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Spatiotemporal characteristics of nitrogen and phosphorus in the benthos of nearshore Lake Erie

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ABSTRACT

Even though nutrient loading targets for Lake Erie have been met for almost 20 years, the lake is still showing signs of eutrophication. In-lake nutrients usually originate from the outside of the lake boundaries; however, there are significant nutrient pools within the lake which potentially are cycled back to the water column from the benthic zone. A better accounting of sediment and benthic macroinvertebrate nutrient pools might further our understanding of why the lake still displays symptoms of eutrophication. We examined the spatiotemporal patterns in nitrogen and phosphorus concentrations of the numerically dominant amphipods, oligochaetes, chironomids, and dreissenid mussels, plus surficial sediments along the southern shoreline. Sediment nutrients and organic matter content increased from nearshore-to-offshore, and sediment nitrogen, but not phosphorus, showed significant differences among the basins. More than 98% of the benthic P and 94.5% of the benthic N were sequestered in the sediments whereas the remainder was in the biota. Dreissenid mussels accounted for approximately 95% of the non-sediment nutrients in the benthic zone. In 2011, an extremely wet year, the concentration of suspended solids was roughly 3.75× higher compared to the dry year (2012), and contained roughly 2.5× and 7.5× as much phosphorus and nitrogen, respectively. All benthic taxa showed significant annual differences in tissue nutrient content, potentially responding to the extreme meteorological differences between study years. There were no significant spatial differences in organism tissue nutrient concentrations either among lake basins or along the nearshore–offshore transects. We estimated that there were 41,691 t of P and 116,544 t of N in the benthic coastal zone. This updated accounting of the benthic nutrient pools, coupled with information on organism and sediment flux rates, might prove insightful in understanding nutrient dynamics in the Lake Erie nearshore.

Introduction

Although the nutrient abatement strategies implemented in the Lake Erie watershed since the 1970's have reduced phosphorous inputs to target levels (i.e., ~10,000 t/yr), not all of the anticipated responses have been realized (Charlton and Milne, 2004; DePinto et al., 1986). The ongoing occurrence of hypoxia in the central basin (i.e., the 'dead-zone'), extensive *Cladophora* and *Lyngbya* growth in the eastern and western basins, and repeated outbreaks of nuisance algal blooms in the western basin have all occurred since the reduction in nutrient inputs (Bridgeman and Penamon, 2010; Burns et al., 2005; Higgins et al., 2005; Michalak et al., 2013). This seemingly contradictory set of observations has been called the 'Lake Erie Trophic Paradox' (Matisoff and Ciborowski, 2005), and suggests that we require a deeper understanding of Lake Erie nutrient dynamics. Early modeling efforts used to establish target nutrient load levels assumed that Lake Erie would mix like a large beaker where no single zone of the system had overriding control over other parts of the system. Additionally, only pelagic biota played a major role in the mass balance kinetics of early models (Di Toro et al., 1987). One major difference between early model representations of lake behavior and current conditions has been the invasion of dreissenid mussels to the nearshore environment. The arrival and eventual establishment of *Dreissena* spp. also have led to changes in the ecology of Lake Erie (Heath et al., 1995), including changes in light

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penetration (Barbiero et al., 2006b), increasing Secchi disk depth (Holland, 1993), availability of hard substrates (Wilson et al., 2006), alterations in benthic and phytoplankton communities (Barbiero et al., 2006a; Botts et al., 1996; Kuhns and Berg, 1999; Lederer et al., 2006), and changes in water column nutrient concentrations (Barbiero et al., 2006a). It has been proposed that the success of dreissenid mussels in the nearshore environment has resulted in a cascade of effects which potentially make the nearshore zone dominant in controlling whole lake dynamics (i.e., the nearshore shunt; Hecky et al., 2004). If the nearshore shunt is occurring, then early models used to establish lake-wide nutrient targets will be invalid.

Excess nutrients are the number one stressor responsible for the degradation of almost 45% of impaired lakes in the U.S. (EPA, 1999) and internal sources of nutrients (i.e., those released from the sediments) can often rival external ones (e.g., Nurnberg, 1991; Nurnberg et al., 1986; Welch and Cooke, 1995). Canavan et al. (2006) found that ~56% of the total P deposited on the sediment of Haringvliet Lake (The Netherlands) was returned to the overlying water through diffusion and bioirrigation (the pumping of pore water by benthic macroinvertebrates through their burrows). Globally, lakes are considered "biogeochemical hotspots" (ASLO, 2003). Freshwater lakes store roughly half as much organic carbon/yr as the oceans, but they cover less than 1% of global surface area (Dean and Gorham, 1998). Clearly, lake sediments play important roles in global nutrient dynamics. For Lake Erie, early estimates suggested that roughly 80% of the phosphorus entering the lake eventually settled within the basin (IJC, 1970) and that incoming tributaries contributed roughly 28% of that accumulating external load. Recent water column nutrient studies suggest a reduction in nutrient loading to the lake from 1989 thru 1995 (Charlton and Milne, 2004). Of particular interest is whether or not that decrease in nutrient loading is reflected in a decrease in nutrient storage in the sediment and a decrease in internal nutrient loading. Preliminary modeling results from the ECOFORE project (Rao et al., 2008) suggest a decreased phosphate flux from 1985 to about 1995 and an increase in phosphate release from the sediments since 1995. One compartment often not assessed in internal nutrient loading estimates is the benthos.

Lake benthos refers to animals associated with substrates (Wetzel, 2001), generally those living in or on lake sediments and bottom structure like cobbles, boulders or bedrock. Although Lake Erie benthos is represented by a diverse array of microinvertebrates and macroinvertebrates (Barton and Hynes, 1978; Bouzat et al., 2013; Burlakova et al., 2014–in this issue), the macroinvertebrate community is presently dominated by a relatively small set of animal taxa. The numerically dominant macroinvertebrates include the infaunal chironomid midges and oligochaetes and the epifaunal amphipods and molluscs, most notably *Dreissena* spp. (Burlakova et al., 2014–in this issue).

