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Associations between cyanobacteria and indices of secondary production in the western basin of Lake Erie

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Abstract

Large lakes provide a variety of ecological services to surrounding cities and communities. Many of these services are supported by ecological processes that are threatened by the increasing prevalence of cyanobacterial blooms which occur as aquatic ecosystems experience cultural eutrophication. Over the past 10 yr, Lake Erie experienced cyanobacterial blooms of increasing severity and frequency, which have resulted in impaired drinking water for the surrounding communities. Cyanobacterial blooms may impact ecological processes that support other services, but many of these impacts have not been documented. Secondary production (production of primary consumers) is an important process that supports economically important higher trophic levels. Cyanobacterial blooms may influence secondary production because cyanobacteria are a poor-quality food resource and cyanotoxins may be harmful to consumers. Over 3 yr at 34 sites across the western basin of Lake Erie, we measured three indices of secondary production that focus on the dominant bivalve taxa: (1) growth of a native unionid mussel, (2) the size of young-of-year dreissenid mussels, and (3) the mass of colonizing animals on a Hester-Dendy sampler. Associations between these indices and cyanobacterial data were estimated to assess whether cyanobacteria are associated with variation in secondary production in the western basin of Lake Erie. The results suggest cyanobacterial abundance alone is only weakly associated with secondary production, but that cyanotoxins have a larger effect on secondary production. Given recurring late-summer cyanobacterial blooms, this impact on secondary production has the potential to undermine Lake Erie's ability to sustain important ecosystem services.

Lake Erie is a large lake located on the border between the U.S. and Canada with strong environmental and economic influence on human communities of the region (Hushak et al. 1988; GLMRIS 2012; U.S. Army Corps of Engineers 2014). Over the past 50 yr, Lake Erie has experienced major changes in its phytoplankton community spurred by changing nutrient loads, invasive species and climate change (Michalak et al. 2013; Kane et al. 2014; Scavia et al. 2014; Carmichael and Boyer 2016). After being absent for most of the late 1980s and 1990s, cyanobacterial blooms have again become prevalent seasonally in the western basin of Lake Erie, which provides drinking water to large coastal communities (Kane et al. 2014). These cyanobacterial blooms have resulted in episodic drinking water shutdowns along Lake Erie and the creation of a large international effort to identify causes and potential management options (Wilson 2014; Bullerjahn et al. 2016).

Ecosystem services provided by Lake Erie extend beyond the use of the lake as a drinking water supply. For example, Lake Erie fisheries are valuable both economically and culturally (Hushak et al. 1988; GLMRIS 2012). These fisheries are supported by production of primary consumers in a highly productive lake (Friedland et al. 2012), but there is concern that recent cyanobacterial blooms could reduce production of primary consumers and, in turn, affect fish

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Additional Supporting Information may be found in the online version of this article.

production. Although we are aware of no field studies that directly link cyanobacteria to measurements of secondary production (i.e., the production of primary consumers), cyanobacterial blooms may influence primary consumers in at least two direct ways. First, cyanobacteria are a poor-quality food resource as they lack essential fatty acids that are necessary for most animal consumers (Brett and Muller-Navarra 1997; Ahlgren et al. 2009; Arts and Kohler 2009). Studies on zooplankton have shown that when cyanobacteria are the primary food source, growth is often reduced (Brett and Muller-Navarra 1997; DeMott and Muller-Navarra 1997). The second mechanism by which cyanobacteria negatively impact primary consumers is via toxin production. Cyanobacteria produce several different classes of cyanotoxins, which are harmful to most animal life, including aquatic consumers (Wiegand and Pflugmacher 2005; Bownik 2016).

Although common cyanotoxins such as anatoxins, cylindrospermopsins, and saxitoxins have not been routinely detected above known adverse health effect thresholds in Lake Erie, microcystin regularly occurs in the lake and is a known health concern (Rinta-Kanto et al. 2009; Carmichael and Boyer 2016). Microcystin is toxic to most animals, but bivalves appear to be fairly resistant to microcystin, often having little or no mortality at concentrations that cause mortality to zooplankton (Wiegand and Pflugmacher 2005; Contardo-Jara et al. 2008; Burmester et al. 2012). However, more recent studies have shown that microcystin can cause inflammatory responses and immune system alterations in dreissenid mussels when present either in dissolved form or in the cells of ingested cyanobacteria (Contardo-Jara et al. 2008; Burmester et al. 2012; Juhel et al. 2015). This is of particular interest in Lake Erie, where invasive dreissenid mussels support the majority of overall secondary production (Johannsson et al. 2000).

Direct measurements of secondary production are difficult, and even substantial effort may yield results that are best thought of as an index (Stead et al. 2005). Instead of direct measurements, here we use indices of secondary production. Specifically, we deployed ecological process monitoring stations (EPS) that included a common consumer and a standardized invertebrate sampler (Hester and Dendy 1962; Larson et al. 2016*a*). In the common consumer method, members of a single taxon (and preferably of a single cohort) are deployed across an environmental gradient, given time to react to those locations and associations between the reactions and the gradient are examined. This is similar to sentinel species methods, which use naturally occurring populations (Hunt and Slone 2010). In this study, the common consumer was a native, unionid mussel (*Lampsilis siliquoidea*) that occupies a similar ecological niche as the invasive dreissenid mussels (Baker and Levinton 2003).

