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Dynamic hypoxic zones in Lake Erie compress fish habitat, altering vulnerability to fishing gears[1]

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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.

Résumé : Une dégradation saisonnière des habitats aquatiques découlant de l'hypoxie caractérise de nombreux systèmes marins côtiers et d'eau douce et peut entraîner la mortalité directe ou le déplacement de poissons. Cela dit, les débarquements provenant de ces systèmes sont bien souvent peu sensibles aux changements de l'intensité et de l'étendue de l'hypoxie, et les effets à l'échelle de la population sont difficiles à mesurer sauf pour les espèces sensibles à l'hypoxie dans des conditions d'hypoxie extrême. Nous avons étudié la variabilité temporelle et spatiale à petite échelle de l'oxygène dissous dans le lac Érié et son lien avec la répartition de poissons et l'efficacité d'engins actifs (chaluts de fond) et passifs (filets-pièges). Des enregistreurs de température et d'oxygène dissous placés près de la bordure de l'hypolimnion témoignaient d'une variabilité beaucoup plus grande que prévu. Des épisodes hypoxiques de durée variable étaient fréquemment ponctués de périodes de normoxie, ce qui concorde avec la présence de vagues internes de haute fréquence. Des interpolations de haute résolution des résultats de levés hydroacoustiques et de la qualité de l'eau donnent à penser que l'habitat des poissons est comprimé durant les périodes hypoxiques, produisant des densités de poissons plus élevées en bordure de zones d'hypoxie. Aux emplacements fixes d'engins de pêche commerciale passifs, les plus grandes prises se produisaient quand les eaux de fond étaient hypoxiques pour des proportions de temps intermédiaires. La proximité de l'hypoxie explique des variations significatives des prises au chalut de fond, dont des taux de prises plus grands en bordure des zones d'hypoxie. Ces résultats soulignent comment l'hypoxie peut rehausser les taux de prises de divers types d'engins de pêche, se traduisant par l'absence de lien entre les indices d'hypoxie et les débarquements. Des taux de prises accrus en bordure de zones hypoxiques ont d'importantes conséquences pour les modèles d'évaluation des stocks reposant sur l'hypothèse de l'homogénéité spatiale de la capturabilité. [Traduit par la Rédaction]

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

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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 (*Callinectes sapidus*) 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 (~5000 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. 2011). 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. 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. 2009*a*).

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 (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. 2014; 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 data; 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).

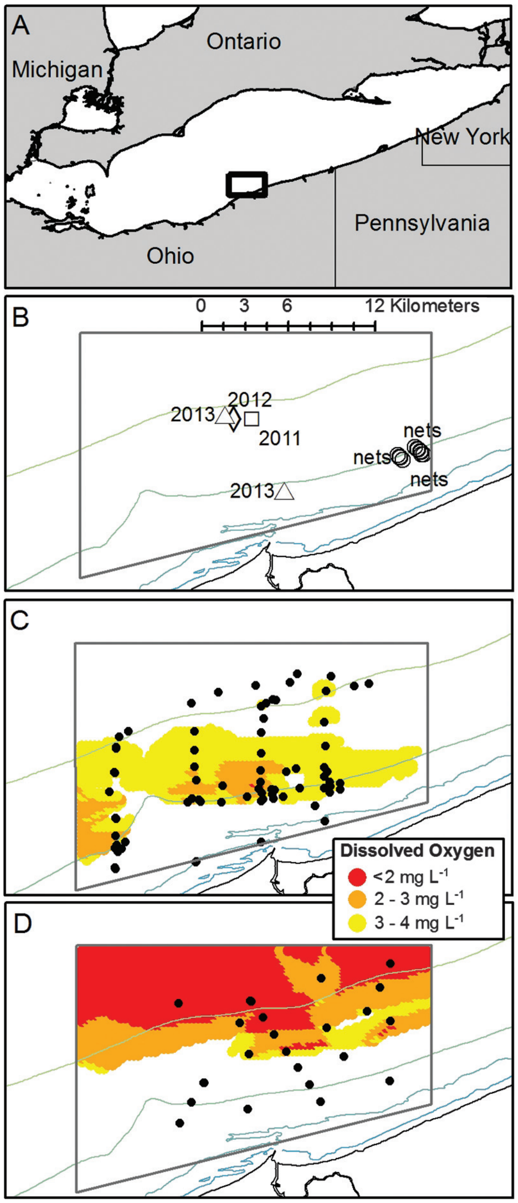
Here, we addressed the need for better information on the influence of hypoxia on fish distribution in Lake Erie through diverse field sampling approaches and retrospective analysis of historical data. The US Environmental Protection Agency (US-EPA) has monitored the hypoxic zone in Lake Erie since the 1980s (Burns et al. 2005; Zhou et al. 2013). Owing 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 (Fig. 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 (Fig. 1), encompassed approximately 243 km², with depths ranging 11–22 m (Fig. 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