Benthic organisms can affect nutrient dynamics in several ways. Animals typically have higher concentrations of nutrients within their tissues relative to the surrounding environment (e.g., Sterner and Elser, 2002). Their bodies can act as nutrient reservoirs, retaining nutrients in their tissues until death. Animals also will ingest particulate nutrients and excrete both particulate and dissolved nutrients at a rate dictated by individual physiology and tissue demands for specific nutrients. Mussels, in particular, are noted for their production of nutrient-rich feces and pseudofeces and urine (Arnott and Vanni, 1996; Ozersky et al., 2009). Thus, living organisms function as storage reservoirs for nutrients while alive and also as nutrient recyclers. Additionally, benthic organisms can affect nutrient dynamics through bioturbation activities associated with feeding, locomotion, or bioirrigation (Bachteram et al., 2005; Chaffin and Kane, 2010; Fisher et al., 1980; Hansen et al., 1998; Matisoff and Wang, 2000), bringing nutrients bound within the sediments to the sediment–water interface. How benthic organisms interact with sediment nutrients may have significant impacts for understanding lake trophic status.

Hecky et al. (2004) provided some testable assumptions necessary for the nearshore shunt to be operational (their Table 1). In particular, they suggest that offshore, water column nutrient concentrations should decline relative to the nearshore, but that offshore benthic material should be greater and have higher P concentrations compared to the nearshore. Thus, we estimated the nutrient concentration within four major benthic animal groups, plus the surficial sediments, across basins and depths in Lake Erie over three years to provide an accounting of the benthic nutrient pools within the coastal zone. We focused on these organisms as they are the most abundant members of the benthic community and most likely to play a role in internal nutrient cycling since these organisms will consume and excrete nutrients, and are known to engage in bioturbation activities.

Methods

We used nearshore-to-offshore transects with fixed sample stations at 2, 5, 10, and 20 m to assess phosphorus and nitrogen nutrient pools in four benthic biological compartments and surficial sediments along the U.S. shoreline of Lake Erie. The benthic organisms targeted included the numerically dominant infaunal Oligocheata and Chironomidae and the epifaunal Amphipoda and *Dreissena* spp. mussels. All of these organism groups are reported as bioturbators, and these four groups account for over 98% of the living benthic biomass and density in nearshore Lake Erie, exclusive of fish, bacteria, and algae (Burlakova et al., 2014–in this issue). We also assessed these same nutrients in the surficial sediment pool at the same locations.

Samples were collected in June of 2009, 2011, and 2012, early September in 2009, and late August in 2011 and 2012 as part of the NOLENS (Nearshore and Offshore Lake Erie Nutrient Study) and LENONS (Lake Erie Nearshore and Offshore Nutrient Study) research projects. These two projects were multi-investigator, multi-institution efforts to document the nearshore and offshore nutrient standing stocks in Lake Erie. The findings relevant to the non-benthic pools (i.e., water column nutrients, plankton communities, productivity) can be found elsewhere in this issue. Six transects were employed in 2009 (NOLENS), bracketing the major tributaries of the central and eastern basins of the lake (Fig. 1, Table 1); Sandusky and Grand Rivers (central basin) and Cattaraugus Creek (eastern basin). In 2011/2012, we employed eight transects roughly equidistant along the southern Lake Erie shoreline resulting in two western basin, four central basin, and two eastern basin transects (Fig. 1, Table 1). Two of these transects (GRE and CCW) also were used in 2009. We consider open water/offshore to be areas of the lake with depths ≥20 m (eastern/central basins), or ≥5 km offshore (in western basin). Hall et al. (2003), working in Lake Ontario, also used depth to reflect nearshore and offshore habitats (i.e., ≤10 m defined as 'nearshore' and ≥20 m defined as 'offshore'). We restrict our nearshore zone to depths <20 m (eastern/central basins) or closer than 5 km in the western basin since depth in that basin never exceeds 15 m.

Three replicate grab samples were taken at each depth on each date and processed separately. All samples were collected with a petite Ponar grab (area 0.0231 m^{-2}) or Ekman grab (area 0.0225 m^{-2}), with the exception of 9 samples in 2009, which were collected by SCUBA divers from 2 to 5 m (GRE transect) and 10 m (CCW) using an air-lift sampler (area 0.0625 m^{-2}, Pennuto et al., 2012). The air-lift sampler allowed us to easily collect at sites encrusted with mussels, but resulted in loss of sediment material through the mesh of the collection nets. Thus, the air-lift sampler was abandoned in later years in lieu of Ponar or Ekman grabs. Samples were washed through a 500-μm mesh net and sorted live. The target organisms (oligochaetes, amphipods, chironomids, mussels) were blotted dry on absorbent paper, counted, and weighed to the nearest 0.0001 g (total wet mass). Dry mass conversion ratios were obtained from Ricciardi and Bourget (1998) for amphipods and oligochaetes, and from Dermott and Paterson (1974) for chironomid larvae. All macroinvertebrates were fixed with 10% neutral buffered formalin, and identified to the lowest possible taxonomic level (usually species, genus, or family) at a later date. We did not attempt to count

Table 1
Sample sites as part of the NOLENS and LENONS projects to assess nutrient pool mass and concentrations in benthic compartments of nearshore Lake Erie. In descriptions, sample depths are in m and the predominant substrate is indicated in () after the sample depth. S = sand, C = cobble/boulder, B = bedrock, and M = mud. Latitude/longitude values represent the 10-m depth station on each transect.

Year	Basin	Site designation	Description	North Lat., West Long.
2009 (NOLENS)	Central	SRW	Sample depths of 2 (S), 5 (S), 10 (S,M), and 14 (M) m west of the Sandusky River mouth	41.53722, −82.64278
		SRE	Sample depths of 2 (S), 5 (S), 10 (S,M), and 14 (S,M) m east of the Sandusky River mouth	41.45002, −82.31380
		GRW	Sample depths of 2 (S), 5 (S), 10 (S), and 20 (S,M) m west of Grand River mouth	41.76218, −81.33585
		GRE	Sample depths of 2 (B,S), 5 (S,C,B), 10 (S), and 20 m east of Grand River mouth	41.79055, −81.22565
	Eastern	CCW	Sample depths of 2 (S), 5 (S), 10 (C,B), and 20 (M) m west of Cattaraugus Creek mouth	42.57090, −79.17352
		CCE	Sample depths of 2 (B,C), 5 (B,C), 10 (S), and 20 (M) m east of Cattaraugus Creek mouth	42.59421, −79.14393
2011/12 (LENONS)	Western	SSP	Sample depths of 2, 5, and 8 14 m offshore easterly from Sterling State Park, MI.	41.85631, −83.33423
		TC	Sample depths of 2, 5, 10, and 14 m offshore northerly from Turtle Creek Bay, near Crane Creek State Park, OH.	41.85528, −83.22806
	Central	HUR	Sample depths of 2 (S), 5 (S), 10 (S), and 20 (S,M) m offshore northerly from just east of Cedar Point amusement park and west of Huron, OH.	41.48346, −82.63344
		GRE	Sample depths of 2 (B), 5 (B,C), 10 (S,C), and 20 (M) m east of Grand River mouth. Same transect as 2009. Fairport Harbor, OH.	41.78336, −81.21685
		ASH	Sample depths of 2 (S), 5 (S), 10 (S,C,M), and 20 (M) m northerly offshore from Ashtabula, OH and west of the Ashtabula River mouth.	41.91036, −80.81231
		ERI	Sample depths of 2 (S,M), 5 (B,C), 10 (S,B,C), and 20 (M) m east of Presque Isle State Park offshore from Erie, PA.	42.16978, −80.03423
	Eastern	WSF	Sample depths of 2 (S), 5 (S,B,C), 10 (S,B), and 20 (M) m offshore northerly from Westfield/Barcelona, NY.	42.33347, −79.60015
		CCW	Sample depths of 2 (S), 5 (B,C,S), 10 (S,C), and 20 (M) m west of Cattaraugus Creek mouth. Same transect as 2009 off village of Silver Creek, NY	42.57473, −79.18306