Because cyanobacteria are poor quality food resources, we would predict (1) negative associations between our indices of secondary production and cyanobacterial abundance. Although we did not see this relationship in a previous study (Larson et al. 2016*a*), this study expands the available data from 1 yr to 3 yr and includes direct phytoplankton biovolume (BV) measurements at a subset of sites. We also predict (2) negative associations between our indices of secondary production and direct measurements of total microcystin. Although cyanobacteria are the source of microcystin, not all taxa produce microcystin, and microcystin production is dependent on nutrient conditions (Davis et al. 2010), so microcystin and cyanobacterial abundance are not necessarily tightly correlated.

Cyanobacteria and mussel growth rates tend to be positively correlated to water temperature (Hanson et al. 1988; O'Neil et al. 2012) and competition between toxic and nontoxic strains of cyanobacteria may be influenced by water temperature (Davis et al. 2009). For this reason, direct and indirect effects of water temperature on our indices of secondary production may obscure cyanobacterial effects. In addition to identifying simple associations between cyanobacteria and secondary production, we also looked for associations that took into account the possible effects of water temperature.

Methods

Study sites

EPS were deployed at 34 sites in the western basin of Lake Erie and the lower Maumee River (Ohio; Fig. 1). Many of the sites were sampled repeatedly from 2013 to 2015 (Supporting Information Table S1). Stations were deployed at the end of May/beginning of June and retrieved at the end of August, encompassing the peak growing season for cyanobacteria. Many of these sites correspond to water quality monitoring stations operated by other research agencies (University of Toledo, Ohio Environmental Protection Agency, etc.) or to research being conducted by other U.S. Geological Survey studies. Other sites were added to fill spatial gaps between other water quality sampling locations. No stations were placed in less than 1 m of water to minimize the likelihood of dewatering during wind-driven seiche events. Specific deployment locations and years are included in Supporting Information Table S1. EPS deployed at additional locations in Lake Erie that lacked any accompanying cyanobacterial data are not reported here.

Unionid mussel growth

For each year, *L. siliquoidea* mussels were used as common consumers. Within a particular year, only mussels from a single generational cohort were used. The origins of the cohorts used in 2013 and 2014 are described in previous publications (Larson et al. 2016*a*,*b*, respectively). *L. siliquoidea* used in 2015 were from the same cohort used in 2014, except that only males were used to avoid distributing any potentially gravid females into the study areas. The 2013

