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Measuring spatial variation in secondary production and food quality using a common consumer approach in Lake Erie

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Abstract. Lake Erie is a large lake straddling the border of the USA and Canada that has become increasingly eutrophic in recent years. Eutrophication is particularly focused in the shallow western basin. The western basin of Lake Erie is hydrodynamically similar to a large estuary, with riverine inputs from the Detroit and Maumee Rivers mixing together and creating gradients in chemical and physical conditions. This study was driven by two questions: (1) How does secondary production and food quality for consumers vary across this large mixing zone? and (2) Are there correlations between cyanobacterial abundance and secondary production or food quality for consumers? Measuring spatial and temporal variation in secondary production and food quality is difficult for a variety of logistical reasons, so here a common consumer approach was used. In a common consumer approach, individuals of a single species are raised under similar conditions until placed in the field across environmental gradients of interest. After some period of exposure, the response of that common consumer is measured to provide an index of spatial variation in conditions. Here, a freshwater mussel (*Lampsilis siliquoidea*) was deployed at 32 locations that spanned habitat types and a gradient in cyanobacterial abundance in the western basin of Lake Erie to measure spatial variation in growth (an index of secondary production) and fatty acid (FA) content (an index of food quality). We found secondary production was highest within the Maumee river mouth and lowest in the open waters of the lake. Mussel tissues in the Maumee river mouth also included more eicosapentaenoic and docosapentaenoic fatty acids (EPA and DPA, respectively), but fewer bacterial FAs, suggesting more algae at the base of the food web in the Maumee river mouth compared to open lake sites. The satellite-derived estimate of cyanobacterial abundance was not correlated to secondary production, but was positively related to EPA and DPA content in the mussels, suggesting more of these important FAs in locations with more cyanobacteria. These results suggest that growth of secondary consumers and the availability of important fatty acids in the western basin are centered on the Maumee river mouth.

Key words: *ecosystem process; fatty acids; Lake Erie;* Lampsilis siliquoidea; *nearshore; river mouths.*

Introduction

Lake Erie is a Laurentian Great Lake on the border between the USA and Canada with a productive fishery that accounts for US$7 billion in economic activity in commercial and recreational fishing (USDA 2005). Unlike other Great Lakes (Evans et al. 2011), Lake Erie has become increasingly eutrophic in recent years (Michalak et al. 2013, Steffen et al. 2014). Eutrophic conditions are particularly intense in the western basin of Lake Erie (Stumpf et al. 2012, Michalak et al. 2013). The western basin is hydrodynamically similar to a large estuary, with riverine inputs from the nutrient-rich Maumee River and the low-nutrient (by concentration) Detroit River mixing together and creating gradients in chemical and physical conditions (Moorhead et al. 2008). These spatial gradients in conditions result in spatial gradients in the abundance and composition of primary producers (Bridgeman et al. 2012, Steffen et al. 2014). The effect of these gradients on other ecological processes is less well understood. This study had two main questions: (1) How does secondary production and food quality for consumers vary across this large mixing zone? and (2) Are there correlations between cyanobacterial abundance and secondary production or food quality for consumers?

To address our research questions, we opted to use a common consumer approach. In this approach, animals of similar condition are placed across a gradient of interest (e.g., cyanobacterial abundance), allowed some period of time to react and then reactions are measured across that gradient. This is analogous to the sentinel species approach, where variation in the properties of a naturally occurring

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species is used to infer something about ecosystem properties (e.g., Hunt and Slone 2010, Larson et al. 2013). However, use of individuals from a common source population solves several problems facing the sentinel species approach. For example, natural populations may not occur across the gradient of interest, longer-lived species may be responding to conditions from before the study period, and genetic differences in resident populations may occur.

As our common consumer, we used a unionid mussel (*Lampsilis siliquoidea*). *Lampsilis siliquoidea* occurs widely throughout North America in varied habitats (NatureServe 2014) and is often propagated for use in experimental studies (e.g., Wang et al. 2007). Unionid mussels also appear to consume similar food resources and occupy a similar ecological niche as dreissenid mussels (Baker and Levinton 2003). *Dreissena polymorpha* and *D. rostriformis bugensis* may be the most important primary consumers in Lake Erie, heavily impacting nutrient dynamics, light penetration, phytoplankton abundance, and other ecosystem properties (North et al. 2012, Ozersky et al. 2013). Previous studies have also suggested that dreissenids make up a large fraction of total benthic secondary production (~90% at times; Johannsson et al. 2000). Unfortunately, using dreissenids directly as a common consumer is difficult. Dreissenids are not reared in hatchery systems, and, as invasive species, moving individuals is complicated legally. Dreissenids also begin diverting resources into reproduction at very small sizes (<5 mm; Mackie 1993), making sampling very difficult. Logistically, it is also difficult to distinguish experimental dreissenids from dreissenids that would colonize substrates after deployment. For these reasons, unionids seemed to be a more suitable choice, and we inferred that spatial variation in the growth of unionids was an index of variation in secondary production in Lake Erie. However, we also looked at the size of colonizing dreissenids as a comparison to unionid growth.

Certain aspects of food quality can also be indexed with the common consumer approach. For example, consumer fatty acid (FA) content varies considerably in response to the FAs available in the food supply (Iverson 2009). As a result, consumer FA content has often been used as a biomarker of food sources (Iverson 2009) and as an indicator of habitat quality (Larson et al. 2015). Fatty acids are an important aspect of food quality for consumers because most metazoans cannot synthesize de novo many of the long-chained polyunsaturated FAs (PUFAs) necessary for development and immune system function (Ahlgren et al. 2009, Arts and Kohler 2009). Polyunsaturated FAs such as eicosapaentanoic acid (EPA) and docosahexaenoic acid (DHA) must be obtained from the diet or produced at great energetic cost from shorter chained precursors such as α-linolenic acid (ALA; Parrish 2009). Studies on the abilities of freshwater mussels to elongate precursors into metabolically essential PUFAs are lacking. Unionids do appear to have large quantities of arachidonic acid (ARA; Newton et al. 2013), and it is likely that mussels do manipulate tissue FA content to some degree relative to the food supply. The presumption of the common consumer approach is that the individuals sampled would have similar responses to a given food. For example, we assume that if EPA content of the food supply increased, individual mussels would generally respond to that change in a similar manner. By measuring spatial variation in the FA content of our common consumer, we infer this relates to spatial variation in the FA content of the available food resources and is also an indication of the food quality available to higher trophic levels (i.e., predators of unionids and other filter feeders).

Methods

Study sites

Mussel cages were deployed at 39 sites from the Maumee river mouth into the western basin of Lake Erie. Of these 39 deployments, 32 were successfully recovered (Fig. 1). During deployment, one cage was placed at each site, and between four and 10 sites were placed by a single crew each day. Cages were deployed from 1 June–4 June in six groups. Retrievals occurred from 26 August–29 August. Sites were grouped into three habitat types: the channelized portion of the Maumee River mouth (RM, sites 1–8), the greater Maumee Bay (MB, sites 12–18 and 20), and the open waters of the western basin (OL, the remaining sites; Fig. 1). These habitat types represent areas with relatively consistent unidirectional flow (RM sites), deeper and more lentic conditions (OL sites), and conditions that are intermediate between these (MB sites).

