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PRIMARY RESEARCH PAPER

Identifying the influence of zebra and quagga mussels on sedimentary phosphorus dynamics in western Lake Erie

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Abstract Dreissenid mussels can alter nutrient cycling and algal productivity in many freshwater ecosystems. But their effects on sedimentary phosphorus dynamics remain largely undefined. Here, we report evidence that dreissenids affect the concentrations of five sedimentary phosphorus fractions and total phosphorus. During our study, zebra mussels were still common and coexisted with quagga mussels in many parts of the basin. The relative abundances varied across the basin, which we characterized as five west-to-east alternating zones where zebra mussels dominated zones I (coastal) and III, quagga mussels dominated zones II and IV, and few dreissenids were present in zone V. The phosphorus fractions exhibited variation concordant with and therefore potentially influenced by dreissenids. Concentrations of all fractions and TP were consistently greater in sediments where quagga mussels dominated than in sediments where zebra mussels dominated. The responses to the absence versus presence of dreissenids were mixed, with Res-P being significantly affected, NaCl-Pi and HCl-Pi being moderately affected, and NaOH-Pi being least affected. Although such dreissenid effects were somewhat altered by in-lake biogeochemical cycling and transfer, we found that elevated levels of NaCl-Pi in dreissenid-present sediments, especially in quagga-dominated sediments, could be linked to recent eutrophication and harmful algal blooms in the basin.

Keywords Algal blooms · Dreissenidae · Phosphorus fractions · Sediments · Great Lakes · Eutrophication

Introduction

Cyanobacterial harmful algal blooms (HABs) can produce cyanotoxins, foul odors, poor water clarity, summer hypoxia, and fish kills (Cheung et al., 2013). Over the past century Lake Erie experienced two episodes of massive HABs (Conroy et al., 2005b; Yuan et al., 2014). During the 1950–1960s, Lake Erie experienced the first episode of eutrophication and HABs due to an excess nutrient loading largely from the discharge of inadequately treated municipal wastewater, including abundant phosphorus detergents (FWPCA, 1968). With the passage of the Great Lakes Water Quality Agreement (GLWQA) of 1972,

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phosphorus loading from municipal sources decreased considerably, reducing total algal biomass and improving water quality (Bertram, 1993; Makarewicz, 1993). Although external phosphorus loading has since remained below the GLWQA target loading of 11,000 Mg/year, symptoms of eutrophication and cyanobacterial HABs have become a recurring feature in western Lake Erie over the past couple of decades with record-setting blooms in 2011 and 2015 (Conroy et al., 2005b; Stumpf et al., 2012; Michalak et al., 2013; Ho et al., 2017).

These blooms serve as a reminder that the Lake Erie ecosystem and water quality can change rapidly, and there are two competing hypotheses for the return of eutrophication and HABs. First is increases in bioavailable phosphorus loading from changes in agricultural land use and farming practices in the Maumee River basin (Michalak et al., 2013; Baker et al., 2014; Smith et al. 2015). Second is changes in phosphorus cycling and internal loading potentially mediated by the invasive dreissenids (zebra mussels, *Dreissena polymorpha* (Pallas, 1771), and quagga mussels, *D. bugensis* (Andrusov, 1897) (Arnott & Vanni, 1996; Hecky et al., 2004; Conroy et al., 2005a).

The invasions of zebra and quagga mussels began in 1986 and 1989, respectively, which produced the most profound ecosystem change in the recent history of Lake Erie (Griffiths et al., 1991; Mills et al., 1993; Carlton, 2008). Both species expanded rapidly, destroying assemblages of native mussel species (Unionidae) and altering food-web dynamics across the lake (Karatayev et al., 2015). The massive density of these filter-feeding mussels had mixed effects on water quality, first to increase water clarity by reducing seston levels and increasing the downward flux of particulate matter (Klerks et al., 1996; Dobson & Mackie, 1998). Later they facilitated cyanobacterial HABs by expediting phosphorus cycling and regeneration (Arnott & Vanni, 1996; Conroy et al., 2005a). Both processes can presumably impact sedimentary phosphorus dynamics. To date, only a few studies have dealt with dreissenid effects on sedimentary phosphorus, particularly soluble reactive phosphorus in microcosms (Turner, 2010) and potential impacts of phosphorus dynamics on the Lake Erie nearshore (Pennuto et al., 2014).

Over one million metric tons of phosphorus from point and nonpoint sources has flowed into Lake Erie since European settlement, much of which has been retained and deposited in sediments (IJC, 1970; Chapra, 1977; Maccoux et al., 2016). These sediments can act as a source of internal phosphorus loading that can exceed external phosphorus loading (Boström et al., 1985; Søndergaard et al., 2003). Potentially facilitating such release, dreissenids interact with sediments through bioturbation and recycling, yet unknown is whether the effect of dreissenids may vary from place to place due to different morphological, trophic, and hydrodynamic conditions (Williamson & Ozersky, 2019).

The main purpose of our work is to yield useful insights into the recent return of eutrophication and HABs and increase development of a better management scheme for this already eutrophic system. Past surveys of surface sediments show few changes in average total phosphorus (TP) across Lake Erie (Painter et al., 2001; Pennuto et al., 2014), which seemingly contrasts with a west-to-east trend of decreasing algal productivity (Makarewicz et al., 2000). The disparity signals a probable difference in sedimentary phosphorus bioavailability. Indeed, concentrations of the sedimentary NaCl-Pi, a loosely bound form of phosphorus, are significantly greater in the western basin than in the Sandusky basin (Yuan et al., 2020), but unclear is what elevates NaCl-Pi, and how the various forms of phosphorus are distributed bathymetrically. As a first step, we initiated a cross-disciplinary study to contrast sedimentary phosphorus fractions with dreissenid occurrence to examine how dreissenids may mediate or enhance phosphorus cycling in the western basin of Lake Erie. Our working assumption is that changes in interception, retention, and cycling of phosphorus induced by the two dreissenid species may affect concentrations of sedimentary phosphorus fractions. Different sedimentary fractions represent alternative binding forms of phosphorus, and therefore we asked how these different fractions vary in response to dreissenid presence and differential abundance.

