

Do Cyanobacteria Blooms Enhance Parasite Loads in Lake Erie Yellow Perch?

Research Thesis

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ABSTRACT

Harmful Algal Blooms composed of cyanobacteria (HABs) are a major concern globally, especially in ecosystems that support commercial and recreational fisheries. Although HABs have been shown to negatively affect the services provided by ecosystems (e.g., safe water for drinking and recreation), their influence on fish populations, and fish health in particular, remains largely unknown. Given that Lake Erie has been experiencing large HABs during the past 15 years and supports important commercial and recreational fisheries, I sought to help Lake Erie agencies understand if HABs are posing a health risk to their valued fish populations. To this end, I explored the relationship between parasite loads in yellow perch (*Perca flavescens*), which supports Lake Erie's largest commercial fishery and second largest recreational fishery, and cyanobacteria concentration. Specifically, I tested the hypothesis that parasite loads in the liver of young-of-year yellow perch would increase with increasing cyanobacteria concentration, as cyanotoxins associated with HABs (e.g., microcystin) have been shown to cause liver damage and physiological stress in other fish species. To answer this question, I measured parasite loads in 519 individuals captured from 54 sites across the western basin of Lake Erie during 2011-2019. My results were opposite of my expectations with mean liver parasite loads being negatively correlated with HAB severity. This finding, which was supported by other non-fish studies, suggests that HABs may actually benefit yellow perch by reducing parasite infections. Ultimately, my research points to the need for more research, if fisheries management agencies are truly to understand the net effect of HABs on their valued fishery resources.

INTRODUCTION

Harmful algal blooms dominated by cyanobacteria (HABs) have become an increasingly important management concern during the past 15 years, owing primarily to human activities in the watershed (Berardo et al. 2017; Stumpf et al. 2012). The increase in HABs worldwide is mainly driven by water pollution, especially nutrient runoff from nonpoint agricultural sources in ecosystems with fertile watersheds such as Lake Erie, USA-Canada (Michalak et al. 2013). The extent to which HABs affect aquatic ecosystems remains an open question, but it is well understood that HABs hold the potential to cause massive ecological and economical damage (Anderson et al. 2000). This notion is especially true in large ecosystems like Lake Erie, which provide numerous ecological services to society (e.g., potable water, food, recreational opportunities).

For the past 15 years, HABs have dominated both nearshore and offshore waters of Lake Erie during the summer growing season (Stumpf et al. 2012). HABs negatively affect tourism (Anderson, et al. 2000), cause the accumulation of cyanotoxins (e.g., microcystin) in fishes (Briland et al. 2020), and promote bottom hypoxia that negatively affects fish habitat use and food web interactions (Scavia et al. 2014). Additionally, HABs hold the potential to negatively affect fish health by altering individual growth, physiology, and survival (Landsberg 1995). This potential for negative effects on fish health is especially evident in Lake Erie's shallow, quick-warming western basin, which provides important nursery areas for many fishes of ecological and economic importance. Among these fishes are yellow perch (*Perca flavescens*) and walleye (*Sander vitreus*), the two most valuable commercially and recreationally fished species in Lake Erie (Blore et al. 2014; Hudson & Zeigler 2014; Coldwater Task Group 2019). Most of the

work that has explored linkages between fish and HABs (including their toxins), however, has been conducted in the laboratory, or with fish species not found in the Great Lakes region (see review by Malbrouck & Kestemont 2006). Thus, our understanding of how HABs influence the health of fish species in the Great Lakes remains uncertain.

Harmful algal blooms are thought to negatively affect fish health in several ways. First, HABs may directly impair fish health by producing toxins that can accumulate in tissues (Briland et al. 2020). In most freshwater ecosystems, including Lake Erie, microcystin (MC) tends to be the dominant toxin produced (Dyble et al. 2008). Well-established as a hepatotoxin, microcystin causes liver damage in fish (Råbergh et al. 1991), and can promote cancer in mammals (Nishiwaki-Matsushima et al. 1992). Furthermore, microcystin negatively affects the behavior, physiology, development, growth, and survival of fish, especially during early life stages (e.g., eggs, larvae; Malbrouck & Kestemont 2006; Ortiz-Rodríguez et al. 2012; also see review by Hu et al. 2016). Wei et al. (2009) also showed that MC-LR, the most common strain of MC, can suppress expression of several immune genes.

Of all the health impacts MCs are capable of producing in fish, I was particularly interested in its ability to suppress the immune system. First, I theorized that the combined negative effects of MC on an individual could compromise its immune system and increase susceptibility to parasites in individuals. Second, I expected that reduced feeding opportunities and foraging efficiency associated with Lake Erie becoming more eutrophic would compound this effect. Because juvenile and adult yellow perch depend heavily on benthic macroinvertebrates as prey, which are known to be sensitive to eutrophication (Knight et al. 1984; Tyson & Knight 2001), it is conceivable that the recent re-eutrophication of Lake Erie

(Scavia et al. 2014) might exacerbate the effects of cyanotoxin (microcystin) exposure on parasite susceptibility by reducing yellow perch foraging opportunities. Third, I expected that reduced water clarity associated with algal and cyanobacteria turbidity, which has been shown to negatively affect consumption by juvenile yellow perch in the laboratory (Wellington et al. 2010), could potentially magnify reductions in foraging, unless zooplankton levels remained high enough to offset reduced foraging efficiency. For these reasons, I expected fish condition, health, and the ability to defend against pathogens or parasites to be lower inside of HABs than outside of them.

Although previous research has not explored the consequences of a compromised immune system from HABs on fish health and performance in the wild, one might postulate that HAB-induced stress and immunosuppression would increase the susceptibility of fish to parasite infections. This notion is based on studies with other organisms, both aquatic and terrestrial, which demonstrated increases in disease, parasite infection, and general physiological dysfunction following exposure to HABs and other contaminants (e.g., cylindrospermopsin, gymnodimine, brevetoxins, saxitoxins, DSP toxins, heavy metals, etc.) that are known to induce stress and (or) compromise the immune systems (Poulin 1992; see review by Landsberg 2002; Fire & Van Dolah 2012; Dragun et al. 2013).

