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# Modelling effects of nutrients and hypoxia on Lake Erie's central basin foodweb

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*Hypoxia (dissolved oxygen < 2 mg $l^{-1}$) has long been a prevalent feature of the central basin of Lake Erie. Studies of the sublethal impacts of hypoxia on fishes have focused on individual species feeding rates, behavior and spatial distributions over short time periods, but the long-term effects on the fish community and its foodweb are poorly known. Sublethal effects of hypoxia on fish include: interrupting their vertical migration, displacing them from bottom habitats either up into the water column or away from the hypoxic zones, altering predator-prey relationships by segregation or aggregation of predators and their prey, and increasing fishing mortality by concentrating fish at the edge of hypoxic zones. We used the Ecopath with Ecosim foodweb model to investigate the singular and combined effects of nutrient concentration and hypoxia on the foodweb structure in Lake Erie's central basin. Our model tracked predator-prey interactions and population biomass of 33 model groups. We balanced the model in Ecopath and calibrated it against biomass time series data from 1996 up to 2020. Model simulations were run with varied nutrients (from 20 to 220% of the previous nutrient loading target level) and hypoxia (none, average summer value from 1996 to 2017, historical high) as forcing variables on the foodweb. Model results suggested that nutrients had positive, non-linear effects on foodweb biomass, while hypoxia decreased biomass of benthos, benthivorous fishes, and some omnivores, but increased biomass of plankton and planktivorous fishes. Nutrient effects were greater than hypoxia effects on the foodweb. Results of the foodweb model analysis may inform water quality and fisheries management strategies for Lake Erie's central basin.*

*Keywords:* Ecopath with Ecosim model, eutrophication, water quality, fish production

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# Introduction

Large regions of hypoxia (dissolved oxygen (DO) concentrations < 2 mg $l^{-1}$) resulting from excessive nutrient loading are a reoccurring global problem in coastal ecosystems (Diaz and Rosenberg, 2008; Scavia et al., 2016, Breitburg et al., 2018). These hypoxic zones are known to impact foodweb structure and function through direct mortality of less mobile species (Diaz and Rosenberg, 1995) and changes in spatiotemporal distributions of more mobile species (Vanderploeg et al., 2009; Zhang et al., 2009; Pothoven et al., 2012; Dillon et al., 2021) that in turn can modify the nature of some trophic interactions and affect overall energy flow (Costantini et al., 2008; Ludsin et al., 2009; Arend et al., 2011; Brandt et al., 2011; Stone et al., 2020). The relationships between nutrient loading, hypoxia, and consequent effects on foodweb productivity and the fisheries are further complicated as increased nutrients may enhance the production of some foodweb groups while reducing the availability of suitable habitats for others (de Mutsert et al., 2016). Thus, the effects of nutrients and hypoxia on foodwebs are realized through direct and indirect pathways and may not always be clear.

Hypoxia and excessive nutrient loading have long been prevalent in the central basin of Lake Erie, where the size, magnitude and duration of the hypoxic event varies annually (Scavia et al., 2014, Del Giudice et al., 2018). The biomass of some trophic groups can vary in direct response to the interactive effects of nutrients and hypoxia, reducing availability of some species to predators (e.g. benthos, zooplankton and planktivorous fishes) (Vanderploeg et al., 2009; Pothoven et al., 2012), squeezing cold-water planktivores between two sub-optimal habitats, a warm epilimnion and a hypoxic hypolimnion (Arend et al., 2011; Stone et al., 2020), modifying large-scale and lake-wide spatial distributions of piscivorous fishes (e.g. Walleye) (Brandt et al., 2011), and affecting fisheries harvest (Kraus et al., 2015; Stone et al., 2020).

Lake Erie has a long history of nutrient abatement and management strategies (e.g. Great Lakes Water Quality Agreement (GLWQA), 2012) intended to control hypoxia, harmful algal blooms (HAB) and other water quality issues (Ludsin et al., 2001). In 2016, basin water quality managers agreed to a 40% reduction in nutrient loads from the previous nutrient loading target of 11,000 metric tonnes $yr^{-1}$ (Scavia et al., 2016; GLWQA Nutrients Annex Subcommittee, 2019). However, concerns remain with respect to having too much or too few nutrients for managing hypoxia, and overall foodweb and fish production. Here, we use a foodweb model to quantify the separate and interactive effects of nutrients and hypoxia on Lake Erie's central basin foodweb and discuss the implications of our results for management of nutrient targets, hypoxia and the fishery.