Fig. 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-metre 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).



repeated this sampling schedule for 3 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, USA) 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, USA). Hypolimnetic volume was calculated at a thermocline threshold of 16.5 °C, but results did not vary appreciably if other thresholds between 15 and 18 °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., Fig. 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 (Fig. 1B). We conducted a longer deployment with a galvanic-style oxygen sensor (RBRDuo 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 (RBRDuo with galvanic-style oxygen sensors till 25 September and HOBO loggers, model U26, with optical oxygen sensors for the last part; Fig. 1B). Each logger recorded temperature and dissolved oxygen continuously at either 5 or 10 min 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 h from other such periods. This threshold is a typical convention for defining hypoxia (Vaquer-Sunyer and Duarte 2008), but because of 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°, 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, USA). 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 mean 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_v 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 owing 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 min) and vessel speed (2.5 knots; 1 knot = 1.852 km·h^{-1}), 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 to October. The overall goal of the survey was 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 four to eight 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 interagency 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 dataset 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*); lake whitefish (*Coregonus clupeaformis*); logperch (*Percina caprodes*); channel catfish (*Ictalurus punctatus*); johnny darter (*Etheostoma nigrum*); burbot (*Lota lota*); and slimy sculpin (*Cottus cognatus*). Owing 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 (i.e., 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 homogeneous 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 $\alpha = 0.05$).

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 10 min tow (TMT) along the bottom. This sample was called the "down–up" (DU). The catch from the DU was quickly removed, and the net was immediately redeployed in standard fashion to conduct a TMT. The proportion of the total catch from the pair that was in the DU was calculated as DU/(DU + TMT), here "midwater catch index" (MCI), and plotted against bottom dissolved oxygen measured at the start of the sequence. Note that the TMT also has a DU 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; 1 n.mi. = 1.852 km) to one of our temperature and dissolved oxygen loggers (Fig. 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 composed of the target species, yellow perch. Commercial trap net deployments (hereinafter 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.

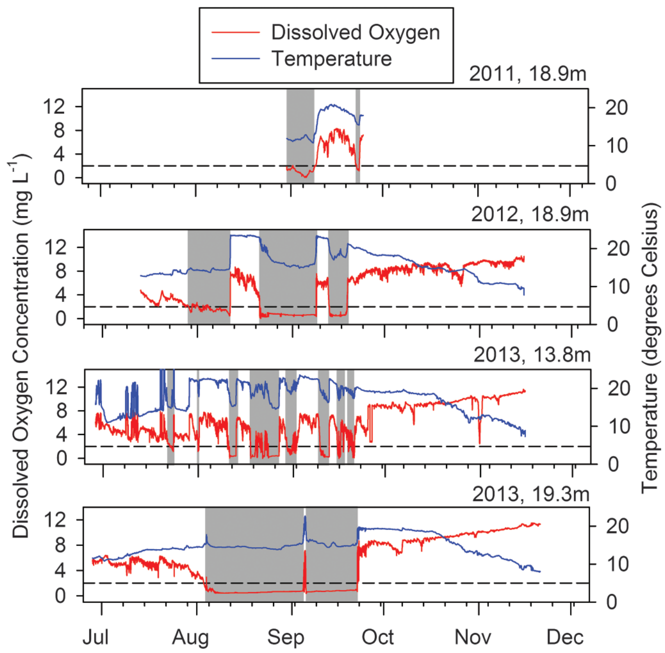
Results

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} (Fig. 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 <3.0 mg·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} (Fig. 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 3 years, dissolved oxygen fluctuated multiple times between normoxia and hypoxia, coincident with changes in temperature (Fig. 2). Typical epilimnetic temperatures were >20 °C,

Fig. 2. Time series of dissolved oxygen (red line, left-hand axis) and temperature (blue line, right-hand axis) observed within the Fairport Harbor study area from 3 consecutive years (labeled by year and sensor depth in the upper right-hand corner of each plot; the sensor was positioned 0.5 m above the bottom). 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 h 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.



whereas hypolimnetic temperatures ranged from 12 to 17 °C (Fig. 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}·day^{-1} and often exceeded 7.5 mg·L^{-1}·day^{-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 (Fig. 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 3 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 (Fig. 2).