Although counterintuitive, it is also important to acknowledge that *Microcystis* spp. exposure could actually reduce disease and parasite infections, given the possibility that cyanobacteria and (or) its toxins might more negatively affect the pathogens or parasites than the host itself. For example, a recent study showed that exposure to a non-toxin producing strain of *Microcystis* reduced parasite loads and bacterial infection in zooplankton (*Daphnia*; Coopman et

al. 2014), suggesting that HABs could have health-promoting properties. Similar results were observed in Manila clams (*Ruditapes philippinarum*) exposed to a harmful dinoflagellate, *Karenia selliformis* (Da Silva et al. 2008). Given the likelihood that MC suppresses the immune system, which counters findings from studies that have shown reduced parasite burdens as a result of cyanobacteria exposure, the question of whether HAB exposure would impair or benefit fish health and affect parasite loads remains open.

To explore how HAB exposure might impair fish health, and contribute to parasite loads in particular, I quantified infections of the parasitic worm, *Neoechinorhynchus*, in the livers of young-of-year yellow perch collected inside and outside of HABs in western Lake Erie during 2011–2019. I focused on yellow perch because this species is both recreationally and commercially important in Lake Erie (Yellow Perch Task Group 2019) and is an abundant secondary consumer (Tyson & Knight 2001), meaning the species is ecologically important as well. Additionally, western Lake Erie’s yellow perch population has demonstrated variable recruitment during recent years (Yellow Perch Task Group 2019), which may relate to the variability in HAB severity. To explore the HAB-health relationship in yellow perch, I tested the hypothesis that young-of-year yellow perch residing in waters with a low cyanobacteria concentration would have lower parasite loads than those living in water with higher cyanobacteria concentrations, owing to anticipated reduced exposure to MCs and reduced foraging opportunities associated with HABs.

METHODS

Fish Collections

Young-of-year (YOY) yellow perch were collected in the western basin of Lake Erie during August of 2011, 2015, 2017, and 2019. All collections were made as part of annual bottom-trawl assessment surveys conducted by the Ohio Department of Natural Resources – Division of Wildlife and Ontario Ministry of Natural Resources and Forestry (Yellow Perch Task Group 2019). These surveys sampled ~80 sites per year. Sites were stratified (by depth) randomly across the entire west basin. Following capture by Lake Erie agencies, fish were held at -20°C until processing.

August trawl samples were used because this is typically the peak of cyanobacteria blooms in Lake Erie and is, therefore, a likely time for MC exposure. Additionally, this month offers the most intense sampling of YOY fishes by Lake Erie agencies in the western basin, thus ensuring access to fish samples collected both inside and outside a bloom. The years 2011, 2015, 2017, and 2019 were selected for analysis because HABs were especially severe (Figure 1) and sufficient samples of YOY yellow perch were available.

HAB Severity

To examine the influence of HAB exposure on the parasite loads of YOY yellow perch, a minimum of three and a maximum of 20 individuals per site were processed from 54 sites (n = 4-18 sites/year; Figure 2) during 2011, 2015, 2017, 2019 (Table 1). These sites were chosen to reflect a range of cyanobacteria densities, which were estimated using remote-sensing surface reflectance data gathered by the National Oceanic and Atmospheric Administration (NOAA,

https://www.glerl.noaa.gov/res/HABs_and_Hypoxia/habTracker.html). Surface reflectance data were converted to a cyanobacteria index following Wynne et al. (2008) and then to cell density following Wynne et al. (2010).

Fish Preparation and Measurement

Yellow perch were thawed prior to examination for the prevalence and severity of parasite loads. For each individual, the total length (TL, nearest 1 mm), and wet mass (nearest 0.1 g) were recorded. Body condition (a proxy of energetic health) was calculated for each individual as the deviation of each individual from a least-squares regression line fit to all of the TL and wet mass data. In this way, individuals with a deviation above this line were considered in better health than those below the line (Scavia et al. 2014). The liver, which is the organ most targeted by MCs (Dabholkar & Carmichael 1987), was then excised through an incision in the peritoneal cavity and examined under 40x magnification using a dissecting microscope to identify individual parasites.

Parasite Loads

Infections by *Neoechinorhynchus*, a genus of parasitic worms that parasitizes other Lake Erie fishes, including northern pike (*Esox lucius*), quillback carpsucker (*Carpionodes cyprinus*), and walleye (Dechtiar 1968; Amin & Muzzall 2009; Melo et al. 2015), results in characteristic nodules seen on the surface of infected tissues (Verweyen et al. 2011; de Matos et al. 2017; Figure 3). Parasite loads were quantified by counting the characteristic nodules embedded in the

tissue surface, with each nodule counting as one parasite (Jithendran and Kannappan 2010; Verweyen et al. 2011; Melo et al. 2015).

Statistical Analysis

To quantify the relationship between cyanobacteria cell counts and mean parasite loads, I used a generalized linear model. In the model, the response variable was mean parasite load (i.e., mean number of parasites in the liver of fish captured at each station). I included cyanobacteria concentration ($\text{cells}\cdot\text{mL}^{-1}$), bottom temperature (nearest 0.1°C), dissolved oxygen (nearest $0.1\text{mg}\cdot\text{L}^{-1}$), Secchi depth (nearest 0.1m ; to represent turbidity), and catch per unit effort (number of individuals $\cdot\text{ha}^{-1}$; as a representation of the abundance of target species) as predictors. I included fish condition as a continuous covariate to account for a possible interaction with parasite loads. A Gamma distribution was assumed, given the right-skewed distribution of response. Because the Gamma distribution does not allow zero to be a dependent variable value, I added 0.001 to zero values in order to use the distribution. Any predictor effects were considered significant at the α -level of 0.05. All analyses were conducted using R version 1.2.5033 (R Core Team 2019).