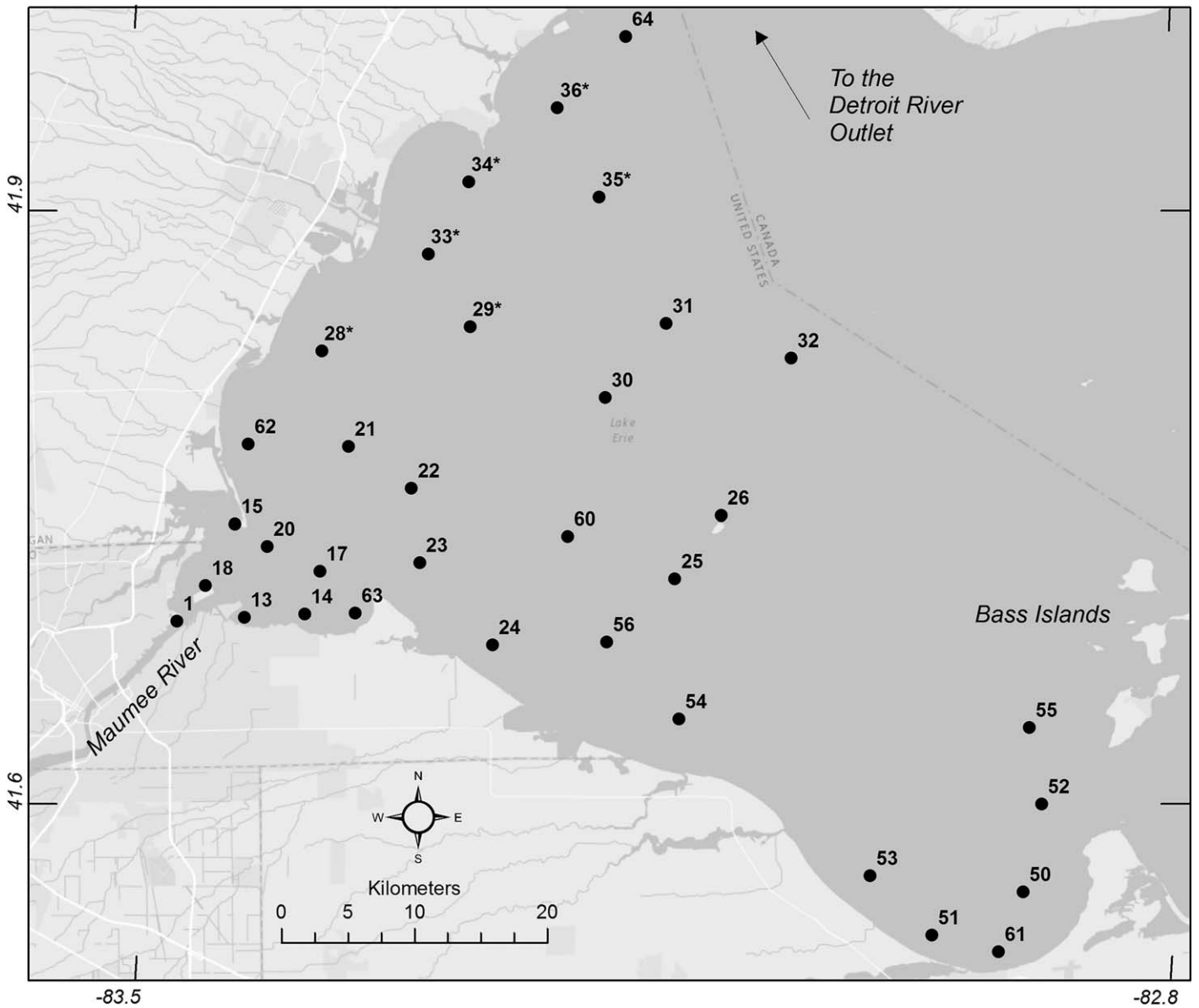

Fig. 1. Locations where stations were deployed from 2013 to 2015. * indicates sites where cyanobacterial biovolume (2014, 2015) and MC (2013–2015) were collected. Many sites were only sampled for 1 yr or 2 yr.

and 2015 cohorts were approximately aged 2+, while the 2014 cohort was age 1+.

Mussel cages used in this study are identical to those previously reported in Larson et al. (2016*a*) and Larson et al. (2016*b*). Briefly, mussel cages were made using plastic-coated mesh with diamond-shaped openings that have a maximum width of 1.4 cm. The mesh was wrapped into a cylindrical shape around two PVC drain caps and tightened with stainless steel hose clamps to form the mussel cage. These cages were then affixed to a rope connecting a cement block (~ 13 kg) to a submerged buoy. The buoy was suspended approximately 1 m off the sediment, and the cages were suspended about half-way between buoy and the cement block. The first cement block was connected to a second cement block, forming a dual anchoring system to facilitate surface retrieval. Mussels (five per cage in 2013, three per cage in 2014, and two per cage in 2015) were randomly assigned to cages, and cages were haphazardly assigned to individual sites.

Mussel shell dimensions were measured as in previous publications (e.g., Larson et al. 2014). Other than in the post-deployment measurements of 2014, length, width, and height were all recorded using a digital caliper accurate to the nearest 0.01 mm. Due to equipment failure in 2014, mussel shell dimensions were measured using calipers accurate to the nearest 0.254 mm (i.e., 0.1 inch). We remeasured

35 individuals two or three times, and found the median relative standard deviation was less than $< 0.5\%$ with either set of calipers. Length is the maximum anterior-to-posterior dimension of the shell measured roughly parallel to the hinge; width is the maximum left–right dimension with both valves appressed; height is the maximum dorsal-ventral dimension of the shell measured roughly perpendicular to the hinge. As previously reported, in 2013 sometimes mussels grew in atypical shapes due to crowding in the cages (Larson et al. 2016*a*), this did not occur in other years. For this reason, we did not use length as our index of growth, but instead report change in nominal volume (length $\times$ width $\times$ height) on a per-day basis. Using data from a previously published analysis of length-weight regressions in this species, we determined that volume is a better predictor of dry mass than any individual dimension, but length, weight, height and volume are all highly correlated (Pearson's $r > 0.90$; Larson et al. 2014).

One individual in 2013 (site 18) and one individual from 2015 (site 36) showed signs of stress prior to deployment (mucous discharge). Based on past experience handling mussels, this is an indication of imminent mortality (N. Eckert pers. comm.; M. Bartsch pers. comm.). Both of these individuals died prior to retrieval. For the individual from 2013, the shell dimensions barely changed (suggesting death occurred soon after deployment), while in the individual from 2015 the shell dimensions decreased (suggesting the shell began to dissolve; Haag 2012).

Two individuals in 2015 (from site 23 and site 29) experienced a loss of nominal volume. Unionid mussels do seem to occasionally exhibit losses in shell size without dying (Downing and Downing 1993). The mechanism for loss of shell size seems to be controlled by dissolution mediated by water quality and stress related to handling. Haag (2012, p. 12) suggested that shell dissolution can occur because the mantle retracts during stress (i.e., caused by handling the mussel) and then does not reconnect at the same location. We suspect these individuals were stressed prior to deployment, but their distress was unnoticed. Because this type of shell loss is mediated by handling and abiotic factors (and presumably not cyanobacteria), we excluded these two individuals from statistical analysis in this study. They also appear as substantial outliers in the data, but make up only 1% of all the mussels in the study.