Vertical fish distributions and hypoxia

The density from hydroacoustic surveys was significantly lower in the hypolimnion when comparing August (hypoxia present) with September (normoxic) both for 2011 (P < 0.0001) and 2013 (P < 0.0001; Fig. 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

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

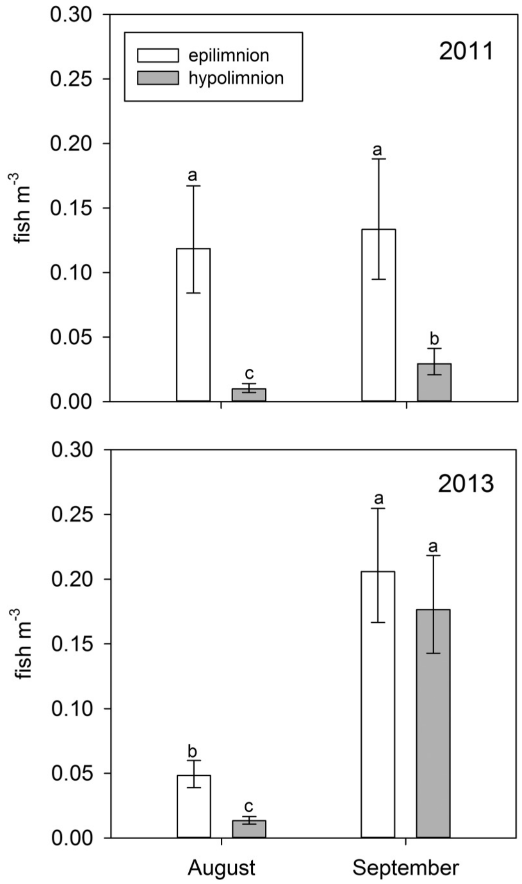
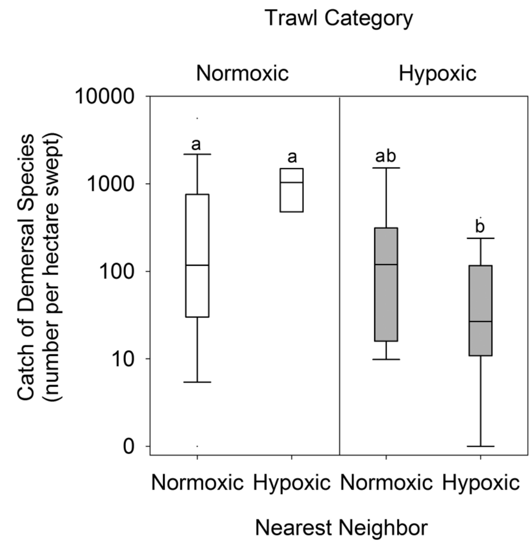


Fig. 4. Box and whisker plots of demersal fish catch rates (numbers per hectare swept) from historical recruitment surveys conducted by the Ohio Department of Natural Resources from 1990 to 2009. Four categories are compared based upon classification of a trawl relative to the nearest neighboring trawl: 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's HSD multiple comparisons.



($P < 0.0001$; Fig. 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 ($P < 0.0001$; Fig. 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; Fig. 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 ($P = 0.0025$); Fig. 4). Some of the variability in trawls near the edge of hypoxia could be due to misclassification of hypoxia category owing 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 to normoxic between end points of a trawl, complicating our ability to classify trawls by hypoxic category. Across 2 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}; Fig. 5). These samples had total catches that were fewer than 500 fish per haul, and most (n = 19) were typically <150 fish per haul (Fig. 5). Except for four 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 (Fig. 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 (Fig. 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; Fig. 5).

The second survey protocol modification, which entailed paired DU and TMT, 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 DU was highly variable. For some trawls conducted in these conditions, the vast majority of the total catch was caught during the DU (MCI > 0.75). For other trawls conducted in these same conditions, the vast majority of the total catch came from the TMT (MCI < 0.1; Fig. 6). This discontinuous pattern contrasted with normoxic conditions when all but one of the catches had an MCI < 0.5 (Fig. 6).