RESULTS & DISCUSSION

Harmful algal blooms (HABs) can influence fish health either directly (e.g., through toxin exposure) or indirectly (e.g., by altering food web interactions) (Briland et al. 2020). Both direct and indirect effects can induce stress and compromise the immune system (Wei et al. 2009), potentially leading to greater susceptibility of individuals to disease and parasitic infection (Schwaiger et al. 1997). Because HABs are a common occurrence in western Lake Erie during

the summer growing season, when juvenile fishes such as yellow perch are using these waters as nursery habitat, I predicted that parasite loads in individuals residing in waters with high cyanobacteria concentrations would be greater than individuals captured in areas with lower concentrations of cyanobacteria. I tested this hypothesis by quantifying the prevalence of infections of parasitic worms of the genus *Neoechinorhynchus* in the livers of YOY yellow perch.

Yellow Perch Attributes

The yellow perch analyzed for this study were generally the same size and body condition across the study years. Mean (± 1 SE) TL of fish ranged from 56.5 ± 0.7 mm (2015) to 75.4 ± 0.9 mm (2017). Mean body condition (measured as a deviation from a best-fit regression line) varied from -0.02 ± 0.02 SD (2019) to 0.07 ± 0.05 SD (2011).

Parasite Loads

To test whether parasite infections increased with increasing cyanobacteria density, I examined the parasite loads of yellow perch collected at 54 sites across western Lake Erie during August of 2011, 2015, 2017, and 2019. These sites spanned a wide gradient in HAB severity with cyanobacteria cell counts ranging from $184,354$ cells·mL⁻¹ to $1,353,648$ cells·mL⁻¹.

Parasite counts varied both within and among years (Table 1). During all years, individuals with parasites were documented with maximum parasite loads among years ranging from 9 per individual (2017) to 2 per individual (2015). Similarly, the proportion of individuals with parasites in their liver varied among years, ranging from 0.09 (2015) to 0.70 (2019) (Table 1). As

expected, I found that parasite load was related to cyanobacteria cell counts across the sampling sites. However, the relationship was opposite of my expectations, with the mean liver parasite counts being negatively related to cyanobacteria cell densities (log-adjusted coefficient: $1.55e^{-6}$; $t = 2.20$; $P = 0.03$; Table 2; Figure 4).

While contrary to my prediction, the negative relationship between cyanobacteria concentration and parasite loads is supported by research conducted with other species (Coopman et al. 2014; Da Silva et al. 2008). Despite HABs and their toxins negatively affecting fish health (see review by Landsberg 2002; Wei et al. 2009; Schwaiger et al. 1997), my results suggest that stress caused by HABs reduces the health and survivability of parasites more so than that of the host fish. This explanation is partially supported by a recent study with Manila clams, where high-level doses of the dinoflagellate *Karenia selliformis*, which forms dense blooms, including red tides that can cause fish kills (Landsberg 1995), showed the potential to reduce parasite burdens while minimally altering clam health metrics (Da Silva et al. 2008). Coopman et al. (2014) also provided evidence to indicate that HABs have health-promoting effects on potential hosts such as *Daphnia*, suggesting that their HAB-derived secondary metabolites (i.e., toxins) have antibacterial properties. These studies, combined with the unexpected result, suggest that HABs confer advantages to organisms like yellow perch by reducing the prevalence of disease and parasite burdens.

Interestingly, the relationship between parasite burdens and cyanobacteria cell counts appeared to depend on fish body condition in an unexpected manner. Specifically, I found that, in waters with relatively severe HABs ($>500,000$ cyanobacteria cells·mL⁻¹), yellow perch in poor condition (condition factor < 0) had lower mean parasite values than fish in good condition

(condition factor > 0). My expectation was that fish in poorer body condition would have higher parasite loads.

I am perplexed as to why this relationship emerged. One possibility is that fish in poorer condition are unable to support high numbers of parasites. Because body condition is based on expected mass according to length compared with actual mass, an individual with less than expected mass at a given length would be in poor condition. It makes sense, then, that fish with lower than expected mass (thus, poor condition) may not be able to support large numbers of parasites due to lack of biomass for the parasites to feed on and/or space for the parasites to grow. This occurrence would lead to the results that we observed, that individuals in poor condition had less parasites on average than individuals in good condition.

Because of the finding that individuals in poor condition found in HABs have fewer parasites than those in good condition, I am drawn to the idea that HABs may not be particularly harmful to fish and may actually provide some benefits. Small fish in poor condition may receive more benefit than harm from a HAB bloom in the form of protection from predators, a source of abundant food, and potential anti-pathogenic properties of cyanobacteria. To this point, Briland et al. (2020) found that small-bodied prey fish, including YOY yellow perch, resided in HABs during the day—perhaps as a refuge from predators – and fed just as well within blooms as outside of them, despite these blooms being highly toxic (with MC). Indeed, the authors found an abundance of zooplankton prey available in western basin blooms, with YOY yellow perch also consuming benthic macroinvertebrate prey. Studies in other ecosystems also have demonstrated the likely use of HABs during the day by small-bodied fishes, with avoidance of them at night, suggesting HABs to be beneficial as a prey-rich environment with minimal predation risk

(Engström-Öst, et al. 2006; Godlewska et al. 2018). Collectively, the results of my study, combined with these other findings, suggest that the net effect of HABs on fish such as yellow perch could be positive. Clearly, more research is needed to determine the validity of this statement.

Study Limitations

The present study has limitations that should be addressed with future research. For instance, while the locations at which yellow perch were caught are known, exactly where the fish resided during the hours, days, or weeks prior to capture is not. Thus, the possibility exists that the individuals analyzed for my study could have moved from sites with differing bloom conditions than those in which they were captured. This limitation could be addressed by tagging fish to track their locations, or perhaps conducting an experiment in which cyanobacteria conditions and fish movement are monitored in a laboratory setting. Additionally, future studies should try to determine the exact amount of MC to which fish are exposed. This could be done by taking water samples at the collection site to quantify MC content in the water (Foss & Auel 2015). Not only would this have allowed for a clearer connection between MC and parasite loads, but it would have made the connection clearer between HAB cell density and the amount of MC taken up by fish in a bloom.