Unionid mussel cages

Unionid mussel cages were made using plastic-coated mesh with diamond-shaped openings having a maximum width of 1.4 cm. A 25 cm tall piece of mesh was wrapped into a cylindrical shape around two PVC drain caps (approximately 10 cm in diameter) 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 halfway between buoy and the cement block. For sites with <2 m depth, buoys and cages were slightly closer to the bottom to minimize navigation hazard. The cement anchor was connected to a second cement block to form a dual anchoring system to facilitate retrieval. Deployment and retrieval (via grappling hook) were conducted from the surface.

Unionid mussels

Lampsilis siliquoidea used in this study were part of the cohort analyzed for size variability in Larson et al. (2014). Larval unionid mussels are parasitic, being released from gravid females to fish gills via a variety of mechanisms. Mussels for this study were reared artificially from gravid females collected from the St. Croix River in April 2011 and

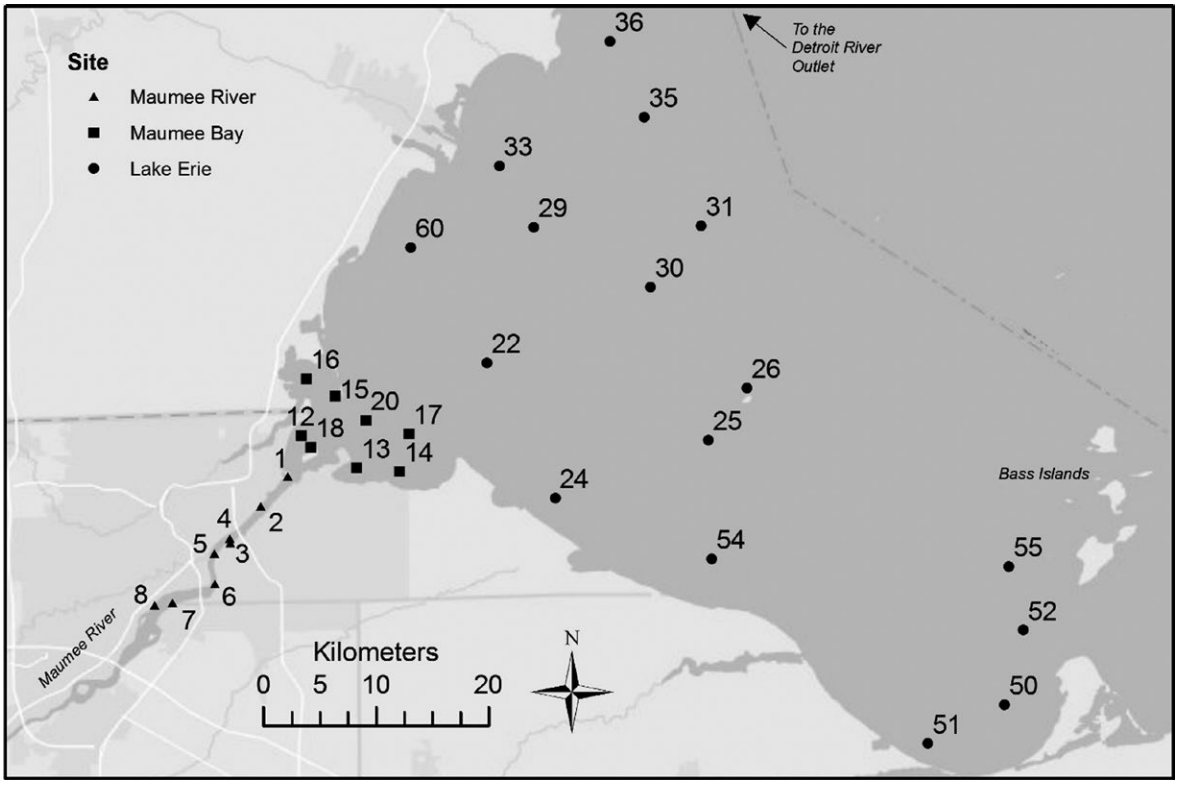

FIG. 1. Sites where caged *Lampsilis siliquoidea* were deployed in the western basin of Lake Erie during the summer of 2013.

used to inoculate largemouth bass *Micropterus salmoides* at Genoa National Fish Hatchery (GNFH; Genoa, Wisconsin, USA). Initially the host fish were placed in enclosures in the St. Croix River (Wisconsin, USA), and mussels that transformed from parasitic to juvenile stage were retrieved in September 2012. From September 2012 to May 2013, mussels were kept in raceways at the GNFH supplied by pond water at ambient temperatures. Prior to use in this study, mussels were depurated for 2 weeks in groundwater. Initial size of mussels was 38.6 mm (standard deviation 4.0).

Mussels used in this study were randomly assigned to cages. Five individually marked mussels were placed in each cage. Marking was done using an electric grinding tool. Mussel shell dimensions were measured as in Larson et al. (2014): Length, width, and height were all recorded using a digital caliper that reported to the nearest 0.01 mm. Length here 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. Mussel shell dimensions were measured at the beginning and end of deployment as an index of secondary production.

Six extra cages were prepared, carried into the field, and then returned to the lab and sampled as a quality control sample (QC). Each quality control cage contained five mussels for a total of 30 QC samples. All control mussels appeared healthy when sampled.

After retrieval (or after deploying mussels for the quality control samples), mussel foot tissues were sampled for the purpose of fatty acid analysis by cutting the adductor muscles and then removing as much of the foot tissue as could be obtained without disturbing or including other tissue types. Foot tissue was immediately placed into individually labeled cryovials, frozen in liquid nitrogen, and brought back to the Upper Midwest Environmental Sciences Center (UMESC; La Crosse, Wisconsin, USA) for lipid analysis. Dissection equipment was rinsed with ethanol and wiped down with disposable tissues between individual samples. None of the recovered individuals showed obvious signs of sexual development.

Dreissenid mussels

At each site we attached a modified Hester-Dendy sampler (Hester and Dendy 1962) to the rope directly beneath the unionid cage and above the cement block to measure the size of dreissenid mussels 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 and placed into 2-L 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. Dreissenid mussel abundance was counted on subsamples of the scraped biota, and dreissenid mussels were then lumped together by station to measure mass. Dreissenids were dried for >24 h at 60°C and then weighed to the nearest 0.01 g on a balance that was calibrated daily. When dreissenid abundance was extremely low (<10 individuals), dry mass was not measured.