Fig. 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.

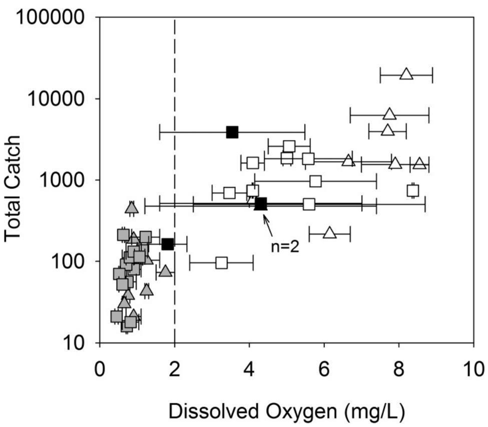


Fig. 6. Paired down-up (DU) and 10 min trawl (TMT) sample results showing the midwater catch index (see description in text) as a function of the bottom dissolved oxygen concentration. The dashed line shows the reference threshold (2.0 mg·L^{-1}) used to classify hypoxic trawls.

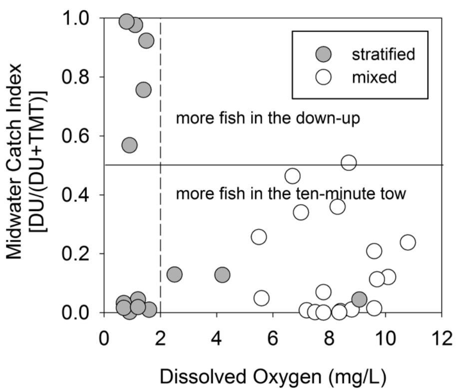
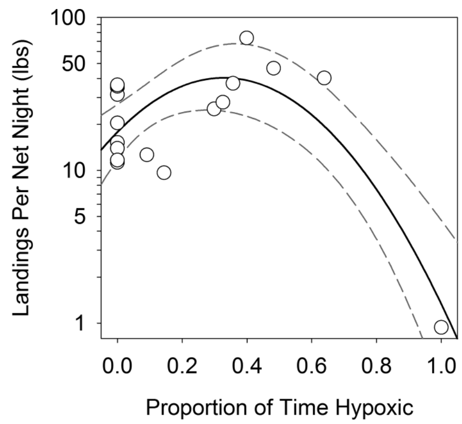


Fig. 7. Catch rates (pounds per net night; 1 lb = 0.453 kg) from commercial trap nets that were set adjacent to one of the data loggers in this study during a portion of the 2013 season. The proportion of fishing time that was hypoxic was determined from time series of dissolved oxygen recorded by the data logger. A best-fit quadratic relationship (solid line) with 95% confidence bands (dashed lines) is also plotted.



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 (Fig. 7). The best-fit relationship was log(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 (Fig. 7). With continuous hypoxia, few yellow perch were landed (0.98 pounds (0.4 kg) per net night; Fig. 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. 2009*b*) 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 h) are a prominent feature of the variability in Lake Erie's thermocline (Bouffard et al. 2012). In addition, large-scale anticyclonic 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 important 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 because of 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 3-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 (Fig. 2), supporting basin-wide inferences from the US-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 and 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. 2009*a*). 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 midwater trawls in areas with low oxygen, demonstrating suspension of fish above the hypoxic zone (Roberts et al. 2009, 2012) or horizontal displacement into normoxic regions of the hypolimnion (Vanderploeg et al. 2009*b*). 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. Because of their collective dominance in our filtered dataset, 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 depends more on understanding the processes occurring within these edge zones than those occurring in central areas of the lake with persistent seasonal hypoxia.

Because of size selectivity characteristics of the research trawls and typical young-of-the-year growth rates of target species, interagency 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 considerable 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, owing 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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References

Arend, K.K., Beletsky, D., DePinto, J.V., Ludsin, S.A., Roberts, J.J., Rucinski, D.K., Scavia, D., Schwab, D.J., and Höök, T.O. 2011. Seasonal and interannual effects of hypoxia on fish habitat quality in central Lake Erie. Freshw. Biol. **56**(2): 366–383. doi:10.1111/j.1365-2427.2010.02504.x.