Hester-Dendy samplers

At each site, a Hester-Dendy sampler was attached (Hester and Dendy 1962) to the rope directly beneath the unionid cage and above the cement block to measure biota colonizing that site (the base of the Hester-Dendy sampler was < 30 cm from the bottom of the unionid cage). These samplers had 14 round plates consisting of eight single spaces (3.2 mm), one double space (6.4 mm), two triple spaces (9.6 mm), and two quadruple spaces (12.8 mm). Total surface area was approximately 1300 cm^2 in each sampler. Immediately upon retrieval of the cage/block/sampler assembly, samplers were cut free of the rope, placed into 2-liter jars of 95% ethanol for preservation, and returned to the lab. Samplers were disassembled, and all biota were carefully scraped off the samplers into individually labeled storage containers. Each sampler was subsetted using a Folsom splitter (McEwen et al. 1954), and individuals were identified and separated into broad taxonomic groups. Each group was then dried for > 24 h at 60°C and weighed to the nearest 0.0001 g on a balance (Mettler-AT200) with daily calibration checks.

Water temperature

During 2014 and 2015, water temperature data loggers (iButton Thermochron loggers; Maxim Integrated, San Jose California, U.S.A.) were deployed with the EPS. These recorded temperatures every 2 h for the entire course of the summer. Instead of simply using average temperatures, we calculated degree days (Chezik et al. 2014). Degree days are useful for calculating the amount of ambient thermal energy that an animal has experienced, which is directly related to growth and other metabolic processes in ectotherms (Trudgill et al. 2005). Degree days have been used in wide variety of applications to relate temperature to growth (Trudgill et al. 2005; Chezik et al. 2014). For each day, the following equation is used to calculate the degree days for that day:

$$\mathrm{DD} = \left[\frac{T_{\max} + T_{\min}}{2}\right] - T_x$$

where T_x is the threshold temperature under consideration (e.g., 0°C or 5°C) and $T_{\max}$ and $T_{\min}$ are the daily maximum and minimum temperatures, respectively. Negative daily DD estimates are discarded, and the positive daily DD estimates are summed for the year. We calculated DDs for a T_x of 0°C, 5°C, 10°C, 15°C, and 20°C. However, the choice of threshold temperature does not matter much for this temperature range, since DD0, DD5, DD10, DD15, and DD20 are all highly correlated (Pearson's $r > 0.9$ for all). In this data set, these DD estimates are strongly correlated with average temperatures (Pearson's $r > 0.9$ with DD15). For statistical analysis, we used DD15 to represent the effects of water temperature, both because it was highly correlated to other choices of temperature threshold and because this is close to the threshold temperature for growth in dreissenid mussels (Neumann et al. 1993).

Indices of secondary production

From the unionid mussels and the Hester-Dendy data, we derived three indices of secondary production: growth of the unionid mussel, average dry mass of dreissenid mussels that accumulated on the Hester-Dendy, and total dry mass of all animals that accumulated (or colonized) the Hester-Dendy. The first is simply growth of the unionid mussel, expressed as increase in nominal volume per day. Variation in growth

of this common consumer is intended to provide a standard index of growth potential among sites. The second index was the average dry mass per individual of dreissenid mussels (i.e., the average size) that had accumulated on the Hester-Dendy sampler. This assumes that all of the dreissenid mussels accumulating on the Hester-Dendy sampler have settled there from veliger stage, and so increases in size since that time are indications of growth rates while on the sampler. The final index is the accumulation of animal mass on the Hester-Dendy, as an indicator of the site's potential to support secondary production. In our data, dry mass and ash-free dry mass were highly correlated (Pearson's $r = 0.94$), so we have just used dry mass in this analysis. Although the Hester-Dendy samplers were colonized by a variety of taxa (insects, amphipods, individual and colonial *Hydra* spp., bryozoans, etc.), the vast majority of the mass in most cases was dreissenid mussel tissue (Supporting Information Fig. S1). Variation in dreissenid mussel mass was highly correlated to overall variation in the mass of all colonizing animals (Pearson's $r = 0.99$).

Cyanobacterial index data

For stations surrounded by sufficient open water, a satellite derived cyanobacterial index (CI; cells mL^{-1}) was used as an indicator of cyanobacterial abundance. This CI is described in Wynne et al. (2010) and Stumpf et al. (2012) and is adapted to use the Moderate Resolution Imaging Spectroradiometer (MODIS) imagery available for the study period (Wynne et al. 2013). To compensate for shallow optical depth, satellite images are taken during low wind conditions when it is assumed the dominant *Microcystis* will float to the surface (Wynne et al. 2010). The CI was calculated for each pixel in 10-d composite images and then averaged by pixel from June–August 2013–2015.

