Distribution of Native Mussel (Unionidae) Assemblages in Coastal Areas of Lake Erie, Lake St. Clair, and Connecting Channels, Twenty-five Years After a Dreissenid Invasion

David T. Zanatta[1,*], Jonathan M. Bossenbroek[2], Lyubov E. Burlakova[3], Todd D. Crail[2], Ferenc de Szalay[4], Traci A. Griffith[1], Douglas Kapusinski[4], Alexander Y. Karatayev[3], Robert A. Krebs[5], Elizabeth S. Meyer[6], Wendy L. Paterson[1], Trevor J. Prescott[5], Matthew T. Rowe[1], Don W. Schloesser[7], and Mary C. Walsh[6]

Abstract - Over the past 25 years, unionid mussels in the Laurentian Great Lakes of North America have been adversely impacted by invasive dreissenid mussels, which directly (e.g., by attachment to unionid shells) and indirectly (e.g., by competing for food) cause mortality. Despite the invasion, unionids have survived in several areas in the presence of dreissenid mussels. We investigated current spatial patterns in these native mussel refuges based on surveys for unionid mussels across 48 sampling locations (141 sites) in 2011 and 2012, and documented species abundance and diversity in coastal areas of lakes St. Clair and Erie. The highest-quality assemblages of native mussels (densities, richness, and diversity) appear to be concentrated in the St. Clair delta, where abundance continues to decline, as well as in in Thompson Bay of Presque Isle in Lake Erie and in just a few coastal wetlands and drowned river-mouths in the western basin of Lake Erie. The discovery of several new refuge areas suggests that unionids have a broader distribution within the region than previously thought.

Introduction

The decline of native unionid mussels in the Laurentian Great Lakes of North America after the introduction and population increases of exotic dreissenid mussels (*Dreissena polymorpha* (Pallas) [Zebra Mussel] and *Dreissena rostriformis bugensis* (Andrusov) [Quagga Mussel]) has been well documented (Lucy et al. 2014, McGoldrick et al. 2009, Nalepa et al. 1996, Schloesser and Nalepa 1994, Schloesser et al. 1996, Strayer and Malcolm 2007). Native mussels in lakes Erie

[1]Central Michigan University, Institute for Great Lakes Research, Biology Department, 217 Brooks Hall, Mount Pleasant, MI 48859. [2]University of Toledo, Department of Environmental Science, Lake Erie Center, 6200 Bayshore Road, Oregon, OH 43616. [3]SUNY Buffalo State, Great Lakes Center, 1300 Elmwood Avenue, Buffalo, NY 14222. [4]Kent State University, Dept. of Biological Sciences, Department of Biological Sciences, 256 Cunningham Hall, Kent, OH 44242. [5]Cleveland State University, Dept. of Biological, Geological, and Environmental Sciences, 2121 Euclid Avenue, Cleveland, OH 44115. [6]Pennsylvania Natural Heritage Program, Western Pennsylvania Conservancy, 800 Waterfront Drive, Pittsburgh, PA 15222. [7]US Geological Survey, Great Lakes Science Center, 1451 Green Road, Ann Arbor, MI 48105. [*]Corresponding author - zanat1d@cmich.edu. (All other authors listed alphabetically).

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and St. Clair had been in decline for decades as a result of pollution and habitat destruction (Nalepa et al. 1991), and the invasion of dreissenids in the late 1980s and early 1990s sparked fears of complete extirpation of unionids (Mackie and Schloesser 1996, Ricciardi et al. 1998). Dreissenids attach to shells of other species, thereby hampering filter feeding, respiration, and reproduction (Schloesser et al. 1996). Dreissenid mussels also impede movement of native mussels, leading to their burial in soft and unconsolidated sediments, and increasing drag and likelihood of their dislodgment by water currents (Burlakova et al. 2000, Karatayev et al. 1997, Schloesser et al. 1996). Conservation programs for these species have become increasingly crucial to prevent species loss (Haag 2012, Strayer 2006, Strayer et al. 2004) because unionid mussels are among the most endangered groups of animals in North America (Bogan 1993, Lydeard et al. 2004).

