Journal of Great Lakes Research 39 (2013) 201–210

Contents lists available at SciVerse ScienceDirect

Journal of Great Lakes Research

journal homepage: www.elsevier.com/locate/jglr

Assessment of remnant unionid assemblages in a selection of Great Lakes coastal wetlands

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ARTICLE INFO

Article history:
Received 21 March 2012
Accepted 29 January 2013
Available online 2 April 2013

Communicated by Anett Trebitz

Keywords:
Unionid
Coastal wetland
Dreissenid
Remnant assemblages

ABSTRACT

Populations of native unionids have been in steady decline over the past century. The invasion of dreissenid mussels (*Dreissena polymorpha* and *Dreissena rostriformis bugensis*) in the mid-1980's impacted already imperiled unionid populations by greatly increasing their regional extinction rates. A selection of Great Lakes coastal wetlands around Michigan was surveyed to locate remnant populations of native unionids. Physical and chemical parameters were measured in coastal wetlands to evaluate the importance of these habitat parameters to remnant unionid assemblages. We assessed fouling rates by dreissenids on unionids and used artificial substrates to estimate dreissenid colonization densities. Live unionids were found in coastal wetlands of the Les Cheneaux Islands, the Lake St. Clair delta, and North Maumee Bay with significantly higher unionid fouling in the Les Cheneaux Islands compared to the other two sampling areas ($F_{2,76} = 4.97, p = 0.0095$). No live unionids were documented in Beaver Island, Garden Island, Grand Traverse Bay, or Saginaw Bay wetlands. *Dreissena* colonization densities on artificial substrates averaged 19,213 m^{-2} at one site in North Maumee Bay, and 10,425 m^{-2} in Saginaw Bay, but no colonization occurred in the wetlands of Beaver Island, Garden Island, the Les Cheneaux Islands, or Grand Traverse Bay while *Dreissena* presence in the open water of these regions was evident. *Dreissena* colonization densities on artificial substrates increased with measures of anthropogenic disturbance and decreased with higher water level fluctuations and aerial exposure. Specific conductance, turbidity, and magnitude of water level fluctuations were important predictors of *Dreissena* colonization on artificial substrates.

Introduction

There are approximately 1000 described species of freshwater mussels (Order: Unionoida) around the world, with roughly 300 species (belonging to two families: Unionidae and Margaritiferidae) occurring in North America (Graf and Cummings, 2007; Strayer et al., 2004; Williams et al., 1993). Approximately 70% of the freshwater mussels that live in North America are listed as endangered, threatened, or as species of special concern (Master et al., 2000; Williams et al., 1993). Unionids, the colloquial term for members of Unionidae, are considered one of the most imperiled groups of organisms in North America and are critically jeopardized in other parts of the world (Strayer et al., 2004; Watters et al., 2009). Many factors have contributed to unionid population declines including overharvesting, habitat loss from dams or river channelization, pollution, loss of obligate host fish species, and the introduction of invasive species (e.g., *Dreissena* spp.) (Hallac and Marsden, 2001; Lydeard et al., 2004; Strayer et al., 2004; Watters et al., 2009). Historically, unionid richness in the Great Lakes varied considerably with lakes Erie and St. Clair playing host to the largest species richness (33–40 species for Erie and 20–27 species for St. Clair), Lake Huron having 17 documented species, and lakes Michigan and Superior having the lowest unionid species richness (10 and 6 species, respectively) (Goodrich and Vander Schalie, 1932; Metcalfe-Smith et al., 1998).

Populations of native unionids, already in decline from anthropogenic influences prior to dreissenid invasions, were expected to show a ten-fold increase in extinction rates throughout the Mississippi River Basin after dreissenid introductions (Ricciardi et al., 1996, 1998). Zebra mussels (*Dreissena polymorpha*, Bivalvia: Dreissenidae), native to the Black and Caspian Sea region of eastern Europe, were introduced into the Great Lakes region around 1986 from the ballast waters of transoceanic ships (Carlton, 2008; Hebert et al., 1989). By the early 1990s, a close relative also from the Ponto-Caspian region, the quagga mussel (*Dreissena rostriformis bugensis*) was introduced to the Great Lakes (May and Marsden, 1992; Mills et al., 1993).