The CI has been calibrated with field radiometry (Wynne et al. 2008) and same day cyanobacteria cell counts (Wynne et al. 2010). Published model validation also included other inland freshwater bodies (Lunetta et al. 2015) and simulation tests (Wynne et al. 2011). The results from the Medium Resolution Imaging Spectrometer (MERIS) and MODIS sensors were comparable when corrections were made (Wynne et al. 2013). This index has been used extensively in Lake Erie for determining annual bloom severity and for analyzing causes of bloom severity, seasonal bloom forecasting, and for short term forecasting and real-time warnings (Stumpf et al. 2012; NOAA 2014; Wynne and Stumpf 2015).

Cyanobacterial biovolumes

The CI is only able to directly measure conditions at the surface. As the mussel cages and Hester-Dendy samplers sit ~ 1 m off the bottom, we also measured cyanobacterial abundance using direct measurements of phytoplankton biovolume (BV) at a limited number of sites. Phytoplankton samples were collected using an integrating tube from the surface to the thermocline or to 1 m above the bottom if no thermocline was present. One hundred fifty milliliters samples were preserved in Lugol's Iodide solution within 4 h of collection and stored in the dark until analysis. Samples were analyzed for phytoplankton abundance, BV, and community composition by membrane filtration and microscopy by BSA Environmental, using a 400 natural unit threshold for counts and measuring 10 specimens of each taxon in each sample to obtain BV estimates. BV of all cyanobacteria taxa were summed for the present analysis.

Microcystin concentrations

Water samples for microcystin analysis were collected using an integrating tube from the surface to the thermocline, or to 1 m above the bottom if no thermocline was present. Total microcystin concentrations (MC) were evaluated in surface water samples screened by the Abraxis, LLC ADDA polyclonal enzyme-linked immunosorbent assay (ELISA) (Warminster, Pennsylvania). Methods have been previously reported (Loftin et al. 2016). Briefly, total microcystin samples were collected as whole water and frozen. Samples were shipped overnight to the U.S. Geological Survey Organic Geochemistry Research Laboratory (Lawrence, Kansas; 2014–2015 samples) or were retained at the U.S. Geological Survey Great Lakes Science Center (Ann Arbor, Michigan; 2013 samples). Samples were sequentially freeze-thawed (–20°C/25°C) three times in the absence of ambient light followed by syringe filtration with 0.7-micron glass fiber filters. All processed samples were stored frozen (–20°C) prior to analysis by ELISA. The minimum reporting level (MRL) for microcystin-LR equivalents reported by ELISA was 0.10 μg/L. Quality assurance included reanalysis of ~ 10% of samples. All kit controls and sample replicates had to be within 28.3% relative standard deviation (RSD) and kit diluent with values below the MRL for an analysis to be considered acceptable. Values higher than the maximum calibration standard of 5.00 μg/L were diluted back on to the calibration curve. The calibration curve was fit using a four-parameter curve. At times, microcystin values were below the minimum reporting level (0.10 μg/L) so summer-long site means were calculated using Kaplan-Meier methods as suggested by (Helsel 2005).

Statistical analysis

All statistical analyses were performed in R (R Development Core Team 2014). Pearson's correlation coefficients were calculated with the base R statistical function cor().

To assess cyanobacteria effects on our indices of secondary production we fit regression models that had the following form:

$$P = b * C + Y$$

where P is the index of secondary production (*L. siliquoidea* growth, average dreissenid mussel size, or the total mass of animals on the Hester-Dendy); C is the cyanobacterial data (cyanobacterial BV, the CI or microcystin concentration); b

Table 1. Associations between cyanobacterial data and three indices of secondary production. Measures of cyanobacterial abundance are cyanobacterial biovolume (BV) and the cyanobacterial index (CI; derived from satellite data). Cyanotoxin concentration is indicated by microcystin concentration (MC). Both standardized slopes (*b*, with 95% confidence intervals) and the marginal R^2 of regression models that include the indicated cyanobacterial data are reported as indications of the effect size. The number of observations is listed as the *N*. Models relating cyanobacterial data to *L. siliquoidea* growth are multi-level with year-specific differences to account for differences among year in *L. siliquoidea* cohorts (Y_{INT}).

Index of secondary production	Effect	*N*	*b*	Marginal R^2
L. siliquoidea growth	BV (Y_{INT})	25	−0.37 (–0.60, −0.12)	0.16
	CI (Y_{INT})	201	−0.23 (–0.38, −0.09)	0.05
	MC (Y_{INT})	45	−0.42 (–0.66, −0.17)	0.19
Average dreissenid mussel mass	BV	11	−0.08 (–0.83, 0.67)	0.01
	CI	57	−0.26 (–0.53, −0.004)	0.07
	MC	15	−0.35 (–0.89, 0.19)	0.12
Total Hester-Dendy animal mass	BV	11	−0.61 (–1.21, −0.01)	0.37
	CI	57	−0.29 (–0.55, −0.03)	0.08
	MC	15	−0.73 (–1.12, −0.34)	0.54