# Methods

## The Ecopath with Ecosim Model

Ecopath with Ecosim Model (EwE) is a free ecological/ecosystem modelling software suite (www.ecopath.org), and is designed for the construction, parameterization and analysis of mass-balance trophic models of aquatic and terrestrial ecosystems. EwE has been thoroughly described in earlier publications (Pauly et al., 2000, Christensen and Walters 2004, Steenbeek et al., 2016). A brief introduction of EwE's governing equations is provided in Supplementary Material (SM1). EwE has been used widely to study the impacts of natural and anthropogenic stressors on ecosystems worldwide (Colléter et al., 2015) and in all five of the Laurentian Great Lakes (Kitchell et al., 2000; Stewart and Sprules, 2011; Rutherford et al., 2021).

## The Ecopath with Ecosim Model for Lake Erie's central basin

We constructed an EwE model for the central basin of Lake Erie to simulate interactive effects of nutrients and hypoxia on the foodweb. This model has 2 algal groups, 1 bacterial group, 1 protozoan group (including ciliates and flagellates), 5 zooplankton groups, 6 benthic groups, and 18 fish groups including 3 fish species modelled with multiple age classes (Supplementary Material SM2, Table SM3.1). Walleye *Sander vitreus* and Yellow Perch *Perca flavescens* were modelled with multiple age classes because of their ecological and economic importance in the central basin of Lake Erie, while Rainbow Trout *Oncorhynchus mykiss* is stocked annually at age-1 with minimal natural reproduction and was modelled as two groups: stocked, and age 1 and older. Data used to construct and parameterize the model were from published stock assessment reports, peer-reviewed journal publications, and government reports. When data were available for parameter estimates from multiple studies, we used average values from those studies. Otherwise, we used the data collected close to 1996 and modified with data collected from other years. Data sources can be found in Supplementary Material (SM2 – SM3). Model calibration also can be found in Supplementary Material (SM2 - SM3).

## Hypoxia impacts and hypoxia forcing functions

Since most animals are quite mobile, direct effects of low DO (i.e. death) are rare compared to its indirect effects (Rao et al., 2014). One of the most documented indirect effects of hypoxia is the displacement or movement of organisms from optimal to suboptimal habitats and interruption/decoupling of predator-prey interactions (Zhang et al., 2009). In general, mesozooplankton that can tolerate low DO conditions can find a refuge from their fish predators in strong hypoxia zones, except for predatory cladocerans that are less affected by hypoxia or can avoid the hypolimnion when it is hypoxic (Vanderploeg et al., 2009). Thus, we assumed that the availability of zooplankton (i.e. herbivorous cladocerans and copepods) to zooplanktivores is negatively correlated with hypoxic conditions. Similarly, mobile benthic fish (e.g. Round Goby *Neogobius melanostomus*) can actively avoid hypoxia and aggregate in normoxic bottom waters. Cold-water pelagic fish (e.g. Rainbow Smelt *Osmerus mordax*) often are forced to move up into the water column and aggregate in a thin metalimnetic layer, thereby increasing their vulnerability to their predators.

For sessile and small benthic invertebrates (our 6 benthic groups), we assumed that seasonal hypoxia causes mortality, although some benthic groups can tolerate low DO (Wetzel, 2001; Cornette et al., 2015). Field observations have shown that Dreissenid Mussels are absent in most of the deepest regions of Lake Erie's central basin where long-lasting hypoxia and anoxia often exists (Karatayev et al., 2018). We constructed a mortality time series based on the hypoxia condition and applied this to benthic groups to represent mortality due to hypoxia. This mortality time series was implemented through a fishing module in the model, and the "fished" biomass was discarded back into water as dead biomass/detritus.

Based on monthly hypoxic area and volume in the central basin, we constructed four time series of hypoxia functions (two volume-based and two aerial-based) that modified the effective search rate of predators on the prey items (a parameter equivalent to the attack rate in Holling's response functions), and also implemented hypoxia-caused mortality on benthic invertebrates (Supplementary Material Table SM3.6, Figure SM3.3). Specifically, one hypoxia function (*f1*) was the volumetric ratio of normoxic water to the whole central basin (Supplementary Material Table SM3.6, Figure SM3.3A), and was applied to the search rates on zooplankton prey groups. Thus, low ratios (strong hypoxia) lead to low search rates on zooplankton groups by their predators, and high ratios (mild hypoxia) lead to high search rates on zooplankton groups by their predators. To reflect the hypoxia-caused increases in the vulnerability of Rainbow Smelt to predators by their aggregation in the metalimnion, the second hypoxia function (*f2*) was constructed as 1 plus the volumetric ratio of hypoxic water to the total water volume of the central basin, so at high ratios there is a greater search rate on Rainbow Smelt by their predators. Similarly, to reflect the hypoxia-caused increases in vulnerability of benthic fish (e.g. Round Goby) by aggregating them in the normoxic area on the bottom, the third hypoxia function (*f3*) was 1 plus the areal ratio of hypoxic bottom area to the total basin. The fourth hypoxia function (*f4*) was a function of the areal ratio of hypoxic bottom area to the total basin area (described below) (Supplementary Material Table SM3.6, Figure SM3.3B), which was applied to the immobile or less mobile benthic groups. We assumed that monthly hypoxia-induced mortality ($m_i$) was the fraction of hypoxic bottom area of the total basin area for each month, and annual instantaneous hypoxia-induced mortality (*f4*) was calculated as:

$$f_4 = -\ln \left(\prod_{i=1}^{12}(1 - m_i)\right)$$

We applied this time series of annual instantaneous mortality as a “fishing” mortality on benthic invertebrates to reflect losses due to hypoxia for benthic invertebrates.

The volumes and areal extents of hypoxia were obtained from the output of three models, including two water quality models and a geostatistical model. The annual estimates of hypoxia volume from 1996 to 2005 were calculated based on DO vertical distribution from a 1D water quality model (Rucinski et al., 2010) and the depth-dependent water volumes of the basin. The annual areal extent of hypoxia from 1996 to 2005 was estimated by Zhou et al., (2013), while both volume and area extent of hypoxia from 2006, and 2010 to 2020 were available from a 3D hydrodynamic and water quality model (Rowe et al., 2019). Hypoxia data from 2007, 2008 and 2009 were an average of values in 2006 and 2010.

### Simulation scenarios

To assess the interactive effects of nutrient concentrations and hypoxia on Lake Erie’s central basin foodweb, we ran scenarios that used various combinations of nutrient concentration levels and hypoxia in a factorial design. Nutrient concentration levels varied from 20% to 220% (historical high) of the previous nutrient loading target level (NLTL) in increments of 40%. Under each nutrient level, we ran three hypoxia scenarios: no hypoxia, average hypoxia and severe hypoxia. We removed all hypoxia effects under the no-hypoxia scenario. Average hypoxia was calculated from monthly hypoxia values averaged across years from 1996 to 2020, while severe hypoxia used the monthly maximal value across years from 1996 to 2020. We ran our contrasting scenarios for 120 years beginning in 2021 to reach a new ecosystem equilibrium (Supplementary Material Figure SM3.3B). To reflect how foodweb groups responded to hypoxia across nutrient levels, we plotted the percent change in biomass of each foodweb group relative to their Ecopath biomass (Y-axis) under a no-hypoxia, average-hypoxia and severe-hypoxia condition versus nutrient levels ranging from 20 to 220 percent of the previous NLTL (X-axis). To better reflect the positive and negative effects of hypoxia on the foodweb, we also plotted the percent change in biomass of a foodweb group under average and severe hypoxia scenarios relative to no-hypoxia scenario under the previous NLTL. To further understand mechanisms underlying hypoxia effects on the foodweb, we analyzed simulation results on select model group consumption and predation. To test the relative effects of hypoxia on foodweb biomass, we conducted an ANCOVA on the relationships between species biomass (dependent variable) and hypoxia (categorical variable) while controlling for nutrient levels (continuous variable). Significant differences in slopes of the species biomass-nutrient relationships among hypoxia levels would indicate hypoxia modified the influence of nutrients on species biomass.

## Results

### Nutrient effects on the foodweb

Nutrient levels showed obvious effects on biomass of all modelled foodweb groups (Figure 1, Supplementary Material Figure SM3.6). Simulated biomass of most foodweb groups increased monotonically as nutrient levels increased. Biomass of some groups increased quickly when nutrients were low ( from 20% to 60% of the previous NLTL), then decreased in slope (e.g. non-blue green algae, meso-zooplankton groups, Rainbow Smelt, and Walleye 3+). Other groups showed the opposite trend, with slow increases in biomass as nutrients increased from 20% to 60% of the previous NLTL, then sharp biomass increases as nutrients continued to increase (e.g. blue green algae, shiners, and White Perch *Morone americana*). Biomass of benthic invertebrates and benthivorous fish showed an almost linear relationship to nutrient levels. Biomass of Amphipoda and ‘other fish’ did not show consistent increases with increasing nutrients (Supplementary Material Figure SM3.6).

