time on each sampling trip. At the Erie study area, we sampled all three transects during night time on each sampling trip. We used a 4 ping \(s^{-1}\) rate with a 0.4 ms pulse duration during active echosounding, and we determined background noise values with passive listening in each study area on each sampling trip. Water quality sampling provided temperature values for estimation of speed of sound in water. We processed acoustic data using the method 2 algorithm for echo integration in Echoview (version 5.4; Myriax, Inc., Tasmania, Australia). To accomplish this, we partitioned the water column into epilimnetic and hypolimnetic strata and 500m cells along each transect. During non-stratified periods the stratum depths from an adjacent sampling event within the same calendar year were applied. Volumetric densities (fish targets per \(m^3\)) were calculated for each cell-stratum combination. Details are described in Kraus et al. (2015), appended to this report.
Target strengths (TS) were converted to fish total length (TL) using Love’s (1971) multispecies equation for 120 kHz echosounder: TS=19.1*\log_{10}(TL) - 63.85. We compared epilimnetic and hypolimnetic target densities and estimated total lengths across study areas, years, and seasons in an analysis of variance (ANOVA).

**Fish Diets and Condition**

From each trawl sample, we collected fish for diet and condition analyses. We targeted 6 common species with contrasting feeding and habitat use behaviors: i) pelagic planktivores (native Emerald Shiner, and non-native Rainbow Smelt), ii) mid-trophic level predators (native Yellow Perch, and non-native White Perch), and iii) benthic feeders (native Freshwater Drum, and non-native Round Goby). Freshwater Drum were rarely captured, and were completely absent in Erie samples in 2012 and 2013; therefore, we dropped this species from consideration in diet and condition analyses. During trawling operations, subsamples of fish from these categories were preserved frozen at -20 °C for subsequent laboratory analysis. In the laboratory, fish were thawed for diet analysis. Total length (mm) and weight (to the nearest 0.1 g) of each fish was measured prior to processing. These data along with length-weight measurements taken in the field were used to develop a somatic index of condition. Other measures of condition (e.g., C:N ratios) are available for exploration from the data sets accompanying this report. Additionally, we developed data for an organo-somatic index of condition using the liver. During extraction of the stomach, the liver was excised and weighed (to the nearest 0.001g) on a high precision electronic balance. Stomach contents were weighed in aggregate and then rinsed into a 250 μm sieve. Items were identified to the lowest possible taxon using light microscopy, and each taxon was weighed in aggregate to the nearest 0.001g. When diet items were too small for our balance, we counted the total number of individuals and measured individual lengths (e.g., head capsule width, or body length) microscopically on a subset (n=10) for conversion to weight using published regressions (available upon request).

We focused on six fish taxa for analysis of condition and diets: Emerald Shiner, Freshwater Drum, Rainbow Smelt, Round Goby, White Perch, and Yellow Perch. To develop a somatic condition index, we fitted a power function to weight and length, and used a least-squares approach to estimate mean weight at a specified length for each species. Separate regressions were carried out by area, year, and month for comparative analysis with confidence intervals. This index allowed us to understand whether different species were heavier or lighter for a specified length throughout the study. Similarly, we developed a hepato-somatic index of condition to understand how the liver’s weight proportion of the body might signify changes in energy status of fish (Wootton et al. 1978) across areas, years, and months. We compared diets of these six species based upon frequency of occurrence of diet items, which provides a more robust measure of diet composition than numerical or gravimetric methods (Baker et al. 2013). One exception to this was in the calculation of diet overlap, which is based upon the proportions of prey in stomachs instead of just presence-absence. To ensure sufficient sample sizes, we pooled the diet data across years (low sample size prevented robust testing of interannual
differences prior to pooling). We used non-metric multi-dimensional scaling (or NMDS) of diet items to understand how much diet overlap between fish species existed. For the NMDS, we evaluated multivariate distances in k=2 dimensions with Bray-Curtis similarity and the Wisconsin square root transformation to achieve acceptable stress levels (<0.3, an indication of model fit) for 2-dimensional plotting. In the NMDS, we exclude diet taxa with low occurrence (present in less than <10 stomachs: gastropoda, Hexagenia spp., hydracarina, nematoda, and oligocheata). We evaluated the results graphically in a two-dimensional plot with 80% confidence ellipses for each fish species and for each study area.

Additionally, we examined diet overlap for two pairs of fishes with similar modes of habitat use: pelagic planktivores (Emerald Shiner and Rainbow Smelt), and demersal predators (White Perch and Yellow Perch). We calculated Schoener’s overlap index (Schoener 1970) for fish diets (Wallace 1981). Wallace and Ramsey (1983) recommended that Schoener’s index be calculated using weight or volume, but we used counts instead due to overestimation biases from length-weight predictions of small prey (typically, partially digested zooplankton). Therefore, Schoener’s index was calculated as follows: $1 - 0.5 \times (\sum |p_{xi} - p_{yi}|)$, where the absolute differences between the numerical proportions of prey item $i$ in species pair, $x$ and $y$, are summed for all prey items. Frequency of occurrence was not used for the reasons described above, and because summation of frequency of occurrence values can lead to totals >1.0, which results in spurious overlap index values (i.e., <0).

Stable Isotopes

We developed information on stable isotope tracers of diet to complement stomach content analyses. Nitrogen stable isotopes quantified trophic position, carbon stable isotopes discerned whether the energy in a fish originated in pelagic or benthic primary producers, and hydrogen isotopes discriminated between in-lake (autochthonous) and terrestrial (allochthonous) energy sources (Doucett et al. 2007, Hoffman et al. 2010, Solomon et al. 2011). Samples were analyzed by external laboratories at the University of New Hampshire (carbon and nitrogen) and Northern Arizona University (deuterium). During laboratory dissections of fish, a plug of light muscle tissue was sampled from each fish for stable isotope analysis. In addition, a subset of benthic macro invertebrates was also prepared for stable isotope analyses. Each sample was dried, powdered with an agate mortar, and weighed into prescribed quantities following standard operating procedures required by each laboratory (see: http://www.isotope.unh.edu/facilities.shtml, http://www.isotope.nau.edu/). Deuterium isotope ($\delta^{2}D$) values were determined with a Delta Plus XL stable isotope mass spectrometer, and expressed as the proportion of deuterium relative to Vienna Standard Mean Ocean Water (VSMOW). Carbon ($\delta^{13}C$) and nitrogen ($\delta^{14}N$) isotopes were determined with a Delta Plus XP spectrometer and expressed as proportions relative to Vienna Pee Dee Belemnite (VPDB) or atmospheric air, respectively.
Paired isotope bi-plots of the results were examined for comparison with published values for terrestrial, benthic, and pelagic energy sources from freshwater lake ecosystems in Solomon et al. (2011). We used a three-isotope Bayesian mixing model based upon source values in Solomon et al. (2011) to estimate the proportional contributions of primary production sources to each macroinvertebrate group and fish species. We performed this analysis with the Stable Isotope Analysis in R package (ver. 4.2, Parnell & Jackson 2013) with generic trophic enrichment factors for nitrogen (3.54), carbon (1.63), and hydrogen (0). Observed variation in isotope values for each taxon was much lower than variation in energy sources. Additionally, we primarily examined juvenile and yearling-and-older fishes, which were expected to exhibit turnover rates on the order of several months to more than a year, dependent upon growth rate and temperature (Herzka 2005). Thus, we expected these dietary tracers to be most representative of a particular study area, and we did not expect to be able to discern variability due to seasons or years. To confirm this, we tested for differences between areas and years singly for each isotope with ANOVA, but observed no significant differences. Accordingly, we examined posterior probability distributions of source contributions by taxon, and study area.

**Project Results, Analysis and Findings**

*Fish Community Structure*

We found substantial variability in fish species dominance and composition among years, months, and study areas, with relatively few species comprising most of the catch during any one sampling event. At the Fairport study area, dominance was the most variable, shifting five times among five species (Figure 4). In August 2011, Yellow Perch and White Perch were similar in proportions (33% and 32%, respectively, out of 6959 fish total). This dominance shifted in September 2011 to similar proportions of Emerald Shiner and Round Goby (each represented 28% of the 14,021 fish total). In 2012, catches were dominated by dominated by White Perch in June and August (31% and 45% of 4,219 and 22,754 fish totals, respectively). In September 2012, Emerald Shiner dominated (66% of 27,933 fish total). In 2013, Rainbow Smelt dominated in June (90% of 104,637 fish total), and Yellow Perch dominated in August and September (36% and 55%, respectively of 5,744 and 14,150 fish total). By comparison, the Erie study area

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1 Appendix II gives samples sizes for each of the field collection events.
was less variable with Rainbow Smelt dominating catches in five of the eight sampling periods (Figure 4): August 2011 (60% of 833 fish total), September 2012 (37% of 5,027 fish total), June 2013 (98% of 3,084 fish total), August 2013 (95% of 10,350 fish total), and September 2013 (84% of 1,566 fish total). During September 2011 and June and August of 2012, Yellow Perch (53% of 4,852 fish total), Round Goby (73% of 3,223 fish total), and Emerald Shiner (87% of 21,792 fish total), respectively dominated catches at the Erie study area (Figure 4). At the Erie study area, White Perch were only observed during two of the sampling periods and only as a small fraction of the total catch (Figure 4).

While the study areas shared the same dominant species overall, they were distinct in composition (Figure 5). As viewed in two-dimensional NMDS space, the trawl samples showed a limited amount of similarity in species composition. Most of the separation between study areas was evident in the secondary axis, with Burbot, Alewife, Rainbow Smelt, and Round Goby contributing most to the separation of the Erie study area from Fairport (Figure 5). By comparison, White Perch, Freshwater Drum, Channel Catfish, White Sucker, White Bass, and Gizzard Shad primarily distinguished the Fairport study area from Erie in terms of fish community composition. Yellow perch and Emerald Shiner contributed very little to the second NMDS axis, emphasizing similarity in trawl catch rates between study areas with respect to these species. This view of the fish community primarily represents the
most abundant species in the catches, and we specifically excluded species that were rare (see previous section). Thus, we also characterized each sampling period using the full data set with Shannon’s diversity index, which accounts for both species richness and relative abundance and is sensitive to rare species. Shannon’s diversity also distinguished study areas, but this was highly dependent upon month and year (Figure 6). Overall, fish diversity was either similar between study areas or higher at the Erie study area (Figure 6). In particular, significantly higher diversity in Erie (as measured by overlap of 25th or 75th quantiles with the median) was evident in August of 2012 and every sampling period in 2013 (Figure 6). Moreover, August 2012, and August and September 2013 in Erie represented the highest fish diversity observed in this study (Figure 6).