Baker, D.B., Confesor, R., Ewing, D.E., Johnson, L.T., Kramer, J.W., and Merryfield, B.J. 2014. Phosphorus loading to Lake Erie from the Maumee, Sandusky and Cuyahoga rivers: The importance of bioavailability. J. Gt. Lakes Res. **40**(3): 502–517. doi:10.1016/j.jglr.2014.05.001.

Beletsky, D., Hawley, N., Rao, Y.R., Vanderploeg, H.A., Beletsky, R., Schwab, D.J., and Ruberg, S.A. 2012. Summer thermal structure and anticyclonic circulation of Lake Erie. Geophys. Res. Lett. **39**(6): L06605. doi:10.1029/2012GL051002.

Belore, M., Cook, A., Hartman, T., Kayle, K., Knight, C., Markham, J., Murray, C., Thomas, M., and Witzel, L. 2014. Report of the Lake Erie Yellow Perch Task Group to the Great Lakes Fishery Commission, Windsor, Ont.

Blumberg, A.F., and Di Toro, D.M. 1990. Effects of climate warming on dissolved oxygen concentrations in Lake Erie. Trans. Am. Fish. Soc. **119**(2): 210–223. doi:10.1577/1548-8659(1990)119<0210:EOCWOD>2.3.CO;2.

Bouffard, D., Boegman, L., and Rao, Y.R. 2012. Poincaré wave-induced mixing in a large lake. Limnol. Oceanogr. **57**(4): 1201–1216. doi:10.4319/lo.2012.57.4.1201.

Brady, D.C., Targett, T.E., and Tuzzolino, D.M. 2009. Behavioral responses of juvenile weakfish (*Cynoscion regalis*) to diel-cycling hypoxia: Swimming speed, angular correlation, expected displacement, and effects of hypoxia acclimation. Can. J. Fish. Aquat. Sci. **66**(3): 415–424. doi:10.1139/F09-007.

Brandt, S.B., Costantini, M., Kolesar, S., Ludsin, S.A., Mason, D.M., Rae, C.M., Zhang, H., and Kraft, C. 2011. Does hypoxia reduce habitat quality for Lake Erie walleye (*Sander vitreus*)? A bioenergetics perspective. Can. J. Fish. Aquat. Sci. **68**(5): 857–879. doi:10.1139/f2011-018.

Breitburg, D. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. Estuaries, **25**(4): 767–781. doi:10.1007/BF02804904.

Breitburg, D.L., Pihl, L., and Kolesar, S.E. 2001. Effects of low dissolved oxygen on the behavior, ecology and harvest of fishes: a comparison of the Chesapeake and Baltic systems. *In* Coastal hypoxia: consequences for living resources and ecosystems. *Edited by* N.N. Rabalais and R.E. Turner. American Geophysical Union, Washington, D.C. pp. 241–267.

Breitburg, D.L., Hondorp, D.W., Davias, L.A., and Diaz, R.J. 2009. Hypoxia, nitrogen, and fisheries: Integrating effects across local and global landscapes. Annu. Rev. Mar. Sci. **1**: 329–349. doi:10.1146/annurev.marine.010908.163754.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multimodel inference. Springer, New York.

Burns, N.M., Rockwell, D.C., Bertram, P.E., Dolan, D.M., and Ciborowski, J.J.H. 2005. Trends in temperature, secchi depth, and dissolved oxygen depletion rates in the central basin of Lake Erie, 1983–2002. J. Gt. Lakes Res. **31**(Suppl. 2): 35–49. doi:0.1016/S0380-1330(05)70303-8.

Caddy, J.F. 1993. Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. Rev. Fish. Sci. **1**(1): 57–95. doi:10.1080/10641269309388535.

Campbell, L.A., and Rice, J.A. 2014. Effects of hypoxia-induced habitat compression on growth of juvenile fish in the Neuse River estuary, North Carolina, USA. Mar. Ecol. Progr. Ser. **497**: 199–213. doi:10.3354/meps10607.

Conroy, J.D., Kane, D.D., Dolan, D.M., Edwards, W.J., Charlton, M.N., and Culver, D.A. 2005. Temporal trends in Lake Erie plankton biomass: Roles of external phosphorus loading and dreissenid mussels. J. Gt. Lakes Res. **31**: 89–110. doi:10.1016/S0380-1330(05)70307-5.