Dreissenid mussels are epifaunal organisms that attach to hard surfaces with byssal threads and filter feed from the water column (Mackie, 1991). Unionid shells provide a suitable attachment site for dreissenids (Burlakova et al., 2000) and are often preferentially colonized over other hard substrates (Mackie, 1990; Ricciardi et al., 1996). Dreissenid mussels are an efficient competitor and by attaching

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http://dx.doi.org/10.1016/j.jglr.2013.03.001

to the exterior of the unionid shell (a process referred to as fouling) can inhibit feeding, respiration, reproduction, and burrowing and can cause unionid mortality (Haag et al., 1993; Ricciardi et al., 1996; Schloesser and Nalepa, 1994). Significant fouling on unionids has been recorded in the Great Lakes with some studies documenting up to 100% of surveyed unionids being fouled (Gillis and Mackie, 1994; Griffiths, 1993; Haag et al., 1993; Hebert et al., 1989; Masteller and Schloesser, 1992).

Refuge habitats are typically described as areas that provide protection from hazardous or inhospitable conditions and, in some cases, are considered to be habitats with relatively unaltered characteristics that allow survival during times of environmental change. Previous studies on the Great Lakes have found that habitats that provide unionid refuges tend to be characterized by the presence of soft or fine sand sediments that allow unionid burrowing, increased productivity to reduce food competition with dreissenids, high water level fluctuations, high wave action, shallow water depths, and the presence of offshore currents (Bowers and de Szalay, 2004, 2005; McGoldrick et al., 2009; Nichols and Amberg, 1999; Nichols and Wilcox, 1997; Schloesser and Masteller, 1999; Schloesser et al., 1997; Zanatta et al., 2002). Previous studies suggest that water level fluctuation and dewatering events play a large role in unionid–dreissenid interactions and may contribute to unionid survival (Balogh et al., 2008; Baumgärtner et al., 2008; Bowers and de Szalay, 2004, 2005). The frequency and duration of water level fluctuation greatly impact the colonization and survival of dreissenids which can decrease their presence in wetlands (Bowers and de Szalay, 2005) and littoral zones (Balogh et al., 2008; Baumgärtner et al., 2008). Bowers and de Szalay (2004) found that as little as 1% temporal exposure to open air due to water fluctuations resulted in dramatically lower colonization rates. Unionids can endure longer periods of aerial exposure than dreissenids; therefore, unionid populations found in shallow waters or areas that have frequent water level fluctuations are less likely to be impacted by dreissenids (Bowers and de Szalay, 2004).

Identifying ecological characteristics that enable unionids to persist among dreissenids is important for survival of unionid populations, for locating potential refuge sites for unionid propagation, and for selecting sites for conservation and protection programs (Bowers and de Szalay, 2004; Hunter and Simons, 2004). Great Lakes coastal wetlands may contain many key characteristics (e.g., high water level fluctuation and soft substrates) to support unionids in the presence of dreissenids and may serve in general as refuge habitats throughout the Great Lakes.

The objectives of this study were to: 1) evaluate coastal wetlands for the presence of unionids and determine what factors may relate to their survival; 2) measure dreissenid colonization in wetlands and identify which physical and chemical factors are associated with their presence/absence; and 3) determine which coastal wetlands are potential refuges for unionids in Michigan, based on chemical and physical habitat characteristics and fouling pressure. We hypothesized that the unique chemical (e.g., dissolved oxygen and pH) and physical (e.g., water level fluctuations and substrate type) properties of Great Lakes coastal wetlands would provide refuge for native unionids from fouling by invasive dreissenids or allow these organisms to co-exist. Specifically, we expected to find decreased dreissenid colonization and lower fouling rates in coastal wetlands with greater water level fluctuations, higher emergent macrophyte densities, low dissolved oxygen, and low pH. We also hypothesized that soft, benthic substrates in coastal wetlands would reduce dreissenid fouling and be a contributing characteristic of unionid presence.