One of the limitations to diversity indices is that if there are complementary changes in abundance between two species (or one species is exactly replaced by another), diversity indices will not change. As an alternative approach to synoptic indices of fish community structure, we evaluated weighted mean trophic level of the trawl catches. Mean trophic level accounts for the roles of fish within the food web both in terms of their trophic position and their relative abundances. Thus, changes in abundance within a trophic level (such as increases in lower trophic level planktivores relative to piscivores) will cause shifts in the mean trophic level of the catch. We observed a wide range of variation in mean trophic levels of trawl catches, and very little consistency in patterns across sampling periods. Mean trophic level at the Fairport study area declined steadily from August 2011 to September 2012, and with the exception of September 2012 it was similar to Erie (Figure 6). In September 2012 (Erie only), and June and August of 2013 (both study areas), mean trophic level was high compared with other sampling periods (Figure 6). At the Fairport study area, these changes most closely track fluctuations in abundance of Emerald Shiner, a lower trophic level species planktivore (Figures 5 and 6). At the Erie study area, a more

![Figure 7. Fish guilds in Lake Erie expressed as a ratio or proportion of trawl catches. Species membership of each group is defined in the text for: piscivores:forage (upper), pelagic:demeral (middle), and coldwater (lower). No sampling occurred in June 2011.](image)
complex dynamic was occurring with contributions to the mean trophic level from changes in both lower trophic level Emerald Shiner, as well as mid-trophic level Rainbow Smelt and Round Goby (Figures 5 and 6).

We further considered variation in catch composition among sampling periods with respect to functional groups based upon feeding mode, habitat, or thermal preferences (defined above). At both study areas, piscivores were often present in catches at a similar level (ratio ≤ 1) with forage fishes (Figure 7, upper). Forage fish outnumbered piscivores (ratio > 1) only in September 2011 in Erie, and in August and September 2013 in Fairport (Figure 7, upper). Pelagic fishes (defined above) were more frequently present in great numbers than demersal species, especially at the Erie study area (ratio >1; Figure 7, middle). At the Fairport study area on average, demersal fishes were present in abundance equal to or greater than pelagic species in all sampling periods except September 2012 and June 2013 (Figure 7). By comparison at the Erie study area, pelagic fishes were present in greater abundance than demersal fishes in all sampling periods except September 2011 and June 2012. Finally, we examined the fraction of the catch comprised of coldwater fish species (defined above). Overall at the Fairport study area, the fraction of coldwater species was low (< 0.25), and it was generally higher at the Erie study area than Fairport (Figure 7). Exceptions to these patterns occurred in June 2013 (both study areas) and August 2013 (Erie only), when catches were predominately made up of coldwater species, and in September 2011, when the fraction of coldwater species was lower on average at the Erie study area (Figure 7).

**Water quality**

To understand how water column structure changed across sampling periods, we examined temperature in relation to dissolved oxygen. In particular, we were interested in relating hypoxic episodes with results from other types of biological sampling. Temperature varied predictably in most sampling periods with relatively uniform conditions during pre- and post-stratification (Figure 8). Temperature ranged from 6 to 25°C in these data, and hypolimnetic (bottom) temperature tended to show more variability than the epilimnion within a sampling period (Figure 8). The coldest temperatures were in the hypolimnion at the Erie study area followed by Fairport (Figure 8). As illustrated by the degree of overlap in the confidence ellipses, stratified conditions...
were present to varying degrees at both study areas and during all sampling periods except September 2011 (Figure 8). This situation was primarily a result of unusually warm summer season in 2012 and delayed fall turn-over in 2012 and 2013. We observed two hypoxic events (dissolved oxygen <2mg/L), one each in 2011 and 2013, and both occurred during August (Figure 8). There was a single hypoxic observation in September 2013, but due to the majority of samples from the bottom layer having normoxic conditions, we did not classify this sampling period as hypoxic. In addition, hypolimnetic hypoxia was heterogeneous throughout the hypolimnion. We used 3-dimensional anisotropic interpolation with inverse distance weighting to map hypoxic zones. We found a striking contrast in the distribution of hypoxia between these events. In 2011, the hypoxic zone was smaller and concentrated near where the thermocline contacted the bottom of the lake (Figure 9). In contrast with our expectations, deeper portions of the hypolimnion transitioned back to normoxic conditions (Figure 9). In August 2011, the hypolimnion was 23% of the volume of the study area, and hypoxic waters made up 38.2% of the hypolimnion. By comparison, August 2013 was more consistent with our expectations of a hypoxic zone that began at the thermocline and became more intense with depth (Figure 9). This more continuous pattern of hypoxia was associated with a smaller hypolimnetic volume (13.5% of the study area), and hypoxic conditions constituted 79.5% of the hypolimnion.

**Zooplankton**

Zooplankton species richness ranged from between 2 and 24 taxa per sample (copepod nauplii and dreissenid veligers were counted as distinct taxa because they could not be identified to species). On average, zooplankton species richness was 17.8 (s.e. = 2.6), and no significant differences (α=0.05) were observed as a function of year, month, area,
or all possible interactions between these variables. By comparison, zooplankton species diversity (Shannon’s index) ranged from 0.2 to 2.6 per sample (again, copepod nauplii and dreissenid veligers were counted as distinct taxa because they could not be identified to species). On average, the diversity index was 2.5, and no significant differences ($\alpha=0.05$) were observed as a function of year, month, area, or all possible interactions between these variables.

Functional groups of zooplankton primarily represented different sized groups of potential prey for zooplanktivorous fishes in Lake Erie. Overall, densities of each group were higher and more variable at the Erie study area (Figure 10). At the Erie study area, the highest zooplankton densities were observed in 2011, and the lowest were observed in 2012. By comparison at the Fairport study area, zooplankton densities were more stable with less variation on average across years and months (Figure 10). Whereas predatory cladocerans were always present at lower densities, other groups were frequently present at densities similar to each other during most sampling periods (overlapping confidence intervals, Figure 10). Calanoid and cyclopoid copepods dominated during every sampling period, and with the exception of August 2011 at the Erie study area, were similar in abundance to each other (Figure 10). Non-daphnid cladocerans ranked third in abundance overall, but were often similar in density to copepods (Figure 10). Though more variable, Daphnidae showed a declining trend at Erie throughout the time of this study, and no trend in Daphnidae was evident at the Fairport study area (Figure 10).

### Benthos

Ponar samples of surficial sediments revealed an average of 2.2 (s.e. = 3.2) benthic macroinvertebrates per sample, with no significant differences between years, months, areas, or all possible interactions between these variables. The composition of benthic macroinvertebrate species was strikingly different between study areas, and in particular the dominant taxon at the Fairport study area often shifted between several taxa across sampling periods. In 2011, Chironomids (38% of 29 organisms) and Dreissenids (28% of 171organisms) dominated in August and September, respectively. In 2012, isopods dominated in June (35% of 336 organisms) and August (56% of 337 organisms) followed by gastropods in September (40% of 30 organisms). At the Erie study area, Dreissenid mussels dominated benthic samples in every sampling period, comprising between 59% and 97% of macroinvertebrate counts (Figure 11). By comparison at the Fairport study area, Dreissenid mussels typically represented a minor fraction of benthic species counts. With the exception of isopods in June 2012, other taxa were more evenly mixed at the Erie study area with no single taxon comprising more than half of the total count (Figure 11).
Hydroacoustics

Hydroacoustic transect surveys provide an overall view of the distribution of fish-sized organisms in the water column at each study area. Across all sampling periods, average target densities were higher in the epilimnion (Figure 12), and given that this layer represented, on average, 80% of the depth range, the greatest abundance of fish were located in the epilimnion. Further, with the exception of September 2011, epilimnetic target densities were higher at the Erie study area (Figure 12). To a lesser degree, hypolimnetic target densities were higher at the Erie study area. We also considered that during August 2011 and 2013, the hypolimnion was affected by hypoxic conditions, and no significant differences were observed in fish target densities in adjacent months from the same area (Figure 12). We further examined fish total length as estimated from target strength estimates, and found that size of targets in the hypolimnion was always larger on average (Figure 13). Whereas at the Fairport study area, estimated total length was often similar between layers and more stable through time, the Erie study area showed a broader range of sizes with significant differences between layers in every sampling period except September 2012 (Figure 13). No consistent shift in pattern of fish total length was apparent during the August 2011 and 2013 hypoxic episodes.

Fish Diets & Condition

We examined fish diets and conditions for six representative fishes; however, catches of freshwater drum were low and this species was available for analysis from only a few sampling sites. To understand similarity in diets between fish species and compare diet similarity between study areas, we examined an NMDS ordination plot of diet samples. We observed broad overlap in diets across species and locations. Except for Round Goby, all the species showed complete overlap in diet composition with a mixture of taxa that included zooplankton, macroinvertebrates, and some fishes (Figure 14). Round goby diets were most similar to yellow perch as evidenced by the overlap in confidence ellipses, and dreissenid mussels contributed most to the separation of round goby diets from other species (Figure 14). Also illustrated by the
area of the confidence ellipsoids, dietary breadth was greatest for White Perch and least for Round Goby (Figure 14).