Conroy, J.D., Boegman, L., Zhang, H., Edwards, W.J., and Culver, D.A. 2011. "Dead zone" dynamics in Lake Erie: the importance of weather and sampling intensity for calculated hypolimnetic oxygen depletion rates. Aquat. Sci. **73**(2): 289–304. doi:10.1007/s00027-010-0176-1.

Craig, J.K. 2012. Aggregation on the edge: Effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the northern Gulf of Mexico. Mar. Ecol. Progr. Ser. **445**: 75–95. doi:10.3354/meps09437.

Craig, J.K., and Bosman, S. 2013. Small spatial scale variation in fish assemblage structure in the vicinity of the northwestern Gulf of Mexico hypoxic zone. Estuar. Coasts, **36**(2): 268–285. doi:10.1007/s12237-012-9577-9.

Craig, J.K., and Crowder, L.B. 2005. Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. Mar. Ecol. Progr. Ser. **294**: 79–94. doi:10.3354/meps294079.

Diaz, R.J. 2001. Overview of hypoxia around the world. J. Environ. Qual. **30**(2): 275–281. doi:10.2134/jeq2001.302275x. PMID:11285887.

Diaz, R.J., and Rosenberg, R. 2008. Spreading dead zones and consequences for marine ecosystems. Science, **321**(5891): 926–929. doi:10.1126/science.1156401. PMID:18703733.

Eby, L.A., and Crowder, L.B. 2002. Hypoxia-based habitat compression in the Neuse River estuary: context-dependent shifts in behavioral avoidance thresholds. Can. J. Fish. Aquat. Sci. **59**(6): 952–965. doi:10.1139/f02-067.

Eby, L.A., Crowder, L.B., McClellan, C.M., Peterson, C.H., and Powers, M.J. 2005. Habitat degradation from intermittent hypoxia: Impacts on demersal fishes. Mar. Ecol. Prog. Ser. **291**: 249–261. doi:10.3354/meps291249.

Hawley, N., Johengen, T.H., Rao, Y.R., Ruberg, S.A., Beletsky, D., Ludsin, S.A., Eadie, B.J., Schwab, D.J., Croley, T.E., and Brandt, S.B. 2006. Lake Erie hypoxia prompts Canada–US study. Eos, Trans. Am. Geophys. Union, **87**(32): 313–319. doi:10.1029/2006EO320001.

Hosack, G.R., Peters, G.W., and Ludsin, S.A. 2014. Interspecific relationships and environmentally driven catchabilities estimated from fisheries data. Can. J. Fish. Aquat. Sci. **71**(3): 447–463. doi:10.1139/cjfas-2013-0236.

International Joint Commission. 2012. Great Lakes Water Quality Protocol of 2012, with the annexes and terms of reference, between the United States and Canada signed at Washington, September 7, 2012.

Knight, C., Lundquist, M., Buenger, J., and Stein, R.A. 1993. Ecology and population dynamics of Lake Erie fishes. Ohio Department of Natural Resources, Lake Erie Fisheries Research Unit, Fairport Harbor.

Kocovsky, P.M., Rudstam, L.G., Yule, D.L., Warner, D.M., Schaner, T., Pientka, B., Deller, J.W., Waterfield, H.A., Witzel, L.D., and Sullivan, P.J. 2013. Sensitivity of fish density estimates to standard analytical procedures applied to great lakes hydroacoustic data. J. Gt. Lakes Res. **39**(4): 655–662. doi:10.1016/j.jglr.2013.09.002.

Leming, T.D., and Stuntz, W.E. 1984. Zones of coastal hypoxia revealed by satellite scanning have implications for strategic fishing. Nature, **310**(5973): 136–138. doi:10.1038/310136a0.

Ludsin, S.A., Kershner, M.W., Blocksom, K.A., Knight, R.L., and Stein, R.A. 2001. Life after death in Lake Erie: nutrient controls drive fish species richness, rehabilitation. Ecol. Appl. **11**(3): 731–746. doi:10.1890/1051-0761(2001)011[0731:LADILE]2.0.CO;2.

Ludsin, S.A., Zhang, X., Brandt, S.B., Roman, M.R., Boicourt, W.C., Mason, D.M., and Costantini, M. 2009. Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: Implications for food web interactions and fish recruitment. J. Exp. Mar. Biol. Ecol. **381**(Suppl. 1): S121–S131. doi:10.1016/j.jembe.2009.07.016.