Lipid analysis

Lipid analysis followed methods previously described in Larson et al. (2013). After being returned to UMESC, mussel foot tissue samples were freeze dried in a Virtis freeze dryer (SP Scientific; Gardiner, New York, USA) and stored at −80°C until analysis. Tissues were homogenized by grinding in liquid nitrogen in preparation for FA analysis. On about 4.5% of the samples, we ran procedural replicates (i.e., splitting the sample in half and separately extracting and methylating each half). These replicates showed small variation (<2%) in total FAs. Procedural replicates were averaged for a single sample. Raw data for all FA samples (including replicates) are included in the data appendix (*available online*).[5]

A total of 42 fatty-acid methyl esters (FAME) were identified in the unionid foot tissues by comparison of their retention times with known standards (see data appendix for complete list). Only unionid foot tissue FAs were measured in this study. The nomenclature *A*:*B*n-*C* is used, where *A* is the number of carbon atoms, *B* is the number of double bonds, and *C* is the position of the first double-bond relative to the terminal (n) methyl carbon atom. Structurally, FAs vary in the length of the carbon (C) chain, the number of unsaturated C-C bonds (i.e., a double bond between adjacent C atoms), and the position of the unsaturated C-C bonds (Parrish 1998). Of the 42 fatty acids measured in unionid foot tissue, five FAs thought to be important for many consumers were individually used as indicators of FA quality in the mussel food supply (Brett and Muller-Navarra 1997, Parrish 2009): 18:3n-3 α-linolenic acid (ALA), 20:4n-6 arachidonic acid (ARA), 20:5n-3 eicosapentaneoic acid (EPA), 22:5n-3 docosapentaenoic acid (DPA), and 22:6n-3 docosahexaenoic acid (DHA). Several other FA metrics that are thought to be indicative of FA sources or quality were also calculated for the mussel foot tissue. We calculated total PUFAs (18:2n-6, 18:3n-3, 18:3n-6, 20:2n-6, 20:3n-3, 20:3n-6, 20:3n-9, 20:4n-6, 20:5n-3, 22:2n-6, 22:4n-6, 22:5n-3, 22:5n-6, 22:6n3) as well as the unsaturation index (UI), by taking the mass fraction of each FA and multiplying by the number of double bonds and then summing across all FA; similar to Novo and Fonseca (1989). PUFAs and UI are thought to be higher in algal than terrestrial or cyanobacterial sources (Ahlgren et al. 2009). Several odd-chain, branched, or uncommon isomers were summed and used as an indicator of bacterial FA sources (Ederington et al. 1995, Napolitano 1999): 14:0 iso, 15:0, 15:0 ante-iso, 15:0 iso, 16:0 ante-iso, 16:0 iso, 17:0, 17:0 anteiso, cis-9, 10-methylenehexadecanoic acid (17:0d9d10), 17:0 iso, and 19:0. Mussel FAs are reported as μg FAME/mg dry mass.

Cyanobacterial index

For stations surrounded by sufficient open water, a satellite-derived cyanobacteria index (cells/mL) was used as an explanatory variable for mussel response. This index could not be used for 13 near shore sites because the corresponding satellite pixel was dominated by land (RM sites and Maumee Bay sites 12–14, 16, and 18). For the remaining 19 sites, we used the CI described in Wynne et al. (2010) and Stumpf et al. (2012) adapted to use Moderate Resolution Imaging Spectroradiometer (MODIS) imagery (Wynne et al. 2013). The cyanobacteria index was calculated for each pixel in 10-d composite images then averaged by pixel from June to August 2013.

This cyanobacteria index has been calibrated with in situ field radiometry (Wynne et al. 2008) and same day cell counts (Wynne et al. 2010). Published model validation also includes other inland freshwater bodies (Lunetta et al. 2015) and simulation tests (Wynne et al. 2011). The results from the MERIS and MODIS sensors are comparable when corrections are done (Wynne et al. 2013). This index has been used extensively in Lake Erie for determining annual bloom severity and 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).

Statistical methods

All statistical analyses were performed in R (R Core Team 2014). Average, standard deviation (SD), coefficient of variation (CV), and 95% credible intervals were estimated using a Bayesian approach described by McCarthy (2007) and implemented using the BRugs package in R (Best and Lunn 2007), which connects R to OpenBUGS (Thomas et al. 2006). Differences among habitat types were evaluated by comparing 95% credible intervals of response variables among habitats (i.e., if 95% credible intervals did not overlap, we considered differences significant). Bayesian correlation coefficients (with 95% credible intervals) were generated using the BayesianFirstAid package (Bååth 2014); these correlation coefficients have uninformative priors. Correlations were done between unionid response variables and (1) other unionid response variables, (2) dreissenid mass, and (3) the cyanobacterial index. Data used in this analysis and additional details related to the statistical procedures used here are available in the data appendix (see footnote 5).

Maps of the spatial distribution of growth and FA metrics across the western basin of Lake Erie were generated using the "Spline with Barriers" spatial analyst function in ArcMap (ESRI 2011). The barrier in this case was drawn

[5] http://dx.doi.org/10.5066/F7BZ6426

to match the boundaries of Lake Erie and the Maumee River (exact barrier shape-file available upon request).

Results

Unionid mussel growth

Of the 160 mussels recovered from the field deployed cages, only one was dead (an individual noted as slightly malformed when deployed did not appear to grow after deployment). Some unionid mussel shells grew in a non-typical fashion, perhaps due to high densities of dreissenid mussels colonizing the cages and individual mussels. Mussel shells in these conditions had skewed length to width ratios. The average length:width ratio of the mussels initially was $2.84_{[2.82–2.86]}$ (95% credible interval) with a coefficient of variation (CV) of 0.8%, while the length:width ratio of the mussels after field deployment was $2.60_{[2.57–2.63]}$ with a CV of 1.6%. Because mussel shape varied in this way, we used an index of volume (length × width × height) instead of shell length or width to estimate growth. However, variation in length, width, or height were all strongly correlated to volume, so choice of growth index does not impact the results substantially (Bayesian correlation = $0.96_{[0.95–0.97]}$, $0.95_{[0.93–0.97]}$, and $0.96_{[0.95–0.97]}$, respectively).

All mussels that survived increased their volume. Reported as a percent increase from initial size, these increases ranged from 1.6% to 266.2%. Mean percent growth was $63.6\%_{[55.1–72.1\%]}$ for all field samples. Comparisons across habitat types revealed significant differences. Average growth of mussels deployed in the channelized portion of the river mouth (RM sites) was 125.2% (95% credible interval, 105.6–144.5%), while growth of mussels from the Maumee Bay (MB) and open waters of Lake Erie (OL) were considerably lower (MB sites = $53.5\%_{[41.9–65.1\%]}$; OL sites = $37.3\%_{[31.6–42.9\%]}$). Site