### Hypoxia effects on the foodweb

We compared biomass changes in foodweb groups between scenarios of hypoxia and no hypoxia

(Figure 1 and Table 1). Hypoxia had negative effects on biomass of benthos and benthivores (Table 1) by hypoxia-induced mortality and decreases in consumption (Figure 2), which declined by 7-32% under the average hypoxic condition, and by 22 to 63% under the severe hypoxic condition and the previous NLTL (Supplementary Material Figure SM3.7). For example, Dreissenid Mussel biomass decreased by 8% under average hypoxia and 25% under severe hypoxia, mainly due to hypoxia-induced mortality and decreases in consumption (Figure 2, Supplementary Material Figure SM3.7). Round Goby biomass decreased by 25% under average hypoxia and 48% under severe hypoxia due to decreases in consumption. Adult Yellow Perch biomass decreased by 13% under average hypoxia and 22% under severe hypoxia due to decreases in consumption and increases in predation mortality. There were negligible changes in biomass of adult Walleye and Rainbow Smelt under average and severe hypoxia (Table 1). In contrast, hypoxia increased the biomass of most pelagic groups (Table 1). Under the previous NLTL, biomass of pelagic groups and planktivorous fish increased by 3-93% under average hypoxia and 10-272% under severe hypoxia (Supplementary Material Figure SM3.7). For example, blue green algae biomass increased by 93% under average hypoxia, and 272% under severe hypoxia. Shiner biomass increased by 13% under average hypoxia and 35% under severe hypoxia due to increased consumption (Figure 2). Compared to normoxic water ratios of average hypoxia, under the severe hypoxia scenario the volume of normoxic water decreased by up to 7%, and the normoxic area decreased by up to 34%. The differences in biomass changes between scenarios of average hypoxia and severe hypoxia were often greater than 100%, indicating the effects of severe hypoxia were stronger.

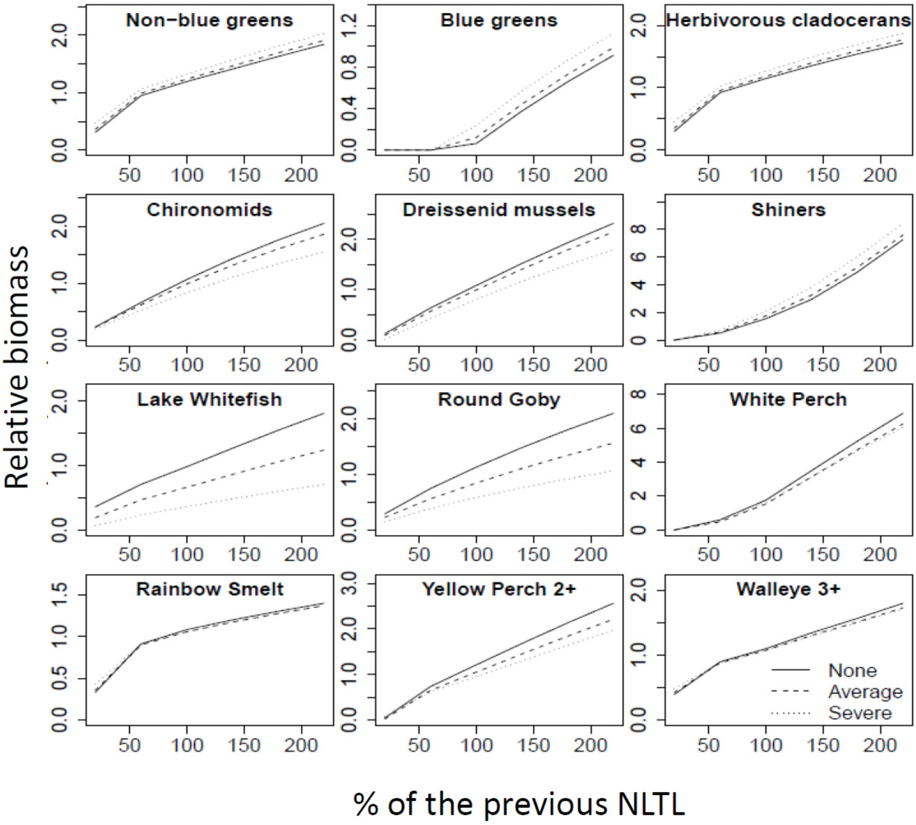

**Figure 1.** Changes in relative biomass of select central basin Lake Erie foodweb model groups under combination scenarios of TP levels and hypoxia conditions (no hypoxia, average hypoxia and severe hypoxia). See Figure SM3.6 for biomass response of all foodweb model groups. Relative biomass of foodweb groups refers to biomass relative to the initial biomass in Ecopath. Average hypoxia reflects the average of monthly hypoxia values from 1996 to 2020. Severe hypoxia reflects the highest monthly hypoxia value from 1996 to 2020.