In the 25 years since the invasions by dreissenid mussels in the Laurentian Great Lakes of North America, several locales were identified where native mussels continue to survive the dreissenid impacts (Bowers and de Szalay 2004, 2005, 2007; Bowers et al. 2005; Carlton 2008; Hebert et al. 1989; McGoldrick et al. 2009; Nichols and Amberg 1999; Nichols and Wilcox 1997; Schloesser and Masteller 1999; Schloesser et al. 1997; Sherman et al. 2013; Zanatta et al. 2002). We refer to such sites as unionid "refuges". Some localities in Lake Erie and Lake St. Clair contained remnants of once-diverse assemblages (Brown et al. 1938, Goodrich and van der Schalie 1932, LaRoque and Oughton 1937), and communities may even have recovered (Crail et al. 2011) in a few areas of Lake Erie where habitat conditions have somewhat mitigated the impacts of the dreissenids (e.g., Bódis et al. 2014, Bowers and de Szalay 2007, Bryan et al. 2013, Lucy et al. 2014, McGoldrick et al. 2009, Sherman et al. 2013, Strayer and Malcom 2007).

Knowledge of the extent of unionid refuges in coastal Lake Erie and Lake St. Clair is limited, as no single comprehensive and cohesive study has been made to compare mussel assemblages and habitats. Monitoring change is necessary to develop predictive models and strategies for protecting remaining native mussel populations in the Great Lakes. Each of the published papers on native mussel refuges in the Great Lakes cited above focuses on a small number of locations, and none address how frequently native mussels occur in coastal habitats and how often they are absent in what appears to be suitable habitat. Toward this end, the objectives of our study were to : 1) identify the extent of unionid assemblages in coastal areas in lakes St. Clair and Erie; 2) estimate relative abundance, density, and diversity of these assemblages, and compare modern and historical species assemblages; and 3) document shell-size distribution in refuges as potential evidence of recruitment and/or population stability.

Study area

The 48 localities surveyed in 2011–2012 (Table 1, Fig. 1) included embayments, coastal wetlands, drowned river-mouths, and deltaic and other shallow-water areas along shorelines of the United States in Lake St. Clair, the Detroit River, Lake Erie, and the Niagara River. The sampling localities consisted of areas where either

Table 1. Mean numbers of unionids collected per site (± S.E. for locations having multiple sites), species richness (S_R), and effective number of species ($e^{H'}$; Jost 2006) at 49 locations visited in 2011–2012 from coastal areas of Lake St. Clair, the Detroit River, Lake Erie, and the Niagara River.