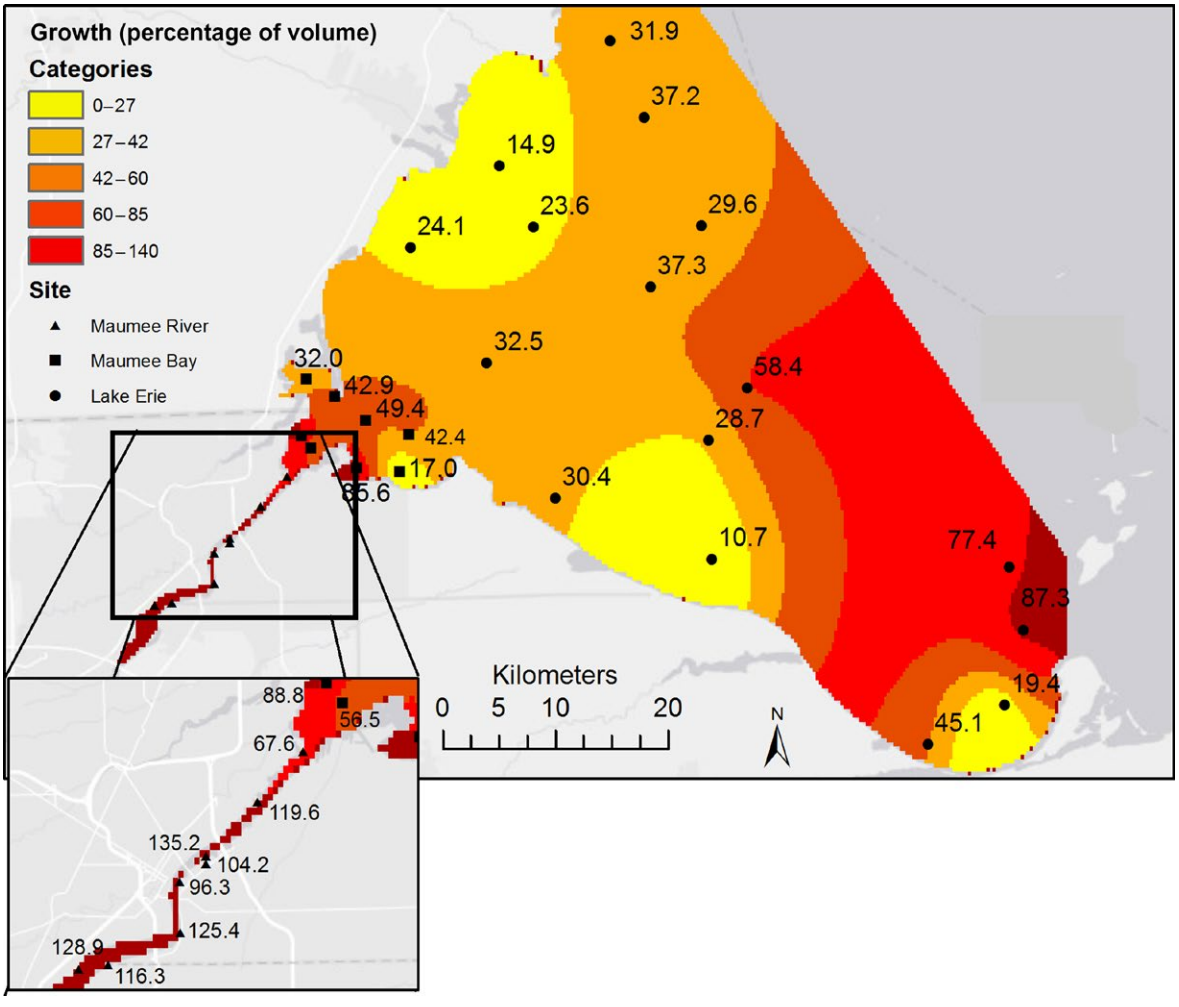

FIG. 2. Growth of mussels (percentage of increase in volume) from June to August of 2013. Caged *Lampsilis siliquoidea* were deployed at points in the western basin of Lake Erie. Color coding reflects interpolated growth value from measured sites. Site-average growth rates are shown for each site.

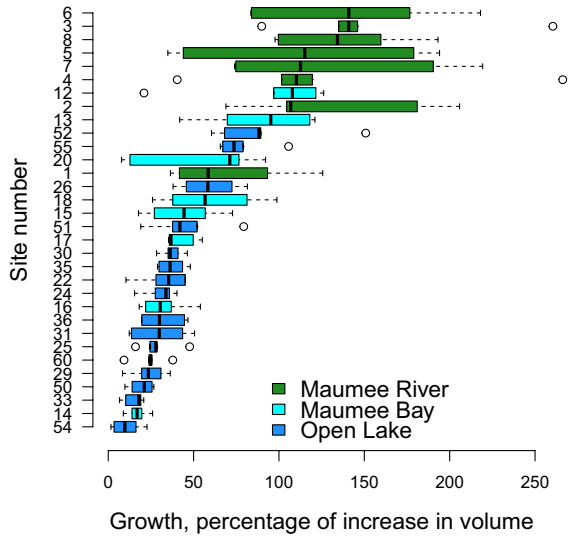

FIG. 3. Percentage of increase in mussel volume (length × width × height) by site in *Lampsilis siliquoidea* deployed in Lake Erie. The thick middle line is the median, and boxes encompass the first and third quartile. The lines (whiskers) show the largest or smallest observation that falls within 1.5 times the box size. Observations that fall outside the lines are shown individually. Each site had five individuals, except for site 18, which had four.

averages were highest in the river mouth and lower across much of the western basin, with a few exceptions near the Bass Islands (sites 55 and 52; Figs. 2 and 3).

Unionid mussel fatty acid composition

Palmitic acid (17.9%), ARA (15.2%), DPA (10.7%), and stearic acid (10.4%) together accounted for >50% of the total measureable fatty acids (FA) in mussel tissue, and 13 FA accounted for >90% of the total measurable FA in mussel tissue (see footnote 5). Most of the FA metrics measured here were lower in mussels after deployment in Lake Erie than in the mussels that were collected as initial controls (Table 1). The one exception to this trend was ALA, which was higher in field-exposed mussel tissues (Table 1).

Mussel FA composition differed significantly by habitat type (Table 2, Fig. 4). The ARA content of mussels increased from RM to MB to OL sites, while EPA decreased across those habitat types (i.e., no overlap of 95% credible intervals between habitat types; Table 2). Bacterial FAs were lower in the RM sites than the OL sites, with MB sites overlapping the other habitat types (Table 2). Mussels from the RM sites had a lower percentage of lipid than other habitat types (no overlap of 95% credible intervals). Mussel PUFA content and UI were highest in the MB sites, but the credible intervals did overlap with values observed in the OL and RM sites, respectively (Table 2).

Some FAs that are most likely derived from algal sources (EPA and DHA) showed strong positive correlations to unionid growth (percentage of increase in volume), while percentage of lipids, bacterial FAs, and ARA were negatively correlated with unionid growth (i.e., 95% credible intervals not overlapping 0; Fig. 5).

Dreissenid mussel abundance and size

Dreissenid length was not measured in this study, but the observed dreissenid mussels were small and likely to represent young-of-year individuals (see *Discussion*). Dreissenid mussel colonization of Hester-Dendy samplers in the RM sites was less than a tenth that in the MB or OL sites (Table 3). Because there were so few, dreissenid mussel masses were only measured for three of the eight RM sites. As a result, the estimate of RM dreissenid mussel size has a wide credible interval and overlaps the credible intervals

TABLE 1. Differences in fatty acids between mussels deployed in Lake Erie and mussels sampled prior to deployment. Negative differences indicate a decline from the initial samples to the field-deployed samples. Mean values (with 95% credible intervals) are reported.