Summary & Conclusions

In summary, I found that mean parasite loads decreased with increasing cyanobacteria cell density, and that YOY yellow perch in poor condition had lower mean parasite loads than those

in good condition. Both of these findings were opposite of my expectations. Even so, they were somewhat supported by the invertebrate literature, where for both zooplankton and a mollusk, disease and parasite burdens declined with exposure to toxic algae or cyanobacteria. Given the many ways in which HABs can directly and indirectly affect fish (Briland et al. 2020), and the many ways that remain poorly understood (e.g., this study), more research in this area is warranted. Only with a better understanding of the effect of HABs on fish health and growth can fishery management agencies truly understand the importance of HABs to fisheries management. In addition, given that HABs are expected to continue to increase with continued climate change (Wells et al. 2015), continued research in this area would offer agencies a means to predict how fish production and recruitment dynamics might change in the future.

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Table 1. Details on collection sites and parasite loads from young-of-year yellow perch collected in western Lake Erie during August, 2011, 2015, 2017, and 2019.

Year	Number of fish	Number of collection sites	Mean \pm 1 SE cyanobacteria concentration (cells·mL ⁻¹)	Proportion of fish with liver parasites	Mean \pm 1 SE parasite counts (parasites·liver ⁻¹)
2011	70	11	651,979 \pm 34,235	0.15	0.24 \pm 0.83
2015	70	4	649,962 \pm 16,181	0.09	0.14 \pm 0.47
2017	60	20	483,456 \pm 45,127	0.60	1.23 \pm 1.67
2019	316	18	372,205 \pm 8,477	0.70	1.51 \pm 1.41

Table 2. Data from the model showing predicted parasite loads for each value of cyanobacteria concentration with standard error and a 95% confidence interval.

Cyanobacteria concentration (cells·mL ⁻¹)	Predicted parasite values	Standard Error	95% confidence interval
184,000	1.33	0.20	[2.67, 0.87]
330,000	1.03	0.15	[1.49, 0.78]
476,000	0.84	0.16	[1.14, 0.66]
622,000	0.70	0.23	[1.02, 0.54]
770,000	0.61	0.31	[0.97, 0.44]
916,000	0.54	0.40	[0.93, 0.33]
1,062,000	0.48	0.50	[0.90, 0.33]
1,354,000	0.39	0.70	[0.86, 0.26]

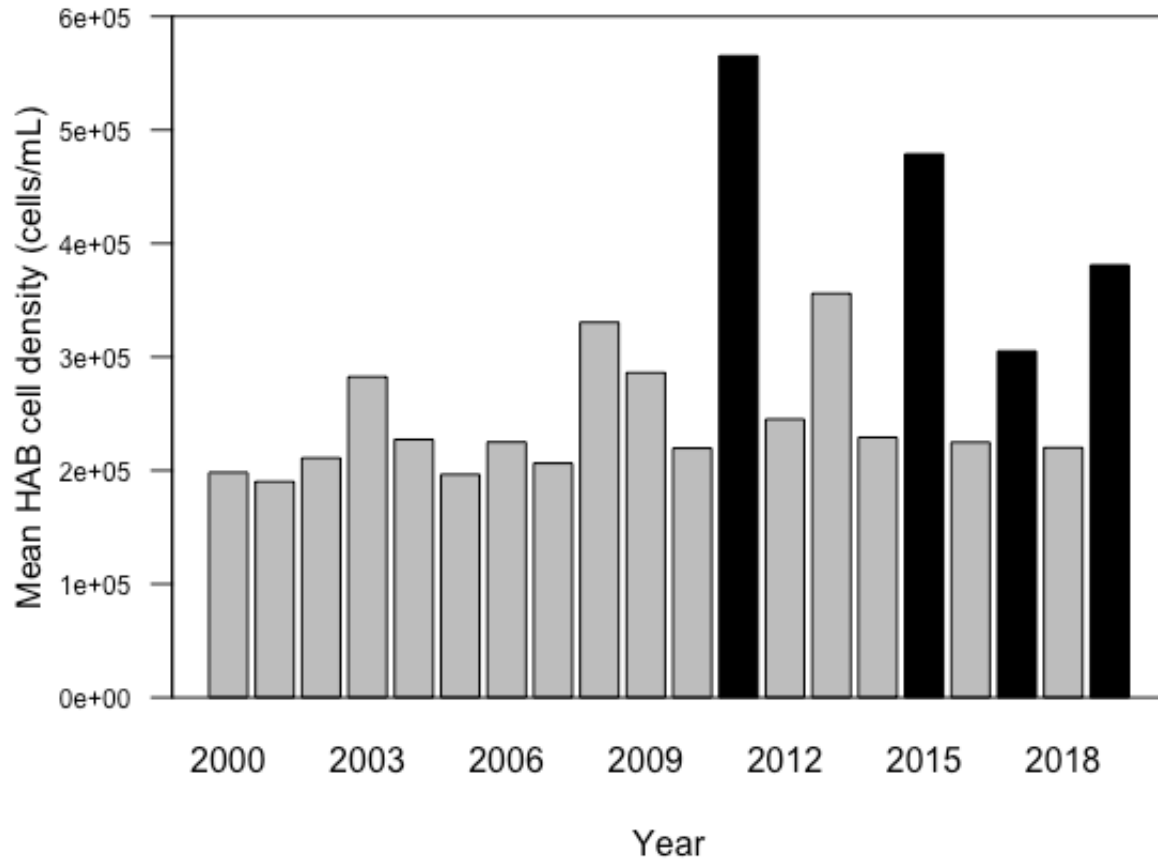


Figure 1. Average annual cyanobacteria cell densities in western Lake Erie, 2000-2019. Cell density values were calculated from reflectance data using methods defined by Wynne et al. (2010). The years during which I collected yellow perch are highlighted in black.