Methods

Study sites

Sampling sites were selected in lakes Michigan, Huron, Erie and St. Clair (Fig. 1; Table 1). There is a general lack of documentation on the current distribution of unionids in coastal areas of the Great Lakes (except for Lake St. Clair; McGoldrick et al., 2009; Zanatta et al., 2002) therefore, regions where unionid presence was suspected (i.e., Beaver Archipelago, Lake St. Clair delta, North Maumee Bay, and Grand Traverse Bay) were selected based on discussions with regional biologists. To expand the geographic range of our study and to avoid biasing our results based on likely presence, we randomly selected additional wetlands in the Les Cheneaux Islands and Saginaw Bay. We attempted to reduce latitudinal differences temporally by sampling the southern sites first and then sampling the northern sites.

We surveyed bulrush (*Schoenoplectus* spp.) dominated wetlands during June, July, and August in 2010 and 2011. We used emergent stem density to determine an inner and an outer wetland. Vegetation zones in coastal wetlands are commonly divided into two stem density categories: a sparse (outer) bulrush zone (<25 stems m^{-2}) which is subjected to heavier wave action, and a protected (inner) bulrush zone (>25 stems m^{-2}) which receives less wave action (Burton et al., 1999; Uzarski et al., 2004). Substrate was visually assessed and assigned a dominant and subdominant classification from the following designators: cobble, gravel, sand, silt, clay, and detritus based on texture and the Wentworth Grain Size Scale (Wentworth, 1922).

Unionid presence, species richness, and abundance

Unionid search techniques were based on methods previously shown to be effective for sampling very low density populations (McGoldrick et al., 2009; Zanatta et al., 2002). A minimum 1-person hour search for live unionids was conducted using snorkeling gear, underwater viewers, and tactile sensory with hands, or clam rakes. When a live unionid was found, a re-bar pole with a 4.55 m line was staked into that position. Using the line as a guide, concentric inward circles around the re-bar were searched to cover a total area of 65 m^2. Live mussels were identified to species, measured, photographed, and returned to their original location. Attached dreissenids were removed, enumerated, and dreissenid fouling rates were recorded.

Water clarity and habitat limitations at two sites in North Maumee Bay reduced the feasibility of circle-plot surveys so an alternative technique was implemented to survey unionids. A clam rake, manufactured by the Clam Out™ Equipment Co. (Mohnton, PA), was utilized to trawl an area of 67 m^2. The plot and clam rake methods were compared at one site in Lake St. Clair where the circle-plot method produced a unionid density of 0.056 m^{-2}. The clam rake method produced a unionid density of 0.015 m^{-2}; therefore, this method may have underestimated unionid densities in two sites within North Maumee Bay. Conversely, the circle-plot method may have provided an overestimate of unionid densities (McGoldrick et al., 2009; Zanatta et al., 2002).

Dreissenid colonization

Dreissenid colonization densities were estimated using artificial substrates made from unglazed clay tiles similar to those implemented by Nelson et al. (2009). Ten tiles (16 × 16 cm) per inner and outer wetland zones were attached to metal poles and installed vertically 1 cm above the substrate surface to represent the typical position of unionids in the habitat. Prior to placement in the wetlands, tiles were soaked in water to obtain a bio-film (Bowers and de Szalay, 2004, 2005). Three tiles were randomly selected after six and 12 weeks of being placed in the wetlands. Attached dreissenids were removed, preserved, enumerated, and identified to species level. Dreissenids larger than 7 mm were identified to species using distinguishing external characteristics such as the placement of the byssal groove, symmetry of the midventral line, and the shape of the shell (Benson et al., 2012). All dreissenids measuring less than 7 mm were recorded as *Dreissena* juveniles.