Methods

Lake Erie consists of a shallow western basin, a large central basin, and a deep eastern basin (Fig. 1a), with a lake surface area of 26,000 km^2 and a total catchment area of 85,000 km^2 (Jasechko et al., 2014). The western basin, the shallowest and most productive

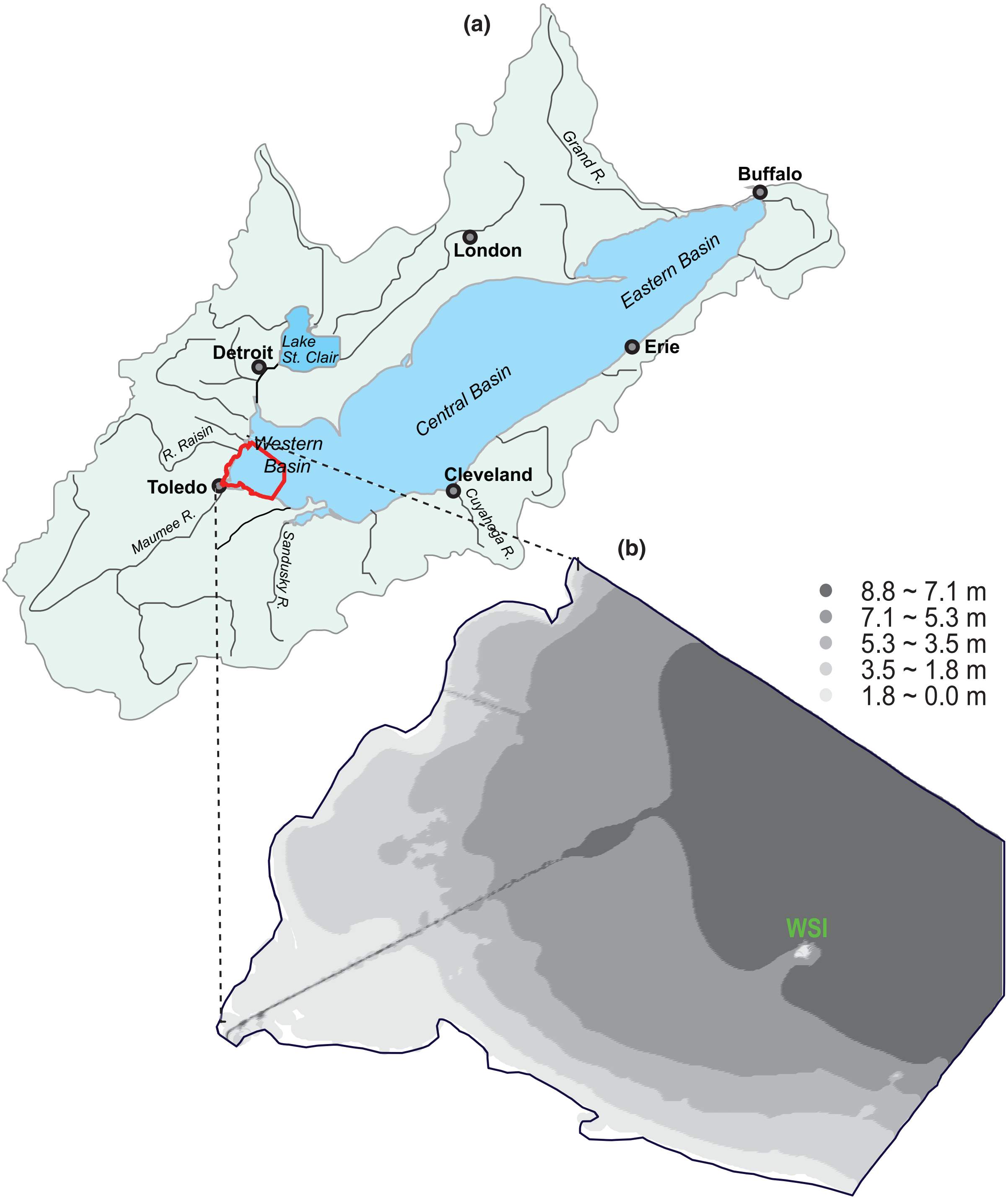

Fig. 1 **a** Map showing the location of the study area (the red polygon) within Lake Erie (in cyan) and its surrounding watersheds (in gray), and **b** a bathymetric map of the study area in western Lake Erie. Original bathymetric data from the National Geophysical Data Center (NOAA, 1999). *WSI* West Sister Island

system within Lake Erie (Makarewicz et al., 2000), has a high surface area/volume ratio, lacking stable thermal stratification during summer warm seasons (Beeton, 1963). Lake Erie receives the majority of surface water from the Detroit River (5,500 m^3/s) and, to a much lesser extent, from its tributaries such as the Maumee River and the River Raisin (Bolsenga & Herdendorf, 1993).

Despite its small flow, the Maumee River contributes nearly half of the external phosphorus loading into the western basin (Maccoux et al., 2016). Owing to the disproportionally high nutrient loading from the Maumee River, an area of 1,000 km^2 in the US half of this basin where water depth ranges from 2 to 9 m was chosen for investigation (Fig. 1b). Surface sediment samples were collected using a 9″ standard Ponar stainless steel grab, and transferred to 500-ml wide-mouth plastic bottles, as described elsewhere (Yuan et al., 2018, 2020). An aliquot of the sediment sample was processed for sequential extractions and subsequent phosphorus determinations. The rest of the sample was wet sieved to separate and collect zebra and quagga mussel shells, which were cleaned, identified, and counted. Additionally, the sediment sites were divided into a dreissenid-absent group and a dreissenid-present group. The latter was further divided into zebra-dominated sites and quagga-dominated sites. Occurrences and relative abundances of the two invasive mussel species were mapped and examined visually to characterize the study area.

As described in Yuan et al. (2020), a modified protocol of five-step sequential extractions was used to quantify five phosphorus fractions, namely sodium chloride extractable inorganic phosphorus (NaCl-Pi), sodium bicarbonate and sodium dithionite extractable inorganic phosphorus (NaBD-Pi), sodium hydroxide extractable inorganic phosphorus (NaOH-Pi), hydrochloric acid extractable inorganic phosphorus (HCl-Pi), and refractory phosphorus (Res-P). These fractions are commonly used to represent loosely bound Pi, redox-sensitive (Fe, Mn bound) Pi, Al and non-reducible Fe oxyhydroxide bound Pi, apatite and other calcium bound Pi, and refractory organic P, respectively (Lukkari et al., 2007; Tu et al., 2019). Additionally, a potassium persulfate digestion method was adopted to extract sedimentary TP (Nelson, 1987; Berthold et al., 2015). All extracts were filtered with 0.45 µm syringe filters and determined using an automated discrete analyzer (AQ2), using the protocol EPA-118-A Rev. 5. The detection limit was 0.004 mg/g, the average relative error was less than 5%, and the average recovery rate was greater than 95% (Yuan et al., 2020).

Other analytical data such as sediment grainsize score (GS) and concentrations of acid-extractable iron (Fe) and total organic carbon (TOC) were included and analyzed to better evaluate the dreissenids influence on sedimentary phosphorus dynamics. As described in Yuan et al. (2018), the sediment GS was assigned discretely: clay (1), silty clay (2), clayey silt (3), silt (4), and fine sand (5). Concentrations of TOC were determined on dried decarbonated sediments with a LECO carbon and sulfur analyzer (CS-200) and concentrations of Fe were measured on acid extracts using an ICP-AES, with a detection limit of 0.005 mg/g.

Multiple statistical procedures were taken to evaluate differences in the five phosphorus fractions, TP, TOC, Fe, GS, and combined mussel counts. First, a chi-squared test was used to detect sampling sites with or without a significant deviation from a 50–50 frequency of the two dreissenid species. Second, a Student's *t*-test was performed to examine the difference of the five fractions and TP between dreissenid-absent and dreissenid-present sites and between zebra-dominated and quagga-dominated sites. Lastly, an empirical bootstrap resampling was carried out to estimate and contrast the confidence intervals for all five fractions and TP between dreissenid-absent and dreissenid-present sites and between zebra-dominated and quagga-dominated sites, using the *R* package *boot* with 10,000 iterations (DiCiccio & Efron, 1996).