Markham, J., Hosack, M., Deller, J., Kocovsky, P., MacDougall, T., Perez-Fuentetaja, A., Trometer, E., Weimer, E., and Witzel, L. 2012. Report of the Lake Erie Forage Task Group, presented to the Great Lakes Fishery Commission, Windsor, Ont.

Ohio Division of Wildlife. 2014. Ohio's Lake Erie Fisheries, 2013. Annual status report. Federal Aid in Fish Restoration Project F-69-P; Ohio Department of Natural Resources, Lake Erie Fisheries Units, Fairport and Sandusky.

Paerl, H.W., Pinckney, J.L., Fear, J.M., and Peierls, B.L. 1998. Ecosystem responses to internal and watershed organic matter loading: consequences for hypoxia in the eutrophying Neuse River Estuary, North Carolina, USA. Mar. Ecol. Progr. Ser. **166**: 17–25. doi:10.3354/meps166017.

Parker-Stetter, S.L., Rudstam, L.G., Sullivan, P.J., and Warner, D.M. 2009. Standard operating procedures for fisheries acoustic surveys in the great lakes. Great Lakes Fishery Commission Special Publication 09-01.

Pavela, J.S., Ross, J.L., and Chittenden, M.E., Jr. 1983. Sharp reductions in abundance of fishes and benthic macroinvertebrates in the Gulf of Mexico off Texas associated with hypoxia. Northeast Gulf Sci. **6**(2): 167–173.

Pihl, L., Baden, S., Diaz, R., and Schaffner, L. 1992. Hypoxia-induced structural changes in the diet of bottom-feeding fish and crustacea. Mar. Biol. **112**(3): 349–361. doi:10.1007/BF00356279.

Pothoven, S.A., Vanderploeg, H.A., Ludsin, S.A., Höök, T.O., and Brandt, S.B. 2009. Feeding ecology of emerald shiners and rainbow smelt in central Lake Erie. J. Gt. Lakes Res. **35**(2): 190–198. doi:10.1016/j.jglr.2008.11.011.

Rao, Y.R., Howell, T., Watson, S.B., and Abernethy, S. 2014. On hypoxia and fish kills along the north shore of Lake Erie. J. Gt. Lakes Res. **40**(1): 187–191. doi:10.1016/j.jglr.2013.11.007.

Richards, R.P., Baker, D.B., and Crumrine, J.P. 2009. Improved water quality in Ohio tributaries to Lake Erie: a consequence of conservation practices. J. Soil Water Conserv. **64**(3): 200–211. doi:10.2489/jswc.64.3.200.

Richards, R.P., Baker, D.B., Crumrine, J.P., and Stearns, A.M. 2010. Unusually large loads in 2007 from the Maumee and Sandusky rivers, tributaries to Lake Erie. J. Soil Water Conserv. **65**(6): 450–462. doi:10.2489/jswc.65.6.450.

Roberts, J.J., Höök, T.O., Ludsin, S.A., Pothoven, S.A., Vanderploeg, H.A., and Brandt, S.B. 2009. Effects of hypolimnetic hypoxia on foraging and distributions of Lake Erie yellow perch. J. Exp. Mar. Biol. Ecol. **381**: S132–S142. doi:10.1016/j.jembe.2009.07.017.

Roberts, J.J., Grecay, P.A., Ludsin, S.A., Pothoven, S.A., Vanderploeg, H.A., and Höök, T.O. 2012. Evidence of hypoxic foraging forays by yellow perch (*Perca flavescens*) and potential consequences for prey consumption. Freshw. Biol. **57**(5): 922–937. doi:10.1111/j.1365-2427.2012.02753.x.

Rose, G.A., and Kulka, D.W. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. Can. J. Fish. Aquat. Sci. **56**(S1): 118–127. doi:10.1139/f99-207.

Rudstam, L.G., Parker-Stetter, S.L., Sullivan, P.J., and Warner, D.M. 2009. Towards a standard operating procedure for fishery acoustic surveys in the Laurentian Great Lakes, North America. ICES J. Mar. Sci. **66**(6): 1391–1397. doi:10.1093/icesjms/fsp014.

Saito, M. 2005. Living on earth: Dead zones [online]. Available from http://loe.org/shows/segments.html?programID=05-P13-00040&segmentID=8. [accessed 29 September 2014].