ostracods and nematodes. The oligochaete, *Branchiura sowerbyi* Beddard, was identified to species, but all others were categorized as oligochaetes. These data were used to determine benthic density (#/m^2) and biomass (g/m^2) and results for the entire community are found in Burlakova et al. (2014–in this issue). For Dreissenids, fresh wet-blotted weight, wet–weight minus shell weight, and dry weight were determined as per Karatayev et al. (2014–in this issue). Extra Ponar and Ekman grabs were collected to accumulate enough target organism tissue for determination of nutrient content (see below: Nutrient analyses section). These samples were washed through a 500-μm mesh net, sorted live, and the four target groups frozen separately in 50-mL centrifuge tubes until processed at a later date. Dreissenids had their flesh removed from the shells prior to freezing.

Surficial sediments were collected using replicate Ekman grabs (n = 3) when substrates were not bedrock, boulder, or cobble. At each depth we attempted to find depositional patches between boulder or bedrock outcrops where some sediment material could be collected. Upon retrieval, grab flaps were carefully opened and the upper 1 cm of substrate was scraped into a 50-mL centrifuge tube using a disposable plastic spoon. The spoon was inserted horizontally into the sediment to half the depth of the spoon width and pulled across the sediment surface until enough material was collected. We focused on the upper 1 cm of sediment as this would represent the 'freshest' sediments with the highest organic matter content and the depth to which we expected significant interactions with epifaunal organisms. Kemp et al. (1977) calculated a maximum sedimentation rate for Lake Erie of 0.74 cm/yr in its western basin. Thus, the upper 1 cm might reflect roughly one year of sedimentation at the maximum rate. Previous assessments of surficial sediment in Lake Michigan (Rossman, 2002; Rossman and Edgington, 2000) used a depth of 1 cm to study mercury deposition, and the upper 1 cm is defined as 'surficial sediment' by the U.S. EPA (U.S. EPA, 2001). These samples were frozen until further processing at a later date.

Water column total suspended solids (TSS) and seston were collected at each depth station on each date to provide an estimate of the mass of nutrients available to settle to the sediment. Here we present only the data from June 2011/2012 and only from the central and eastern basin sites since analysis of samples from the western basin sites is still not

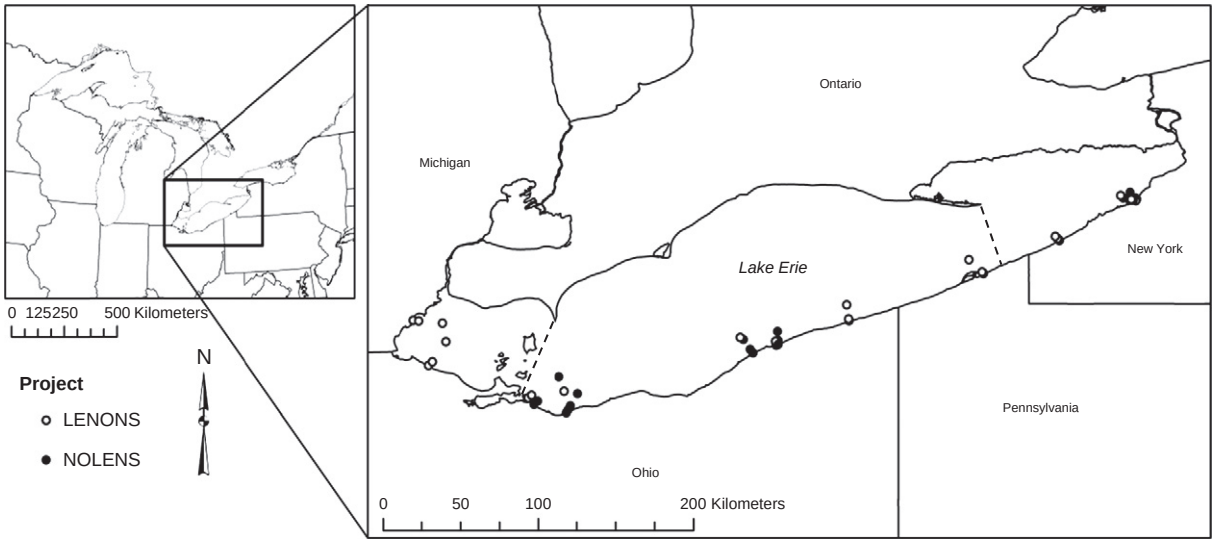

Fig. 1. Sampling locations for the 2009 NOLENS and 2011/2012 LENONS projects on Lake Erie. Closed circles = NOLENS; open circles = LENONS. Dashed lines divide western, central, and eastern basins.

completed. Depth-integrated water samples with particulate material (zooplankton, phytoplankton, POM) were collected using a tube sampler (2.5-cm diameter clear Tygon). The tube was lowered repeatedly to within 1 m of the bottom for nearshore stations or to 10 m (approximately twice the depth of the thermocline) for the deeper stations. About 15 L was collected and homogenized in a large bucket. A 500-mL, plastic bottle was immersed into the bucket to collect a representative TSS sample and the bottle was stored on ice until analysis was performed, usually within 48 h. Seston was filtered through a conditioned and pre-weighed GF/F filter until enough mass accumulated on the filter for analysis. GF/F filter conditioning included soaking in distilled water for 24 h and drying in an oven at 60 °C for 24 h. The volume of sample water filtered was recorded. Filters were placed in small Petri dishes and frozen at −20 °C immediately. Seston filters and TSS sample bottles were transported to the National Center for Water Quality Research (NCWQR) at Heidelberg University for analyses. The product of seston nutrient concentration and TSS mass was used as an estimate of the nutrient mass potentially available for settling to the sediment.