is the standardized coefficient relating *C* to *P*; and *Y* is an intercept term. We interpret *b* values < 0.1 to be near zero, *b* values between 0.1 and 0.4 to be weak effects, and *b* between 0.4 and 0.8 to be moderate effects. When *P* was derived from the Hester-Dendy sampler, *Y* is a simple constant. When *P* is *L. siliquoidea* growth, *Y* was allowed to vary by year (i.e., instead of a simple linear model, we used a mixed effects model with year as a grouping variable). This is because mussels differed in age or origin among years. These differences in mussel ages and origins are reflected in substantial differences in initial size and perhaps some differences in the range of potential growth rates (Supporting Information Fig. S2). Mixed effects models were fit using the "lme4" package in R (Bates et al. 2015), and marginal R^2 values were calculated using the methods of Nakagawa and Schielzeth (2013) as implemented in the piecewiseSEM package in R (Lefcheck 2016). Simple linear models were fit using the base R function lm() (see details in the Supporting Information Statistical Appendix).

Inspection of diagnostic plots suggested that residuals from models using untransformed data were non-normal and did not meet the assumption of homoscedasticity. Natural log transformations were performed on these data which resulted in diagnostic plots that did not reveal any serious deviations from model assumptions (see details in the Supporting Information Statistical Appendix). After log transformation, data were standardized so that each variable had a mean 0 and a standard deviation of 1, so that standardized slopes could be calculated (see Supporting Information Table S2)T. Standardized coefficients (or beta coefficients) are then comparable despite differences in the underlying measurement scale (Hair et al. 1998).

To incorporate the possibility that water temperature might influence our ability to detect cyanobacterial effects, we ran the regression models described above that include the CI with degree days above 15°C (DD15) as a covariate. For other cyanobacterial data, there were too few observations to parameterize a multiple regression model (Hair et al. 1998).

All of the data used in the statistical analysis are available in the data appendix (doi: 10.5066/F7G15ZB8).

Results

Prediction 1: Secondary production negatively associated with cyanobacterial abundance

Cyanobacterial abundance was measured using either direct measurements of cyanobacterial BV or the CI. BV was negatively related to all three indices of secondary production, but this association was near-zero for average dreissenid mussel mass ($b = -0.08$) and weak for *L. siliquoidea* growth ($b = -0.37$; Table 1). The effect size of the association between BV and total Hester-Dendy dry mass was moderate ($b = -0.61$; Table 1). By contrast, the CI had weak associations with *L. siliquoidea* growth ($b = -0.21$), the average dreissenid mussel mass ($b = -0.26$), and total Hester-Dendy dry mass ($b = -0.29$; Table 1; Fig. 2). Of the six different secondary production-cyanobacterial abundance models, only the one relating BV to total Hester-Dendy dry mass explained more than 20% of the variation in the index of secondary production ($R^2 = 0.37$; Table 1). Somewhat unexpectedly, the CI and measured BVs were not strongly correlated at sites where they overlapped (Pearson's $r = -0.20$), perhaps reflecting differences in cell counts (CI) vs. BV.

Prediction 2: Secondary production negatively associated with cyanotoxins

Water column MC were measured at six sites over 3 yr. The standardized coefficient for MC suggested a weak effect on average dreissenid mussel mass (–0.35), but moderate effects for *L. siliquoidea* growth and total Hester-Dendy