Results

Dreissenid shells were present at 55 (70.5%) of the 78 sampled sites, including 50 sites with quagga mussels and 53 sites with zebra mussels (Fig. 2). Five samples contained only a few zebra mussels without quagga mussels and two samples contained a single or a few quagga mussels without zebra mussels. At the other 48 sites with dreissenids, shells of both species occurred; 17 sites had more than 50% zebra mussels, 27 sites contained more than 50% quagga mussels and 4 provided 50% of each. Although only 38.6% of all shells pooled for all sites were zebra mussel shells, the overall abundance was similar when averaging by site,

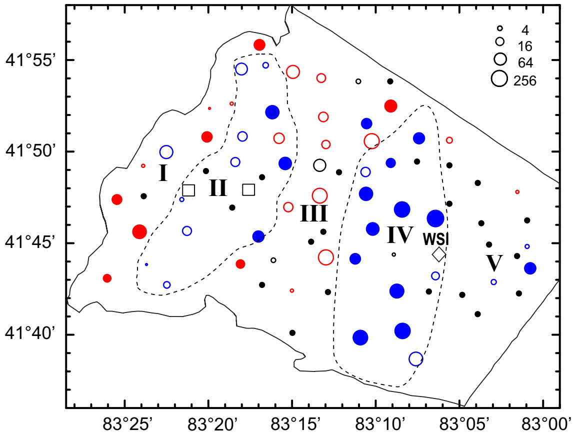

Fig. 2 Occurrences, abundance, and dominance of zebra and quagga mussels across the study area. Filled black circles denote samples where dreissenids were absent. Filled circles denote samples dominated significantly by zebra (red) or quagga (blue) mussels, while open circles denote samples without significant deviation from a 50–50 frequency as revealed by a χ^2 test. Size of circles represents abundance of the combined dreissenid species. Open squares denote two dumping sites for dredged material from the Toledo shipping channel within the lower Maumee River. The open diamond denotes West Sister Island (WSI). Roman numerals demarcate five apparent zones with different dreissenid characteristics of which the dashed lines denote areas where quagga mussels dominated

with zebra mussels comprising 48.6% of the dreissenids.

Variation in the relative abundance of the two dreissenid species was apparent from west to east across the study area that can be represented as zonal change (Fig. 2). Visually, zebra mussels dominated the western coastal zone (I), where they made up 68.3% of the dreissenid mussels and showed significant dominances at five sites. Zebra mussels were also slightly more common than quagga mussels in a south-north elongated zone (III) east of two dredged material disposal sites. Zebra mussels accounted in total for 56.5% of the mussels though only one site showed significant dominance, and at three sites, the frequency of each species was 50%. At area (II) sandwiched between zones I and III, quagga mussels accounted for 62.4% of the dreissenids with significant dominance at three sites. Between zone III and West Sister Island (WSI), a south-north elongated zone (IV) was more heavily biased for quagga mussels, which in total accounted for 79.1% of the dreissenid shells. An area (V) east of WSI comprised only 2% of the total dreissenids found and included 10 of 23 dreissenid-absent sites in the study area. Despite variation in frequency, the average combined dreissenid count changed little from zone I to zone III, peaked in zone IV, and diminished in zone V.

Average concentrations of the five phosphorus fractions varied between dreissenid-absent and dreissenid-present sediments, and ranged from 0.002 mg/g for NaOH-Pi to 0.026 mg/g for HCl-Pi (Table 1). Average concentrations of NaCl-Pi (15.2%, $P = 0.22$) and HCl-Pi (6.8%, $P = 0.31$) were greater in the dreissenid-present sediments than in the dreissenid-absent sediments, while average concentrations of NaBD-Pi (6.3%, $P = 0.50$) and Res-P (at 20.8%, a significant difference, $P = 0.02$) were greater in the dreissenid-absent sediments. The average concentration of TP in the dreissenid-present sediments was 0.765 mg/g, slightly (8.2%, $P = 0.07$) less than that in the dreissenid-absent sediments (0.834 mg/g). The 95% bootstrap confidence intervals for all but TP were greater in the dreissenid-absent sediments than in the dreissenid-present sediments (Table 2). All the fractions and TP had overlapping confidence intervals (CI; Fig. S1), with Res-P being the least percent overlapping CI (7.3%) and NaOH-Pi being the most percent overlapping CI (88.8%).

Concentrations of the five fractions and TP also appeared to have changed in the western basin where dreissenid species frequencies differed (Table 1). In quagga-dominated sediments (where quagga mussels accounted for 50% or greater of the combined mussels found), average concentrations of the five phosphorus fractions and TP were consistently greater than those in the zebra-dominated sediments (where zebra mussels accounted for over 50% of the combined mussels), with percent differences at 28.9% for NaCl-Pi ($P = 0.04$), 7.1% for NaBD-Pi ($P = 0.42$), 21.2% for NaOH-Pi ($P = 0.04$), 12.3% for HCl-Pi ($P = 0.16$), 24.9% for Res-P ($P = 0.04$), and 21.9% for TP ($P = 0.01$). The 95% bootstrap CI for all but HCl-Pi were slightly to moderately greater in the zebra-dominated sediments than in the quagga-dominated sediments (Table 2). All but TP had overlapping CI (Fig. S2), with NaCl-Pi, NaOH-Pi, and Res-P being among the least percent overlapping CI (10.1 to 12.6%) and NaBD-Pi being the most percent overlapping CI (52.3%).

Characteristics of the sediments also varied across the study area (Fig. 3), suggesting physical differences in the zones characterized by variation in dreissenids.

Table 1 Concentrations (mean ± standard error, mg/g) of phosphorus in sediments with different dreissenid characteristics

	Dreissenid-absent sediments Mean ± SE ($N = 23$)	Dreissenid-present sediments Mean ± SE ($N = 55$)	t	P-value	Zebra-dominated sediments Mean ± SE ($N = 22$)	Quagga-dominated sediments Mean ± SE ($N = 33$)	t	P-value
NaCl-Pi	0.038 ± 0.004	0.045 ± 0.003	− 1.23	0.22	0.037 ± 0.004	0.050 ± 0.004	− 2.16	0.04
NaBD-Pi	0.239 ± 0.020	0.225 ± 0.009	0.68	0.50	0.215 ± 0.015	0.231 ± 0.012	− 0.82	0.42
NaOH-Pi	0.107 ± 0.006	0.106 ± 0.006	0.19	0.85	0.092 ± 0.007	0.114 ± 0.007	− 2.07	0.04
HCl-Pi	0.365 ± 0.018	0.391 ± 0.017	− 1.02	0.31	0.363 ± 0.023	0.410 ± 0.024	− 1.43	0.16
Res-P	0.079 ± 0.005	0.064 ± 0.004	2.45	0.02	0.055 ± 0.006	0.071 ± 0.005	− 2.08	0.04
TP	0.834 ± 0.017	0.765 ± 0.033	1.85	0.07	0.667 ± 0.047	0.831 ± 0.042	− 2.63	0.01

t and *P* values are derived from Welch two sample *t*-test

Table 2 Bootstrap confidence intervals (CI) and % overlap of intervals (% CI) of phosphorus in sediments with different dreissenid characteristics