Nutrient analyses

All biological tissue, sediment samples, and seston filters were analyzed for nitrogen (total Kjeldahl nitrogen, TKN) and phosphorus (total phosphorus, TP) content on a dry mass basis. These results were multiplied by the areal density and biomass results to determine standing stock of nutrients within each of the four taxonomic compartments plus the surficial sediments. Total area of the 0–20 m contours (6690 km^2) was obtained from the Great Lakes Program, SUNY Buffalo (Dr. Joseph Atkinson, pers., comm.) and this was used to estimate the potential nutrient pool throughout the nearshore zone.

Frozen sediment and biological tissue samples were thawed at room temperature in a preweighed aluminum weigh boat and dried at 60 °C until reaching a constant mass. Samples were cooled in a dessicator and ground with a mortar and pestle. The sample was repackaged into plastic shell vials, labeled, and shipped to the National Center for Water Quality Research (NCWQR) at Heidelberg University for analysis. Once at Heidelberg, 0.10 g of dried material was measured into a bottle with 200 mL of de-ionized water. This bottle provided a sample for both TP and TKN analyses. The sample was homogenized with a sonic disruptor and shaken before a subsample was taken. A 50-mL subsample was measured into a 125-mL glass flask with 1 mL of 12 N sulfuric acid and 0.04 g of ammonium persulfate. The flask was covered with a disposable beaker and autoclaved for 45 min at 15 PSI. Upon cooling the contents of the flask were filtered through a GFF filter and analyzed on a B&L AutoAnalyzer II for TP. For TKN analysis, a 25-mL subsample was added to a digestion tube with 4 mL of TKN digestion reagent and placed in a digestion block for 4 h. Upon cooling, 10 mL of distilled water was added to dissolve the precipitate and analysis was completed on an AutoAnalyzer II.

Laboratory blanks and spiked matrix samples were performed once per 20 samples with each sample batch. All data quality indicators were within expected acceptance criteria (TKN: % recovery = 102.8 ± 12.6, blanks = 0.009 ± 0.031; n = 39, and TP: % recovery = 98.1 ± 6.8, blanks = 0.002 ± 0.004). Detection limits were 0.07 μmol/L for TKN and 0.003 μmol/L for TP.

Sediment calculations

In 2009 only, sediment dry bulk density (g/cm^3, Dadley et al., 1992) was determined for transects to allow estimation of surficial sediment nutrient pools. Samples of the upper 1-cm layer were collected as described above and frozen in 50-mL centrifuge tubes. Samples were later thawed in their centrifuge tubes and homogenized. A 1-cm^3 subsample of wet sample was removed and placed in a preweighed aluminum weigh boat. The wet-weight was recorded to the nearest 0.1 g. Samples were oven-dried at 60 °C until a constant weight and reweighed. Samples were then combusted at 550 °C for 2 h, cooled in a desiccator, and reweighed. The resultant dry weight represented the surficial sediment bulk density in g/cm^3. Subtraction of the post-combustion weight from the dry weight represented the organic fraction of the sediment. Bulk density (BD) and percent organic matter (OM) estimates were examined for differences based on depth using ANOVA. Additionally, we determined correlations of BD and OM with each other and with TKN and TP concentrations. Various other reports on Lake Erie sediment have used a bulk density value between 2.0 and 2.3 g/cm^3 (Klump et al., 2005; Pilasky and Matisoff, 2010) for determination of nutrient mass values. We applied our mean bulk density values of 1.7 g/cm^3 for the shallowest sites (0–10 m) and 1.4 g/cm^3 for deepest sites (20 m). Nutrient concentrations (mg/g) were determined as outlined above on dry sediments, multiplied by sediment bulk density (g/m^3), and multiplied by the lake bed area bound within each depth contour sampled (0–10 m = 2540.2 km^2; 10–20 m = 4149.7 km^2) to provide a gross estimate of the amount of nutrient in the upper 1-cm depth of sediment.

Statistical analyses

All tissue and sediment nutrient concentration data were transformed as log(n + 1) to meet variance assumptions prior to analyses. ANOVA procedures were used to detect differences in nutrient concentrations among years (n = 3), basins (n = 3), and depths (n = 2; nearshore (0–10 m) vs offshore (20 m or >5 km)). When enough samples were collected, we also examined seasonal effects (n = 2) on tissue nutrient concentration. Alpha levels were set at 0.05, and appropriate Bonferroni adjustments were made for multiple contrasts following a significant main effect. Water column TSS concentrations and seston nutrient concentrations were examined for differences between years (n = 2; 2011 and 2012), basins (n = 2; central vs eastern), and location (NS vs OS) using ANOVA. Pearson product–moment correlations were used to examine sediment nutrient correlations with BD and TSS.

Results

A total of 78 benthic organism samples were assessed for biomass across the three years of sampling and nutrient mass pools were compared on a dry weight basis. Chironomid midges and oligochaetes were the most cosmopolitan of the four organism groups assessed, occurring in all samples. Dreissenids occurred in nearly all samples, exclusive of shallow stations with sand substrate. Amphipods were never collected at the offshore sites (20 m or >5 km). In all years, dreissenid mussels were the most common organisms, representing 47% to 95% of the dry biomass among the sites (Table 2). In all three years of sampling, mussels were most abundant in the eastern basin of the lake, followed by the central basin, and least abundant in the western basin (Table 2).

We were unable to recover enough dry mass tissue for nutrient analysis of all benthic groups among the different year, basin, season, and depth combinations (Table 3). Overall, oligochaetes ranked the highest in total tissue nutrient concentration (mean nitrogen = 90.9 mg/g, mean phosphorus = 11.2 mg/g). Mussels had the overall lowest concentration of P (mean = 6.7 mg/g) whereas amphipods held the least N (mean = 68.0 mg/g) (Table 3).