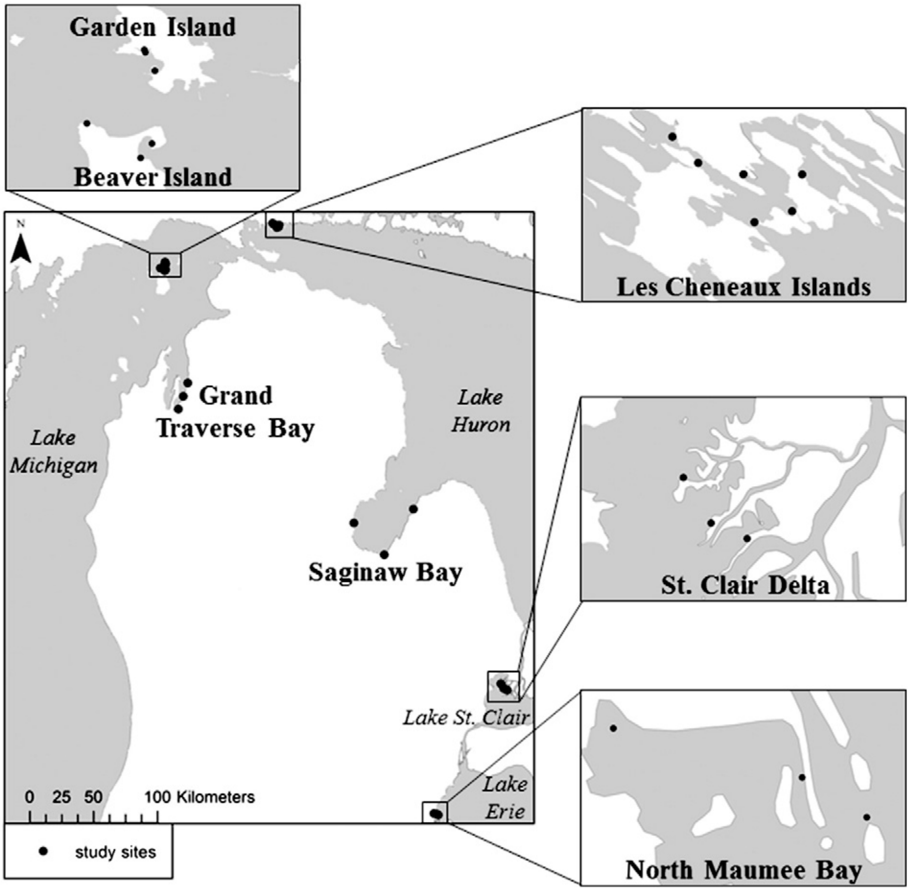

Fig. 1. Coastal wetland study sites surveyed for dreissenid and unionid populations. All sites were located in the state of Michigan, USA. Information about the sites is provided in Table 1.

Physical and chemical habitat characteristics of study areas

Water chemistry procedures were conducted according to procedures described in Standard Methods for the Examination of Water and Wastewater (APHA, 1992). In situ parameters of the wetlands were measured (in triplicate) using a Multi-parameter Water Quality Sonde (Yellow Springs International, model 6600 V2), including: water temperature (°C), specific conductance (μS/cm), dissolved oxygen

Table 1
Description of sites sampled for this study with reference to specific site names and distinguishing geomorphic characteristics. All sites were located in the state of Michigan, USA (See map Fig. 1 for locations). All field seasons took place from June–September.