Code and locality		Waterbody	No. sites	# specimens	S_R	$e^{H'}$
1	Pollet Bay	Lake St. Clair	2	6.0 ± 6.0	6	5
2	Goose Bay	Lake St. Clair	3	40.5 ± 15	11	4
3	Fisher Bay	Lake St. Clair	1	20.0	6	4
4	Big Muscamoot Bay	Lake St. Clair	5	9.5 ± 3.9	11	6
5	Little Muscamoot Bay	Lake St. Clair	3	47.5 ± 13	10	3
6	Pocket Bay	Lake St. Clair	1	19.0	2	1
7	Bass Bay	Lake St. Clair	2	19.5 ± 19.5	6	4
8	Humbug Island	Detroit River	1	0.0	0	0
9	Calf Island	Detroit River	1	0.0	0	0
10	Huron River (MI) mouth	Detroit River	3	6.0 ± 4.0	9	7
11	Celeron Island	Detroit River	1	0.0	0	0
12	La Plaisance Bay	Lake Erie	1	9.0	2	1
13	North Maumee Bay	Lake Erie	3	46.5 ± 18	6	4
14	North Maumee Bay - Dyked	Lake Erie	3	0	0	0
15	Monroe Power Plant Discharge	Lake Erie	2	42.0 ± 15	4	1
16	Potters Pond - Ottawa NWR	Lake Erie	2	0	0	0
17	Brest Bay	Lake Erie	1	0	0	0
18	Cedar Creek/Meinke Marina	Lake Erie	1	2.0	2	2
19	Crane Creek Marsh - Ottawa NWR	Lake Erie	5	56.0 ± 26.5	10	3
20	Turtle Creek	Lake Erie	4	26.0 ± 9.0	4	2
21	Toussaint River - Gath Kurdy Preserve	Lake Erie	4	48.0 ± 27.5	7	2
22	Portage River mouth	Lake Erie	4	40.0 ± 2.7	5	1
23	Muddy Creek Bay	Lake Erie	17	10.0 ± 3.1	10	3
24	Young Marsh	Lake Erie	2	22.0 ± 2.0	8	5
25	Sandusky Bay	Lake Erie	11	1.3 ± 1.0	5	4
26	Port Clinton Beach	Lake Erie	1	1.0	1	1
27	East Harbor	Lake Erie	2	23.0 ± 17	3	1
28	Cedar Point - Sandusky Bay	Lake Erie	3	1.0 ± 0.6	3	3
29	Griffith Airport - Sandusky Bay[A]	Lake Erie	3	3.8 ± 2.7	2	2
30	Huron River (OH) mouth	Lake Erie	3	4.4 ± 3.4	5	3
31	Old Woman Creek mouth	Lake Erie	3	0.7 ± 0.4	1	1
32	Chapel Creek mouth	Lake Erie	1	0.0	0	0
33	Sugar Creek mouth	Lake Erie	1	0.0	0	0
34	Raccoon Creek mouth	Lake Erie	1	0.0	0	0
35	Elk Creek mouth	Lake Erie	2	0.0	0	0
36	Presque Isle Bay	Lake Erie	15	0.9 ± 0.4	3	2
37	Thompson Bay – Presque Isle	Lake Erie	3	10.0 ± 4.6	7	4
38	Gull Point - Presque Isle	Lake Erie	2	0.0	0	0
39	Duck Pond - Presque Isle	Lake Erie	2	11.0 ± 10	4	2
40	Twelve Mile Creek mouth	Lake Erie	1	0.0	0	0
41	Sixteen Mile Creek mouth	Lake Erie	1	0.0	0	0
42	Twenty Mile Creek mouth	Lake Erie	1	0.0	0	0
43	Silver Creek mouth/ Walnut Creek mouth	Lake Erie	1	0.0	0	0
44	Cattaraugus Creek mouth	Lake Erie	1	0.0	0	0
45	Big Sister Creek mouth/ Bennett Beach	Lake Erie	1	0.0	0	0
46	Eighteen Mile Creek backwater	Lake Erie	2	0.0	0	0
47	Strawberry Island	Niagara River	3	28.0 ± 14	3	1
48	Spicer Creek mouth/ Grand Isle	Niagara River	1	45.0	4	2
49	Bayshore – South Maumee Bay[B]	Lake Erie	4	1201.5 ± 400.5	13	4
	Mean values (locations 1–48)			13.1	3.33	1.75

[A]From D. Kapusinski (unpubl. data).
[B]From Bryan et al. (2013) and not included in the analyses (of 48 sites) used herein.

live unionids had been observed in recent years (~10 y), shells had been collected recently (Crail et al. 2011, McGoldrick et al. 2009, Zanatta et al. 2002), or where unionids were thought to possibly occur based on habitat features including water depth (<1 m, protected embayments, drowned river mouths), substrate type (soft sand or mud), and vegetation (e.g., chara, bullrushes). At each locality, one or more sites were surveyed depending on areal extent (totaling 141 sites across the 48 locations). For example, we sampled 17 sites at Muddy Creek Bay (location 24, ~7.4 km^2) and 11 sites at inner Sandusky Bay (location 26, ~73 km^2), but only sampled single sites at the mouths of small tributaries (<0.1 km^2).