We focused on two species pairs for further analysis of diet overlap as determined with Schoener’s index (described above). These pairs were representative of pelagic zooplanktivorous species, Emerald Shiner and Rainbow Smelt, and demersal mid-trophic level predators, White Perch and Yellow Perch. Sufficient sample sizes were available to compare months within each study area, but finer division of the data into years was not warranted. In addition, one or the other species of each pair was missing in June of each year at the Erie study area; therefore, no indices were available for either species pair in this instance. Schoener’s Index ranges from zero (no overlap) to one (complete overlap), and values >0.6 are considered to indicate an ecologically meaningful degree of diet overlap. In all cases, there was greater overlap for the pelagic zooplanktivorous species pair, and in three cases this species pair exhibited a high degree of overlap, indicating high similarity in diet composition between these species (>0.6, Figure 15). The demersal mid-trophic level predator species pair exhibited great overlap at Fairport, but only in one instance was this overlap considered significant (>0.6, Figure 15).

While diet composition provides a short-term view of recent feeding performance of fishes, diets can be subject to multiple biases such as faster digestion of soft-bodied prey, which may lead to underestimation of their contribution to diets. Because it was necessary to pool data across years to understand seasonal and study area variability in diet overlap, we also sought to understand interannual changes in the nutritional...
status of fish via measures of somatic condition. Data on the weight proportion of liver to body (hepatosomatic index) were spotty and could not support a fully crossed comparison for all species; therefore, we focused on the length-weight based estimate of somatic condition, which had more complete representation in each year and study area. Exceptions were a lack of samples of White Perch and Emerald Shiner from Erie. Patterns varied by species. Emerald Shiner exhibited a significant increase in condition after 2011, and condition was higher in Fairport than Erie in the one year with comparable data (Figure 16). Round goby condition was variable with no obvious trend across years or between study areas (Figure 16). Yellow Perch condition was significantly higher in Fairport during the first two years of the study, but this pattern reversed in 2013 (Figure 16). At Fairport, rainbow smelt condition showed a significant decline each year (assessed via non-overlapping confidence intervals in Figure 16), and a similar pattern was observed for Erie. A declining trend in condition was also observed for White Perch at the Fairport study area, but comparison with the Erie study area could not be made due to lack of samples (Figure 16).

**Stable Isotopes**

Due to slower turnover in muscle tissue, stable isotopes provide a longer-term integrated view of dietary sources that can complement analysis of stomach contents. In general, relative to benthic macroinvertebrates, fish were enriched (i.e., higher δ) in the heavier isotope for all three tracers: $^{13}$C, $^{15}$N, and $^2$H (Table 1). One exception to this pattern was with deuterium for oligochaetes, where we observed the lowest value across all taxa. For carbon and nitrogen, this trophic enrichment is consistent with empirical and theoretical expectations from predator-prey interactions (Post 2002). Relative to other freshwater systems (but still consistent with previous work from Lake Erie), values for nitrogen were high, reflective of a primarily agricultural watershed (Guzzo et al. 2010).
Trophic enrichment of deuterium is negligible (Solomon et al. 2011); therefore, differences between fish and benthic macroinvertebrates reflect consumption of other prey types (Table 1). This result could not be explained by consumption of oligochaetes, because they were rarely consumed by demersal fishes (frequency of occurrence <5%) and never consumed by pelagic species. Further, higher values (less negative $\delta$) of deuterium in fishes indicated a greater contribution of allochthonous primary production sources (i.e., terrestrial subsidies) relative to benthic macroinvertebrates (Table 2).

Results from the three-isotope mixing model emphasize an approximately equal mixture of primary production sources (Table 2) for most taxa. For all fish species, the contribution of pelagic primary production was slightly less than benthic or terrestrial sources, which were similar to each other (Table 2). One exception was for Emerald Shiner, where bentic sources contributed 6% more than terrestrial (Table 2). For benthic macroinvertebrates, pelagic primary production typically contributed more than other sources, with three notable exceptions (Table 2). Hirudinea (leeches), which often parasitize fishes, were more similar to fishes than other macroinvertebrates (Table 2). Oligochaetes showed a strong contribution of terrestrial sources, indicating a reliance on organic matter from terrestrial plants (45%; Table 2). Finally, Dreissenid mussels, which primarily filter-feed on phytoplankton, were primarily composed of pelagic primary production sources (62%) with a negligible contribution from terrestrial sources (6%) (Table 2).

**Conclusions and Recommendations**

This study addressed three key questions, concerning food webs that support important Great Lakes fisheries. We asked 1) how predator-prey interactions between cool- and coldwater fish guilds change as environmental conditions increase spatial overlap, and 2) whether prey choice became more selective, segregating diets as a result of environmental change. Further, we asked 3) how the structure of the foodweb and trophic levels were affected by changes in distribution of fishes. Contrast in environmental conditions was primarily expected due to hypoxia in the central basin compared with eastern basin sites, which were stratified but normoxic. We observed hypoxic events during two sampling periods, and noted a mixture of cold- and cool-water species as well as highly variable proportions of pelagic and piscivorous fishes in trawl catches. In terms of fish community composition, these hypoxic events were similar to adjacent sampling periods, emphasizing the potential for overlap of fish species from
different guilds. Unexpectedly, our sampling revealed evidence that fish aggregated near the edges of hypoxic zones (Kraus et al. 2015), which would tend to intensify competitive interactions. Despite increases in fish density near hypoxia and independent variation of the fish community composition, diets of selected species were broadly overlapping and exhibited only weak evidence of segregation during hypoxic events. Dietary overlap was greater at the mesotrophic Fairport study area compared with the oligotrophic Erie study area, and pelagic competitors (Emerald Shiner and Rainbow Smelt) showed greater diet overlap than demersal species (Yellow Perch and White Perch). Weak reduction in dietary overlap for both species pairs was evident in August (the hypoxic month), approaching the same levels of overlap observed at the Erie study area. These data suggest that greater dietary overlap (rather than less) within a fish guild may serve as an indicator of environmental changes such as increasing temperature, hypoxia, and nutrient enrichment that is expected to accompany climate change. In addition, mean trophic level of the catch and stable isotope values of nitrogen (proxy for trophic position) for selected species showed no consistent patterns with respect to hypoxic events or variation between study areas. Consideration of additional isotopes did not improve discrimination across months or study areas, and a three-isotope model emphasized that the fish community represents a mixture of primary production sources with similar contributions from benthic, pelagic, and terrestrial sources. Finally, condition of selected fish species varied spatially and annually, indicating that it may be useful indicator of changes in nutritional condition, but the variation was not associated with proximate environment conditions such as hypoxia.

The objectives of this study were achieved with the development of diverse ecological data sets, which permitted novel seasonal and interannual comparisons across a productivity gradient (i.e., between mesotrophic Fairport and oligotrophic Erie study areas). Trawl catches and hydroacoustic surveys provided quantitative information on the vertical and horizontal distribution of fishes, fish community composition, and mean trophic position of the fish community (Objectives 1, 2, and 4). Laboratory derived information on diets, condition, and stable isotopes of selected species provided individual level characterization of trophic interactions (Objectives 2 and 3). Further, quantification of zooplankton and benthic prey communities supports more involved analyses beyond the scope of this report. These results are relevant to large lake and inland fishery managers to understand how climate change and related environmental forcings can influence fishery food webs and the sustainability of fisheries and to incorporate ecosystem considerations into the management of fisheries in Lake Erie and other systems. We found that some methods may provide more useful information for tracking changes in food webs (e.g., dietary overlap measures, spatial distribution, and somatic condition), but all of the approaches can be implemented with relatively small investments in existing fishery monitoring programs. Some of the uncontrollable challenges that delayed this project were: high turn-over of technicians, sample processing delays from contracted laboratories, and loss of samples due to freezer failure.
One of the hallmarks of these data was high seasonal and interannual variation in the distribution of fishes. This emphasized not only the importance of multi-year investigations but also the need to examine seasonal changes in the distribution of fishes. For example, for a brief time, coldwater species dominated at the Fairport study area, but across the three years of this study, coldwater species made up a minor fraction of the fish community. In contrast with Fairport, the Erie study area was characterized by a preponderance of non-native species (e.g., Dreissenid mussels, and Rainbow Smelt), higher fish community diversity, lower fish density, and greater ranges of temperature and zooplankton prey. Climate change is expected to intensify and to expand the extent of seasonal hypoxia, but bi-national nutrient management is aimed at mitigating hypoxia (GLWQA, 2013). Further, longer-term indicators of fish status in the food web indicated that condition measures as opposed to natural tracers of diet (i.e., stable isotopes) have more potential to inform managers about the status of fisheries food webs. There was little difference between study areas or across years in stable isotopes, but condition varied significantly by year and study area with patterns that were unique for each fish.

Our data have already served policy decisions regarding the influence of hypoxia on recruitment indices for fisheries stock assessments in Lake Erie. Additionally, this work played an important role in the development of an effective Great Lakes Restoration Initiative project, forming the basis for a lake-wide food web study as part of the Coordinated Science and Monitoring Initiative (CSMI) in 2014 (each Great Lake is on a 5-year CSMI assessment cycle). The same study areas and methods were utilized in this study as the CSMI study; therefore, data from both projects are being combined in a broader analysis of fish diets and food web analyses that are currently underway. Through joint funding, this study represents an example of successful coordination between Great Lakes Science Center, the Northeast Climate Science Center, and the Upper Midwest Great Lakes Landscape Conservation Cooperative. Next steps will to be complete analyses of combined data sources with the publication of manuscripts, and utilize these data and published results in annual cycles of fishery resource assessment in Lake Erie via task group participation. Changes in the approach to fishery management in the Great Lakes are slow but deliberate, and generally based on consensus of managers informed by scientific information and the identification of needs. Studies such as this one, which dovetails with CSMI, provide a unique longer-term view with interjurisdictional spatial coverage. This type of data collection has the potential to improve modeling efforts (evidenced by the adoption of our dissolved oxygen data and collection methods by US-EPA and NOAA-GLERL researchers to retool biophysical models of Lake Erie), and thus represents an important component of the sponsored program portfolios of NECSC, UMGL-LCC, and USGS. Efforts to maintain this type of funding portfolio diversity could have positive synergistic impacts on both resource policies and the advancement of scientific knowledge.
Outreach and Products

Articles

Conference presentations
Kraus, R. T., Gorman, A. M., Farmer, T., Knight, C., Warren, G., and Collingsworth, P. 2014. Highly Variable Dissolved Oxygen in Lake Erie has Implications for Fish Kills and Vulnerability of Fish to Capture. Annual Research Review of the Aquatic Ecology Laboratory at The Ohio State University, Columbus, Ohio, 16-17 January.
Kraus, R.T., Kocovsky, P.M., Knight, C.T., Gorman, A.M., and Rogers, M.W. 2016. Fish Trophic Interactions as Indicators of Climate Change in the Great Lakes. Annual meeting of the American Fisheries Society, Kansas City, Missouri, 21-25 August.