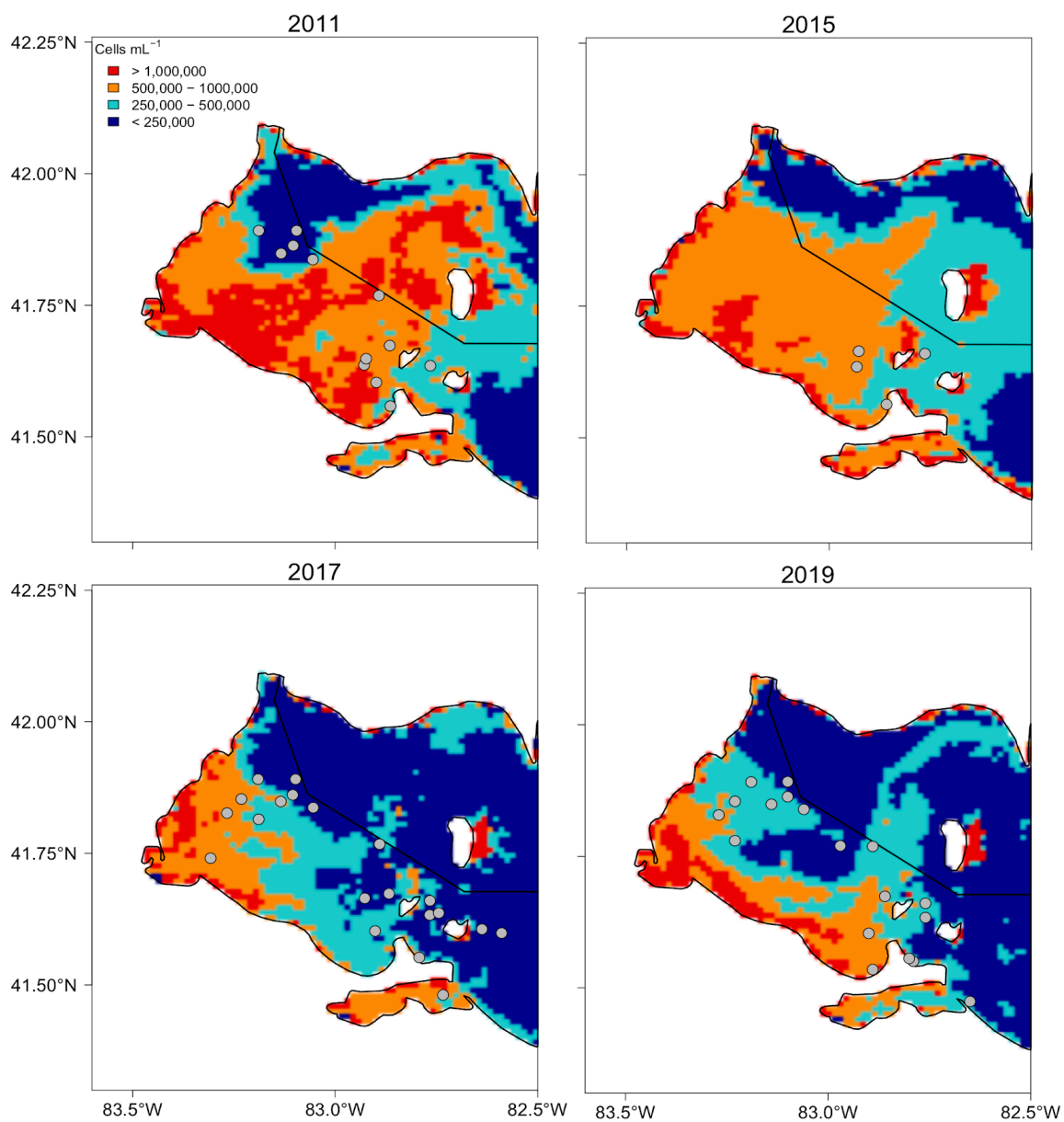


Figure 2. Maps of cyanobacteria cell densities in western Lake Erie during August 2011, 2015, 2017, and 2019, which were sampled for this study. Red indicates high cyanobacteria cell densities, whereas dark blue indicates low cyanobacteria cell densities. Gray circles on

each panel indicate stations from which young-of-year yellow perch were collected for quantification of parasites.