Amphipods showed a significant year effect on both nitrogen and phosphorous content (N: $F_{2,21} = 4.25$, $P = 0.028$; P: $F_{2,21} = 10.04$, $P < 0.001$), but no differences in nutrient content among basins or seasons. Phosphorous concentrations in amphipods were significantly lower in 2012 compared to both 2009 and 2011 (Bonferroni post-hoc: $P < 0.05$). Nitrogen content also was lowest in 2012, but this was only significantly different relative to 2011 (Fig. 2A). Nutrient concentrations in amphipod tissues varied the least among the organisms as determined by the coefficient of variation (CV) over all samples combined

Table 2
Average dry weight biomass (g/m^2) of select benthic organisms collected between 2 and 20 m in Lake Erie. *Dreissena* includes *Dreissena rostriformis bugensis* plus *D. polymorpha*. Standard error shown in parentheses. N equals the pooled number of June and August samples used to determine mean values. Data summarized from Burlakova et al. (2014–in this issue).

		2009			2011			2012			Total
		Western	Central	Eastern	Western	Central	Eastern	Western	Central	Eastern	
Amphipoda	Mean	0.5(0.49)	0.7(0.56)	0.3(0.25)	0.1(0.05)	0.3(0.23)	0.1(0.06)	0.1(0.11)	0.3(0.16)	0.4(0.24	0.3(0.10)
	N	8	8	8	6	16	8	6	12	6	78
Chironomidae	Mean	1.5(0.82)	0.7(0.37)	0.3(0.10)	0.3(0.13)	1.5(0.73)	1.3(0.50)	1.0(0.52)	4.0(1.81)	0.7(0.34)	1.5(0.35)
	N	8	8	8	6	16	8	6	12	6	78
Oligocheata	Mean	0.7(0.39)	0.5(0.32)	0.6(0.36)	0.4(0.21)	1.7(0.59)	0.6(0.31)	0.3(0.20)	1.9(0.53)	0.8(0.47)	0.9(0.18)
	N	8	8	8	6	16	8	6	12	6	78
Dreissena	Mean	5.3(2.25)	11.1(9.94)	20.8(13.66)	5.7(3.31)	8.4(3.97)	7.0(3.67)	6.9(3.53)	16.9(5.90)	26.7(9.61)	11.9(2.32)
	N	8	8	8	6	16	8	6	12	6	78
Other	Mean	0.9(0.54)	0.8(0.52)	<0.01	3.4(1.43)	0.9(0.41)	0.03(0.02)	6.4(4.23)	3.5(1.07)	0.18(0.14)	1.7(0.42)
	N	8	8	8	6	16	8	6	12	6	78

and nitrogen concentrations varied more than phosphorus concentrations (CV for N = 52.0% and P = 42.1%).

Nitrogen concentrations in chironomid midges did not differ among basins, seasons, or years (all $P > 0.05$), but phosphorus levels exhibited a significant year effect ($F_{2,62} = 10.49$, $P < 0.001$; Fig. 2B). Phosphorus content was highest in 2011 relative to the remaining years (Bonferroni post-hoc: $P < 0.05$). Midge nutrient concentrations showed patterns, both in absolute magnitude and annual changes, very similar to the patterns observed in amphipods. Nitrogen and phosphorus concentrations in midge tissue varied about the same when examined over all samples (CV for N = 71.5% and P = 70.6%).

Not enough oligochaete tissue was collected in 2009 to run nutrient analyses, thus we can only compare 2011 and 2012. Oligochaete tissues had no significant differences in phosphorus content among basins, seasons, or years (all $P > 0.05$), but there was a significant year difference in nitrogen content ($F_{1,38} = 7.17$, $P < 0.011$; Fig. 2C). Nitrogen levels in tissues were higher in 2011 than in 2012. Tissue P content in oligochaetes varied more than twice as much as N content (CV for N = 57.7% and P = 120.0%).

Dreissenid mussels showed significant differences in both N and P content among years (nitrogen: $F_{2,50} = 7.43$, $P = 0.002$; phosphorus: $F_{2,50} = 6.25$, $P = 0.004$; Fig. 2D). Post-hoc tests suggested that nitrogen and phosphorus content were both lowest in 2012 (both Bonferroni post-hoc: $P < 0.05$). There were no significant differences among basins, but there was a marginally significant effect of season. In 2011 only, tissue N and P were lower in late summer relative to spring (Bonferroni post-hoc: $P < 0.05$). Mussel tissue, like amphipod tissue, showed substantial variation across all samples, but varied less than either midge or worm tissue. Tissue phosphorus varied less than tissue nitrogen (N = 62.6% and P = 48%).

Spring seston nutrient and TSS concentrations were compared only for 2011 (extremely wet year) and 2012 (extremely dry year) in the central and eastern basins. Seston samples had a significantly lower concentration of phosphorus in 2011 relative to 2012 (0.091 vs 0.149 mg/kg, respectively; $F_{1,40} = 24.07$, $P \ll 0.001$), but a significantly higher nitrogen concentration (1.758 vs 0.897 mg/kg, respectively; $F_{1,40} = 5.50$, $P = 0.024$). There also was a significant basin effect ($F_{1,40} = 8.07$, $P = 0.007$), with the eastern basin having roughly twice the N concentration compared to the central basin (1.849 vs 0.806, respectively). However, there also was a significant year × basin interaction for nitrogen, making year and basin main effects less definitive ($F_{1,40} = 12.14$, $P = 0.0012$). TSS was significantly higher in the wet year (2011) compared to the dry year (2012) (6.65 vs 1.77 mg/L, respectively; $F_{1,33} = 11.88$, $P = 0.002$), having a concentration that was roughly 3.75x greater. Assuming similar settling dynamics in both years, approximately 2.4× more P and 7.4× more N should have settled on the sediment surface in 2011 relative to 2012 based on the product of nutrients in seston and TSS concentration (Table 4).

Collectively, biological tissue nutrient levels represented a very small fraction of the N and P contained within the benthic zone of

Table 3
Mean nutrient concentration (mg/g dry weight) in benthic organisms and sediment from Lake Erie in different years and seasons. N equal sample size. Standard errors appear in parentheses. For *Dreissena*, mg/g is on a shell-free dry mass (SFDM) basis.