	Dreissenid-absent sediments	Dreissenid-present sediments	Overlapping		Zebra-dominated sediments	Quagga-dominated sediments	Overlapping	
	95% CI	95% CI	CI	% CI	95% CI	95% CI	CI	% CI
NaCl-Pi	0.031–0.046	0.039–0.051	0.039–0.046	36.8	0.029–0.045	0.042–0.057	0.042–0.045	10.1
NaBD-Pi	0.199–0.275	0.206–0.243	0.206–0.243	48.8	0.186–0.244	0.209–0.254	0.209–0.244	52.3
NaOH-Pi	0.096–0.118	0.095–0.117	0.096–0.117	88.8	0.078–0.107	0.101–0.129	0.101–0.107	12.2
HCl-Pi	0.338–0.406	0.358–0.425	0.358–0.406	54.2	0.317–0.404	0.366–0.459	0.366–0.404	27.3
Res-P	0.070–0.088	0.057–0.072	0.070–0.072	7.3	0.044–0.066	0.061–0.080	0.061–0.066	12.6
TP	0.802–0.867	0.702–0.829	0.802–0.829	16.1	0.574–0.750	0.753–0.912	–-	0.0

Percent confidence interval (% CI) is the ratio of overlapping interval to collective interval

First, grainsize (GS) of surface sediments decreased stepwise from zone I to zone III and from zone IV to zone V. This eastward trend mirrored increases in Fe and TOC, as well as for Res-P, NaOH-Pi, and TP (Fig. 4). Second, a more complex pattern was shown by the average concentration of HCl-Pi, which remained nearly constant from zone I to zone III, increased in zone IV, and decreased markedly in zone V, a shift similar to the average combined mussel count. Concurrently, average concentrations of the bioavailable fractions NaCl-Pi, NaBD-Pi, and NaOH-Pi showed high values in zones II–IV and low values in zones I and V.

Discussion

Zebra mussels expanded rapidly in Lake Erie and reached a maximum around 1989–1990 (Griffiths et al., 1991; Nicholls & Hopkins, 1993; Carlton, 2008). Despite a later arrival, quagga mussels outcompeted zebra mussels and soon dominated the deeper eastern and central basins by 1993 (Mills et al.,

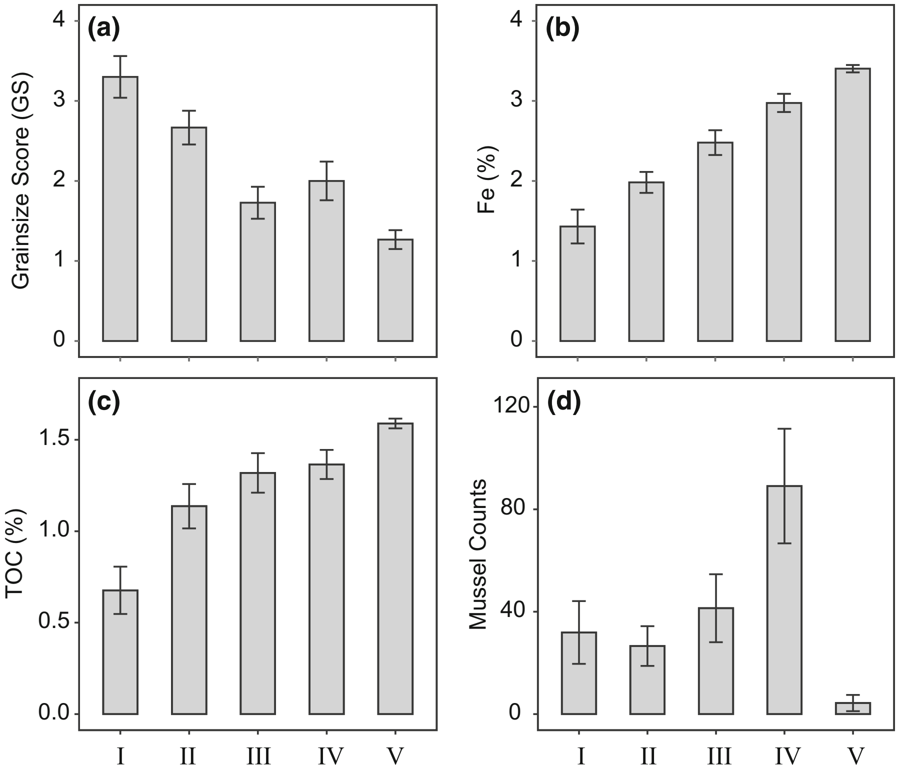

Fig. 3 Bar plots (± 1 standard error) showing changes in sediment characteristics among five zones defined by shifts in dreissenid dominance (Fig. 2): **a** grainsize score (GS), **b** iron concentrations (Fe), **c** total organic carbon (TOC), and **d** combined mussel counts

1993; Jarvis, 2000). In western Lake Erie, however, zebra mussels still were more abundant, accounting for 63–66% of the total dreissenid mussel density in 1998 (Jarvis, 2000; Conroy et al., 2005a), and they remained common in 2002, comprising 45% of dreissenids (Patterson et al., 2005). The prevalence of zebra mussels may have declined thereafter, and were reported at 26% in 2003 and around 30% in 2009–2012 (Conroy et al., 2005a; Burlakova et al., 2014; Karatayev et al., 2014), but our collections from sediments revealed that zebra and quagga mussels continue to coexist, as 43 (86%) of 50 samples contained zebra mussels at between 38 and 49% of the total dreissenid count. Abundant seston from inputs of tributaries and from resuspended materials may ease interspecific food competition and allow the two dreissenid species to continue to coexist in more similar proportions (Conroy et al., 2005a; Karatayev et al., 2014). Suggested in our results is an interplay between presence, the frequency of the two species, and the concentration of various fractions of phosphorus in the substrate. Whether dreissenids are impacting phosphorus or whether both are responding to other lake features to form bands of differential dominance is less clear.

Coexistence of these two similar species is predicted in such a shallow and large system as western Lake Erie (Karatayev et al., 2011, 2014). Zebra mussels often colonize hard substrates in shallow waters while quagga mussels may colonize soft sediments in deep waters, consistent with a benthic habitat partition model (Dermott & Munawar, 1993). Our results suggest more complex partitioning in the basin, most striking being a distinctive west-to-east alternating pattern of zonal change. Zones I and III probably associate with high levels of dissolved oxygen and the ability of zebra mussels to attach more firmly to the substrate where coastal wave actions and circulations driven by large inflows from the Detroit River occur (Kovacik, 1972; Beletsky et al., 2013). Quagga mussels became more abundant in zone II, attributed to poor water quality induced by deposits of dredged materials from the Toledo shipping channel (Hoke et al., 1990; Burris et al., 1993),