Decision-maker communications
Portions of this work were presented to Lake Erie Committee Task Groups in 2012, 2013, 2014, and 2015. These task groups are made up of Federal and State partners representing science and resource management agencies responsible for sustainable fisheries in Lake Erie. This committee is part of the Great Lakes Council of Lake Committees, which is facilitated by the Great Lakes Fishery Commission (www.glfc.org).

Websites
Not Applicable.
Other products
Media interactions:

National Public Radio article on Lake Erie foodwebs related to climate change: www.michiganradio.org/post/too-warm-your-fried-perch-dinner

“Scientists find lake’s ‘dead zones’ move”, Sandusky Register, 4/10/2015

“Lake Erie’s dead zones more dynamic than once believed; impact fish distribution, study shows”, FishSens Magazine, 4/21/2015


Acknowledgements
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Literature Cited


Appendix I: Technical details of the trawl sampling.

From 2011 through August 2012, bottom trawl sampling was conducted from the USGS research vessel Musky II, a 13.7m steel monohull work boat with a single propeller and a split warp trawling system. The bottom trawl was a Marinovich-style semi-balloon otter trawl with a 7.9m headrope and galvanized chain footgear, and was constructed of nylon mesh with a cod end liner with 13mm mesh opening (stretched measure). We used 1 m Biloxi-style wooden trawl doors, and towed the net for ca. 10 minutes at a speed of 3.5 km/hr for an average tow distance of 583m. Previous trials with net mensuration gear revealed an average wingspread of 3.9 m during trawling; therefore, this value and average tow-distance was used to convert catches into numbers per hectare swept. During 2012, the USGS commissioned a new research vessel for Lake Erie, the Muskie – a 21.6m aluminum monohull workboat with twin propellers and a double warp trawling system, and the older Musky II was decommissioned and sold.

The Muskie was used for sampling conducted in September 2012 and all sampling in 2013. Various issues surrounding the use of the old net on the new vessel necessitated a change in trawl gear (i.e., net, doors, and hardware). The new bottom trawl net was a four-seam, three-bridle, bottom trawl, with a fishing circle that was 200 meshes by 12 cm mesh size. The body of the net transitioned from a mesh size of 12 cm to 6 cm and was constructed of polyethylene. The cod end liner was constructed of knotless dyneema mesh with a mesh size of 14 mm (stretched measure). The head rope length was 11.2 m and the foot rope length was 14.2 m. To accommodate hard bottom substrate, the sweep was designed with 20.3 cm rubber discs interspersed between 5.6 cm rubber discs in a configuration called a “rubber cookie sweep”, known to be successful for trawling for squid on glacial moraines in the north Atlantic. The bridle length was 36.6 m overall with a junction between the top and middle bridle at 18.3 m. The bridle was constructed of wire rope, with 1.3 cm diameter cable on the bottom bridle, and 0.953 cm diameter cable on the middle and top bridles. To fish this net we used high performance steel doors, Thyboron Type IV, outfitted with heavy duty ball bearing swivels to reduce asymmetric twisting resistance in the trawl warps. Net geometry was measured with acoustic mensuration gear (NOTUS ®) during trawling to allow site-specific estimates of area swept. Typical wingspread was 6 m with accuracy of 0.1 m based upon stationary harbor tests. Prescribed trawling time was 10 minutes, and the typical tow distance at a target speed of 5.5 km/hr was 930 m, which produced an average swept area of approximately 0.5 hectares for calculating catch per area swept.

We also conducted sampling with a mid-water trawl with the aid of Ohio Department of Natural Resources research vessel, Grandon, a 12.2m monohull workboat with a single propeller and a double warp trawl system. The mid-water trawl was an Aluette-style trawl (built by Innovative Net Systems, http://www.fishtrawls.com) with a 19.8 m head rope and 13.7 m side lines. The cod end liner mesh size was 12 mm (stretched measure), and was fished with 0.5 m Poly-ice doors with a 38.1 m dyneema bridle. The mid-water trawl was towed for 20 minutes at a target speed of 5.5 km/hr for an average tow distance of 1833 m. The Grandon conducted mid-
water trawls with a similar style net from 2011 through August 2012 (Fairport study area only). From September 2012 through 2013, the mid-water trawl was fished from the Muskie using the Thyboron trawl doors. In September of 2013, the last bottom trawl sample from the Muskie at the Fairport study area snagged on a boulder and damaged the trawl, making it unavailable for sampling at the Erie study area. Therefore, we use the mid-water trawl only during September 2013 in the Erie study area, and we fished it with 10 minute tows as close to the bottom as possible (within 2 m) to obtain fish community data that would be comparable with the bottom trawl samples. Average wingspread for the mid-water trawl was 5 m measured with acoustic mensuration gear. Swept area was calculated with net mensuration gear similar to the bottom trawl.

Finally, at various times during 2011 and 2012 sampling rounds at Fairport, supplementary fish samples were collected with the Grandon using a different bottom trawl. The bottom trawl on the Grandon was a Yankee two-seam bottom trawl with a 10.4-m head rope, 25 mm bar mesh in the cod end, 13 mm stretched mesh liner, and 25.4 cm roller gear on the foot rope. These samples were only used to augment sample size for laboratory analyses (e.g., diets and stable isotopes), and these were not used in the comparisons of catch rates. This sampling turned out to be crucial for providing fish samples: many of the samples collected from the Musky II were lost due to freezer malfunction during an extended holiday period in 2012.
Appendix II. Tabulation of samples collected during field activities.

Table AII.1. Sample sizes for each sampling period by study area for each of the field methods employed in this project.

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<th>Area</th>
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Appendix III: CJFAS manuscript

This manuscript is the final accepted version. The journal formatted version can accessed with a subscription via the internet at the follow address:

Dynamic Hypoxic Zones in Lake Erie Compress Fish Habitat, Altering Vulnerability to Fishing Gears

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Abstract

Seasonal degradation of aquatic habitats from hypoxia occurs in numerous freshwater and coastal marine systems and can result in direct mortality or displacement of fish. Yet, fishery landings from these systems are frequently unresponsive to changes in the severity and extent of hypoxia, and population-scale effects have been difficult to measure except in extreme hypoxic conditions with hypoxia-sensitive species. We investigated fine-scale temporal and spatial variability in dissolved oxygen in Lake Erie as it related to fish distribution and catch efficiencies of both active (bottom trawls) and passive (trap nets) fishing gears. Temperature and dissolved oxygen loggers placed near the edge of the hypolimnion exhibited much higher than expected variability. Hypoxic episodes of variable durations were frequently punctuated by periods of normoxia, consistent with high frequency internal waves. High-resolution interpolations of water quality and hydroacoustic surveys suggest that fish habitat is compressed during hypoxic episodes, resulting in higher fish densities near the edges of hypoxia. At fixed locations with passive commercial fishing gear, catches with the highest values occurred when bottom waters were hypoxic for intermediate proportions of time. Proximity to hypoxia explained significant variation in bottom trawl catches with higher catch rates near the edge of hypoxia. These results emphasize how hypoxia may elevate catch rates in various types of fishing gears, leading to a lack of association between indices of hypoxia and fishery landings. Increased catch rates of fish at the edges of hypoxia have important implications for stock assessment models that assume catchability is spatially homogeneous.

Keywords
Hypoxia-based habitat compression, catchability, Great Lakes fisheries

Introduction

Hypoxia in aquatic systems is a worldwide phenomenon often linked to excessive nutrient loadings from human activities (Diaz 2001; Diaz and Rosenberg 2008). Numerous experimental laboratory and field studies on hypoxia have demonstrated lethal effects, avoidance, tolerance, and physiological impairment (Brady et al. 2009; Eby and Crowder 2002; Pavela et al. 1983; Roberts et al. 2009; Vaquer-Sunyer and Duarte 2008); however, population-scale impacts on fisheries tend to be found only in extreme hypoxic conditions with demersal species (Breitburg et al. 2009; Eby et al. 2005). This has led to speculation about compensatory
mechanisms in commercial and recreational fisheries that may mask the true ecological effects of hypoxia on the distribution and density of mobile fauna (Leming and Stuntz 1984; Ludsin et al. 2009; Thompson et al. 2010). For example, fishing effort in the North Carolina (USA) pot fishery is redistributed to target concentrations of blue crabs near the edge of hypoxic zones (Selberg et al. 2001). Likewise, fish and decapod crustaceans in the Gulf of Mexico orient near the edge of hypoxic fronts where fisheries may exploit them more efficiently (Craig 2012; Craig and Bosman 2013; Craig and Crowder 2005). Fish and mobile invertebrates may concentrate in suitable habitats near the edge of hypoxic zones as a consequence of avoidance of stressful conditions – a phenomenon called hypoxia-based habitat compression (Campbell and Rice 2014; Eby and Crowder 2002). Additionally, hypoxia-tolerant organisms may select habitats adjacent to hypoxia to gain a foraging advantage (Pihl et al. 1992; Roberts et al. 2012). Through various aggregative effects, hypoxia may increase the vulnerability of some species to exploitation, but it is unclear to what degree the mechanisms and consequences can be generalized across species, systems, and fisheries.