		2009		2011		2012	
		June	August	June	August	June	August
Phosphorus							
Amphipoda	Mean	10.4(2.04)	12.4(1.67)	12.9(1.09)	11.7(1.02)	5.3(1.29)	5.6(1.29)
	N	2	3	7	8	5	5
Chironomidae	Mean	6.3(1.34)	5.6(1.54)	8.4(1.17)	13.5(1.19)	5.5(1.44)	7.8(1.88)
	N	15	9	17	16	11	6
Oligocheata	Mean	–	–	10.4(3.81)	10.1(3.83)	17.0(4.02)	6.9(5.24)
	N	–	–	14	13	12	7
Dreissena spp.	Mean	9.5(1.44)	7.4(1.54)	8.8(1.22)	5.6(1.22)	3.6(1.96)	5.1(1.13)
	N	7	8	10	10	14	13
Sediment	Mean	0.56(0.081)	0.44(0.089)	0.63(0.077)	0.66(0.075)	0.66(0.082)	0.71(0.105)
	N	15	12	18	20	17	11
Nitrogen							
Amphipoda	Mean	62.9(24.04)	55.7(19.63)	82.1(12.85)	104.9(12.02)	42.7(15.21)	59.9(15.21)
	N	2	3	7	8	5	5
Chironomidae	Mean	81.2(16.45)	64.5(18.90)	79.6(14.30)	102.3(14.55)	43.3(17.66)	92.0(23.01)
	N	15	9	17	16	11	6
Oligocheata	Mean	–	–	91.2(14.61)	130.4(14.68)	78.7(15.41)	65.3(20.09)
	N	–	–	14	13	12	7
Dreissena spp.	Mean	128.4(21.88)	96.8(23.39)	141.2(18.49)	57.3(18.49)	36.0(29.73)	54.5(17.22)
	N	7	8	10	10	14	13
Sediment	Mean	1.78(0.351)	1.18(0.384)	1.70(0.333)	1.31(0.329)	1.91(0.359)	1.97(0.451)
	N	15	12	18	20	16	11

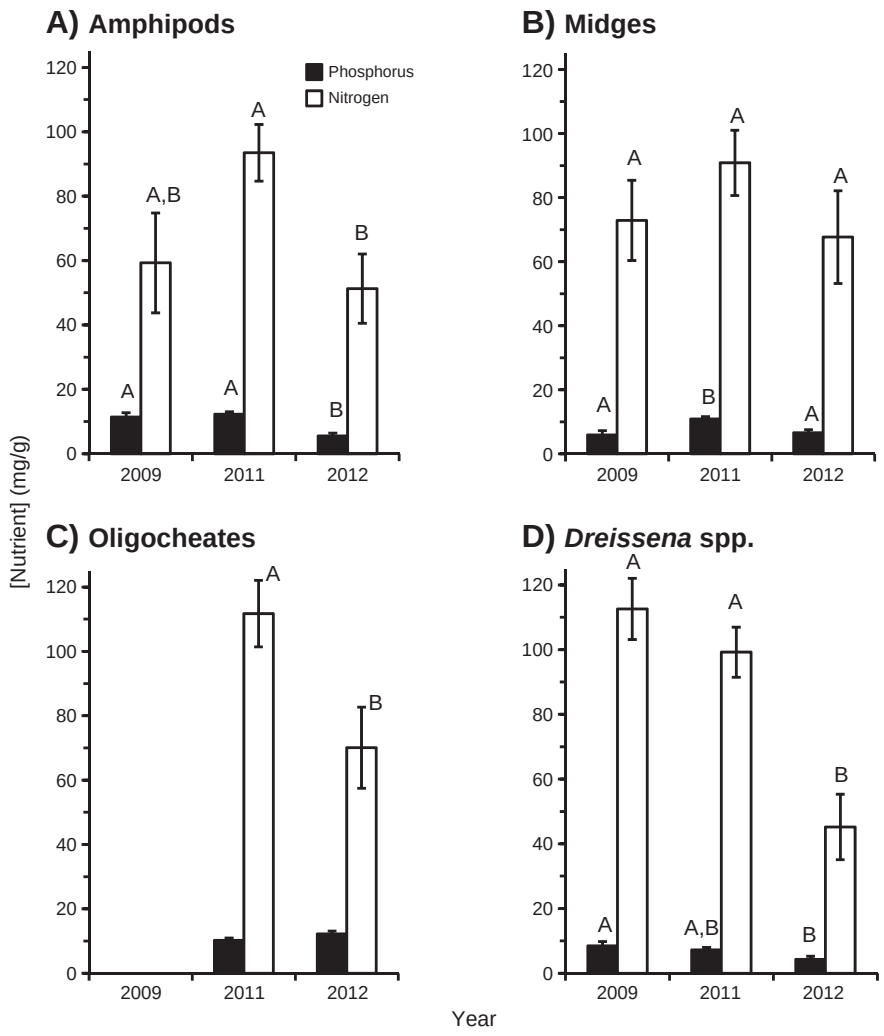

Fig. 2. Mean nutrient concentrations (mg/g dry weight) in the target benthic biological pools in Lake Erie averaged across depths and basins. Error bars equal one standard error. Same letters over P-bars indicate no significant difference in P among years and same letters over N-bars indicate no significant difference in N among years.

Lake Erie even though nutrients were considerably more concentrated in tissues. When averaged across all taxa and years, phosphorus was roughly 14 times more concentrated in living tissue than in the upper 1 cm of surficial sediment (8.6 vs 0.6 mg/g, respectively), and nitrogen was about 50 times more concentrated (79.5 vs 1.6 mg/g, respectively; Table 3). However, the huge difference in and sheer mass of surficial sediments resulted in total nutrient pools of nitrogen and phosphorus that dwarfed the living tissue pools. When multiplied by the 0–20 m area of the south shore (6690 km^2), we estimated that there were 41,691 t of phosphorus and 116,844 t of nitrogen in the benthic zone. Of this, 98.7% of the P and 94% of the N were located within the surficial sediments. Mussels contained 1.2% and 5.5% of the phosphorus and nitrogen, respectively, with amphipods, oligochaetes, and midges each contributing less than 0.5% of either nutrient.

Table 4
Mean spring nutrient (mg/g TP and TKN) and TSS concentrations (mg/L) for the central and eastern basins of Lake Erie in 2011 and 2012. Standard error in parentheses. For F values, df = 1, 40.