**Table 1.** $F_{ratio}$ values for an ANCOVA using the model- *biomass = hypoxia + nutrient + Interaction* where*,* hypoxia is a categorical variable (no hypoxia, average hypoxia, severe hypoxia), nutrient is a continuous variable, and *interaction* refers to *hypoxia* x *nutrient*. Shaded area is where $P < 0.05$. “Direction of biomass change” is for where variable satisfies the condition of $P < 0.05$ with “+” reflecting increase in biomass with increases in hypoxia severity or nutrient concentrations, and “-” reflecting decrease in biomass. See Supplementary Material Table SM3.1 for group code definitions. *Indicates a significant effect at $P < 0.06$ level.

| | | **Variables** | | | **Direction of biomass change** | | |
|---|---|---|---|---|---|---|---|
| **Code** | **ANOVA** | **Hypoxia** | **Nutrient** | **Interaction** | **Hypoxia** | **Nutrients** | **Interaction** |
| WAE Y | 845.64 | 17.557 | 4191.92 | 0.58 | + | + | |
| WAE 1 | 1158.00 | 43.24 | 3703.28 | 1.12 | + | + | |
| WAE 2 | 104.56 | 3.95 | 514.29 | 0.31 | + | + | |
| WAE 3+ | 3948.21 | 50.32 | 19616.00 | 12.01 | - | + | - |
| YPH Y | 817.14 | 23.84 | 4030.90 | 5.59 | + | + | + |
| YPH 1 | 420.78 | 12.80 | 2077.80 | 0.26 | + | + | |
| YPH 2+ | 6788.37 | 1147.76 | 31182.86 | 231.73 | - | + | - |
| RBT 1+ | 206.51 | 0.43 | 1031.10 | 0.30 | | + | |
| WHB | 124.76 | 15.60 | 589.85 | 1.38 | - | + | |
| WHP | 426.75 | 7.81 | 2111.88 | 0.09 | - | + | |
| GIZ | 795.03 | 43.86 | 3886.47 | 0.47 | + | + | |
| RBS | 155.01 | 1.74 | 771.37 | 0.13 | | + | |
| FWD | 642.02 | 829.70 | 1399.08 | 75.80 | - | + | - |
| SHR | 97.75 | 3.97* | 479.18 | 0.82 | + | + | |
| RDG | 1030.34 | 978.94 | 2970.88 | 111.47 | - | + | - |
| LWF | 12809.20 | 17493.40 | 26215.80 | 1421.60 | - | + | - |
| OTH_F | 0.14 | 0.19 | 0.08 | 0.11 | | | |
| DREI | 1332.62 | 233.85 | 6149.87 | 22.77 | - | + | - |
| AMPH | 90.12 | 219.33 | 10.16 | 0.89 | - | + | |
| SPHA | 1207.00 | 406.67 | 5179.27 | 11.62 | - | + | - |
| CHIR | 402.69 | 87.38 | 1810.92 | 13.88 | - | + | - |
| OLIG | 925.14 | 1.48 | 4618.99 | 1.89 | | + | |
| OTH_B | 1164.40 | 113.36 | 5568.77 | 13.36 | - | + | - |
| PRED | 41.75 | 9.70 | 189.29 | 0.04 | + | + | |
| CLAD | 630.76 | 55.93 | 3039.31 | 1.31 | + | + | |
| CYCL | 1810.3 | 168.81 | 8702.02 | 5.92 | + | + | + |
| CALA | 1830.8 | 164.25 | 8814.61 | 5.43 | + | + | + |
| ROTI | 3843.80 | 248.56 | 18640.30 | 10.73 | + | + | + |
| PROT | 35.60 | 2.23 | 171.70 | 0.93 | | + | |
| BACT | 2864.40 | 111.53 | 14089.00 | 4.39 | + | + | + |
| BLUE | 129.30 | 9.52 | 624.22 | 1.61 | + | + | |
| OTH_A | 2373.409 | 219.78 | 11412.59 | 7.56 | + | + | + |
| DET | 1067.20 | 56.48 | 5221.69 | 0.67 | + | + | |