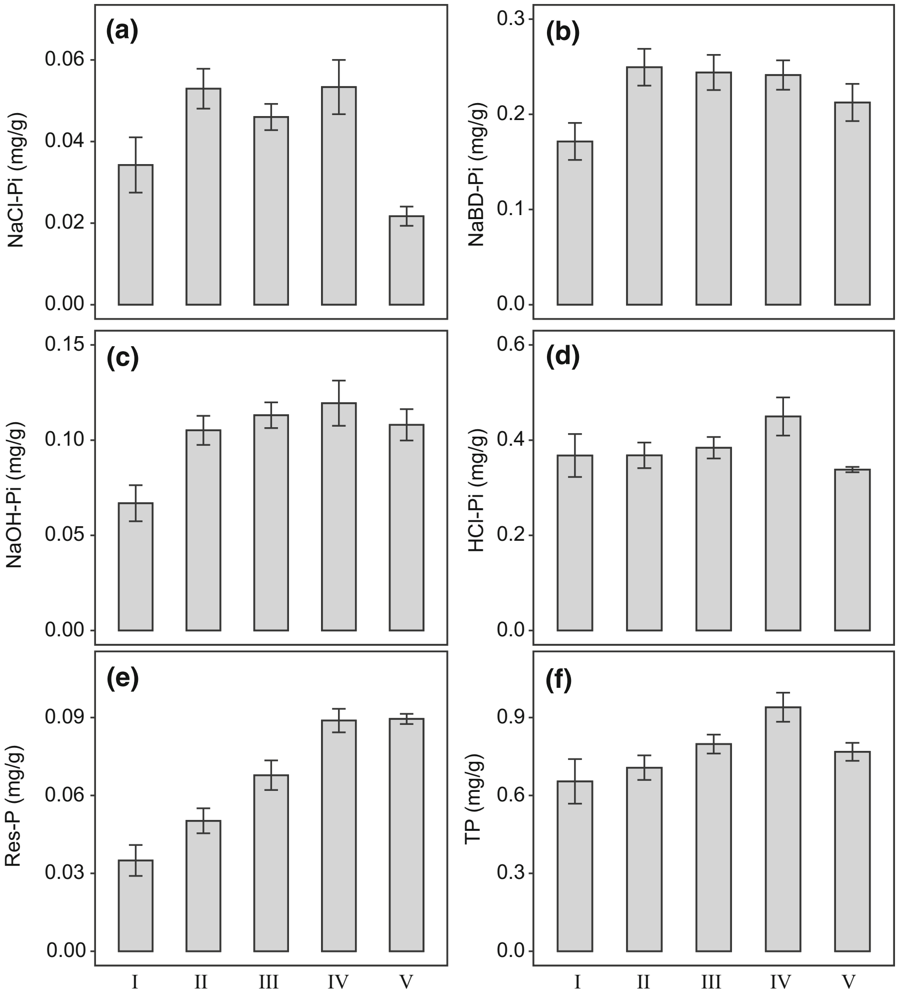

Fig. 4 Bar plots (± 1 standard error) of average phosphorus concentrations among five zones defined by shifts in dreissenid dominance (Fig. 2): **a** sodium chloride extractable inorganic phosphorus (NaCl-Pi), **b** sodium bicarbonate and sodium dithionite extractable inorganic phosphorus (NaBD-Pi), **c** sodium hydroxide extractable inorganic phosphorus (NaOH-Pi), **d** hydrochloric acid extractable inorganic phosphorus (HCl-Pi), **e** refractory phosphorus (Res-P), and **f** total extractable phosphorus (TP)

while in zone IV, quagga mussels dominated perhaps because they tolerate fine-grained sediments or occasional hypoxia (Karatayev et al., 2014). The scarcity of dreissenids in zone V (and some localities in other zones) was likely caused by severe short-lived hypoxia during warm seasons (Beeton, 1963; Coloso et al., 2011).

Zonal changes in sedimentary characteristics are not novel, but the striking zonal changes and possible impacts to phosphorus fractions from variation in dreissenid mussel frequencies and abundances are new (Fig. 3), especially as variation in species dominance appeared both greater and more consistent than simple presence or absence of dreissenids (Tables 1, 2; Figs. S1, S2). The lower differences in NaCl-Pi than in NaBD-Pi suggest that a large portion of phosphorus processed by dreissenids may be released or transferred into the overlying water column without being trapped and preserved in the sediments, and species differences may arise because zebra mussels may have a greater phosphorus excretion rate than quagga mussels (Conroy et al., 2005a). This pattern suggests complex sedimentary phosphorus dynamics that are affected by dreissenid-mediated transformations and in-lake biogeochemical cycling including watershed characteristics, external phosphorus loading, eutrophication history, and water circulation, as well as dreissenid abundance, composition and invasion history (Dittrich et al., 2013; Williamson & Ozersky, 2019; Yuan et al., 2020).

The eastward decreasing grainsize, along with trends of increasing Fe and TOC, may be attributed to inputs of suspended sediments from tributaries, removal of fine particles from nearshore areas, and deposition of organically-coated fine particles in offshore areas (Williams et al., 1976a; Pennuto et al., 2014; Yuan et al., 2018). The relatively coarse sediments found in zone IV were related to exceptionally high dreissenid mussel abundance, as accumulating shells are changing both the substrate characteristics and the benthic fauna in the western basin (Berkman et al., 1998; Crail et al., 2011; Bryan et al., 2013). Much of the area in zones I to III can be considered as a shallow (less than 7 m) high energy nearshore associated with coastal waves and basin circulations (Kovacik, 1972; Beletsky et al., 2013), and much of the area from zone IV to V may be regarded as a relatively deep (more than 7 m), low energy and offshore (Fig. 1b) (Przywara, 1978; Yuan et al., 2018). Except for zone IV, quagga mussel abundance was relatively low for the study area, as compared to the central and eastern basins where quagga mussels predominate (Jarvis, 2000; Patterson et al., 2005). Both species had the lowest abundances in zone V. It is unclear whether the low dreissenid density in zone V was caused by a reduction of food resources from the dense population in zone IV upstream or by a depletion of dissolved oxygen from transient thermal stratifications during summer warm seasons in the basin (Beeton, 1963; Coloso et al., 2011; Giles et al., 2016).

Yet, like the biota, sedimentary phosphorus dynamics can be affected by a variety of other processes. In Lake Erie, the detrital phosphorus fraction HCl-Pi accounted for 70% of TP in the sediments during European settlement (Williams et al., 1976b; Yuan et al., 2020). During the first episode of eutrophication, however, the bioavailable phosphorus fractions, NaCl-Pi, NaBD-Pi, and NaOH-Pi, increased considerably due to excessive external phosphorus loading, largely from municipal sources (IJC, 1970; Chapra, 1977; Yuan et al., 2020). After the dreissenids arrived, sedimentary phosphorus dynamics were presumably further modulated. For instance, concentrations of loosely bound phosphorus represented by NaCl-Pi increased again and potentially contributed to the re-eutrophication and cyanobacterial HABs in the western basin (Yuan et al., 2020). The rise in NaCl-Pi may be ascribed to an increased phosphorus recycling rate mediated by dreissenids (Arnott & Vanni, 1996; Conroy et al., 2005a).