	2011	2012	F	P
Total phosphorus	0.091 (0.008)	0.149 (0.007)	24.07	≪0.001
Total Kjeldahl nitrogen	1.758 (0.259)	0.897 (0.247)	5.50	0.024
Total suspended solids	6.65 (0.878)	1.77 (1.091)	11.88	0.002
Product of TP * TSS	0.61	0.26		
Product of TKN * TSS	11.69	1.59		

Unlike the biological nutrient pools, there was no significant year effect on N or P concentrations in the surficial sediments ($P > 0.05$). Depth (0–10 m vs 20 m) had a significant effect on both nitrogen and phosphorus concentrations (N: $F_{1,73} = 4.24$, $P = 0.043$; P: $F_{1,73} = 8.85$, $P = 0.004$; Fig. 3), both increasing in the offshore direction. There also was a significant basin effect on nitrogen content ($F_{2,71} = 3.65$, $P = 0.031$), with the lowest concentration being found in the eastern basin and the highest in the western and central basins (Bonferroni post-hoc: $P < 0.05$; Fig. 3). Sediment nutrient concentrations varied as much as the biological pool nutrient concentrations, and sediment N levels varied almost twice as much as P levels when comparing across all samples (CV for P = 56.9% and N = 91.5%). There was a significant depth effect on both dry bulk density (BD) and percent organic matter (OM) in the surficial sediment (BD: $F_{3,12} = 13.90$, $P < 0.001$ and OM: $F_{3,12} = 5.76$, $P = 0.011$); BD was negatively correlated with OM ($r = -0.561$, $n = 15$, $P = 0.029$) and decreased with depth whereas OM increased with depth. Bulk density values ranged from a low of 0.9 to a high of 1.7 g/cm^3. Both nitrogen and phosphorus concentrations in the surficial sediments were negatively correlated with BD (nitrogen: $r = -0.515$, $P = 0.049$; phosphorus: $r = -0.611$, $P = 0.016$; both $n = 15$), but neither nitrogen nor phosphorus concentration was correlated with percent organic matter (nitrogen: $r = 0.381$, $P = 0.161$; phosphorus: $r = 0.398$, $P = 0.147$).

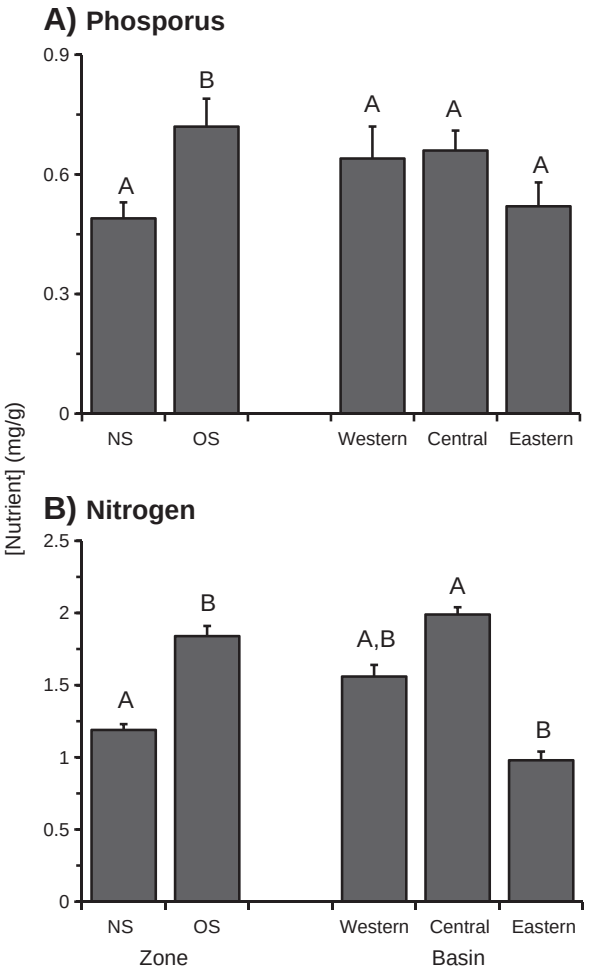

Fig. 3. Phosphorus and nitrogen concentrations (mg/g dry mass) in surficial sediments of Lake Erie. NS = nearshore, 0–10 m depths. OS = offshore, 10–20 m depths. Same letters over bars indicate no significant differences based on Bonferroni post-hoc assessments either between NS and OS or the three basins. Error bars are one standard error.

Discussion

Sediment nutrients accounted for an overwhelming majority of the standing stock of nutrients in the 0–20 m benthic zone of Lake Erie. Unlike the biological samples, surficial sediment nutrient concentrations showed significant spatial, but not temporal differences. Both nitrogen and phosphorus content in the sediments declined in a west-to-east direction (though not significantly for P) and both were significantly higher in the offshore direction (i.e., 20 m sites were greater than the 2–10 m sites, Fig. 3). These results parallel the observations that organic matter increased with depth and sediment bulk density decreased with depth. The west-to-east decline in sediment nutrients in the nearshore is not surprising given that the largest tributary inputs of sediment and nutrients are in the western basin (i.e., the Detroit and Maumee Rivers) or far western-central basin (i.e., Sandusky River). Likewise, the nearshore-to-offshore increase in nutrients is easily explained by lake hydrodynamics and gravity forcing hypolimnetic settling of smaller silt and clay particles as shown by a decreasing bulk density with depth (e.g., Wetzel, 2001).

It was a fortuitous occurrence that 2011 was an extremely wet year whereas 2012 was a drought year throughout the Lake Erie basin. The total phosphorus load entering Lake Erie from the Maumee River in spring 2011 was nearly the largest recorded since 1975, and the dissolved reactive phosphorus (DRP) load was the highest on record since 1975 (Michalak et al., 2013). In contrast, the 2012 total discharge and DRP were 20% and 15% of the 2011 levels over the same spring time frames (Michalak et al., 2013). We measured a 3.75-fold higher suspended solid concentration in 2011 relative to 2012, and estimated that there was roughly 2.5× and 7.5× more phosphorus and nitrogen, respectively, in the water column. Typical settling velocities of even very small seston (about 1.5 m/day for 10–61 μm particles; Burns and Rosa, 1980) suggest that settling particles could reach even the deepest portion of Lake Erie (i.e., 64 m) within about 43 days. Thus, assuming no year differences in settling or consumption dynamics, we anticipated a sediment phosphorus and nitrogen signature that showed high sediment levels of P in 2011 and lower levels in 2012, consistent with the large decline in incoming nutrients. We expected this reduction to be particularly evident east of the Maumee River mouth since this predominately agricultural watershed contributes roughly 36% of the discharge to Lake Erie from U.S. sources (Baker, 2007). However, we did not detect a significant temporal difference in sediment nutrient concentrations over the duration of our study.