Variable	Units	Initial mean	Field mean	Percentage of difference
ALA	µg/mg dry mass	$0.36_{[0.32–0.39]}$	$0.47_{[0.45–0.48]}$	$31.2_{[45.7–18.6]}$
ARA	µg/mg dry mass	$3.66_{[3.45–3.87]}$	$3.35_{[3.25–3.45]}$	$-8.4_{[-2.4\text{ to }-14]}$
EPA	µg/mg dry mass	$2.3_{[2.21–2.4]}$	$1.7_{[1.64–1.76]}$	$-26.0_{[-21.9\text{ to }-30]}$
DPA	µg/mg dry mass	$3.27_{[3.11–3.42]}$	$2.25_{[2.2–2.3]}$	$-31.0_{[-27.4\text{ to }-34.4]}$
DHA	µg/mg dry mass	$1.54_{[1.47–1.62]}$	$1.01_{[0.98–1.04]}$	$-34.6_{[-30.7\text{ to }-38.3]}$
UI†	no units	$60.83_{[58.33–63.31]}$	$46.99_{[46.24–47.74]}$	$-22.7_{[-19.2\text{ to }-26]}$
PUFAs‡	µg/mg dry mass	$13.73_{[13.14–14.32]}$	$11.12_{[10.94–11.29]}$	$-19_{[-15.2\text{ to }-22.6]}$
Bacterial FAs§	µg/mg dry mass	$1.64_{[1.50–1.77]}$	$1.27_{[1.21–1.33]}$	$-22.3_{[-14.6\text{ to }-29.3]}$
Percentage of lipids	percentage	$9.12_{[8.74–9.5]}$	$8.11_{[7.96–8.25]}$	$-11.1_{[-6.9\text{ to }-15.0]}$

†Unsaturation index.
‡Polyunsaturated fatty acids:18:2n-6, 18:3n-3, 18:3n-6, 20:2n-6, 20:3n-3, 20:3n-6, 20:3n-9, 20:4n-6, 20:5n-3, 22:2n-6, 22:4n-6, 22:5n-3, 22:5n-6, 22:6n3.
§Bacterial fatty acids: 14:0 iso, 15:0, 15:0 anteiso, 15:0 iso; 16:0 anteiso, 16:0 iso, 17:0, 17:0 anteiso, 17:0d9d10, 17:0 iso, 19:0.

TABLE 2. Differences in fatty acids between mussels deployed in the Maumee river mouth (RM), the Maumee Bay (MB), and the open waters of Lake Erie (OL). Mean values (with 95% credible intervals) are reported. Differences among habitat types are indicated by superscript letters.

Variable	Units	RM	MB	OL
ALA	µg/mg dry mass	$0.42_{[0.39–0.45]}^{a}$	$0.53_{[0.48–0.58]}^{b}$	$0.46_{[0.44–0.47]}^{a}$
ARA	µg/mg dry mass	$2.63_{[2.54–2.72]}^{a}$	$3.30_{[3.1–3.5]}^{b}$	$3.73_{[3.65–3.82]}^{c}$
EPA	µg/mg dry mass	$2.13_{[2.06–2.2]}^{a}$	$1.86_{[1.75–1.96]}^{b}$	$1.41_{[1.37–1.46]}^{c}$
DPA	µg/mg dry mass	$2.27_{[2.18–2.35]}^{a,b}$	$2.39_{[2.28–2.50]}^{a}$	$2.18_{[2.11–2.24]}^{b}$
DHA	µg/mg dry mass	$1.13_{[1.07–1.18]}^{a}$	$1.09_{[1.03–1.16]}^{a}$	$0.91_{[0.87–0.94]}^{b}$
UI†	no units	$46.71_{[45.6–47.83]}^{a,b}$	$49.05_{[47.41–50.7]}^{a}$	$46.13_{[45.03–47.24]}^{b}$
PUFAs‡	µg/mg dry mass	$10.71_{[10.47–10.96]}^{a}$	$11.49_{[11.09–11.9]}^{b}$	$11.13_{[10.87–11.39]}^{a,b}$
Bacterial FAs§	µg/mg dry mass	$1.15_{[1.07–1.22]}^{a}$	$1.25_{[1.13–1.37]}^{a,b}$	$1.34_{[1.25–1.43]}^{b}$
Percent lipids	percentage	$7.60_{[7.43–7.76]}^{a}$	$8.49_{[8.22–8.75]}^{b}$	$8.18_{[7.95–8.41]}^{b}$

†Unsaturation index.
‡Polyunsaturated fatty acids: 18:2n-6, 18:3n-3, 18:3n-6, 20:2n-6, 20:3n-3, 20:3n-6, 20:3n-9, 20:4n-6, 20:5n-3, 22:2n-6, 22:4n-6, 22:5n-3, 22:5n-6, 22:6n3.
§Bacterial fatty acids: 14:0 iso, 15:0, 15:0 anteiso, 15:0 iso; 16:0 anteiso, 16:0 iso, 17:0, 17:0 anteiso, 17:0d9d10, 17:0 iso, 19:0.

from MB and OL sites (Table 3). Unionid growth and dreissenid mussel mass (per individual) had a strong, positive correlation, suggesting that the same areas that were good for unionid growth were also good for dreissenid growth (Fig. 6). Unionid tissue FAs that were correlated to growth in the unionids were also correlated to larger size in dreissenid mussels from the same sites (Fig. 6).

Cyanobacteria and ecosystem properties

Across the 19 sites where cyanobacterial estimates could be made (Fig. 7), the EPA and DPA content of mussels was positively correlated to this measure of cyanobacterial abundance, as was the unsaturation index (Fig. 8). The 95% credible intervals for correlation coefficients of the other fatty acid metrics measured here overlapped zero. Correlations between cyanobacterial abundance and percentage of lipids and PUFAs had intervals that just barely overlapped zero with a >90% probability that they were also positively correlated. The correlation coefficient between cyanobacterial abundance and unionid growth was small and its 95% credible interval overlapped zero ($-0.11_{[-0.54\text{ to }0.35]}$; Fig. 8), although many of the high-growth sites were absent from this correlation estimate.

DISCUSSION

Each of the individual *L. siliquoidea* mussels deployed in this study was treated similarly up to the moment of deployment. As a result, spatial variation in their growth and fatty acid composition is related to differences in the environmental conditions (e.g., food quality, flow, cyanobacteria abundance, etc.) to which they were exposed during the three months they were in Lake Erie. We measured variation in *L. siliquoidea* growth as an index of the potential to support secondary production. This interpretation is supported by the observed correlations between growth rates of *L. siliquoidea* and the size (mass) of colonizing dreissenid mussels (Fig. 6). Size of the dreissenids collected here is itself likely a good indication of growth, because dreissenids colonizing the Hester-Dendy samplers probably represented first-year individuals. Adult dreissenid mussels are known to move (Toomey et al. 2002), but it seems unlikely they would climb the rope connecting the Hester-Dendy to the substrate. Considering the importance of dreissenids to Lake Erie secondary production (Johannsson et al. 2000), using *L. siliquoidea* growth as an index of spatial variation in potential secondary production appears reasonable. Variation in unionid FA content was used to characterize spatial differences in the availability of FA, both to other consumers that feed on seston and to predators that would potentially eat unionid mussels. These two metrics (growth and FA content) may be causatively linked, as appears to be the case for other invertebrates (Müller-Navarra et al. 2000, Taipale et al. 2013). Confirming this is the case would require experimental work similar to that done previously for *Daphnia* spp. (Galloway et al. 2014). Regardless of causal links between growth and FA content, these individual metrics can identify some of the drivers of ecosystem variation in Lake Erie.