Methods

Each survey site was sampled for unionids within a rectangular-shaped area of 0.5 ha, typically 50 m by 100 m but dimensions were dependent on the layout of available habitat. We marked the rectangle corners and recorded the coordinates with a hand-held GPS unit. Each site was searched by tactile methods (due to poor visibility caused by highly turbid water) for 2 person-hours (e.g., 4 searchers for 30 minutes each). Search method varied due to substrate type, water clarity, and water depth; wading, raking, and snorkeling were used at a majority (90%) of sites. Relatively deep sites (>1.5 m) were sampled by SCUBA. We do not believe that varying methods biased the results among sites. We identified all

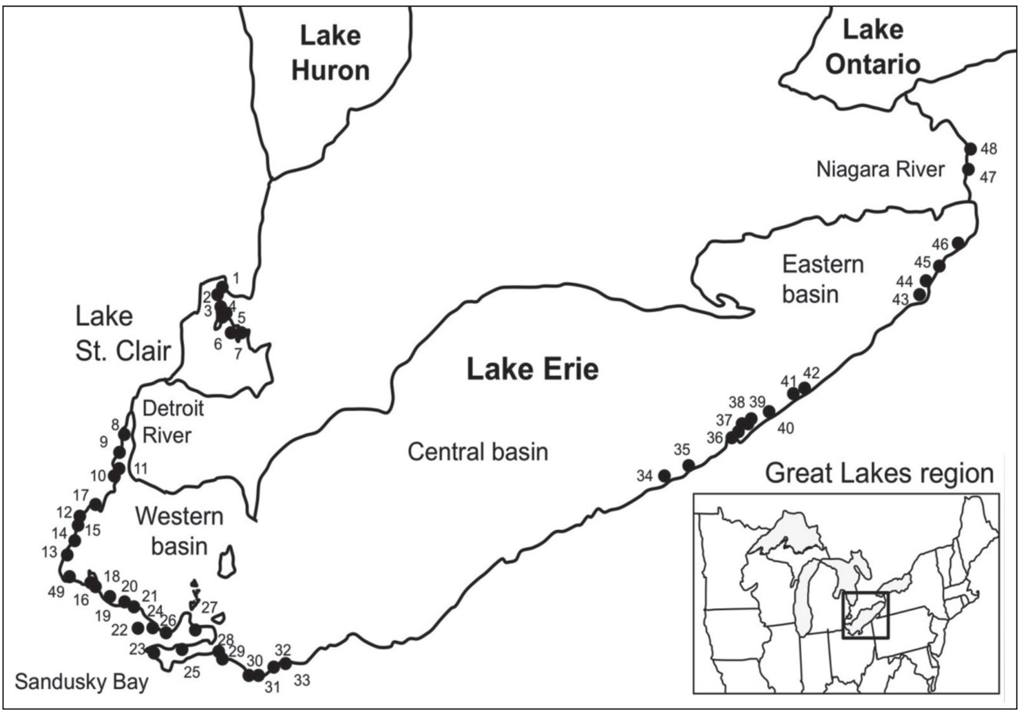

Figure 1. Map showing collection localities (codes from Table 1) in Lake St. Clair, the Detroit River, Lake Erie, and the Niagara River sampled in 2011–2012. The location of the study area in northeastern North America is shown in the insert.

collected material to species, measured standard shell length of all specimens, and determined gender for species that have sexually dimorphic shells. Dreissenid data for these sites was collected as part of another study and is presented there (see Burlakova et al. 2014).

We determined the mean numbers of unionids per site (± standard error [SE]) for each location by averaging data among sites sampled within each location, the species richness (S_R) by enumeration of the number of species present at a location (cumulative across sites), and the diversity by a Shannon diversity index (H'), which we then converted to effective number of species (calculated as $e^{H'}$, Jost 2006). We also calculated the mean shell lengths of the 13 most common or widespread species at each location. The presence of small-size classes (<40 mm length, except <30 mm length for small species and <20 mm length for *Taxolasma parvum* [Lilliput]) in samples was interpreted as evidence of recent recruitment (Haag 2012).