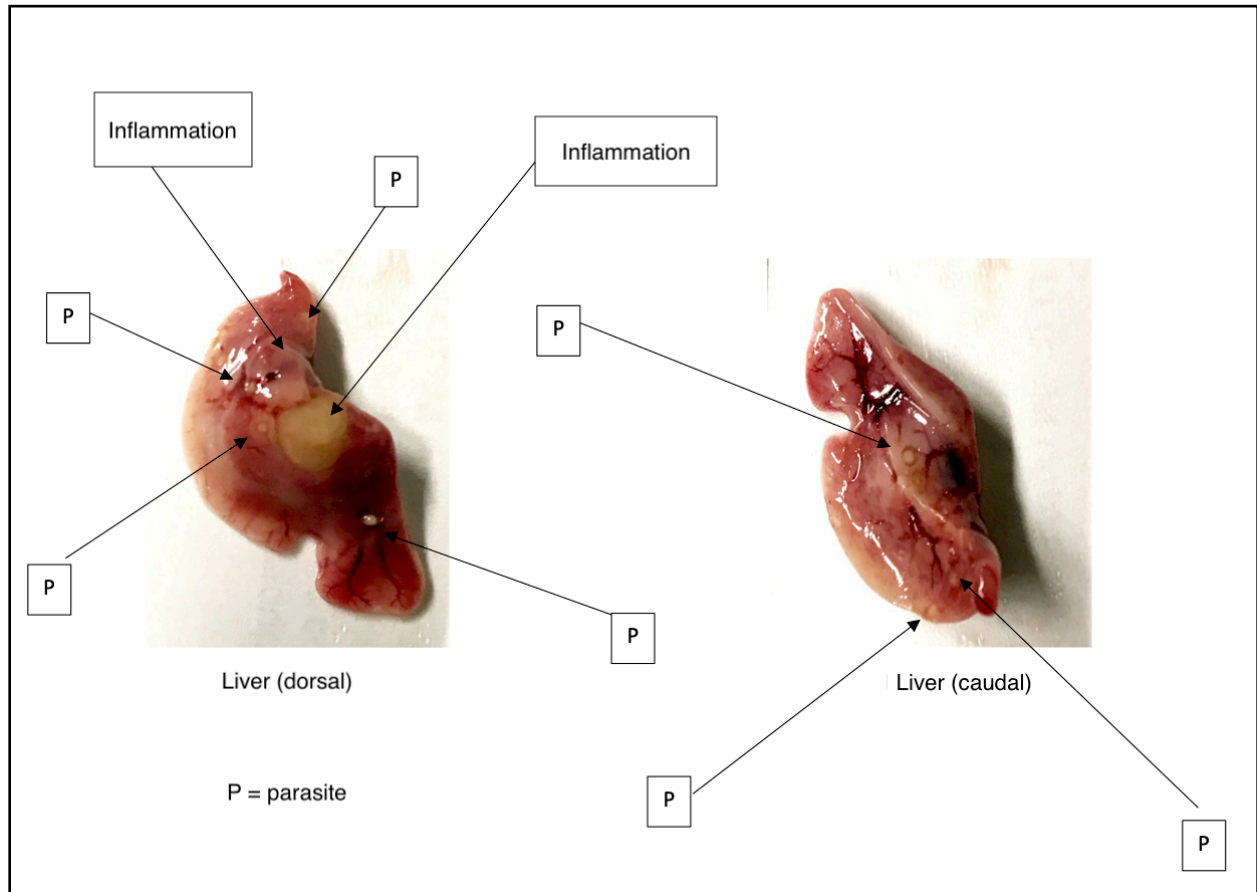


Figure 3. Larval *Neoechinorhynchus* parasites individually appear as embedded nodules within the tissue of fish livers.

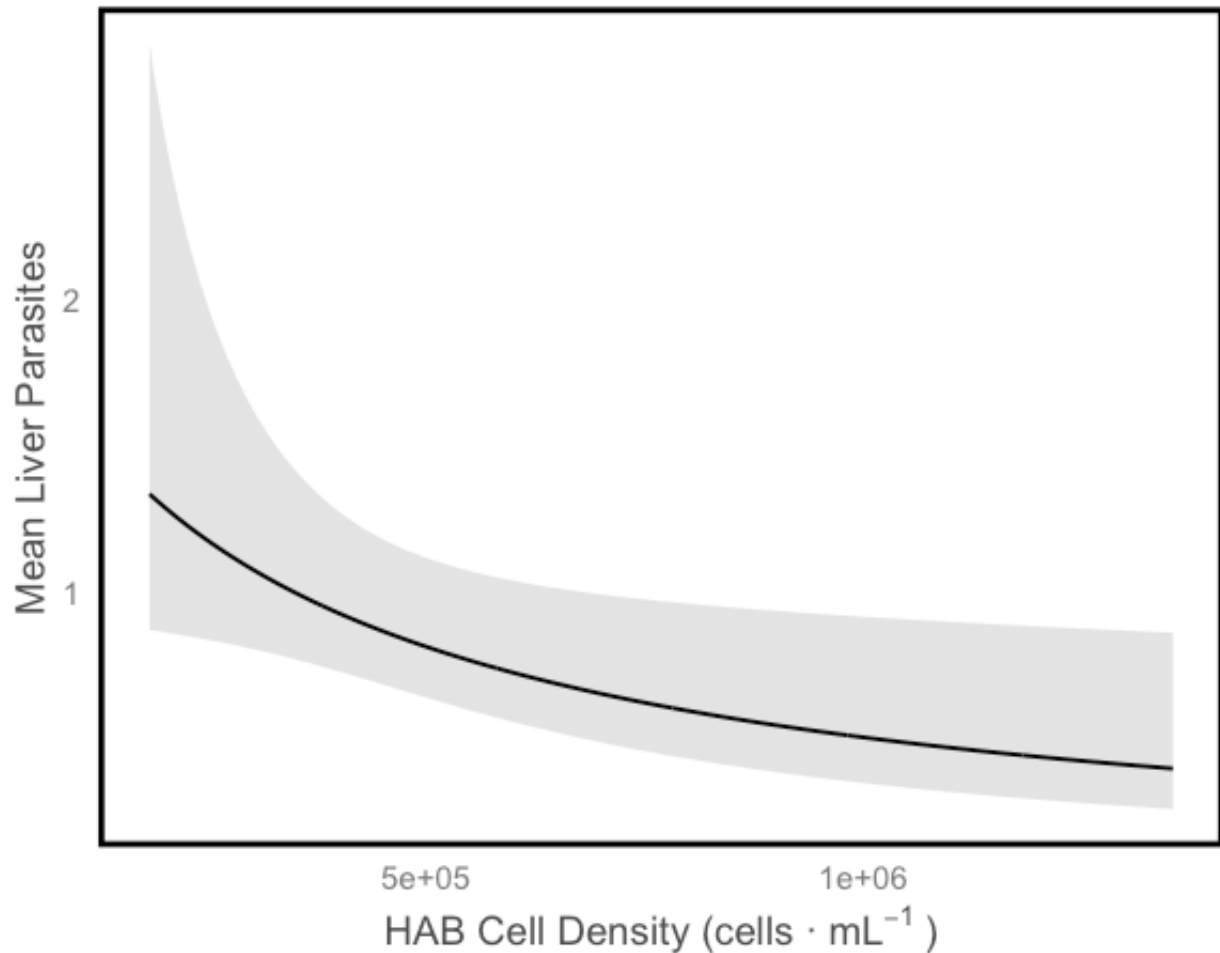


Figure 4. Relationship between cyanobacteria (HAB) cell density and mean liver parasites (number per individual) in young-of-year yellow perch collected in western Lake Erie during 2011, 2015, 2017, and 2019. The gray shading indicates the 95% confidence interval of the best fit line.