Sawada, K., Furusawa, M., and Williamson, N.J. 1993. Conditions for the precise measurement of fish target strength *in situ*. J. Mar. Acoustics Soc. Jpn. **20**(2): 73–79. doi:10.3135/jmasj.20.73.

Scavia, D., David Allan, J., Arend, K.K., Bartell, S., Beletsky, D., Bosch, N.S., Brandt, S.B., Briland, R.D., Daloğlu, I., DePinto, J.V., Dolan, D.M., Evans, M.A., Farmer, T.M., Goto, D., Han, H., Höök, T.O., Knight, R., Ludsin, S.A., Mason, D., Michalak, A.M., Peter Richards, R., Roberts, J.J., Rucinski, D.K., Rutherford, E., Schwab, D.J., Sesterhenn, T.M., Zhang, H., and Zhou, Y. 2014. Assessing and addressing the re-eutrophication of Lake Erie: Central basin hypoxia. J. Gt. Lakes Res. **40**(2): 226–246. doi:10.1016/j.jglr.2014.02.004.

Selberg, C.D., Eby, L.A., and Crowder, L.B. 2001. Hypoxia in the Neuse River estuary: responses of blue crabs and crabbers. N. Am. J. Fish. Manage. **21**(2): 358–366. doi:10.1577/1548-8675(2001)021<0358:HITNRE>2.0.CO;2.

Stumpf, R.P., Wynne, T.T., Baker, D.B., and Fahnenstiel, G.L. 2012. Interannual variability of cyanobacterial blooms in Lake Erie. PLoS ONE, **7**(8): e42444. doi:10.1371/journal.pone.0042444. PMID:22870327.

Thompson, J.S., Rice, J.A., and Waters, D.S. 2010. Striped bass habitat selection rules in reservoirs without suitable summer habitat offer insight into consequences for growth. Trans. Am. Fish. Soc. **139**(5): 1450–1464. doi:10.1577/T09-140.1.

Tyson, J.T., Johnson, T.B., Knight, C.T., and Bur, M.T. 2006. Intercalibration of research survey vessels on Lake Erie. N. Am. J. Fish. Manage. **26**(3): 559–570.

Vanderploeg, H.A., Ludsin, S.A., Cavaletto, J.F., Höök, T.O., Pothoven, S.A., Brandt, S.B., Liebig, J.R., and Lang, G.A. 2009*a*. Hypoxic zones as habitat for zooplankton in Lake Erie: Refuges from predation or exclusion zones? J. Exp. Mar. Biol. Ecol. **381**: S108–S120. doi:10.1016/j.jembe.2009.07.015.

Vanderploeg, H.A., Ludsin, S.A., Ruberg, S.A., Höök, T.O., Pothoven, S.A., Brandt, S.B., Lang, G.A., Liebig, J.R., and Cavaletto, J.F. 2009*b*. Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. J. Exp. Mar. Biol. Ecol. **381**: S92–S107. doi:10.1016/j.jembe.2009.07.027.

Vaquer-Sunyer, R., and Duarte, C.M. 2008. Thresholds of hypoxia for marine biodiversity. Proc. Natl. Acad. Sci. **105**(40): 15 452-15 457. doi:10.1073/pnas.0803833105.

Weimer, E., Castiglione, C., Gorman, A.M., MacDougall, T., Anderson, K., Boase, J., Knight, C., Kraus, R., Mackey, S., Markham, J., Roseman, E., Rutherford, E., Thomas, M., and Zhao, Y. 2012. Report of the Lake Erie Habitat Task Group 2012. Great Lakes Fishery Commission, Windsor, Ont.

Weimer, E., Castiglione, C., Gorman, A.M., MacDougall, T., Anderson, K., Boase, J., Knight, C., Kraus, R., Mackey, S., Markham, J., Roseman, E., Rutherford, E., Wills, T., and Zhao, Y. 2013. Report of the Lake Erie Habitat Task Group, presented to the Great Lakes Fishery Commission, Niagara Falls, New York.

Zhou, Y., Obenour, D.R., Scavia, D., Johengen, T.H., and Michalak, A.M. 2013. Spatial and temporal trends in Lake Erie hypoxia, 1987–2007. Environ. Sci. Technol. **47**(2): 899–905. doi:10.1021/es303401b. PMID:23237424.