Results

A total of 1923 live specimens (22 species) was collected from 30 of the locations sampled between June and August in 2011 and 2012 (Tables 1, 2; Fig. 1). No mussels were found at the remaining 18 locations. The most abundant species were *Quadrula quadrula* (Pimpleback; *n* = 780), *Pyganodon grandis* (Giant Floater; *n* = 311), *Lampsilis siliquoidea* (Fatmucket Clam; *n* = 262), *Amblema plicata* (Three-ridge; *n* = 199), and *Leptodea fragilis* (Fragile Papershell; *n* = 92) (Table 2). Collectively these 5 species accounted for 85.5% of the total number of specimens. The most widespread species (proportion of sites found) were: *P. grandis* (38.9%), *Q. quadrula* (27.3%), *A. plicata* (21.6%), *L. fragilis* (17.3%), and *L. siliquoidea* (14.4%). The assemblages in Lake Erie, the Detroit River, and the Niagara River differed considerably from that in Lake St. Clair (Table 2). In Lake Erie, *Q. quadrula*, *P. grandis*, and *A. plicata* dominated numerically, toogether accounting for 84% of the total assemblage. The most abundant species in Lake St. Clair, in contrast, were *L. siliquoidea*, *Potamilus alatus* (Pink Heelsplitter), *Ligumia nasuta* (Eastern Pondmussel), and *Villosa iris* (Rainbow Mussel), which together accounted for 80% of the assemblage.

The mean abundance of unionids in the St. Clair delta (23.8 ± 6.2 inidviduals/site) was more than twice that of the other sampled regions grouped together (10.9 ± 2.7 individuals/site) (Table 2). However, 5 of the 7 highest-density sites were in western Lake Erie: at Crane Creek Marsh (location 19), Toussaint Creek (21), North Maumee Bay (13), Monroe power-plant discharge (15), and the Portage River mouth (22). Mean unionid abundance in the western basin of Lake Erie was similar to that of the St. Clair delta, although variation among locations was 40% higher than in the latter (Table 3). Evidence of recent recruitment was found for 9 of the 13 most common species, but at only 11 of the 48 locations surveyed (Table 4): 3 in Lake St. Clair, 5 in the western basin of Lake Erie, 2 in Sandusky Bay, and just 1 farther east, at Presque Isle, PA.

Discussion

Our findings provide further evidence that Great Lakes nearshore beach/littoral habitats still contain native mussel populations (Crail et al. 2011, Schloesser et al. 1997) despite the presence of dreissenids and a long history of declining water

Table 2. Comparison between unionid assemblages in Lake St. Clair and Lake Erie and the Detroit and Niagara rivers in 2011–2012. Rel. abund. = relative abundance; % of sites = proportion of all sites in which species was found.

	Waterbody				
	Lake St. Clair		Lake Erie and Detroit and Niagara rivers		
Species	# of mussels	Rel. abund.	# of mussels	Rel. abund.	% of sites
Subfamily Anodontinae					
Anodontoides ferussacianus Lea (Cylindrical Papershell)	1	0.2%	0	0.0%	0.7%
Lasmigona complanata Barnes (White Heelsplitter)	0	0.0%	23	1.5%	8.6%
Lasmigona costata Rafinesque (Flutedshell)	5	1.2%	0	0.0%	2.9%
Pyganodon grandis (Say) (Giant Floater)	13	3.1%	298	19.8%	38.9%
Strophitus undulatus Say (Squawfoot)	12	2.9%	0	0.0%	2.9%
Utterbackia imbecillis (Say) (Paper Pondshell)	0	0.0%	9	0.6%	2.2%
Subfamily Ambleminae					
Tribe Amblemini/Pleurobemini/Quadrulini					
Amblema plicata Say (Threeridge)	12	2.9%	187	12.4%	21.6%
Elliptio dilatata Rafinesque (Spike)	1	0.2%	0	0.0%	0.7%
Fusconaia flava Rafinesque (Wabash Pigtoe)	21	5.1%	22	1.5%	8.6%
Pleurobema sintoxia Rafinesque (Round Pigtoe)	2	0.5%	1	0.1%	1.4%
Quadrula pustulosa Lea (Pimpleback)	0	0.0%	5	0.3%	2.9%
Quadrula quadrula Rafinesque (Mapleleaf)	0	0.0%	780	51.7%	27.3%
Tribe Lampsilini					
Lampsilis cardium Rafinesque (Plain Pocketbook)	14	3.4%	1	0.1%	5.0%
Lampsilis siliquoidea Barnes (Fatmucket Clam)	251	60.5%	11	0.7%	14.4%
Leptodea fragilis Rafinesque (Fragile Papershell)	2	0.5%	90	6.0%	17.3%
Ligumia nasuta Say (Eastern Pondmussel)	24	5.8%	28	1.9%	10.8%
Ligumia recta Lamarck (Black Sandshell)	1	0.2%	0	0.0%	0.7%
Obliquaria reflexa Rafinesque (Three-horn Wartyback)	0	0.0%	10	0.7%	4.3%
Potamilus alatus (Say) (Pink Heelsplitter)	35	8.4%	22	1.5%	12.2%
Toxolasma parvum (Barnes) (Lilliput)	0	0.0%	15	1.0%	7.9%
Truncilla donaciformis Lea (Fawnsfoot)*	0	0.0%	0*	0.0%	0.7%
Truncilla truncata Rafinesque (Deertoe)	0	0.0%	6	0.4%	3.6%
Villosa iris (Lea) (Rainbow Mussel)	21	5.1%	0	0.0%	5.0%
Total unionids	415		1508		
Total collection sites	17 sites		125 sites		
Abundance (unionids/site ± S.E.)	23.8 ± 6.2		10.9 ± 2.7		
Species richness (S_R)	15		16		
Shannon diversity (H')	1.55		1.53		
Effective number of species	5		5		