The Laurentian Great Lakes have often been contrasted with semi-enclosed and open coastal marine systems to develop a more universal understanding of human impacts on aquatic ecosystems (Caddy 1993; Hawley et al. 2006). In particular, Lake Erie has a long history of cultural eutrophication with cascading negative effects on the proliferation of harmful algae, deterioration of water quality, and development of a large area (~5,000 to 10,000 km²) of summer hypoxia (Ludsin et al. 2001). Nutrient abatement efforts, which began in the early 1970s, were successful in reducing point-source inputs of phosphorus to Lake Erie (Richards et al. 2009). This led to gradual change in trophic status (oligotrophication) of the lake through the mid-1990s (Conroy et al. 2005), but during the past two decades the soluble reactive phosphorus component of the total nutrient loadings increased, driving more frequent and intense algal blooms (Baker et al. 2014; Richards et al. 2010; Stumpf et al. 2012). During the same period, the extent and severity of hypoxia has increased (Zhou et al. 2013), prompting water resource managers to establish the goal of reducing hypoxia in the Great Lakes Water Quality Protocol of 2012 (International Joint Commission 2012). Evidence from a sub-basin of Lake Erie shows that the hypolimnetic oxygen depletion rates may have remained constant over this period of trophic change, and that physical properties such as hypolimnion thickness, temperature gradients, and frequency of internal mixing are better predictors of hypoxia than nutrient loads and primary
productivity (Conroy et al. 2010). Further, climate-driven warming is predicted to increase hypoxia in Lake Erie (Blumberg and Di Toro 1990), and this combined with uncertainty in the potential effects of nutrient controls may complicate efforts to achieve water quality goals.

In Lake Erie, direct effects of hypoxia on fishes often have been implicated by coincidence of two circumstances: i) a fish kill event that lacks evidence of a pathogenic or toxic cause, and ii) extreme upwelling of low oxygen waters that mix throughout the water column (Rao et al. 2014). In contrast, the more pervasive effects appear to be indirect ones. Seasonal hypoxia leads to widespread reduction in habitat quality or loss of habitat as measured by reduced growth rate potential in bioenergetics models of temperature, oxygen, and forage density (Arend et al. 2011; Brandt et al. 2011). Loss of suitable habitat for positive growth is thought to be responsible for the observed declines in Lake Erie yellow perch *Perca flavescens* body condition following long durations of hypoxia (Scavia et al. 2014). Indeed, the species most vulnerable to these changes in habitat quality are demersal or cool- and cold-water species, which prefer hypolimnetic environments in a warm summer stratified lake (Arend et al. 2011). In general, the reduction of suitable habitat displaces fish into adjacent habitats of marginal quality with resultant shifts in diet and reduced productivity at higher trophic levels (Pothoven et al. 2009; Roberts et al. 2009; Vanderploeg et al. 2009a).

Less understood are the consequences of fish displacement into marginal habitats to catches in commercial fisheries and fishery-independent population surveys. Anecdotes from the commercial trap net fishery in Lake Erie suggest that fishers set nets near the edge of hypoxia to augment catches of target species, such as yellow perch *Perca flavescens* (Saito 2005). Further, fishery-independent recruitment surveys of yellow perch conducted by the Ohio Department of Natural Resources have observed anomalous high catches from trawls that were conducted either within or adjacent to hypoxic zones (Weimer et al. 2013). Both of these phenomena have implications for fishery managers. In the case of the commercial fishery, the potential increase in catchability of yellow perch due to hypoxia may lead to hyperstability in population dynamics models that are based largely upon fishery-dependent data (Hosack et al. 2013; Rose and Kulka 1999). For fishery-independent surveys, simulations with recruitment data have demonstrated that anomalous high catches influence predictions of fish entering the fishery at older ages by as much as 34%, or 30 million individual fish (C. Knight, unpublished; Weimer et al. 2012). Currently, there is an interim decision rule to censor high catches from survey trawls in hypoxic
zones, and managers have called for an improved understanding of the influence of hypoxia on survey catches (Markham et al. 2012).

Here, we addressed the need for better information on the influence of hypoxia on fish distribution in Lake Erie through diverse field sampling approaches and retrospective analysis of historical data. The U.S. Environmental Protection Agency (US-EPA) has monitored the hypoxic zone in Lake Erie since the 1980s (Burns et al. 2005; Zhou et al. 2013). Due to limited sample locations (n=10) and frequency of observation (approximately every 3 weeks), US-EPA data are too coarse (both temporally and spatially) to define the edge of the hypoxic zone in relation to survey trawl or commercial fishing locations. In response, we developed a study area near Fairport Harbor, Ohio, that has been historically affected by seasonal hypoxia (Figure 1). We sampled this area intensively for three consecutive seasons (2011–2013) and examined historical trawl survey data from the central basin of Lake Erie to address two key hypotheses concerning fish distribution near hypoxic zones. We first hypothesized that fish avoidance of hypoxia would lead to higher catch rates and densities of fish near the edges of hypoxia. In turn, we hypothesized that densities would be further augmented at lower levels of dissolved oxygen. The latter hypothesis required a combination of spatially-intense water-column profiling with continuous near-bottom dissolved oxygen monitoring with data loggers. In 2013, a commercial fisherman set trap nets near one of our continuous monitoring stations, and we took advantage of this opportunity to examine whether commercial trap net catch rates supported inferences gleaned from survey trawls. The results we present here are of particular interest to managers of Lake Erie fisheries who are in the process of improving stock assessment models.

Methods

Study Site and Sampling Approach

The study site near Fairport Harbor, Ohio (Figure 1) encompassed approximately 243 km² with depths ranging 11–22 m (Figure 1). To contrast fish distribution during periods of normoxia and hypoxic periods, we intensively sampled the area for 24-h periods in both August and September of each year. These months represented typical periods of thermal stratification (i.e., August) and post-stratification immediately following autumnal turnover (i.e., September). Contrasts between August and September minimized effects on the redistribution of fish
abundances due to seasonal habitat shifts and migration that occur during cooler spring and fall months and facilitated comparisons of fish distribution. We repeated this sampling schedule for three consecutive years, but only observed thermal stratification in August 2011 and 2013; therefore, we did not consider 2012 data from the intensive sampling herein.

**Determining Spatial and Temporal Variability of Hypoxia**

We developed fine-scale interpolations of temperature and dissolved oxygen from depth profiles (n = 77 in 2011 and n = 22 in 2013) measured with a multiparameter instrument (model 6600, YSI, Inc., Yellow Springs, Ohio, U.S.A.) equipped with an optical dissolved oxygen sensor (calibrated immediately prior to each sampling event). We estimated volumes of both the hypolimnion and hypoxic areas using three-dimensional anisotropic inverse-distance weighted interpolations (Voxler 3.3, Golden Software, Inc., Golden, Colorado, U.S.A.). Hypolimnetic volume was calculated at a thermocline threshold of 16.5 degrees C, but results did not vary appreciably if other thresholds between 15–18 degrees C were applied (analysis not shown). For this portion of the analysis, we used 3.0 mg L\(^{-1}\) as the threshold for hypoxia. Although some studies have shown behavioral reactions at higher dissolved oxygen concentrations (Vaquer-Sunyer and Duarte 2008), this represented a median threshold for potentially unusable habitat for Lake Erie fishes based upon laboratory experiments on consumption (analyzed in Arend et al., 2011). After visualizing the data and quantifying volumes, we determined that the hypoxic zones existed as a thin (~ 2-m) layer contacting the bottom; therefore, we present only a two-dimensional view of bottom hypoxia herein (i.e., Figure 1). While the profiles provided an instantaneous view of the spatial distribution of hypoxia, we learned early in 2011 that temporal variability was potentially higher than expected. In response, we deployed a multiparameter instrument and data logger (model 6600, YSI, Inc.) at a depth of 19.4 m during September 2011 (Figure 1B). We conducted a longer deployment with a galvanic-style oxygen sensor (RBR Duo® series logger, RBR Limited, Ottawa, Ontario, Canada) at approximately the same location in 2012. In 2013, we deployed loggers at shallower (14.3 -m) and deeper (19.8 -m) sites (RBR Duo® with galvanic-style oxygen sensors till September 25\(^{th}\), and HOBO® loggers, model U26, with optical oxygen sensors for the last part; Figure 1B). Each logger recorded temperature and dissolved oxygen continuously at either 5- or 10-minute intervals, and the sensors were
moored 0.5 m above bottom. We plotted time-series of temperature and dissolved oxygen and defined hypoxic periods as intervals with dissolved oxygen < 2.0 mg L\(^{-1}\) separated by at least 12 hours from other such periods. This threshold is a typical convention for defining hypoxia (Vaquer-Sunyer and Duarte 2008), but due to the rapid and large magnitude of dissolved oxygen variability in our data, other thresholds between 1.0 and 3.0 mg L\(^{-1}\) would not change the interpretation of hypoxic periods.

**Vertical Fish Distributions and Hypoxia**

We quantified total fish density throughout the water column with hydroacoustics. During the night of each intensive sampling event, we collected data on two (September 2013) or four (all other sampling events) north-south transects (each approximately 8 km long) with a BioSonics DT-X echosounder using 120-kHz, 8.2-degree, split-beam transducers. Data were collected using a 4 s\(^{-1}\) ping rate and 0.4 ms pulse duration with Visual Acquisition (version 6, BioSonics, Inc., Seattle, Washington, U.S.A.). We used water temperature data to define thermocline depth and the speed of sound through water. Background noise values were determined at the study site via passive listening. Fish densities were estimated using echo integration, scaling area backscattering coefficients (minus noise) by average backscattering cross section for individual targets calculated from in-situ target strength (TS). Densities were calculated in 500-m-long epilimnetic and hypolimnetic (determined from temperature profile data) cells. Although the water column was not stratified in September, we used the same depth strata as in August to divide the data vertically for comparison. Single targets were identified using the method 2 algorithm in Echoview (version 5.4, Myriax, Inc., Hobart, Tasmania, Australia) with the following parameters: TS threshold -68 dB (derived from histograms of single targets collected to -80 dB, Rudstam et al. 2009); pulse-length determination level = 6 dB; minimum pulse length = 0.6 and maximum pulse length = 1.5; maximum beam compensation = 6 dB; and, major and minor axis standard deviations = 0.6. A TS-based S\(_t\) threshold of -74 dB was used to include all fish targets within the half-beam angle (Kocovsky et al. 2013). Bias in cell density estimates was examined using the N\(_v\) statistic (Sawada et al. 1993). For cells with biased in-situ TS we used the mean TS from unbiased cells in the same depth layer. Data
collection and analysis followed the Great Lakes Standard Operating Procedure (GLSOP; Parker-Stetter et al. 2009).