How does secondary production and food quality for consumers vary across this large mixing zone (the western basin of Lake Erie)?

Sites in the channelized portion of the Maumee river mouth had the highest secondary production (i.e., most unionid growth) of habitats studied here. These are sites dominated by Maumee River waters that tend to have unidirectional flow. This is not the first time Maumee River waters have been shown to be very important for consumer production. Reichert et al. (2010) showed that the production of yellow perch in Lake Erie was significantly influenced by Maumee River waters.

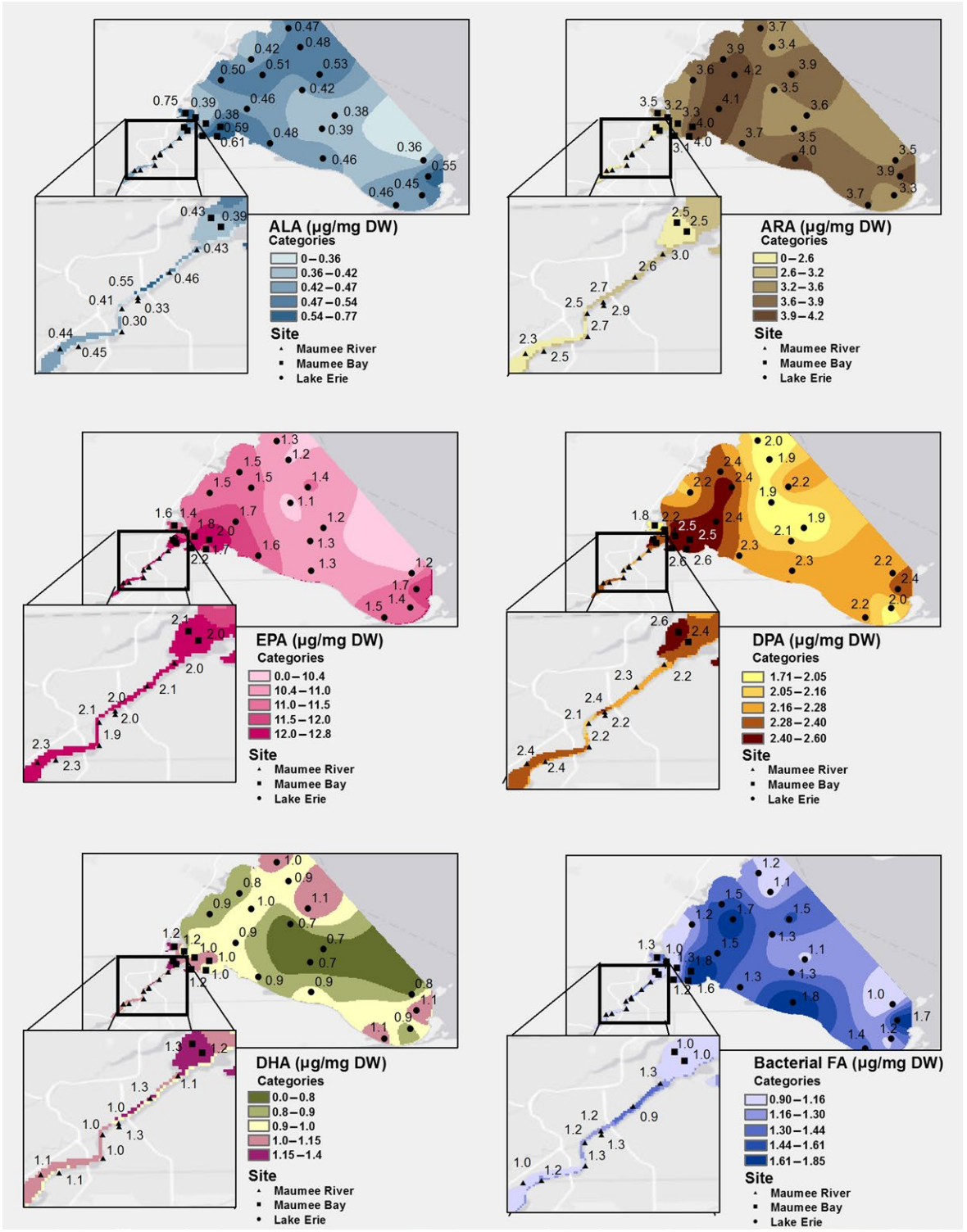

FIG. 4. Spatial distribution of fatty acids in *Lampsilis siliquoidea* deployed in cages from June to August 2013 in the western basin of Lake Erie. Color coding reflects interpolated growth value from measured sites. Abbreviations are: ALA, α-linolenic acid, 18:3n-3; ARA, arachidonic acid, 20:4n-6; EPA, eicosapentaenoic acid, 20:5n-3; DPA, docosapentaenoic acid, 22:5n-3; DHA, docosahexaenoic acid, 22:6n-3; bacterial FA, fatty acids from bacterial sources.

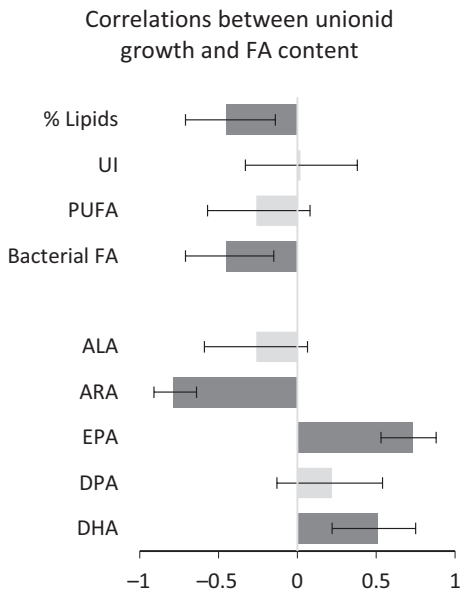

FIG. 5. Bayesian correlation coefficients between average fatty acid (FA) metrics and growth in *Lampsilis siliquoidea* deployed in cages in the western basin of Lake Erie from June to August 2013. Bars extend to the median correlation coefficient estimate and error bars denote the 95% credible intervals of the estimated correlation coefficient. Shaded bars are those that do not overlap zero. Abbreviations are: UI, unsaturation index; PUFA, polyunsaturated fatty acids; bacterial FA, fatty acids from bacterial sources; ALA, α-linolenic acid, 18:3n-3; ARA, arachidonic acid, 20:4n-6; EPA, eicosapentaenoic acid, 20:5n-3; DPA, docosapentaenoic acid, 22:5n-3; DHA, docosahexaenoic acid, 22:6n-3.