*Many were collected during a fall seiche at Bayshore (Maumee Bay) in October 2011 (Bryan et al. 2013).

quality (Nalepa et al. 1991). The present study encompassed a much wider geographic area than previous investigations (e.g., Lake St. Clair delta [McGoldrick et al. 2009, Zanatta et al. 2002], Crane Creek [Bowers and de Szalay 2004], and Presque Isle Bay of Lake Erie [Masteller et al. 1993]), and all surveys were obtained within a 2-year time frame, which allowed for comparison of abundance, richness, and diversity among locations not possible with previous data .

Five of the seven sites surveyed in the St. Clair delta had among the highest species richness and diversity in the entire region surveyed. Interestingly, the composition of the unionid assemblages in Lake St. Clair has changed little since 1986, prior to the Zebra Mussel invasion (Nalepa and Gauvin 1988). However, assemblages on the Canadian side of the delta (Pocket Bay and Bass Bay), which

Table 3. Mean unionid abundance by location visited in 2011–2012 across 6 bathymetrically separate regions of the Lake Erie watershed, and the coefficient of variation (*V*) among locations in each region.

Regions	Number of locations	Mean number of unionids/site	SE	*V*
Lake St. Clair	7	23.8	6.2	34.4
Detroit River	4	3.0	1.5	100.0
Lake Erie western basin	13	22.5	6.0	48.2
Lake Erie Sandusky Bay	5	9.3	4.4	59.2
Lake Erie central basin	10	2.7	1.4	80.7
Lake Erie eastern basin	9	8.1	5.6	102.6
Niagara River	48	12.1	2.5	69.4

Table 4. Shell lengths, locations (codes from Table 1) with evidence of recent recruitment (length < 40 mm*,†), and proportion of locations with evidence of recent recruitment for common and/or widely distributed species in coastal areas of Lake St. Clair, the Detroit River, Lake Erie, and the Niagara River visited in 2011–2012.