REFERENCES

- Amin, O. M., & Muzzall, P. M. (2009). Redescription of *Neoechinorhynchus tenellus* (Acanthocephala: Neoechinorhynchidae) from *Esox lucius* (Esocidae) and *Sander vitreus* (Percidae), among other percid and centrarchid fish, in Michigan, USA. *Comparative Parasitology*, 76(1), 44-50.
- Anderson, D. M., Hoagland, P., Kaoru, Y., & White, A. W. (2000). Estimated annual economic impacts from harmful algal blooms (HABs) in the United States (No. WHOI-2000-11). National Oceanic and Atmospheric Administration National Severe Storms Lab, Norman, OK.
- Berardo, R. & Formica, F., & Reutter, J., & Singh, A. (2017). Impact of Land Use Activities in the Maumee River Watershed on Harmful Algal Blooms in Lake Erie. *Case Studies in the Environment*. University of California Press, Oakland, CA.
- Coldwater Task Group (2019). 2018 Report of the Lake Erie Coldwater Task Group, March 2019. Presented to the Standing Technical Committee, Lake Erie Committee of the Great Lakes Fishery Commission, Ann Arbor, Michigan, USA.
- Coopman, M., Muylaert, K., Lange, B., Reyserhove, L., & Decaestecker, E. (2014). Context dependency of infectious disease: the cyanobacterium *Microcystis aeruginosa* decreases white bacterial disease in *Daphnia magna*. *Freshwater Biology*, 59(4), 714-723.

- Dabholkar, A. S., & Carmichael, W. W. (1987). Ultrastructural changes in the mouse liver induced by hepatotoxin from the freshwater cyanobacterium *Microcystis aeruginosa* strain 7820. *Toxicon*, 25(3), 285-292.
- Da Silva, P. M., Hégaret, H., Lambert, C., Wikfors, G. H., Le Goïc, N., Shumway, S. E., & Soudant, P. (2008). Immunological responses of the Manila clam (*Ruditapes philippinarum*) with varying parasite (*Perkinsus olseni*) burden, during a long-term exposure to the harmful alga, *Karenia selliformis*, and possible interactions. *Toxicon*, 51(4), 563-573.
- Dechtiar, A. O. (1968). *Neoechinorhynchus carpiodi* n. sp. (Acanthocephala: Neoechinorhynchidae) from quillback of Lake Erie. *Canadian Journal of Zoology*, 46(2), 201-204.
- de Matos, L. V., de Oliveira, M. I. B., Gomes, A. L. S., & da Silva, G. S. (2017). Morphological and histochemical changes associated with massive infection by *Neoechinorhynchus buttnerae* (Acanthocephala: Neoechinorhynchidae) in the farmed freshwater fish *Colossoma macropomum* Cuvier, 1818 from the Amazon State, Brazil. *Parasitology Research*, 116(3), 1029-1037.
- Dyble, J., Fahnenstiel, G. L., Litaker, R. W., Millie, D. F., & Tester, P. A. (2008). Microcystin concentrations and genetic diversity of *Microcystis* in the lower Great Lakes. *Environmental Toxicology*, 23(4), 507-516.
- Engström-Öst, J., Karjalainen, M., & Viitasalo, M. (2006). Feeding and refuge use by small fish in the presence of cyanobacteria blooms. *Environmental Biology of Fishes*, 76(1), 109-117.

- Foss, A. J., & Aibel, M. T. (2015). Using the MMPB technique to confirm microcystin concentrations in water measured by ELISA and HPLC (UV, MS, MS/MS). *Toxicon*, *104*, 91-101.
- Greer, B., Maul, R., Campbell, K., & Elliott, C. T. (2017). Detection of freshwater cyanotoxins and measurement of masked microcystins in tilapia from Southeast Asian aquaculture farms. *Analytical and Bioanalytical Chemistry*, *409*(16), 4057–4069.
- Godlewska, M., Balk, H., Kaczkowski, Z., Jurczak, T., Izydorczyk, K., Długoszewski, B., Jaskulska, A., Gagala-Borowska, I., & Mankiewicz-Boczek, J (2018). Night fish avoidance of *Microcystis* bloom revealed by simultaneous hydroacoustic measurements of both organisms. *Fisheries Research*, *207*, 74-84.
- Hudson, J. C., & Ziegler, S. S. (2014). Environment, culture, and the Great Lakes fisheries. *Geographical Review*, *104*(4), 391-413.
- Jithendran, K. P., & Kannappan, S. (2010). A short note on heavy infection of acanthocephalan worm (*Neoechinorhynchus agilis*) in grey mullet, *Mugil cephalus*. *Journal of Parasitic Diseases*, *34*(2), 99-101.
- Knight, R. L., Margraf, F. J. & Carline, R. F. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. *Transactions of the American Fisheries Society*, *113*: 677–693.
- Landsberg, J. H. (1995). Tropical reef-fish disease outbreaks and mass mortalities in Florida, USA: what is the role of dietary biological toxins? *Diseases of Aquatic Organisms*, *22*(2), 83-100.