Unionids in the river mouth sites also had more EPA and DHA in their tissues than open lake sites (Table 2). The increased abundance of EPA and DHA in unionid tissues likely indicates these FAs are more available in the unionid food supply at these locations. Collectively, the FA data suggest significant variation among these three habitat types in the available food resources, with more algal food resources in the river mouth (as indicated by increased EPA and DHA) and more bacterial food resources in the open lake waters (as indicated by greater bacterial FAs; Table 2; Ahlgren et al. 1992). Predators of unionids (or predators of other species that consume similar food resources) would likely find the river mouth provides higher quality food resources than the open waters of the western basin. Relative to the open water areas sampled here, these results suggest the Maumee river mouth probably fuels a disproportionate (per unit area) amount of the total secondary production in the western basin due to both high production of primary consumers and higher quality food resources for consumers and predators.

Are there correlations between cyanobacterial abundance and secondary production and food quality for consumers?

The cyanobacterial index was not correlated to secondary production (unionid growth), but was positively related to the EPA and DPA content in the unionids (Fig. 8). Cyanobacteria are generally thought to have low quantities of EPA and other long-chained PUFAs (Ahlgren et al. 1992, Burns et al. 2010), so at first glance the results here are difficult to reconcile with that understanding. The most likely possibility is that some underlying mechanism improves conditions for both cyanobacteria and algal primary producers that have higher EPA content. For example, phosphorus concentrations may be highest in these locations, fueling higher production of other algae (e.g., greens or diatoms). Differences in food quantity might also cause the observed trends. Cyanobacteria are the numerically dominant phytoplankton in the western basin of Lake Erie during the summer and often make up a very large portion of the total phytoplankton biovolume (Reavie et al. 2014). Hence, variation in the cyanobacterial index may correspond to variation in total available food. Although elongation of ALA to EPA is energetically costly, in places with abundant food, consumers may have extra energy available to perform this conversion (Parrish 2009). However, this has never been demonstrated in unionid mussels. Either way, it seems likely that either more EPA or more energy is available to fuel consumers in areas with higher cyanobacterial abundance.

The cyanobacterial index used here is widely available and used for a variety of environmental management purposes (Stumpf et al. 2012, NOAA 2014), and for that reason it is useful to assess how it relates to other important ecological parameters. At the spatial scale of this study, the cyanobacterial index represents the best data available on cyanobacterial abundance. However, the cyanobacterial index does have drawbacks in terms of establishing a direct connection between cyanobacteria and consumers. For example, satellite imagery is only able to directly characterize surface conditions. Many cyanobacteria are buoyant, and thus vertical gradients in cyanobacteria often occur in lakes (Sejnohova

TABLE 3. Differences in dreissenid mussel abundance and size between sites in the Maumee river mouth (RM), the Maumee Bay (MB), and the open waters of Lake Erie (OL). Mean values (with 95% credible intervals) are reported. Differences among habitat types are indicated by superscript letters.

Variable	Units	RM	MB	OL
Abundance	count	$117.9_{[9.532–281.5]}{}^{a}$	$4738_{[1492–8173]}{}^{b}$	$7968_{[4991–10950]}{}^{b}$
Size	g/individual	$0.062_{[0.007–0.173]}$	$0.021_{[0.004–0.04]}$	$0.003_{[0–0.008]}$

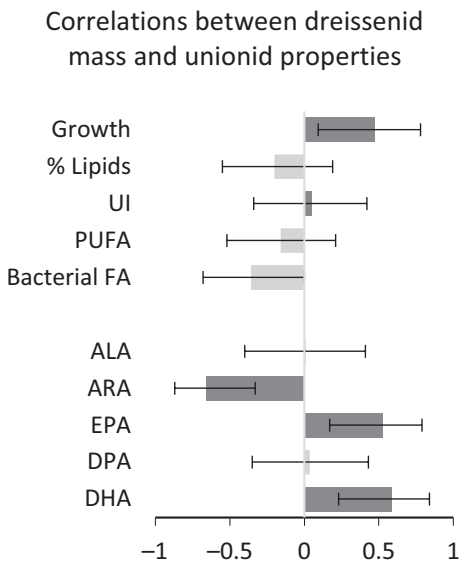

FIG. 6. Bayesian correlation coefficients between dreissenid mussel size and *Lampsilis siliquoidea* growth and fatty acid composition. *Lampsilis siliquoidea* were deployed in cages in the western basin of Lake Erie from June to August 2013 and dreissenid mussels were collected from samplers attached to the cages. Bars extend to the median correlation coefficient estimate and error bars denote the 95% credible intervals of the estimated correlation coefficient. Shaded bars are those that do not overlap zero. UI, unsaturation index; PUFA, polyunsaturated fatty acids; bacterial FA, fatty acids from bacterial sources; ALA, α-linolenic acid, 18:3n-3; ARA, arachidonic acid, 20:4n-6; EPA, eicosapentaenoic acid, 20:5n-3; DPA, docosapentaenoic acid, 22:5n-3; DHA, docosahexaenoic acid, 22:6n-3.

and Marsalek 2012). However, vertical stratification of cyanobacteria is probably less pronounced in the western basin of Lake Erie than it is in deeper lakes or lakes with less fetch. For instance, studies by Carrick et al. (2005) and Ghadouani and Smith (2005) found no evidence for vertical stratification of phytoplankton at depths of less than 10 m in Lake Erie and nowhere in the western basin is the depth greater than 10 m. Further, wind speeds of 2–3 m/s will "mix floating phytoplankton cells (or colonies)" from the surface into the water column (Sejnohova and Marsalek 2012: p. 203). During the summer of 2013, wind speeds only dipped below 2 m/s on about 9% of observations from a weather station in the western basin (observations are made every 15 min; station THLO1, maintained by the National Oceanic and Atmospheric Administration; *data available online*).[6] For these reasons, surface conditions are likely a good index of conditions in the water column, and the cyanobacterial index has been shown to be correlated to field observations (Wynne et al. 2010).

The other significant drawback is the lack of cyanobacterial index data at sites close to land. The channelized portion of the Maumee river mouth and the Maumee Bay are frequently the site of intense cyanobacterial blooms during the months when sampling occurred (Bridgeman et al. 2012, Stumpf et al. 2012, Michalak et al. 2013), but most of these sites lack cyanobacterial index estimates. For example, in 2013 the first dense blooms to occur in the western basin of Lake Erie were centered around Maumee Bay (reported on 31 July; NOAA 2014). Cyanobacteria in these locations may have been much denser or occurred for a longer duration (thus being more likely to influence the mussels' growth or FA content), but are not measured with this technique. Since these were places where EPA content was high, this is consistent with the cyanobacterial correlation identified above, but cannot be quantified with the available data. Vertically integrated, repeated measures from the water column of cyanobacterial abundance would no doubt have improved the precision and accuracy of cyanobacterial measurements, but satellite imagery certainly seems to provide a very good index of cyanobacterial abundance at the large spatial scales needed for understanding Lake Erie (Wynne et al. 2010, Stumpf et al. 2012).