## Interactions between hypoxia and nutrients on the foodweb

Biomass values of many foodweb groups were very low at the 20% of the previous NLTL (Figure 1), and exhibited minor hypoxia effects, so we excluded this nutrient level from the ANCOVA analysis. Analysis of covariance of hypoxia effects on modelled group biomass across a range of nutrient levels (60% to 220% of the previous NLTL) indicated most groups were affected by hypoxia (28 of 33), and nearly all groups were affected by nutrients (32 of 33 groups) (Table 1). Nutrients had a much greater influence than hypoxia on biomass of all groups (higher F-ratio, Table 1). Nutrients had a significant positive effect on biomass of foodweb groups, whereas hypoxia had a significant but smaller negative effect on benthos, benthivores, and piscivores that ate benthivorous fish (e.g. age 1 and 2+ Yellow Perch and adult Walleye), and positive effects on biomass of detritus, phytoplankton, zooplankton, and pelagic fishes (shiners, young Yellow Perch and Walleye life stages). Interactive effects of hypoxia and nutrients on foodweb group biomass were significant for nearly half of all foodweb groups, indicating hypoxia amplified the effects of nutrients on pelagic foodweb groups and depressed effects of nutrients on demersal foodweb groups.

# Discussion

Our overall model results generally matched survey observations made on benthos, plankton and fish in Lake Erie and elsewhere (Ludsin, et al., 2001, Pothoven et al., 2009, 2012; Vanderploeg et al., 2009, Karateyev et al., 2014, Stone et al., 2020). For example, increases in nutrients had a positive effect on the biomass of most foodweb groups. Similarly, Ludsin et al., (2001) analyzed temporal patterns of fish community composition in Lake Erie's western and central basins from 1969 to 1996 and found a unimodal response of

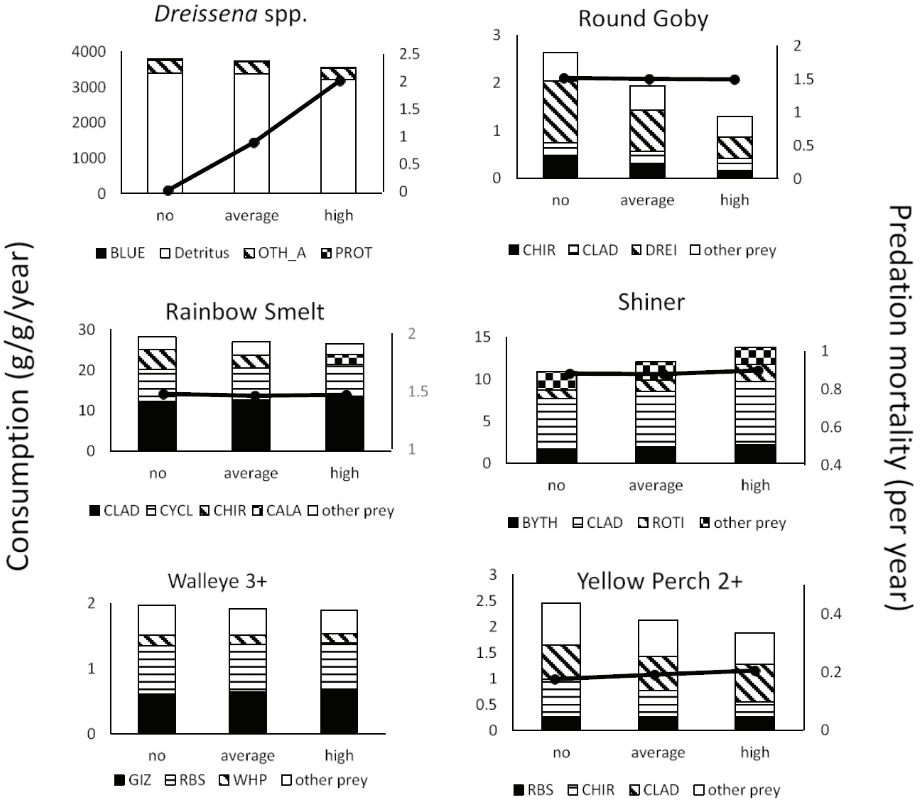

**Figure 2.** Average annual consumption of prey groups (bars) and annual predation mortality (lines) for chironomids, herbivorous cladocerans, Rainbow Smelt, shiners, Round Goby and Yellow Perch under different hypoxia scenarios and the previous NLTL. Note mortality for *Dreissena* spp. included hypoxia-induced mortality.

species richness to nutrients, with central basin taxa responding positively to nutrients. When we considered scenarios of average or severe hypoxia, our model suggested that benthos and benthivorous fish would decrease in biomass, while zooplankton biomass and epilimnetic zooplanktivores increased in response to increased phytoplankton biomass. This effect of hypoxia on benthic and pelagic foodwebs has previously been documented in Lake Erie's central basin by several studies (Pothoven et al., 2009, 2012; Vanderploeg, et al., 2009; Karateyev, et al., 2014), and by a longer time series showing the long-term negative relationship between hypoxia and Rainbow Smelt (Stone et al., 2020).