- Landsberg, J. H. (2002). The effects of harmful algal blooms on aquatic organisms. *Reviews in Fisheries Science*, 10(2), 113-390.
- Malbrouck, C., & Kestemont, P. (2006). Effects of microcystins on fish. *Environmental Toxicology and Chemistry*, 25(1), 72-86.
- Melo, F. T. D. V., Costa, P. A. F. B., Giese, E. G., Gardner, S. L., & Santos, J. N. (2015). A description of *Neoechinorhynchus veropesoi* n. sp. (Acanthocephala: Neoechinorhynchidae) from the intestine of the silver croaker fish *Plagioscion squamosissimus* (Heckel, 1840) (Osteichthyes: Sciaenidae) off the east coast of Brazil. *Journal of Helminthology*, 89(1), 34-41.
- Michalak, A., Anderson, E., Beletsky, D., Boland, S., Bosch, N.S., Bridgeman, T.B., Chaffin, J.D., Cho, K., Confesor, R., Daloğlu, I., DePinto, J.V., Evans, M.A., Fahnenstiel, G.L., He, L., Ho, J.C., Jenkins, L., Johengen, T.C., Kuo, K.C., LaPorte, E., Liu, X., McWilliams, M.R., Moore, M.R., Posselt, D.J., Richards, R.P., Scavia, D., Steiner, A.L., Verhamme, E., Wright, D.M., and Zagorski, M.A. (2013). Record-setting algal bloom in Lake Erie caused by agricultural and meteorological trends consistent with expected future conditions. *Proceedings of the National Academy of Sciences*, 110(16), 6448-6452.
- Nishiwaki-Matsushima, R., Ohta, T., Nishiwaki, S., Suganuma, M., Kohyama, K., Ishikawa, T., Carmichael, W. W. & Fujiki, H. (1992). Liver tumor promotion by the cyanobacterial cyclic peptide toxin microcystin-LR. *Journal of Cancer Research and Clinical Oncology*, 118(6), 420-424.

- Ortiz-Rodríguez, R., Dao, T. S., & Wiegand, C. (2012). Transgenerational effects of microcystin-LR on *Daphnia magna*. *Journal of Experimental Biology*, 215(16), 2795-2805.
- Poulin, R. (1992). Toxic pollution and parasitism in freshwater fish. *Parasitology Today*, 8(2), 58-61
- Råbergh, C. M. I., Bylund, G., & Eriksson, J. E. (1991). Histopathological effects of microcystin-LR, a cyclic peptide toxin from the cyanobacterium (blue-green alga) *Microcystis aeruginosa* on common carp (*Cyprinus carpio* L.). *Aquatic Toxicology*, 20(3), 131-145.
- R Core Team (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>.
- Scavia, D., Allan, J. D., Arend, K. K., Bartell, S., Beletsky, D., Bosch, N. S., Brandt, S.B., Briland, R.D., Daloglu, I., DePinto, J.V., Dolan, D. M., Evans, M.A., Farmer, T.M., Goto, D., Han, H., Hook, T.O., Knight, R., Ludsin, S.A., Mason, D., Michalak, A.M., Richards, P.R., Roberts, J.J., Rucinski, D.K., Rutherford, E., Schwab, D.J., Sesterhenn, T.M., Zhang, H., & Zhou, Y. (2014). Assessing and addressing the re-eutrophication of Lake Erie: Central basin hypoxia. *Journal of Great Lakes Research*, 40(2), 226-246.
- Schwaiger, J., Wanke, R., Adam, S., Pawert, M., Honnen, W., & Triebkorn, R. (1997). The use of histopathological indicators to evaluate contaminant-related stress in fish. *Journal of Aquatic Ecosystem Stress and Recovery*, 6(1), 75-86.

- Stumpf, R. P., Wynne, T. T., Baker, D. B., & Fahnenstiel, G. L. (2012). Interannual variability of cyanobacterial blooms in Lake Erie. *PloS one*, 7(8).
- Tyson, J. T., & Knight, R. L. (2001). Response of yellow perch to changes in the benthic invertebrate community of western Lake Erie. *Transactions of the American Fisheries Society*, 130(5), 766-782.
- US Department of Commerce, NOAA. (2018). HAB Tracker 2018. Lake Erie HAB Tracker Archive. NOAA Great Lakes Environmental Research Laboratory, Ann Arbor, MI. www.glerl.noaa.gov/res/HABs_and_Hypoxia/habTracker.html.
- Verweyen, L., Klimpel, S., & Palm, H. W. (2011). Molecular phylogeny of the *Acanthocephala* (class Palaeacanthocephala) with a paraphyletic assemblage of the orders Polymorphida and Echinorhynchida. *PLoS One*, 6(12).
- Wei, L., Sun, B., Chang, M., Liu, Y., & Nie, P. (2009). Effects of cyanobacterial toxin microcystin-LR on the transcription levels of immune-related genes in grass carp *Ctenopharyngodon idella*. *Environmental Biology of Fishes*, 85(3), 231.
- Wellington, C. G., Mayer, C. M., Bossenbroek, J. M., & Stroh, N. A. (2010). Effects of turbidity and prey density on the foraging success of age 0 year yellow perch *Perca flavescens*. *Journal of Fish Biology*, 76(7), 1729-1741.
- Wells, M. L., Trainer, V. L., Smayda, T. J., Karlson, B. S., Trick, C. G., Kudela, R. M., Karlson, B.S.O., Trick, C.G., Kudela, R.M., Ishikawa, A., Bernard, S., Wulff, A., Anderson, D.M., & Cochlan, W. P. (2015). Harmful algal blooms and climate change: learning from the past and present to forecast the future. *Harmful Algae*, 49, 68-93.

Wynne, T. T., Stumpf, R. P., Tomlinson, M. C., Warner, R. A., Tester, P. A., Dyble, J., & Fahnenstiel, G. L. (2008). Relating spectral shape to cyanobacterial blooms in the Laurentian Great Lakes. *International Journal of Remote Sensing*, 29(12), 3665-3672.

Wynne, T. T., Stumpf, R. P., Tomlinson, M. C., & Dyble, J. (2010). Characterizing a cyanobacterial bloom in western Lake Erie using satellite imagery and meteorological data. *Limnology and Oceanography*, 55(5), 2025-2036.

Yellow Perch Task Group (YPTG). 2019. Report of the Yellow Perch Task Group, March 2018. Presented to the Standing Technical Committee, Lake Erie Committee of the Great Lakes Fishery Commission. Ann Arbor, Michigan, USA.