Species	Range of shell lengths in mm (# of individuals)	Locations with evidence of recent recruitment	Proportion of locations with evidence of recent recruitment (# of locations)
Amblema plicata	15–126 (*n* = 199)	13, 19, 21, 23	25% (*n* = 16)
*Fusconaia flava**	26–81 (*n* = 43)	2, 3, 4	27% (*n* = 11)
Lampsilis siliquoidea	34–151 (*n* = 262)	2	13% (*n* = 8)
Lasmigona complanata	24–165 (*n* = 23)	19	20% (*n* = 5)
Leptodea fragilis	11–158 (*n* = 92)	13, 19, 25	20% (*n* = 15)
Ligumia nasuta	49–110 (*n* = 52)	-	- (*n* = 10)
*Obliquaria reflexa**	17–63 (*n* = 10)	15, 19, 25	60% (*n* = 5)
Potamilus alatus	58–138 (*n* = 57)	-	- (*n* = 16)
Pyganodon grandis	11–155 (*n* = 311)	13, 25, 37	12% (*n* = 25)
Quadrula quadrula	11–117 (*n* = 780)	19, 21, 22, 23, 25, 30	50% (*n* = 12)
*Strophitus undulatus**	33–43 (*n* = 12)	-	- (*n* = 3)
Toxolasma parvum†	14–41 (*n* = 15)	19, 25, 30	43% (*n* = 7)
*Villosa iris**	36–67 (*n* = 21)	-	- (*n* = 5)

*Recent recruits for small species considered when length < 30 mm.
†Recent recruits for *T. parvum* considered when length < 20 mm.

contained several rare species and have been considered among the highest-quality refuges in the region (McGoldrick et al. 2009, Zanatta et al. 2002), may be in decline. In Lake Erie, the highest native mussel abundance we found exists near the warm-water discharge of the Bayshore power plant in Maumee Bay (location 49; Fig. 1), where unionids were collected during a seiche (standing wave) event (Bryan et al. 2013) that caused the water levels at that site to drop considerably at that time. However, data collected during a seiche event are not directly comparable to methods used in the present study because sampling is much more effective where large areas of the lake bottom are exposed. The sampling revealed 13 species and >1200 unionids in a 0.5-ha site, which is two orders of magnitude higher than that of any location surveyed in the present study. Other Lake Erie locations in which we found a large number of species were the mouth of the Huron River, MI; several of the large drowned river-mouths of the western basin (Toussaint Creek, Turtle Creek, and the Portage River), and two coastal wetlands (North Maumee Bay and Young Marsh). The latter two locations have habitats similar to Crane Creek (Bowers and de Szalay 2007, Bowers et al. 2005). Similar to the results of Schloesser et al. (2006), we found few unionids around islands at the outlet of the Detroit River. Only one location outside of western Lake Erie (Thompson Bay, outer Presque Isle Bay) still possessed a remnant mussel assemblage that apparently does not contain dreissenids (Burlakova et al. 2014), but populations in that region were much reduced compared to those reported by Masteller et al. (1993).

Many of trhe sampling localities in central and eastern Lake Erie had few or no unionids (e.g., locations 34–46; Fig. 1). While relatively large densities of unionids were found at 2 locations in the upper Niagara River, neither of these had relatively high species richness or diversity (instead they were numerically dominated by *L. siliquoidea* and *P. grandis*), and none showed evidence of recent recruitment. Unexpectedly , and despite intensive sampling, the large, shallow (generally <2 m depth) region of Sandusky Bay (in western Lake Erie) contained small populations. Densities there were low and often below detectable limits, which equated to a large number of coastal sites where no mussels were found (albeit with evidence of recent recruitment for several species). Most individuals in Sandusky Bay were found in the mouth of the Sandusky River where it flows into Muddy Creek Bay (location 23), and few specimens occurred in the bay itself.

Therefore , as abundances declined in Lake Erie, species assemblages have shifted compared to those of the 1950s and 1980s (Nalepa et al. 1991). Lake assemblages were previously dominated numerically by *L. siliquoidea*, *P. grandis*, and *L. nasuta* (Nalepa et al. 1991), as is still the case in Lake St. Clair. The coastal assemblage present in western Lake Erie has become dominated by *Q. quadrula*, *P. grandis*, and *A. plicata*, although unionid richness (S_R) and diversity metrics (H' and effective number of species) have rebounded to levels similar to that found in Lake Erie in the 1950s (Nalepa et al. 1991). A recent geographic expansion is suggested by the present results because *Q. quadrula* was rarely collected in earlier surveys (e.g., Clark 1944, Nalepa and Gauvin 1988).