Region	Site #	Hydrologic system	Dominant substrate type(s)	Field season
Saginaw Bay (Lake Huron)	1- Wildfowl Bay	Lacustrine, open embayment	Sand	2009
	2- Vanderbilt Park	Lacustrine, open embayment	Sand	2009
	3- Pinconning Park	Lacustrine, protected embayment	Silt	2009
Les Cheneaux Islands (Lake Huron)	1- Sheppard Bay	Lacustrine, protected embayment	Clay	2009
	2- Urie Bay	Lacustrine, protected embayment	Clay–detritus	2009
	3- Aldo Leopold Reserve	Lacustrine, protected embayment	Clay	2009
	4- Government Bay	Lacustrine, protected embayment	Sand	2010
	5- Muscallonge Bay	Lacustrine, protected embayment	Sand–gravel	2010
	6- Mackinac Bay	Lacustrine, protected embayment	Clay–sand	2010
Beaver Island (Lake Michigan)	1- North	Lacustrine, open shoreline	Cobble	2009
	2- St. James Bay South	Lacustrine, open embayment	Detritus–clay	2009
	3- St. James Bay East	Lacustrine, open embayment	Sand	2009
St. Clair Delta (Lake St. Clair)	1- Big Muscamoot Bay	Riverine, delta	Sand–silt	2010
	2- Goose Bay	Riverine, delta	Sand–silt	2010
	3- Anchor Bay	Riverine, delta	Sand–silt	2010
North Maumee Bay (Lake Erie)	1- North Maumee Bay Outer	Lacustrine, open shoreline	Silt	2010
	2- NMB- Inner East	Riverine, delta	Sand–silt	2010
	3- NMB- Inner West	Riverine, delta	Sand	2010
Garden Island (Lake Michigan)	1- Garden Harbor North	Lacustrine, protected embayment	Silt	2010
	2- Garden Harbor West	Lacustrine, protected embayment	Silt	2010
	3- Garden Harbor South	Lacustrine, protected embayment	Cobble	2010
Grand Traverse Bay (Lake Michigan)	1- South Elk Rapids	Lacustrine, open shoreline	Cobble–sand	2010
	2- North Elk Rapids	Lacustrine, open shoreline	Sand	2010
	3- Acme Roadside Park	Lacustrine, open shoreline	Sand	2010

(both as a percentage and in mg/L), turbidity (NTU), total dissolved solids (g/L), pH, oxidation reduction potential (mV), and chlorophyll (μg/L, using Relative Fluorescence Units (RFU) as a surrogate).

Water samples were collected in acid washed polyethylene bottles and stored on ice in a dark cooler for alkalinity and nutrient analysis. Alkalinity was determined within 12 h by titrating a 100 mL, unfiltered sample with 0.02 N H_2SO_4 to a pH of 4.5. Water samples collected for nutrient analysis were filtered through a 0.45 μm Millipore filter and processed with a Bran + Luebbe QuAAtro auto-analyzer to measure soluble reactive phosphorous (SRP), ammonium (NH_4^+), and nitrate (NO_3^-) levels. Water and substrate depths (from the organic layer to the resistant layer) were measured in triplicate for both the inner and outer wetlands at each site to assess the potential for unionid burrowing (Bowers and de Szalay, 2004; Bowers et al., 2005; Nichols and Wilcox, 1997; Schloesser et al., 1997).

Water gauges were placed in the inner and outer vegetation zones at each site. These gauges provided the maximum and minimum water levels during each sampling period, but did not provide information on frequency or duration of water level change. From these data, we could estimate the occurrences of aerial exposure on the artificial substrates. We calculated extent of water level fluctuation as the difference between observed maximum and minimum. Gauges were constructed of circular foam floats 28 cm in diameter affixed to PVC poles. The foam floats moved a marker constructed of foam pipe insulation up and down as the water level fluctuated.

Data analysis

Physical and chemical parameters, dreissenid fouling rates, and dreissenid colonization densities were analyzed to assess all sites and determine potential unionid refuges. Physical and chemical factors were related to unionid densities with Pearson correlations (Zar, 2010). Differences in fouling rates (number of dreissenids per unionid) among unionid species and among study areas were assessed using general linear model (GLM) analysis of variance (ANOVA) with post-hoc Tukey pairwise comparisons (Zar, 2010). Dreissenid colonization density was measured and compared to all physical and chemical measurements using Pearson correlations. Colonization densities were compared among sampling areas and between the inner and outer wetland zones using ANOVA and subsequent Tukey's pairwise comparisons. Dreissenid colonization rates on artificial substrates were compared to unionid densities using a Pearson correlation. We did not use Bonferonni corrections; it is therefore important to note the possibility that some relationships may be spurious. Significance was established in all statistical tests by an alpha (α) value of 0.05.