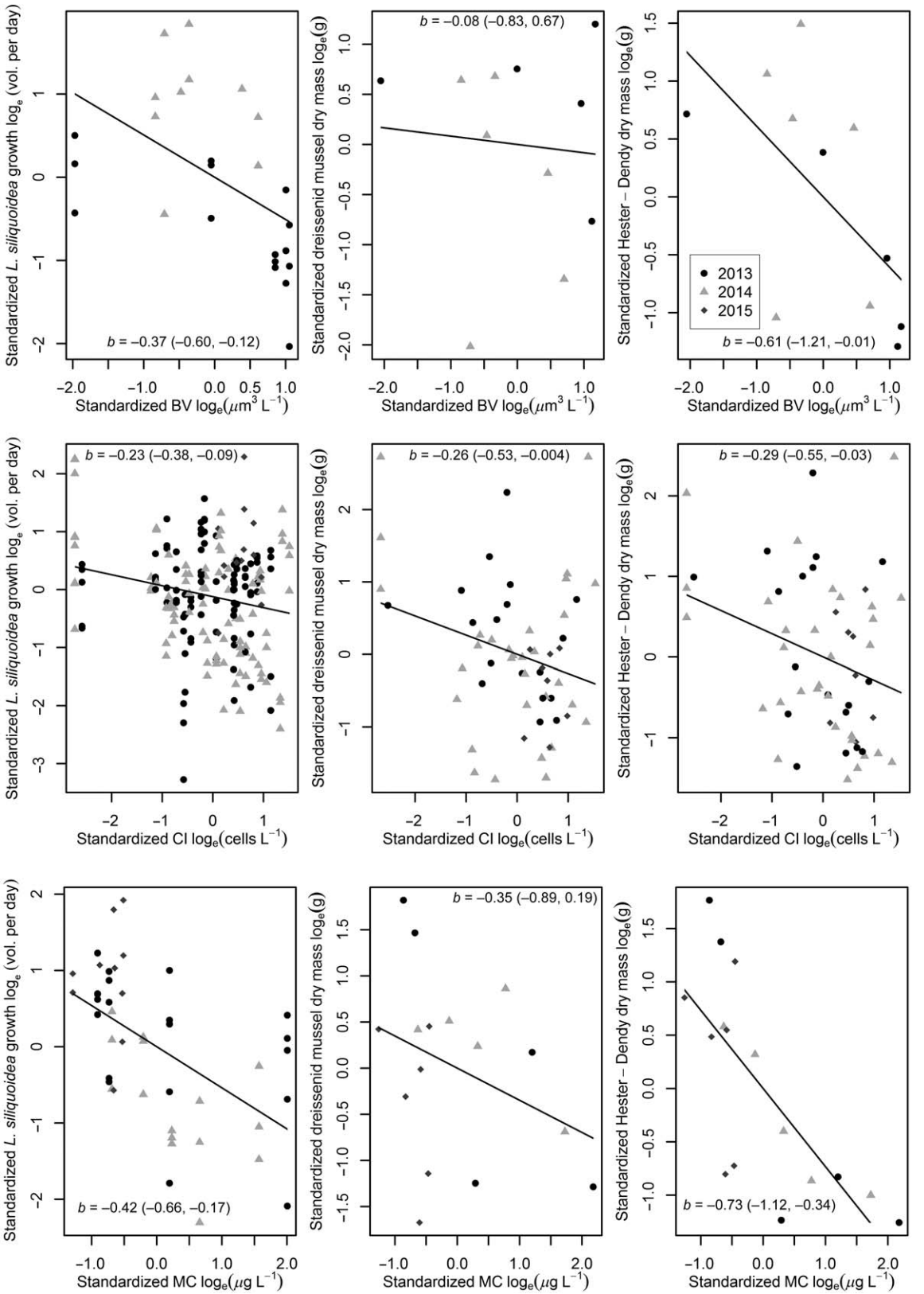

Fig. 2. Plots of associations between indices of secondary production (*L. siliquoidea* growth, dreissenid mussel average dry mass, and total Hester-Dendy dry mass) and cyanobacterial data (cyanobacterial biovolume, cyanobaterial index, and microcystin concentration). Solid lines are the fitted regression between cyanobacterial data and secondary production, with the standardized slope with 95% confidence interval (*b*). BV, cyanobacterial biovolume; CI, cyanobacterial index; MC, microcystin concentration.

Table 2. Associations between the cyanobacterial index (CI) and three indices of secondary production with degree days (15°; DD15) as a co-variate. The standardized slopes (b and b_{DD15}, with 95% confidence intervals) and the marginal R^2 of regression models that include the indicated cyanobacterial data are reported as indications of the effect size. The number of observations is listed as the *N*. The model relating CI to *L. siliquoidea* growth is multi-level with year-specific differences to account for differences among year in *L. siliquoidea* cohorts (Y_{INT}).

Index of secondary production	Effect	*N*	b_{DD15}	b	R^2
L. siliquoidea growth	CI (Y_{INT})	98	0.43 (0.23,0.61)	−0.45 (–0.62, −0.26)	0.21
Average dreissenid mussel mass	CI	36	0.49 (0.12,0.86)	−0.40 (–0.76, −0.05)	0.22
Total Hester-Dendy animal mass	CI	36	0.42 (0.09,0.74)	−0.36 (–0.67, −0.05)	0.21

animal mass (–0.42 and −0.73, respectively; Table 1; Fig. 2). The associations between MC and indices of secondary production were always stronger than the associations between cyanobacterial abundance and secondary production, although differences in these effect sizes were not always large. Variation in both *L. siliquoidea* growth and total Hester-Dendy mass was explained more by MC than by either CI or BV (Table 1; Fig. 2).

The role of water temperature

Water temperature data were only collected at a subset of the sites for which cyanobacterial data are available, and therefore estimates of b in Table 2 are only available for the CI (i.e., the cyanobacteria metric for which we have the most data). These models that included temperature did have estimates of b that were slightly higher than those without temperature, especially for *L. siliquoidea* growth, but confidence intervals for those estimates had considerable overlap (Tables 1, 2). Temperature itself had a moderate positive effect on all three indices of secondary production (Table 2).

Discussion

In reviewing the available literature, we have been unable to find any studies that measured in situ associations between secondary production and cyanobacteria. The intention here was to measure the effect of cyanobacteria on three indices of secondary production that would reflect the invertebrate community present in Lake Erie. The reality is that these indices are best reflective of the effects of cyanobacteria on bivalves (specifically, unionid and dreissenid mussels). However, the one study that seems to have quantified total secondary production in Lake Erie since the arrival of dreissenid mussels concluded that dreissenid mussels make up a very high proportion of the total secondary production in the western basin of Lake Erie (Johannsson et al. 2000). Furthermore, while dreissenid mussels have occasionally been labeled a dead end trophic pathway in the Great Lakes, this view has probably been overstated (Madenjian et al. 2010) and the introduction of Round Goby (*Neogobius melanostomus*) provides a pathway for dreissenid mussel biomass to move into the higher food web (Johnson et al. 2005). Therefore, while our indices of secondary production may be limited taxonomically, these indices likely reflect the dominant taxa and an important source of resources for higher trophic levels in Lake Erie.