That dreissenids may shift phosphorus fractions also relates to the small, yet opposing changes where dreissenids were present or not, more NaCl-Pi but less NaBD-Pi (Table 1; Fig. S1). The bioavailable fraction, NaCl-Pi, represents loosely bound phosphorus is subject to diffusive transfer and algal uptake during sediment resuspension (Matisoff & Carson, 2014; Matisoff et al., 2016; Yuan et al., 2020). Phosphorus firmly bound to redox-sensitive Fe oxyhydroxides (NaBD-Pi) may be liberated as soluble phosphorus during passage of oxygenated material in mussel guts (Hecky et al., 2004; Turner, 2010), which may be trapped in pore waters or adsorbed on mineral surfaces as part of NaCl-Pi in surface sediments. Res-P also significantly declined (Tables 1, 2), but this form is bound to organic compounds (Ostrofsky, 1987; Søndergaard et al., 1996) derived from fluvial pathways (Psenner & Pucsko, 1988; Kpodonu et al., 2016). The zonal changes in Res-P may be induced by the eastward transfer and deposition of organically-coated fine-grained particles in the deeper zones (Williams et al., 1976b; Giles et al., 2016; Yuan et al., 2020) from which a large proportion of dreissenid-absent samples came (Fig. 2). The lower concentrations of TP where dreissenids occur represent less organic-bound P, but that may be due to consumption and respiration by dreissenids (Turner, 2010). Moreover, the higher HCl-Pi concentrations with dreissenids present suggest that deposition of mussel shells may influence concentrations, though most of the apatite-bound phosphorus (HCl-Pi) is of detrital origin (Williams et al., 1976b; Yuan et al., 2020).

Dreissenids intercept, retain, and recycle nutrients in nearshore benthic areas (Arnott & Vanni, 1996; Hecky et al., 2004; Conroy et al., 2005a). This nutrient shunt model explains well the contrasting water-quality changes between nearshores and offshores in the Great Lakes, however, details for benthic nutrient redistribution and preservation remain scarce (Pennuto et al., 2014). Our sedimentary data suggest eastward shifts, possibly as zonal changes, in dreissenid distribution and concentrations of phosphorus. Notably, dreissenids may have affected the phosphorus fraction differently, but they are only one contributor to a complex array of in-lake biogeochemical cycling and transferring processes during sediment resuspension and focusing. Loosely bound inorganic phosphorus (NaCl-Pi) in the surface sediments may be accessible to phytoplankton and benthic algae through either diffusive migration of soluble phosphorus across the sediment–water interface during warm, transient stratification periods or sediment resuspension during some storm events in the basin (Ozersky et al., 2009; Giles et al., 2016; Yuan et al., 2020). Although being the smallest fraction in the sedimentary TP, the elevated NaCl-Pi appears to be the most consequential due to an extremely large sediment loading from resuspension as observed by sediment traps (Marvin et al., 2007; James, 2014), and thus increases in this component could be linked to recent eutrophication and algal blooms in the basin (Yuan et al., 2020).

In summary, this work relied on sediments collected from part of the western basin during the spring of 2016 to document several intriguing aspects of sedimentary phosphorus dynamics which are seemingly affected by dreissenid-mediated transformations and in-lake biogeochemical cycling and transfer. Owing to the complexity of interactions between dreissenids, in-lake biogeochemical cycling, and sedimentary phosphorus dynamics, more research is needed. Although laboratory experiments can be insightful of processes (Conroy et al., 2005a; Turner, 2010), future investigations should expand the research area across the entire western basin to better characterize spatial variation and possible seasonal changes. Such efforts would help eliminate some uncertainty in the assessment of dreissenid effects on the phosphorus dynamics and algal productivity in the basin.

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Author contributions FY conceived the study. AW, FY, and RK collected the mussel data. FY and RK conducted the data analysis, prepared all the figures and tables, and wrote the manuscript. All authors contributing to interpreting the results and editing the manuscript.

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Code availability Code is available upon request.

Consent to publication All authors agree to the content for the work.

Declarations

Conflict of interest We declare no competing financial interests.

Ethical approval We did not work with animals by their definition as invasive dreissenids are not animals from a research ethics protocol.

Informed consent All authors agree to participate in the work.

References:

Arnott, D. L. & M. J. Vanni, 1996. Nitrogen and phosphorus recycling by the zebra mussel (*Dreissena polymorpha*) in the western basin of Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 53(3): 646–659.

Baker, D. B., R. Confesor, D. E. Ewing, L. T. Johnson, J. W. Kramer & B. J. Merryfield, 2014. Phosphorus loading to Lake Erie from the Maumee, Sandusky and Cuyahoga Rivers: the importance of bioavailability. Journal of Great Lakes Research 40(3): 502–517.

Beeton, A. M., 1963. Limnological Survey of Lake Erie 1959 and 1960 Great Lakes Fishery Commission. Technical Report. Great Lakes Fishery Commission: 32.

Beletsky, D., N. Hawley & Y. R. Rao, 2013. Modeling summer circulation and thermal structure of Lake Erie. Journal of Geophysical Research: Oceans 118(11): 6238–6252.

Berkman, P. A., M. A. Haltuch, E. Tichich, D. W. Garton, G. W. Kennedy, J. E. Gannon, S. D. Mackey, J. A. Fuller & D. L. Liebenthal, 1998. Zebra mussels invade Lake Erie muds. Nature 393(6680): 27–28.

Berthold, M., D. Zimmer & R. Schumann, 2015. A simplified method for total phosphorus digestion with potassium persulphate at sub-boiling temperatures in different environmental samples. Rostocker Meeresbiologische Beiträge 25: 7–25.

Bertram, P. E., 1993. Total phosphorus and dissolved oxygen trends in the Central Basin of Lake Erie, 1970–1991. Journal of Great Lakes Research 19(2): 224–236.

Bolsenga, S. J. & C. E. Herdendorf, 1993. Lake Erie and Lake St. Clair Handbook. Wayne State University Press, Detroit.

Boström, B., I. Ahlgren & R. Bell, 1985. Internal nutrient loading in a eutrophic lake, reflected in seasonal variations of some sediment parameters. Verhandlungen des Internationalen Verein Limnologie 22(5): 3335–3339.

Bryan, N. J., C. V. Florence, T. D. Crail & D. L. Moorhead, 2013. Freshwater mussel community response to warm water discharge in western Lake Erie. Journal of Great Lakes Research 39(3): 449–454.

Burlakova, L. E., A. Y. Karatayev, C. Pennuto & C. Mayer, 2014. Changes in Lake Erie benthos over the last 50 years: historical perspectives, current status, and main drivers. Journal of Great Lakes Research 40(3): 560–573.

Burris, R., J. Busch, W. Cadet, C. Crook, W. Franz, H. Harrington, K. Kroonemeyer, J. Letterhos, J. Loftus, J. Rupert, W. Van Cott & H. Wirick, 1993. Long-Term Dredged Material Management Plan Within the Context of Maumee River Watershed Sediment Management Strategy. Toledo Harbor, OH: 175.

Carlton, J. T., 2008. The zebra mussel *Dreissena polymorpha* found in North America in 1986 and 1987. Journal of Great Lakes Research 34(4): 770–773.

Chapra, S. C., 1977. Total phosphorus model for the Great Lakes. Journal of Environmental Engineering Division 103(2): 147–161.