Our model results for omnivorous adult Yellow Perch suggested their biomass would decrease in response to hypoxia. These results also matched seasonal field observations of central basin Yellow Perch which indicated generally negative effects of hypoxia for fish including benthos in their diet. For example, Roberts et al., (2009) found Yellow Perch generally avoided hypoxic zones despite some foraging forays into hypoxic waters (Roberts, 2010, Taylor, et al., 2007), and were forced to switch prey consumption from energy rich benthos to less nutritious zooplankton, while the hypoxia-induced refuge for zooplankton (Vanderploeg et al., 2009) decreased predation from planktivores during summer and early fall. Despite finding no decrease in Yellow Perch body condition from August through October, Roberts et al., (2009) speculated that over time, hypoxia would decrease Yellow Perch population growth because it occurs when Yellow Perch store energy in preparation for overwinter and reproduction the following spring. Our long-term model projections also indicated that biomass of adult Yellow Perch would be negatively affected by hypoxia. Further research is needed to determine if and whether hypoxia affects gonadal development and reproductive success of Yellow Perch and other fish species.

Our model results indicated no effect of hypoxia on Rainbow Smelt biomass, but we may have underestimated potential negative effects of hypoxia. The hypoxia function we implemented for Rainbow Smelt was based on the ratio of the volume of hypoxic water to the volume of the whole water column, while the available habitat for Rainbow Smelt during thermal stratification excluded the epilimnion (Arend et al., 2011). In retrospect, this hypoxia function should have been based on the ratio of hypoxic water to the portion of the water column that includes the hypolimnion and metalimnion. Thus, Rainbow Smelt was forced to use the thin metalimnetic stratum during the hypoxia season, and would be more vulnerable to Walleye predation than was implemented in our model.

Model results also suggested that the hypoxia had a significant negative effect on piscivorous adult Walleye. The predicted hypoxia effects on Walleye biomass seemingly contradict findings in habitat quality studies (Brandt et al., 2011) which suggest that short-term (seasonal) episodes of hypoxia may serve to improve Walleye habitat suitability by concentrating prey fish in normoxic water. However, given that the total prey biomass consumed by adult Walleye was predicted to decline under hypoxia, it is not surprising that adult Walleye biomass also declined. The differences also may be an artifact of differences in time frame, wherein our simulations ran for 120 years, while the habitat quality study only focused on a single snapshot in time during the hypoxic season. It is possible that further increases in hypoxia will lead to further reductions in available prey (Round Goby, Yellow Perch, White Perch, and Freshwater Drum *Aplodinotus grunniens*) for Walleye and decrease adult Walleye biomass.

Our ANCOVA analysis indicated a positive effect of hypoxia on modelled shiner biomass, whereas agency surveys showed Emerald Shiner catch rate in trawls was negatively correlated with bottom hypoxia, but not with Walleye abundance estimates (Stone et al., 2020). We believe the negative correlation between shiner catch rate and hypoxia severity is likely spurious as hypoxia would truncate the vertical distribution of shiners and make them less available to bottom trawls. Arend et al., (2011) used a bioenergetics model to estimate a negative impact of hypoxia on Emerald Shiner growth potential. Stone et al., (2020) also found hypoxia reduced the growth potential of Emerald Shiner, but noted that shiner consumption and energetic condition still increased during summer, and concluded the fish found enough suitable habitat in the epilimnion to grow. Our results suggest that increases in zooplankton biomass under hypoxia were adequate to support annual population growth of shiners.

These model simulations can be used to separately examine the single effects of nutrients and hypoxia on the central basin foodweb, and their interactive effects. Model results suggested that nutrients had strong, positive non-linear effects on foodweb biomass. In comparison to nutrients, hypoxia had reduced effects on foodweb biomass, which were negative for demersal and benthic foodweb groups, but positive for pelagic foodweb groups. These results are consistent with modelling studies in the northern Gulf of Mexico (De Mutsert et al., 2014) and the Baltic Sea (Ehrnsten et al., 2019). For example, De Mutsert et al., (2014) used an EwE model with Ecospace to separate positive and negative effects of nutrients on fish biomass and fisheries harvest in the northern Gulf of Mexico. Their results suggested that the positive effects of increased fish biomass from increased nutrients and primary production would outweigh decreases in some species (Red Snapper *Lutjanus campechanus*) resulting from hypoxia.