Within each year we compared months and depth layers (hypolimnion and epilimnion) with ANOVAs of fish target density followed by pairwise multiple comparisons using Tukey’s HSD test (experiment-wise alpha = 0.05). One issue that prevented detailed spatial comparison of hydroacoustics data with interpolations of hypoxia was the acoustic “dead zone” near the bottom, where fish targets were indistinguishable from the bottom due to interference from reflected sound. Following GLSOP we established a 0.5-m bottom line that excluded the bottom acoustic dead zone to ensure quality density estimates (maximum height of the bottom acoustic dead zone at our sites was approximately 0.35 m). This represented approximately one quarter to one half of the volume of the hypoxic zones that we observed, and prevented us from evaluating small-scale differences in fish density near the bottom edges of the hypoxic zones.

**Hypoxia Effects on a Fishery Independent Survey**

To understand how hypoxia affects a fishery independent recruitment trawl survey conducted annually in Lake Erie, we conducted two separate experiments. The first experiment examined historical (1990-2009) bottom trawl recruitment survey catches and concurrent measurements of dissolved oxygen from the Ohio portion of the central basin in Lake Erie. The goal of this experiment was to assess if the proximity to hypoxia affected bottom trawl catch rates. The second experiment involved two experimental modifications to the existing bottom trawl recruitment survey methods to quantify i) the variability in dissolved oxygen across the spatial extent of a single bottom trawl deployment and ii) the effect of these small-scale changes in dissolved oxygen on trawl catch rates. Additional details for each experiment are provided below.

*Experiment 1: Assessing the historical relationship between fish catches and proximity to hypoxia.* In the historical recruitment survey data and the experiments, we used the same gear: a Yankee two-seam bottom trawl with 10.4-m headrope, 25.4-cm roller gear, and 25-mm bar mesh cod end with a 13-mm mesh liner (Ohio Division of Wildlife, 2014; Tyson et al., 2006). All tows were standardized to the same duration (10 minutes) and vessel speed (2.5 knots), which permitted direct comparisons in terms of total catch in each haul. The recruitment survey has
been conducted annually since 1990 with monthly sampling from May–October. The overall goal of the survey is to collect juvenile abundance data on economically and ecologically important fish species (i.e., yellow perch). Juvenile abundances are subsequently used in stock assessments to predict the number of age-2 fish that will recruit to the commercial and recreational fisheries in future years. Typically, monthly trawling was conducted at n = 75 stations distributed across four depth strata and 4-8 transects along the southern lake shore between Vermilion and Conneaut, Ohio (Ohio Division of Wildlife 2014).

In the past, each trawl sample was characterized as having occurred at a normoxic or hypoxic site based on bottom dissolved oxygen measurements made at either the start or end of each trawl. Recently, however, observations of large catches in trawls characterized as hypoxic have led to questions about the validity of this classification approach. To understand better the importance of proximity to the edge of hypoxia, we further classified trawl samples based upon the nearest neighboring sample which resulted in four categories: normoxic trawls where the nearest neighboring site was either 1) normoxic or 2) hypoxic; and, hypoxic trawls where the nearest neighboring site was 3) normoxic or 4) hypoxic. A more restrictive threshold for hypoxia (2.0 mg L\(^{-1}\)) was used in this analysis to help evaluate the interim inter-agency management decision rule to exclude hypoxic trawls from stock assessment analyses. We filtered data to exclude the shallow depth stratum (< 5 m), which was never hypoxic during these surveys and consisted of a different species assemblage. Further, we limited the data set to August and September (months with hypoxia) and limited the nearest neighbor search to sites within 3 nautical miles (5.6 km) of each other. We considered 12 demersal species. The most abundant of these included: white perch, *Morone americana* (proportion of total catch in final dataset = 0.50); yellow perch (0.38); round goby, *Neogobius melanostomus* (0.09); and freshwater drum, *Aplodinotus grunniens* (0.02). The remaining demersal species collectively made up 1% of the total catch in the final dataset: trout perch, *Percopsis omiscomaycus*; white sucker, *Catostomus commersonii*; whitefish, *Coregonus clupeaformis*; log perch, *Percina caprodes*; channel catfish, *Ictalurus punctatus*; Johnny darter, *Etheostoma nigrum*; burbot *Lota lota*; and slimy sculpin *Cottus cognatus*. Due to strong patchiness, high interannual variability, and propensities for vertical migration, pelagic species such as alewife, *Alosa pseudoharengus*; gizzard shad, *Dorosoma cepedianum*; emerald shiner, *Notropis atherinoides*; and rainbow smelt, *Osmerus mordax*; were not included in the analysis. The filtering produced a dataset with n =
136 paired trawl samples (primary trawl and the nearest neighbor) for analysis, with catch data for 12 demersal fish species summarized as catch per hectare.

The primary goal of this analysis was to determine if our four hypoxia categories for paired trawls had a significant effect on catches of demersal fishes. However, we also wanted to account for any large-scale temporal trends that might be present in our data. To accomplish this, we evaluated four different models fit to log-transformed demersal catch-per-hectare data. Our predictor variables in these models were year (to test for large-scale, temporal trends) and our hypoxia category. The four models we evaluated included one, both, or neither of the predictor variables of interest: year and hypoxia category. We had no a priori reason to expect that the effects of hypoxia should vary by year, and did not test for an interaction. To determine the most parsimonious model, we used second-order Akaike’s information criteria (AIC_c: Burnham and Anderson 2002) which accounts for goodness of fit, while assessing a penalty for model complexity (= number of parameters), thereby favoring models with reduced complexity that explain a high degree of variability (Burnham and Anderson 2002). We used Akaike weights (ω) to determine the normalized relative likelihood that a given model was the best among the subset of models (Burnham and Anderson 2002). Based upon AIC_c, the best model with overwhelming support (ω = 99%) was the model with only the hypoxia categories. We determined that residuals from this model were normally distributed and that variances were homogenous across hypoxia categories. Therefore, we compared log-transformed catches of demersal species (catch-per-hectare) across the four hypoxic categories with ANOVA, and conducted pairwise multiple comparisons between hypoxic categories using Tukey’s HSD test (experiment-wise α = 0.05).

Experiment 2: Assessing within-trawl variation in dissolved oxygen and fish catches. To more fully understand how small-scale changes in dissolved oxygen affect bottom trawl catches, our second experiment modified existing bottom trawl protocols for the recruitment survey. Recognizing that characterization of a trawl sample with a single dissolved oxygen measurement at either the beginning or the end is problematic, we experimented with the recruitment survey protocol and instituted water column profiling at both ends for a subset of sites (n = 28 in 2012 and n = 17 in 2013). Because trawl distances were typically 800 m, this approach allowed us to directly compare the spatial variability in hypoxia with trawl catches. For this analysis, we examined total catch as a function of the range of bottom dissolved oxygen observed for each
sample. We were also concerned with quantifying the portion of catch that was captured in the middle of the water column during deployment and retrieval of the net, and we devised a second protocol modification. The second experiment involved paired samples (n=45) in an attempt to index the proportion of the catch obtained from the water column. In the first part of the sample pair, the net was deployed and retrieved without conducting the usual ten minute tow along the bottom. This sample was called the “down-up” (DU). The catch from the down-up was quickly removed and the net was immediately redeployed in standard fashion to conduct a ten-minute tow (TMT). The proportion of the total catch from the pair that was in the down-up was calculated as: DU÷(DU+TMT), here mid-water catch index (MCI), and plotted against bottom dissolved oxygen measured at the start of the sequence. Note that the TMT also has a down-up component, which cannot be quantified separately. Measurements of dissolved oxygen at the end of the pair were also taken, but did not vary between normoxic-hypoxic categories in these data.

**Hypoxia Effects on Commercial Fishery Catch Rates**

We investigated anecdotes from commercial fishers in Ohio, who claimed that the edge of the hypoxic zone in Lake Erie was an advantageous fishing environment because it could aggregate fish and drive them into stationary gears such as trap nets. This claim has proven difficult to test because, although Ohio has a vessel and catch monitoring system for commercial fishers, the geographical locations of the nets are only indexed by 10-minute latitude/longitude grids which may cover a broad gradient of normoxic to hypoxic conditions. Fortuitously in 2013, a commercial fisherman set 10 trap nets at the same depth (~14 m) and in close proximity (within 3 nautical miles) to one of our temperature and dissolved oxygen loggers (Figure 1). Working with the commercial fisherman, we obtained absolute position information of the nets adjacent to our moored data logger. Landings (reported in pounds) were entirely comprised of the target species, yellow perch. Commercial trap net deployments (hereafter soak times) ranged 2–5 nights. All 10 nets were emptied on each day a catch was landed; therefore, we calculated mean catch per net night from Ohio Department of Natural Resources catch records of yellow perch specific to this fisherman’s nets. Using data on soak times, we queried the dissolved oxygen record from the nearby monitoring station and calculated the proportion of time that was
hypoxic for each deployment. Logger data and commercial catch data overlapped during 5 July–30 August 2013. A plot of the log of catch per net night against proportion of hypoxic time suggested a dome-shaped relationship, which we modeled as a quadratic polynomial function fit via maximum likelihood.