The lack of a year effect on sediment nutrient content might be explained by several mechanisms. It could be that incoming nutrients associated with the 2011 nutrient pulse never reached the bottom. Possibly, the rapid turnover rate in Lake Erie (roughly 2-year residence time; Quinn, 1992) transported this nutrient pulse out of the lake and down the Niagara River. Alternatively, Matisoff (1999) suggested that the combination of particle settling velocities plus sediment bioturbation activity allows only a 3-to-7-year resolution sensitivity for sedimentation in Lake Erie. This means that organism activity within the sediments redistributes settled particles into the sediment in such a way as to make it difficult to distinguish annual deposition events. Given these sedimentation dynamics and resolution limits, we would benefit from new techniques that might tease out shorter term temporal distinctions. For example, Green et al. (2002) and Gerino et al. (1998) made efficient use of natural chlorophyll *a* tracers or luminophores to resolve annual sedimentation events in marine systems. Lastly, it is possible that the 2011 nutrient pulse may have been intercepted before reaching the sediment.

Hecky et al. (2004) proposed a nearshore shunt mechanism whereby dreissenid mussels intercepted seston and nutrient particles in transit to the offshore and redirected them to the benthic nearshore zone. Applying a modeling effort to federal water quality data, Cha et al. (2011) showed that dreissenid mussels have restricted the offshore transport of nutrients out of Saginaw Bay, Lake Huron, since their arrival, supporting nearshore shunt dynamics. Our dreissenid tissue nutrient concentration data also might suggest that these mussels took advantage of a large 2011 nutrient pulse followed by a 2012 nutrient shortage since both N and P levels within mussel tissues were lower in 2012 compared to 2011 (Fig. 2D). An explicit assumption of the nearshore shunt hypothesis is an increase in sediment nutrient concentrations from nearshore to offshore (Hecky et al., 2004; Table 1). Presumably this results from benthic mussels filtering out significant fractions of pelagic seston and converting it to feces and pseudofeces which settle in the sediments. The post-dreissenid loss of a spring phytoplankton bloom in Lake Michigan and its resultant nutrient deposition signature would seem to support this assumption (Vanderploeg et al., 2010). Our sediment nutrient data showed an increasing concentration of N and P with depth as predicted by the shunt hypothesis, but this could also be an artifact of lower surficial sediment bulk density values with its associated adsorbed nutrients at the 20-m sites. Further research on the specific fate of mussel feces and psuedofeces as part of the surficial sediment pool would be a valuable contribution in our understanding of shunt dynamics. Although these deposits are clearly dense enough to remain on the bottom near or within mussel beds, both nearshore wave action and periodic upwelling events generate significant water velocities and turbulent energy (e.g., Rao and Schwab, 2007) capable of resuspending deposited particles.

Although not directly implicated in the nutrient shunt hypothesis, the remaining benthos also appeared to respond to the annual differences in incoming nutrients. Amphipod nitrogen and phosphorus tissue

concentrations, chironomid tissue phosphorus concentrations, and oligochaete tissue nitrogen concentrations were all lowest in 2012 (Fig. 2). The changes in tissue nutrient content among years suggest that these benthic taxa are more stoichiometrically malleable than prevailing thought indicates (e.g., Sterner and Elser, 2002). However, there is growing evidence that some benthic taxa may be less homeostatic than many pelagic taxa, and this is particularly true for dreissenids (e.g., Frost et al., 2003; Naddafi et al., 2009). Even though we observed temporal differences in biota nutrient content, we did not record any nearshore-to-offshore or interbasin differences in nutrient content in organism tissue. This is in agreement with Pennuto et al. (2012) who did not find any spatial differences in the P content of dreissenid mussels in the Lake Ontario nearshore. Thus, although benthic organisms appear to be stoichiometrically consistent throughout the lake, future modeling efforts should incorporate some temporal variability and feedback loops since these organisms recycle nutrients and can act as short-term nutrient sources.

Several authors have suggested that benthic organisms can be significant sources of recycled nutrients in lake ecosystems. Dreissenid mussels, chironomid midges, oligochaete worms, and amphipods all have been shown to elevate dissolved nutrient levels in lakes (e.g., Arnott and Vanni, 1996; Conroy et al., 2005; Devine and Vanni, 2002; Gardner et al., 1983; Nalepa et al., 1983; Ozersky et al., 2009; Wilhelm et al., 1999), and this may have important ecosystem effects. For example, Conroy et al. (2005) suggested that dreissenid mussels could turn over the entire nutrient pool in the western basin of Lake Erie in 6 to 50 days, depending on the nutrient, and Ozersky et al. (2009) showed that nutrient release by dreissenid mussels was sufficient to support *Cladophora glomerata* growth over short distances of the Lake Ontario shoreline. Additionally, bioturbation activities like bioirrigation, conveyor-belt feeding, or burrowing have the potential to bring sediment-bound nutrients to the sediment–water interface and into the water column (e.g., Fisher et al., 1980; Gallepp, 1979; Matisoff and Wang, 2000). Thus, the nutrient content within benthic organism tissue, their excretion rates, and their bioturbation activities affect nutrient recycling into the water column.

We estimated that there was a total phosphorus pool of 41,691 t in the 0–20 m contour of the southern Lake Erie shore and a total nitrogen pool of 116,844 t. Of this, approximately 500 t of P (1.2%) and 6426 t of N (5.5%) was sequestered within dreissenid mussel tissues and mussels accounted for up to 95% of the benthic biomass throughout the sampling area. Thus, in terms of living benthos, the remaining organisms possessed a very small fraction of the P and N nutrient pools in Lake Erie. For comparison, Johengen et al. (1995) suggested that there was between 52 and 682 t of P locked up in mussel tissue in Saginaw Bay in the early 1990's after the population reached a stable density. Similarly, our estimated P concentration in mussel tissues (grand mean = 6.2 mg/g) was within the range of concentrations reported by Pennuto et al. (2012) for mussels in the nearshore of Lake Ontario (3.9 to 7.4 mg/g for U.S. and Canadian mussels, respectively), and by Kr lak and Zdanowski (2007) in several Polish lakes (6.6 mg/g). When averaged across all sites and depths and scaled to equivalent areas, Pennuto et al. (2012) found roughly 160 t of phosphorus sequestered in mussel tissue in the Lake Ontario nearshore, or about one third of the total estimated for a comparable depth zone in Lake Erie. Even though a small fraction of the total nutrient pool in the benthic zone is sequestered within biological tissue, the role of the benthos in sediment reworking coupled with the transient nature of nutrient storage in living tissue suggests that more attention is needed on the impact of benthos on lake nutrient dynamics.

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