CONCLUSIONS

Often, successful management or restoration of ecosystems relies on measurements of ecosystem processes or functions to evaluate success (Bernhardt and Palmer 2007, Palmer and Febria 2012). However, for many ecosystem processes, the available methods for quantification are extremely difficult. For difficult-to-measure processes such as secondary production, the available techniques are probably best interpreted as an index of reality (Butkas et al. 2010). The common consumer approach we used in this study is clearly an index as well, but has the advantage of being much easier to implement and interpret than many other approaches. Using this approach, measurements of ecosystem properties could be made at large spatial scales with a relatively fine granularity compared to other techniques. For example, it is easy to imagine deploying unionid mussels into coastal wetlands to monitor the impact of habitat restoration or into agricultural rivers to monitor the effects of pesticide applications.

For Lake Erie, these results suggest that growth of secondary consumers and the availability of important fatty acids in the western basin are centered on the Maumee river mouth. Off-shore oligotrophication of Lakes Michigan, Huron, and Superior over the past 30 years has been suggested due to improved nutrient management and the influence of dreissenid mussels (Evans et al. 2011, Bunnell et al. 2013). Some recent work has suggested that nearshore habitats, especially those influenced by tributary inputs, are becoming increasingly important to overall Great Lakes productivity (Bunnell et al. 2013). These results are consistent with the importance of nearshore habitats, even though Lake Erie itself is considered far more productive than Lakes Michigan, Huron, and Superior. Consumer production supports many important ecosystem services (e.g., fisheries), and therefore the

[6] http://www.ndbc.noaa.gov/station_history.php?station=thlo1

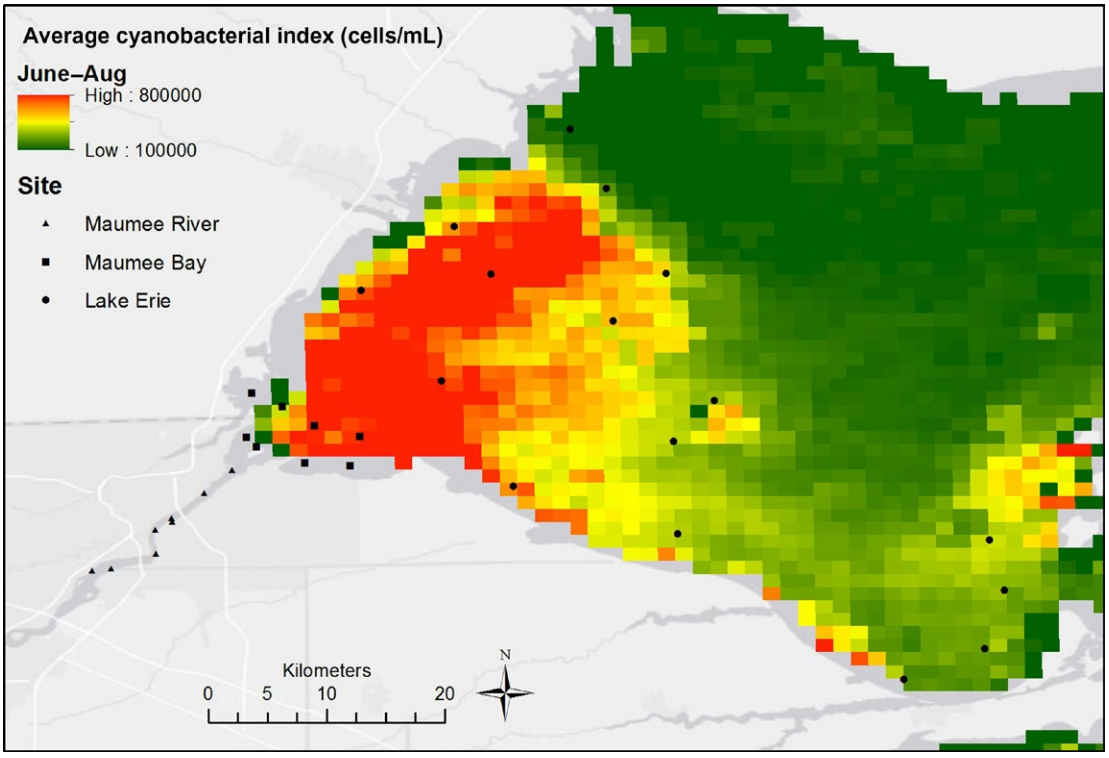

FIG. 7. Spatial distribution of the cyanobacterial index from June to August 2013 in the western basin of Lake Erie. Data derived from satellite imagery.

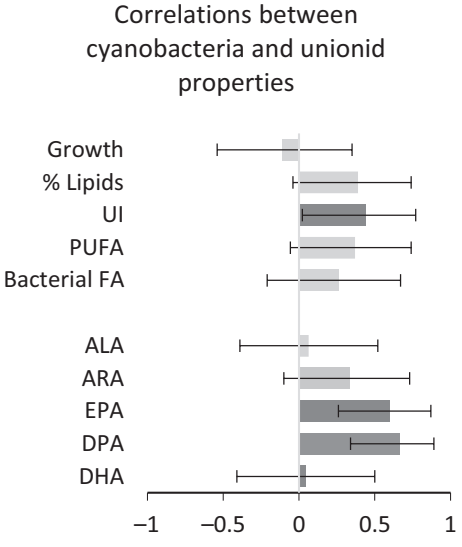

FIG. 8. Bayesian correlation coefficients between average fatty acid (FA) metrics in *Lampsilis siliquoidea* and cyanobacterial abundance in the western basin of Lake Erie from June to August 2013. Bars extend to the median correlation coefficient estimate and error bars denote the 95% credible intervals of the estimated correlation coefficient. Shaded bars are those that do not overlap zero. UI, unsaturation index; PUFA, polyunsaturated fatty acids; bacterial FA, fatty acids from bacterial sources; ALA, α-linolenic acid, 18:3n-3; ARA, arachidonic acid, 20:4n-6; EPA, eicosapentaenoic acid, 20:5n-3; DPA, docosapentaenoic acid, 22:5n-3; DHA, docosahexaenoic acid, 22:46n-3.

Maumee river mouth and other river mouths are probably more important (per unit area) than other habitats for the provisioning of many ecosystem services to the regional economy. For example, the production of fish and wildlife (for recreational and commercial fishing, water fowl harvest, etc.) is probably enhanced by access to locations with higher production of prey items and denser accumulations of essential FAs (Tanentzap et al. 2014). For these reasons, conservation and management actions aimed at improving the production of fish and wildlife may benefit from close attention to conditions in the Maumee river mouth and perhaps in river mouths elsewhere.

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Data Availability

Data associated with this paper have been deposited in the USGS ScienceBase Catalog: http://dx.doi.org/10.5066/F7BZ6426