Results

Spatial and Temporal Variability of Hypoxia

Two contrasting patterns of hypoxia were observed during the intensive sampling events of August 2011 and 2013. In 2011, hypoxia was patchy (on an areal basis) and less intense with bottom dissolved oxygen concentrations rarely < 2.0 mg L\(^{-1}\) (Figure 1). The patchy hypoxia was associated with a thicker hypolimnion (23% of the volume of the study area) and only 38% of this area had dissolved oxygen concentrations < 3.0mg L\(^{-1}\). By comparison, in 2013 hypoxia was continuous (beginning just below the thermocline and continuing offshore) and affected a broad area with oxygen concentrations < 2.0 mg L\(^{-1}\) (Figure 1). In 2013 the hypolimnion was thinner (14% of the volume of the study area) and 80% of this area had dissolved oxygen concentrations < 3.0 mg L\(^{-1}\).

Although the dissolved oxygen concentration distributions from measurements conducted over the study area on a single day in 2011 and 2013 suggested divergent patterns, we found also that conditions near the bottom changed rapidly throughout the study period. In all three years, dissolved oxygen fluctuated multiple times between normoxia and hypoxia, coincident with changes in temperature (Figure 2). Typical epilimnetic temperatures were > 20 degrees C, whereas hypolimnetic temperatures ranged from 12–17 C (Figure 2). Temperature changes indicated rapid movement of the thermocline consistent with internal waves (Bouffard et al. 2012), and in most cases these episodes advected low oxygen waters across the sensors. Corresponding switches from normoxia to hypoxia and back were always greater than 2.0 mg L\(^{-1}\) d\(^{-1}\), and often exceeded 7.5 mg L\(^{-1}\) d\(^{-1}\) (75% of occurrences). The frequency and duration of hypoxic episodes varied with depth such that the shallowest station was the most variable whereas the deepest station exhibited hypoxia of longer, more consistent duration (Figure 2). Therefore, advection of the hypolimnion was primarily responsible for changes in dissolved oxygen at a station, suggesting that the spatial differences between August 2011 and 2013 were
ephemeral. These data also confirmed that, despite the lack of a thermocline during intensive sampling in 2012, the study area was affected by hypoxia in all three years, including a substantial portion of September. During and after the last week in September (2012 and 2013), the stations demonstrated a pattern of steadily declining temperature and gradually increasing dissolved oxygen, indicative of autumnal turnover and increasing oxygen saturation due to colder temperatures (Figure 2).

**Vertical Fish Distributions and Hypoxia**

The density from hydroacoustic surveys was significantly lower in the hypolimnion when comparing August (hypoxia present) to September (normoxic) both for 2011 ($P<0.0001$) and 2013 ($P<0.0001$; Figure 3). In 2011, epilimnetic fish densities were similar in August and September whereas hypolimnetic fish densities were significantly lower than the epilimnion in either month ($P<0.0001$, Figure 3). In 2013, densities of fish in both the epilimnion and the hypolimnion were similar to each other in September and significantly higher than either layer in August ($P<0.0001$, Figure 3).

**Hypoxia Effects on a Fishery Independent Survey**

*Experiment 1: Assessing the historical relationship between fish catches and proximity to hypoxia.* In the analysis of historical recruitment trawl survey data, we found that catches of demersal species differed significantly (ANOVA $F_{3,132}=5.68; P=0.001$) by hypoxic category. In general, catches of demersal species were highly variable (could be either high or low) when trawls were conducted in normoxia and the nearest neighboring trawl within 5.6 km was also normoxic (category 1). When paired trawls straddled hypoxia, with one trawl being normoxic and one being hypoxic (categories 2 and 3), catches were generally elevated above those when both trawls were conducted in hypoxia (category 4; Figure 4). The only significant pairwise differences were between the hypoxic trawls adjacent to other hypoxic trawls (category 4) and either category of normoxic trawls (categories 1 [$P=0.0074$] and 2 [$P=0.0025$], Figure 4). Some of the variability in trawls near the edge of hypoxia could be due to misclassification of hypoxia.
category due to fine spatial heterogeneity in hypoxia, but the single measurements at only one end of the trawl precluded evaluation of this in the historical data.

*Experiment 2: Assessing within-trawl variation in dissolved oxygen and fish catches.* The first survey experiment allowed us to address the spatial heterogeneity through a protocol modification, which entailed measuring bottom oxygen concentrations across a trawl sample. We observed, here, that bottom dissolved oxygen varied from hypoxic and normoxic between end points of a trawl, complicating our ability to classify trawls by hypoxic category. Across two years of sampling, 23 out of 45 trawls were unambiguously classified as hypoxic (i.e., dissolved oxygen at the start and end of a trawl was < 2.0 mg L$^{-1}$, Figure 5). These samples had total catches that were fewer than 500 fish per haul, and most (n=19) were typically < 150 fish per haul (Figure 5). Except for 4 trawls, the rest (n = 18) were classified as normoxic and had catches that were greater than the hypoxic trawls by up to two orders of magnitude (Figure 5). The ambiguous trawls (n=4), which crossed the edge of hypoxia, had higher catches (typically > 150 fish per haul) than most of the hypoxic trawls (Figure 5). Further, some of the normoxic trawls (n = 6) had marginal oxygen values at one end (< 4.2 mg L$^{-1}$) and were similar to the ambiguous trawls with intermediate catches (96–1629 fish per haul; Figure 5).

The second survey protocol modification, which entailed paired down-up and ten-minute tows, illustrated that variance in the catch per haul, due to fish captured in the middle of the water column, increased at lower oxygen concentrations. When the sampling area was stratified and hypoxic (dissolved oxygen concentrations < 2.0 mg L$^{-1}$), the proportion of the total catch from the down-up was highly variable. For some trawls conducted in these conditions, the vast majority of the total catch was caught during the down-up (MCI > 0.75). For other trawls conducted in these same conditions, the vast majority of the total catch came from the ten-minute tow (MCI< 0.1) (Figure 6). This discontinuous pattern contrasted with normoxic conditions when all but one of the catches had a MCI < 0.5 (Figure 6).

**Hypoxia Effects on Commercial Fishery Catch Rates**

A significant amount of variability ($R^2 = 0.63$) in landings from the commercial trap nets within our study area during 2013 could be explained by a quadratic relationship between the log of landings and the proportion of time hypoxic as recorded on the shallow data logger (Figure 7).
The best fit relationship was: \( \log(\text{landings}) = 1.25 + 2.16x - 3.28x^2 \) \((F_{15}=13.1, P=0.0005)\), where \( x \) was the proportion of time hypoxic. Commercial landings varied around 18 pounds (8.2 kg) per net night under normoxic conditions, and then increased to a peak near 40 pounds (18.1 kg) per net night when hypoxia was present 30–50% of the time (Figure 7). With continuous hypoxia, few yellow perch were landed (0.98 pounds [0.4 kg] per net night, Figure 7).

**Discussion**

Habitat quality effects on population dynamics of exploited species is a core issue in fisheries science, which in recent decades has been incorporated into resource management as part of ecosystem-based approaches. In this context, understanding how ecosystem function changes in the presence of hypoxia is complicated by the interaction of behaviors of both human (fisheries) and fish populations that show marked avoidance of degraded habitats. In particular, when seasonal hypoxia affects habitats, vertical and horizontal displacement may intensify interactions between fish and fishing gears at the edges of hypoxic zones. This concept has support from both coastal marine systems (Campbell and Rice 2014; Craig 2012; Selberg et al. 2001), and freshwater lakes (Roberts et al. 2009). We observed evidence of displacement of fish from hypoxic zones and concentration of fish near the edge of hypoxic zones. Further, our results provide novel insights on the spatial and temporal dynamics of the lateral edges of hypoxic zones, which were more variable than expected and a key factor for explaining catches in both fishery-dependent and fishery-independent data. Although the observed environmental variability in hypoxia was unanticipated, our analysis provided valuable insights for fishery managers considering the impact of seasonal hypoxia on fisheries.

The traditional paradigm of seasonal hypoxia in shallow lakes, where warming temperatures and the development of a thermocline establish conditions for oxygen depletion in the hypolimnion, has sometimes been associated with predictable stability of the hypoxic zone. The view that “…advection does not quickly shift the edges of the hypoxic regions” in Lake Erie (Vanderploeg et al. 2009b) is primarily based upon data collected from the center of the basin, while a more dynamic situation along the lateral edges of the hypolimnion (i.e., depths where the thermocline intersects the bottom) has also been found from recent studies, including ours. Physical modeling efforts have revealed that low amplitude, high frequency inertial waves
(Poincaré waves with a dominant period of 17.3 hours) are a prominent feature of the variability in Lake Erie’s thermocline (Bouffard et al. 2012). In addition, large-scale anti-cyclonic circulation patterns generate a bowl-shaped thermocline in Lake Erie’s central basin, which results in varying degrees of upward forcing of the thermocline near the edges of the basin (Beletsky et al. 2012). Thus, instability of the thermocline and fluctuations in the thickness of the hypolimnion can function to increase heterogeneity in the hypoxic zone, especially in regions where the thermocline contacts the sediment. Our data logger and intensive sampling results indicated that this heterogeneity can be observed across a large area in which the thermocline depth changes frequently. Further, we observed that frequent rapid shifts in the quality of fish habitat driven by advection of hypoxic waters tend to displace and concentrate fish in adjacent habitats, and only during extreme events in which hypoxic waters are mixed throughout the water column are fish kill events likely (Paerl et al. 1998; Rao et al. 2014).

Zones of high variability in hypoxia in Lake Erie have significant implications for resource managers as well as for assessment of fish habitat quality and habitat use in Lake Erie. The binational Great Lakes Water Quality Protocol calls for a reduction in the extent of hypoxia with special reference to Lake Erie’s central basin (International Joint Commission 2012). Not only is the current approach to monitor progress on this objective problematic due to infrequent sampling that is limited to deep stations, but our results emphasize that modifications to the monitoring plan will have to address fluctuations in areal extent of the hypoxic zone, which are beyond the limits of what can be efficiently measured with conventional water column profiling. Even within the current US-EPA monitoring of 10 fixed stations sampled at three-week intervals, decadal trends in the basin-wide extent of hypoxia may have been influenced by finer-scale variability. Comparative evaluation between the current monitoring plan and a new network of data loggers with high-frequency dissolved oxygen sampling is being led by some of the authors of this paper (G. Warren, P. Collingsworth, and R. Kraus). Although future insights could potentially discount long-term patterns, our data showed that hypoxia was more chronic with longer hypoxic episodes at the deepest station (Figure 2), supporting basin-wide inferences from the EPA data regarding the deeper hypolimnetic portions of the central basin (Burns et al. 2005; Zhou et al. 2013).