Experimental and field work has suggested that cyanobacteria negatively impact secondary production in consumers by providing poor-quality food resources that limit invertebrate growth rates and by producing harmful toxins that impair invertebrate growth. If these hypotheses are true, then we would anticipate cyanobacterial abundance and microcystin concentration would be negatively associated with indices of secondary production. In our study, all of the associations we examined between cyanobacteria and secondary production were negative, but the magnitude of these negative effects varied substantially. Five of six associations between our indices of secondary production and cyanobacterial abundance suggest near-zero or weak effects. In the context of our hypothesis, this suggests that in Lake Erie, variation in food quality caused by cyanobacterial abundance has only a small effect on spatial variation in secondary production. By contrast, two of three effect sizes of microcystin concentration were moderate and the other was weak. This suggests that variation in microcystin concentration has a larger influence on spatial variation in invertebrate growth rates in Lake Erie, at least for the dominant bivalve species.

Dreissenid mussels may be unusually resilient to the negative impacts of cyanobacteria. Although there is ample evidence that microcystin is toxic to dreissenid mussels (Juhel et al. 2006), bivalves in general appear to be less vulnerable to microcystins than some other invertebrates (see review in Bownik 2016). Dreissenids also appear to be more resilient to microcystin than unionid bivalves (Burmester et al. 2012). Mussels appear to primarily react to microcystin via food (Yokoyama and Park 2002), but dreissenid mussels are known to "sort" their food, often rejecting *Microcystis* colonies (although this sorting may be based on size not toxicity; Vanderploeg et al. 2001). For these reasons, the dreissenid-dominated invertebrate community of western Lake Erie may be more resilient to effects of microcystin than communities where dreissenids have not yet invaded or do not dominate. Despite this presumed resilience, Lake Erie invertebrates still appear to be negatively impacted by microcystin.

Dreissenid mussels dominated our "whole-community" index of secondary production. However, dreissenid mussel

size and the whole community mass did not respond the same way to cyanobacteria. Why might these responses differ? We think the total mass on the Hester-Dendy sampler probably reflects a combination of processes that could each be affected by cyanobacteria for different reasons. For dreissenid mussels to colonize a Hester-Dendy there needs to be veligers present in the water column, those veligers need to transition to settlement on the sampler, and they need to survive and grow after attachment. By contrast, the average dreissenid mussel size only reflects growth after attachment (since they are all approximately the same size at settlement). Cyanobacterial effects on dreissenid mussel size were always less than effects on the total Hester-Dendy mass, suggesting that veliger abundance or settlement is more negatively impacted than growth. Microcystin is known to inhibit the reproduction of other bivalves (Boltovskoy et al. 2013), so perhaps in this case microcystin reduces the viability of dreissenid veligers or the ability of adults to produce veligers. By contrast, dreissenid growth rates may be simply be more heavily influenced by other factors (e.g., crowding).

Spatial and temporal variation in cyanobacteria primary production and microcystin production is strongly associated with variation in nutrient concentrations, temperature and other environmental conditions (O'Neil et al. 2012; Ekvall et al. 2013; Davis et al. 2015). These factors may influence secondary production via effects on cyanobacteria, or may influence secondary production directly. Temperature, for example, is often positively correlated with both cyanobacterial abundance and mussel growth (Hanson et al. 1988; O'Neil et al. 2012), potentially complicating univariate effect measurements, but incorporating temperature into our models only slightly altered estimates of cyanobacterial effects. Field studies rely on existing, real-world gradients in driving factors, which can limit a study's ability to separate direct from indirect effects or co-varying effects. In the case of cyanobacterial effects on invertebrates, there is strong evidence from mechanistic studies that bivalves can be harmed by cyanotoxins (Juhel et al. 2007, 2015; Bownik 2016), so the observed cyanobacterial effects certainly seem plausible.

The increasing frequency of cyanobacteria is a major concern to managers of many aquatic ecosystems because they have major impacts on a variety of ecosystem services (Smith 2003; Smith and Schindler 2009). For example, cyanobacterial blooms in Lake Erie have been associated with disruptions to the drinking water supply (Wilson 2014; Bullerjahn et al. 2016). This analysis suggests that naturally occurring cyanobacteria are negatively impacting secondary production in Lake Erie as well. The potential impacts we observed are independent of any direct impacts of cyanotoxins on fish, but suggest ecosystem services derived from the fish community may be vulnerable under current conditions. Ecosystem services could also be impaired by the accumulation of cyanotoxins in fish tissues at levels that may not be harmful to fish but are harmful to humans (Poste et al. 2011).

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Conflict of Interest

None declared.

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