Nutrient concentration and hypoxia are interactive and have positive feedbacks wherein high nutrients lead to high oxygen demand and strong hypoxia (Rucinski et al., 2014), while strong hypoxia may trigger internal phosphorus loads and increase nutrient concentration in the water column (Anderson et al., 2021, North et al., 2015). Anderson et al., (2021) estimated that internal phosphorus loads could be 11 551 metric tonnes of soluble reactive phosphorus, slightly higher than the previous total external phosphorus load target (11 000 metric tonnes) enacted during the 1970s. Thus, hypoxia may delay a response to the reduction of external phosphorus loads by as long as 10 - 15 years (Jeppesen et al., 2007). We did not develop or implement nutrient and hypoxia functions with complex interactions and time lags in our model as this was beyond the scope of the study. We simulated nutrient and hypoxia effects independently, and changes in one factor were not associated with changes in the other factor. Even so, our simulation scenarios that combine different levels of nutrients and hypoxia conditions reflect some typical combined conditions of these two factors. For example, a scenario of low phosphorus (60%) and average hypoxia represents a situation where short-term external nutrient loads decreased by 40% but hypoxia persisted due to a time lag, while a scenario of low phosphorus (60%) and no hypoxia could represent a situation of long-term phosphorus reduction and minimal area of hypoxic zone.

Our coarse model representation of nutrient and hypoxia effects on the foodweb may have underestimated foodweb effects for several reasons. First, we crudely simulated hypoxia effects by modifying search rates of predators on zooplankton, and implementing mortality on benthic invertebrates. In reality, spatial heterogeneity in species distributions that are caused by hypoxia are known to intensify or weaken predator prey interactions and movements, depending on where the interactions occur. In the deep areas of Lake Erie's central basin, hypoxia separates zooplankton and benthos prey from their predators, while in the nearshore or marginal areas of hypoxic waters hypoxia may increase consumption of zooplankton and benthos (Roberts et al., 2009; Pothoven et al., 2009; Vanderploeg et al., 2009). In addition, recent reports of *Dreissena* biomass suggest we have overestimated biomass of *Dreissena* (Karateyev et al., 2021), and thus may have underestimated response of the planktonic foodweb to hypoxia. In addition, hypoxia causes changes in physiology, behavior and distribution of mobile organisms and increases energy costs in adapting to suboptimal habitats (Randall, 1982, Herbert and Steffensen, 2005, Craig and Crowder, 2005, Petersen and Pihl, 1995), which are affected by other environmental factors as well (e.g. water temperature) and hard to quantitatively evaluate (Roman et al., 2019), thus are not included in our model simulation. Moreover, we defined hypoxia as DO $< 2$ mg $l^{-1}$, while studies showed the fish might already experience stress when DO is lower than 4 mg $l^{-1}$ (Tang et al., 2020).

Results showed that blue-green algae (HAB) biomass increased rapidly when nutrient levels were high, but their negative effects on the foodweb were not implemented as modifiers of predator-prey interactions in the model. HAB may act as an ecotone where predators and prey may concentrate and enhance foodweb interactions or may reduce energy flow from nutrients to fish biomass through algal shading of diatoms and other algae and have toxic effects and retard filtration by filter feeders. Reduction in HAB currently is a water quality target for Lake Erie's nutrient reduction program.

Recent proposed nutrient targets for Lake Erie call for a 40% reduction in phosphorus loads, which should reduce HAB over the long term, in addition to reducing hypoxia, but also will reduce the biomass of most desired fish groups. Simulations showed fish biomass will continue to decrease if nutrients are decreased by 40% from the previous NLTL, but further decreases in nutrients may lead to undesirable regime shifts and potential reductions in fishery harvests. Effects of nutrients on HAB and the foodweb may be altered under climate change scenarios of increased precipitation and warming (Zhou et al.,, 2015) but were not considered here.

# Conclusions

Our analysis is but one step toward a comprehensive projection of foodweb response to nutrients and hypoxia, but future efforts should incorporate spatially explicit effects of temperature and oxygen on predator-prey dynamics, production, and organism movement. It also will be critical to incorporate the positive and negative implications of climate warming for fisheries harvest as shown by De Mutsert et al., (2014) for a Northern Gulf of Mexico foodweb.

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# Supplementary material

Supplementary material for this article is available on-line at the publisher's website.

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