With respect to the seasonal impact of variable hypoxia on fish habitats, our results suggested that decoupling of benthic-pelagic food web linkages has a spatial/depth gradient in
addition to a seasonal one. The strongest evidence for decoupling of benthic-pelagic foodweb linkages in Lake Erie due to hypoxia comes from seasonal diet analyses that show increasing consumption of zooplankton prey and absence of benthic prey during hypoxic events (Pothoven et al. 2009; Roberts et al. 2009; Vanderploeg et al. 2009a). These diet studies were primarily conducted in the deepest portions of the central basin of Lake Erie, and water quality data associated with the diet analyses supported conclusions that chronic hypoxia was the primary influence on diet. Our results indicated that hypoxia is intermittent near the edge of the hypolimnion, and the spatial interpolations in conjunction with the data loggers revealed frequent opportunities for benthic foraging in normoxic conditions within our study area. The edge zone of intermittent hypoxia is at least as wide as our study area (11–16 km). Future studies drawing comparisons and contrasts between this zone and the center of the lake are critical for evaluating population and ecosystem level impacts.

In the more chronically impacted central portions of the lake, yellow perch catch rates declined in bottom trawls and increased in mid-water trawls in areas with low oxygen, demonstrating suspension of fish above the hypoxic zone (Roberts et al. 2012; Roberts et al. 2009) or horizontal displacement into normoxic regions of the hypolimnion (Vanderploeg et al. 2009b). Our results provided novel information on the effects of horizontal displacement of fish near the edge of the hypolimnion, where we observed elevated bottom trawl catch rates of demersal fishes on both sides of the hypoxic front. Due to their collective dominance in our filtered data set, inferences from catch rates apply primarily to white perch and yellow perch. The effect of hypoxia was emphasized with passively fishing commercial trap nets, which exhibited increased catch rates of yellow perch when hypoxia occurred for intermediate proportions of time. Thus, fish in this edge zone are concentrated at small spatial scales (approximately equal to the length of a trawl, 800 m) and in locations that may shift rapidly with fluctuations in the thermocline. In Lake Erie, this region (depths 5–20 m) corresponds to the highest fish abundances for most species during stratified periods (Knight et al. 1993). On the scale of individual research samples or commercial fishing catches, predicting the locations of hypoxia or the thermocline within this zone is not currently possible. Yet, if the importance of a particular habitat is proportional to the abundance of organisms, assessing lake-wide population and ecosystem level responses to hypoxia depend more on understanding of the processes
occurring within these edge zones than those occurring in central areas of the lake with persistent seasonal hypoxia.

Due to size selectivity characteristics of the research trawls and typical young-of-the-year growth rates of target species, inter-agency fish recruitment surveys historically have been conducted in August. Hypoxia affects the efficiency of these recruitment surveys, but there is a pragmatic need to sample in August to avoid disrupting a long time series that is critical for developing a recommended allowable harvest. Our results elucidated some potential approaches to reduce uncertainty in August survey results. In the historical series, information on the spatial proximity of hypoxia to sampling sites can be extracted through the nearest neighbor classification method that we used. This approach accounts for a significant amount of variance and could be used to standardize indices to a normoxic habitat condition through statistical least-squared means approach or similar routine. This is not a panacea and would cease to be useful if hypoxia became more widespread and persistent as predicted with climate change (Blumberg and Di Toro 1990). To better track changes in recruitment with variable hypoxia, additional protocols are warranted. These might include increased profile sampling at both ends of the trawls at the least, and net sensors to record dissolved oxygen and other variables during trawls to gain high spatial resolution water quality data. Similarly, more information is needed from commercial fishing gears to better define the dome-shaped response that we observed. One limitation in our commercial fishing data is the lack of samples when hypoxic durations exceeded 50%. Additionally, due to the spatial mismatch between the nets and our logger, we recommend attaching data loggers to fishing nets to better understand the influence of hypoxia on commercial trap net catches.

The influence of hypoxia on the distribution of Lake Erie fishes is in many ways comparable to coastal marine systems. A key concept for marine coastal systems is that spatial mosaics of hypoxic zones across a waterscape may function to mitigate harmful effects by displacing productivity at higher trophic levels to adjacent areas (Breitburg 2002). Similarly, the edge zones in Lake Erie are part of a larger mosaic of habitats where ecological interactions between fish species and the effects of fishing may mitigate the seasonal loss of deeper habitats due to hypoxia. Although different physical mechanisms (other than tidal forces in coastal marine environments) primarily influence variability in the edge zone, our results demonstrated, similar to other systems, that fish may be concentrated at small spatial scales adjacent to
hypoxia. Consistent with the concept of habitat compression, we showed with both active and passive fishing gears how catches may actually increase in areas affected by hypoxia. This latter insight helps to explain the lack of a relationship between fishery landings and the level of hypoxia across a wide range of enclosed and semi-enclosed systems throughout the world (Breitburg et al. 2001). On the one hand, if the fishing mortality rate is constant through periods of hypoxia in Lake Erie, deleterious effects on landings would only be observed if the rate is unsustainable. The more concerning possibility is that habitat-compression may increase catchability in concert with fishing mortality to an unknown degree above the level estimated in stock assessments. In the age-structured population models currently used for Lake Erie fisheries, catchability is assumed constant across management districts; therefore, if catchability is in reality higher in the vicinity of hypoxia, current models would estimate a larger population of fish than actually exists. We recommend that ongoing efforts to improve the stock assessment and harvest recommendation strategies for Lake Erie (Belore et al. 2014) better account for the effects of hypoxia to provide more accurate estimates of catchability and reduce the risk of overfishing.

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Environmental Protection Agency. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the United States Government. This article is contribution number 1916 of the Great Lakes Science Center.


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Figure Captions

Figure 1. Location of the study area for the intensive sampling effort in Lake Erie (A) and locations of bottom data loggers (symbols labeled by year) and commercial trap nets (circles) as discussed in the text (B). Sampling effort and inferences for spatial interpolation of water quality were limited to the gray polygon in the lower three panels. Five-meter depth contour intervals are also displayed in the lower three panels. The distribution of low oxygen areas was derived from interpolations of water column profiles (dots) in August of 2011 (C) and 2013 (D).

Figure 2. Time series of dissolved oxygen (red, left-hand axis) and temperature (blue, right-hand axis) observed within the Fairport Harbor study area from three consecutive years (labeled by year and sensor depth in the upper right-hand corner of each plot). For reference, a horizontal dashed line is shown, demarcating a dissolved oxygen threshold of 2.0 mg L\(^{-1}\) for hypoxia. In addition the gray-shaded boxes highlight periods of continuous hypoxia that were separated by at least 12 hours from other such periods. The durations of each time series varied dependent upon the availability of data loggers and vessels to deploy and retrieve the devices. Minor tick marks are shown for each Monday. The sensor depth is noted in the upper right-hand corner of each plot: the sensor was positioned 0.5 m above the bottom.

Figure 3. Mean densities of fish determined from north-south hydracoustic transects in the Fairport Harbor study area from August and September in 2011 (upper) and 2013 (lower). Confidence intervals (95%) are plotted, and letters above the symbols denote means that were not significantly different as determined by Tukey HSD multiple comparison tests (separate tests for each year).

Figure 4. Box and whisker plots of demersal fish catch rates (numbers per hectare swept) from historical recruitment surveys conducted by the Ohio Department of Natural Resources from 1990 to 2009. Four categories are compared based upon classification of a trawl relative to the nearest neighboring trawl: normoxic trawls that were adjacent to 1) another normoxic trawl or a 2) hypoxic trawl, and hypoxic trawls that were adjacent to 3) a normoxic trawl or another 4)
hypoxic trawl. Letters above the symbols denote means that were not significantly different as determined by Tukey HSD multiple comparisons.

**Figure 5.** Catches from bottom trawls conducted in August and September in Lake Erie (2012=squares, 2013=triangles) following protocol modification to measure water quality profiles at the beginning and end of each tow. Error bars show the range of bottom dissolved oxygen at the ends of each trawl sample. Trawls were classified as either hypoxic (gray) or normoxic (open), but four of the trawls were ambiguous (black symbols). The dashed line shows the reference threshold (2.0 mg L\(^{-1}\)) used to classify hypoxic trawls.

**Figure 6.** Paired down-up (DU) and ten minute trawl (TMT) sample results showing the mid-water catch index (see description in text) as a function of the bottom dissolved oxygen concentration. The dashed line shows the reference threshold (2.0 mg L\(^{-1}\)) used to classify hypoxic trawls.

**Figure 7.** Catch rates (pounds per net night) from commercial trap nets that were set adjacent to one of the data loggers in this study during a portion of the 2013 season. The proportion of fishing time that was hypoxic was determined from time series of dissolved oxygen recorded by the data logger. A best fit quadratic relationship (solid line) with 95% confidence bands (dashed lines) is also plotted.
Figure 1.
Figure 2.
Figure 3.
Figure 4.
Figure 5.
Figure 6.

The graph illustrates the relationship between Midwater Catch Index [DU/(DU+TMT)] and Dissolved Oxygen (mg/L). Two categories are shown: 
- Stratified (dark grey circles) with a trend indicating more fish in the down-up area.
- Mixed (light grey circles) with a trend suggesting more fish in the ten-minute tow area.

The data suggests that as Dissolved Oxygen levels increase, the Midwater Catch Index decreases, indicating a possible decrease in fish population in the down-up area and an increase in the ten-minute tow area.
Figure 7.