Cheung, M. Y., S. Liang & J. Lee, 2013. Toxin-producing cyanobacteria in freshwater: a review of the problems, impact on drinking water safety, and efforts for protecting public health. Journal of Microbiology 51(1): 1–10.

Coloso, J. J., J. J. Cole & M. L. Pace, 2011. Short-term variation in thermal stratification complicates estimation of lake metabolism. Aquatic Sciences 73(2): 305–315.

Conroy, J. D., W. J. Edwards, R. A. Pontius, D. D. Kane, H. Zhang, J. F. Shea, J. N. Richey & D. A. Culver, 2005a. Soluble nitrogen and phosphorus excretion of exotic freshwater mussels (*Dreissena* spp.): potential impacts for nutrient remineralisation in western Lake Erie. Freshwater Biology 50(7): 1146–1162.

Conroy, J. D., D. D. Kane, D. M. Dolan, W. J. Edwards, M. N. Charlton & D. A. Culver, 2005b. Temporal trends in Lake Erie plankton biomass: roles of external phosphorus loading and dreissenid mussels. Journal of Great Lakes Research 31(Supplement 2): 89–110.

Crail, T. D., R. A. Krebs & D. T. Zanatta, 2011. Unionid mussels from nearshore zones of Lake Erie. Journal of Great Lakes Research 37(1): 199–202.

Dermott, R. & M. Munawar, 1993. Invasion of Lake Erie offshore sediments by *Dreissena*, and its ecological implications. Canadian Journal of Fisheries and Aquatic Sciences 50(11): 2298–2304.

DiCiccio, T. J. & B. Efron, 1996. Bootstrap confidence intervals. Statistical Sciences 11(3): 189–212.

Dittrich, M., A. Chesnyuk, A. Gudimov, J. McCulloch, S. Quazi, J. Young, J. Winter, E. Stainsby & G. Arhonditsis, 2013. Phosphorus retention in a mesotrophic lake under transient loading conditions: insights from a sediment phosphorus binding form study. Water Research 47(3): 1433–1447.

Dobson, E. P. & G. L. Mackie, 1998. Increased deposition of organic matter, polychlorinated biphenyls, and cadmium by zebra mussels (*Dreissena polymorpha*) in western Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 55(5): 1131–1139.

FWPCA, 1968. Lake Erie Report: A Plan for Water Pollution Control. U.S. Department of the Interior, Federal Water Pollution Control Administration (FWPCA), Great Lakes Region: 113.

Giles, C. D., P. D. F. Isles, T. Manley, Y. Xu, G. K. Druschel & A. W. Schroth, 2016. The mobility of phosphorus, iron, and manganese through the sediment–water continuum of a shallow eutrophic freshwater lake under stratified and mixed water-column conditions. Biogeochemistry 127(1): 15–34.

Griffiths, R. W., D. W. Schloesser, J. H. Leach & W. P. Kovalak, 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Canadian Journal of Fisheries and Aquatic Sciences 48(8): 1381–1388.

Hecky, R. E., R. E. Smith, D. R. Barton, S. J. Guildford, W. D. Taylor, M. N. Charlton & T. Howell, 2004. The nearshore phosphorus shunt: a consequence of ecosystem engineering by dreissenids in the Laurentian Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 61(7): 1285–1293.

Ho, J. C., R. P. Stumpf, T. B. Bridgeman & A. M. Michalak, 2017. Using Landsat to extend the historical record of lacustrine phytoplankton blooms: a Lake Erie case study. Remote Sensing of Environment 191: 273–285.

Hoke, R. A., J. P. Giesy, G. T. Ankley, J. L. Newsted & J. R. Adams, 1990. Toxicity of sediments from western Lake Erie and the Maumee River at Toledo, Ohio, 1987: implications for current dredged material disposal practices. Journal of Great Lakes Research 16(3): 457–470.

IJC, 1970. Pollution of Lake Erie, Lake Ontario and the International Section of the St. Lawrence River, Vol. 1. International Joint Commission, Canada and United States: 150.

James, W., 2014. Effects of Open-Lake Dredge Material Placement on Sediment Characteristics and Diffusive Phosphorus Fluxes in Lake Erie, Western Basin. University of Wisconsin-Stout, Sustainability Science Institute, Menomonie: 26.

Jarvis, P., 2000. Zebra (*Dreissena polymorpha*) and quagga mussel (*Dreissena bugensis*) distribution and density in Lake Erie, 1992–1998. Canadian Technical Report of Fisheries and Aquatic Sciences 2304: 1–46.

Jasechko, S., J. J. Gibson & T. W. D. Edwards, 2014. Stable isotope mass balance of the Laurentian Great Lakes. Journal of Great Lakes Research 40(2): 336–346.

Karatayev, A. Y., L. E. Burlakova, S. E. Mastitsky, D. K. Padilla & E. L. Mills, 2011. Contrasting rates of spread of two congeners, *Dreissena polymorpha* and *Dreissena rostriformis bugensis*, at different spatial scales. Journal of Shellfish Research 30(3): 923–931.

Karatayev, A. Y., L. E. Burlakova, C. Pennuto, J. Ciborowski, V. A. Karatayev, P. Juette & M. Clapsadl, 2014. Twenty five years of changes in *Dreissena* spp. populations in Lake Erie. Journal of Great Lakes Research 40(3): 550–559.

Karatayev, A. Y., L. E. Burlakova & D. K. Padilla, 2015. Zebra versus quagga mussels: a review of their spread, population dynamics, and ecosystem impacts. Hydrobiologia 746(1): 97–112.

Klerks, P. L., P. C. Fraleigh & J. E. Lawniczak, 1996. Effects of zebra mussel (*Dreissena polymorpha*) on seston levels and sediment deposition in western Lake Erie. Canadian Journal of Fisheries and Aquatic Sciences 53(10): 2284–2291.

Kovacik, T. L., 1972. Information on the velocity and flow pattern of Detroit River water in western Lake Erie revealed by an accidental salt spill. Ohio Journal of Science 72(3): 81–86.

Kpodonu, A. T. N. K., D. P. Hamilton, A. Hartland, D. C. Laughlin & C. H. Lusk, 2016. Coupled use of sediment phosphorus speciation and pigment composition to infer phytoplankton phenology over 700 years in a deep oligotrophic lake. Biogeochemistry 129(1): 181–196.

Lukkari, K., H. Hartikainen & M. Leivuori, 2007. Fractionation of sediment phosphorus revisited. I: fractionation steps and their biogeochemical basis. Limnology and Oceanographic Methods 5(12): 433–444.

Maccoux, M. J., A. Dove, S. M. Backus & D. M. Dolan, 2016. Total and soluble reactive phosphorus loadings to Lake Erie: a detailed accounting by year, basin, country, and tributary. Journal of Great Lakes Research 42(6): 1151–1165.

Makarewicz, J. C., 1993. Phytoplankton biomass and species composition in Lake Erie, 1970 to 1987. Journal of Great Lakes Research 19(2): 258–274.

Makarewicz, J. C., P. Bertram & T. W. Lewis, 2000. Chemistry of the offshore surface waters of Lake Erie: pre- and post-*Dreissena* introduction (1983–1993). Journal of Great Lakes Research 26(1): 82–93.