The shift in species composition in Lake Erie is potentially a result of differential tolerance to mortality caused by dreissenid mussels. Studies from the 1990s, not long after Zebra Mussels invaded Lake Erie (ca. mid-1980s), suggest that some unionid species were more likely to survive dreissenid fouling than others (reviewed in Schloesser et al. 1996). Explanations for unionid survival included the ability to burrow quickly, gender (males appeared to be less impacted than brooding females), shell robustness (thick/heavy shelled species seemed to be less affected), and the length of brooding period (species with short brooding time were found to be less influenced). These characteristics, which are shared by many of the taxa that live in drowned river-mouths and shallow embayments (e.g., *A. plicata*, species of *Quadrula* and *Fusconaia*) correspond to an equilibrium life-history strategy (Haag 2012). The robust shells and short-term brooding period of these surviving species may well give them some resilience to dreissenid fouling. Two other species predominantly found in Lake Erie, *L. fragilis* and *P. grandis*, possess an opportunistic strategy of high fecundity, early age of reproduction, and short life spans (Haag 2012). Although these 2 species were not especially abundant in the stream mouths, fresh empty shells of both were frequently found on beaches (Crail et al. 2011). Host-fish abundance may have contributed to their persistence as well; *P. grandis* is a host generalist, and *Leptodea fragilis* appears to be dependent on *Aplodinotus grunniens* (Rafinesque 1819) (Freshwater Drum; Watters et al. 2009), a large benthic molluscivore fish that has become very abundant in western Lake Erie since dreissenid mussels invaded (ODW 2013).

Our evidence for recent recruitment correlated well with abundance, richness, and diversity. Although our sampling methods were not especially efficient at detecting juvenile unionids, 9 of the 13 most-common and/or widespread species—including *Q. quadrula*, *P. grandis*, and *A. plicata* in western Lake Erie—showed evidence of recruitment at several locations. In contrast, a concern exists that some of the more common species in the St. Clair delta (e.g., *L. siliquoidea* and *L. nasuta*) and Presque Isle (e.g., *A. plicata*, *F. flava*, and *L. nasuta*) exhibited few signs of recent reproduction.

These results lead to a final important question: what varies between sites with and without unionids? This study described the current distribution of native mussel assemblages in Lake St. Clair and Lake Erie, and research continues to characterize and model habitat variables of refuges that enable unionids to persist at those locations. Sherman et al. (2013) found that while both North Maumee Bay in Lake Erie and the delta of Lake St. Clair contain unionids, they differ in habitat features (drowned river-mouth vs. deltaic), substrate (softer in Lake Erie), and water chemistry (higher pH and turbidity in Lake Erie). The St. Clair deltaic environment may suppress dreissenid impacts because its flow remains river-like with a retention/replacement time of only 7 days compared to 2.6 years for Lake Erie (GLIN 2014). A persistent flow may allow periodic life-history strategists, including *L. siliquoidea* and *L. nasuta*, to sustain populations; we note in this context that the unionid assemblage of the St. Clair delta is similar to those of small streams in the Mississippi watershed (Haag 2012:table 8.1) with the addition of 4 species presumed to use Freshwater Drum as a host fish (*L. fragilis*, *P. alatus*, *Truncilla truncata*, and *T. donaciformis*; Watters et al. 2009) and therefore not typically present in small streams. North Maumee Bay had the highest water-level fluctuations (>1 m water-level changes during seiches) of any of the locations from across the Great Lakes, a characteristic that may largely exclude dreissenid mussels.

The native mussel compositions we found in 2011–2012 are difficult to directly compare to species compositions found in previous studies. Most offshore sampling suggested a limited unionid presence, and therefore coastal refuges may represent the vast majority of what remains in Lake Erie. Within coastal refuges of western Lake Erie, species composition has changed in comparison to historical assemblages. Lake St. Clair populations showed signs of decline, although the aggregate community has not changed substantially. Our main concern is that the remaining species assemblages will succumb to mortality caused by dreissenid mussels. Only time will tell whether shifts that have been observed in Lake Erie will also occur in Lake St. Clair in the future.

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