Marvin, C., M. Charlton, J. Milne, L. Thiessen, J. Schachtschneider, G. Sardella & E. Sverko, 2007. Metals associated with suspended sediments in Lakes Erie and Ontario, 2000–2002. Environmental Monitoring and Assessment 130(1–3): 149–161.

Matisoff, G. & M. L. Carson, 2014. Sediment resuspension in the Lake Erie nearshore. Journal of Great Lakes Research 40(3): 532–540.

Matisoff, G., E. M. Kaltenberg, R. L. Steely, S. K. Hummel, J. Seo, K. J. Gibbons, T. B. Bridgeman, Y. Seo, M. Behbahani, W. F. James, L. T. Johnson, P. Doan, M. Dittrich, M. A. Evans & J. D. Chaffin, 2016. Internal loading of phosphorus in western Lake Erie. Journal of Great Lakes Research 42(4): 775–788.

Michalak, A. M., E. J. Anderson, D. Beletsky, S. Boland, N. S. Bosch, T. B. Bridgeman, J. D. Chaffin, K. Cho, R. Confesor, I. Daloğlu, J. V. DePinto, M. A. Evans, G. L. Fahnenstiel, L. He, J. C. Ho, L. Jenkins, T. H. Johengen, K. C. Kuo, E. LaPorte, X. Liu, M. R. McWilliams, M. R. Moore, D. J. Posselt, R. P. Richards, D. Scavia, A. L. Steiner, E. Verhamme, D. M. Wright & M. A. Zagorski, 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 of USA 110: 6448–6452.

Mills, E. L., R. M. Dermott, E. F. Roseman, D. Dustin, E. Mellina, D. B. Conn & A. P. Spidle, 1993. Colonization, ecology, and population structure of the “Quagga” mussel (Bivalvia: Dreissenidae) in the Lower Great Lakes. Canadian Journal of Fisheries and Aquatic Sciences 50(11): 2305–2314.

Nelson, N. S., 1987. An acid-persulfate digestion procedure for determination of phosphorus in sediments. Communications in Soil Science and Plant Analysis 18(4): 359–369.

Nicholls, K. H. & G. J. Hopkins, 1993. Recent changes in Lake Erie (North Shore) phytoplankton: cumulative impacts of phosphorus loading reductions and the zebra mussel introduction. Journal of Great Lakes Research 19(4): 637–647.

NOAA, 1999. Bathymetry of Lake Erie and Lake Saint Clair. National Geophysical Data Center, NOAA. https://doi.org/10.7289/V5KS6PHK. Accessed 11 November 2014.

Ostrofsky, M. L., 1987. Phosphorus species in the surficial sediments of lakes of eastern North America. Canadian Journal of Fisheries and Aquatic Sciences 44(5): 960–966.

Ozersky, T., S. Y. Malkin, D. R. Barton & R. E. Hecky, 2009. Dreissenid phosphorus excretion can sustain *C. glomerata* growth along a portion of Lake Ontario shoreline. Journal of Great Lakes Research 35(3): 321–328.

Painter, S., C. Marvin, F. Rosa, T. B. Reynoldson, M. N. Charlton, M. Fox, P. A. Lina Thiessen & J. F. Estenik, 2001. Sediment contamination in Lake Erie: a 25-year retrospective analysis. Journal of Great Lakes Research 27(4): 434–448.

Patterson, M. W. R., J. J. H. Ciborowski & D. R. Barton, 2005. The distribution and abundance of *Dreissena* Species (Dreissenidae) in Lake Erie, 2002. Journal of Great Lakes Research 31: 223–237.

Pennuto, C. M., L. E. Burlakova, A. Y. Karatayev, J. Kramer, A. Fischer & C. Mayer, 2014. Spatiotemporal characteristics of nitrogen and phosphorus in the benthos of nearshore Lake Erie. Journal of Great Lakes Research 40(3): 541–549.

Przywara, M. S., 1978. Characterizations of the Detroit, Raisin, and Maumee Sediment Plumes in Western Lake Erie Using Grain-size and Heavy-Mineral Analyses. Bowling Green State University, Bowling Green.

Psenner, R. & R. Pucsko, 1988. Phosphorus fractionation: advantages and limits of the method for the study of sediment P origins and interactions. Archiv fur Hydrobiologie Beih Ergebn Limnologie 30: 43–59.

Smith, D. R., K. W. King & M. R. Williams, 2015. What is causing the harmful algal blooms in Lake Erie? Journal of Soil and Water Conservation 70(2): 27A–29A.

Søndergaard, M., J. Jensen & E. Jeppesen, 2003. Role of sediment and internal loading of phosphorus in shallow lakes. Hydrobiologia 506–509(1–3): 135–145.

Søndergaard, M., J. Windolf & E. Jeppesen, 1996. Phosphorus fractions and profiles in the sediment of shallow Danish lakes as related to phosphorus load, sediment composition and lake chemistry. Water Research 30(4): 992–1002.

Stumpf, R. P., T. T. Wynne, D. B. Baker & G. L. Fahnenstiel, 2012. Interannual variability of cyanobacterial blooms in Lake Erie. PLoS ONE 7(8): e42444.

Tu, L., K. A. Jarosch, T. Schneider & M. Grosjean, 2019. Phosphorus fractions in sediments and their relevance for historical lake eutrophication in the Ponte Tresa basin (Lake Lugano, Switzerland) since 1959. Science of the Total Environment 685: 806–817.

Turner, C. B., 2010. Influence of zebra (*Dreissena polymorpha*) and quagga (*Dreissena rostriformis*) mussel invasions on benthic nutrient and oxygen dynamics. Canadian Journal of Fisheries and Aquatic Sciences 67(12): 1899–1908.

Williams, J. D. H., J. M. Jaquet & R. L. Thomas, 1976a. Forms of phosphorus in the surficial sediments of Lake Erie. Journal of Fisheries Research Board of Canada 33(3): 413–429.

Williams, J. D. H., T. P. Murphy & T. Mayer, 1976b. Rates of accumulation of phosphorus forms in Lake Erie sediments. Journal of Fisheries Research Board of Canada 33(3): 430–439.

Williamson, F. & T. Ozersky, 2019. Lake characteristics, population properties and invasion history determine impact of invasive bivalves on lake nutrient dynamics. Ecosystems 22(8): 1721–1735.

Yuan, F., J. D. Chaffin, B. Xue, N. Wattrus, Y. X. Zhu & Y. Sun, 2018. Contrasting sources and mobility of trace metals in recent sediments of western Lake Erie. Journal of Great Lakes Research 44(5): 1026–1034.

Yuan, F., R. Depew & C. Soltis-Muth, 2014. Ecosystem regime change inferred from the distribution of trace metals in Lake Erie sediments. Scientific Reports 4: 1–7.

Yuan, F., H. Li, R. Kakarla, C. Kasden, S. Yao, B. Xue & Y. Sun, 2020. Variability of sedimentary phosphorus fractions in the western and Sandusky basins of Lake Erie. Journal of Great Lakes Research 46(4): 976–988.