Physical and chemical parameters were analyzed using principal components analysis (PCA) to evaluate shared patterns of the measured abiotic and biotic variables among sampling areas (McGarigal et al., 2000). Principal components (PCs) were constructed using all physical and chemical data, water level fluctuations, and substrate depth. Relationships between PCs and dreissenid colonization and unionid abundance were explored to identify environmental gradients with the strongest influence on mussel presence.

We also investigated the environmental factors related to dreissenid presence/absence using discriminate analysis (DA) (McGarigal et al., 2000). Seventy-five percent of the data were used to develop the discriminant model, while the remaining 25% of the data were retained for model validation. Similar analyses could not be conducted on unionid data because there were too few sites with unionid presence.

Statistical analyses were conducted in Minitab® Statistical Software version 14 (Minitab Inc., State College, PA, U.S.A.), SAS version 9.1 (SAS Institute Inc., Cary, NC, U.S.A.), and PC-ORD version 5 (MjM Software, Gleneden Beach, Oregon, U.S.A.).

Results

Unionid presence, species richness, and abundance

Live unionids were found in three sampling areas: the Les Cheneaux Islands, the Lake St. Clair delta, and North Maumee Bay. We did not observe live unionids in the wetlands of Beaver Island, Garden Island, Grand Traverse Bay, or Saginaw Bay. Species richness was highest in the Lake St. Clair delta and lowest in the Les Cheneaux Islands (Table 2). Fouling was significantly higher ($F_{2,76} = 4.97$, $p = 0.0095$; Fig. 2) on unionids surveyed in the Les Cheneaux Islands (100%) compared to the Lake St. Clair delta and North Maumee Bay (85% and 50%, respectively) (Table 2).

Unionid densities found in this study are similar to those found in other studies identifying potential refuges in the Great Lakes (Crail et al., 2011; McGoldrick et al., 2009; Zanatta et al., 2002). We found live unionids in densities of 0.015–0.056 m^{-2} while previous research in coastal wetlands described unionid refuge sites containing population densities of 0.09 m^{-2} in the western basin of Lake Erie (Crail et al., 2011), and densities in the Lake St. Clair delta of 0.03–0.07 m^{-2} (Zanatta et al., 2002), and 0.02–0.12 m^{-2} (McGoldrick et al., 2009). No live unionids were found in Saginaw Bay, although historically the area was habitat for at least 13 species (Goodrich and Vander

Table 2
Unionid statistics for each site with species richness, mean length of unionids, mean fouling (the number of dreissenids attached to each unionid), and fouling range (the span between lowest and highest number of attached dreissenids per unionid species). SEM represents standard error for the mean.

Site	Date	Richness	Species	N	Mean length in mm (SEM)	Mean fouling (SEM)	Fouling range
Les Cheneaux, site 1	20-Jul-09	1	*Elliptio complanata*	5	91 (2)	22.8 (8.3)	3–49
Les Cheneaux, site 4	17-Aug-10	1	*Elliptio complanata*	1	79.0	19.0	
St. Clair delta, site 1	12-Jul-10	7	*Fusconaia flava*	8	30.9 (2.3)	11.9 (3.3)	0–28
	12-Jul-10		*Lampsilis cardium*	4	76.3 (2.7)	8.5 (3.3)	3–18
	12-Jul-10		*Lasmigona costata*	2	64.8 (14.8)	23 (2)	21–25
	12-Jul-10		*Lampsilis siliquoidea*	27	52.3 (1.3)	12.4 (2.3)	0–39
	12-Jul-10		*Pyganodon grandis*	1	59.0	20.0	
	12-Jul-10		*Strophitus undulatus*	7	41.6 (1.7)	9.6 (3.6)	0–25
	12-Jul-10		*Villosa iris*	2	53.5 (6.5)	8 (2)	6–10
	21-Aug-10		*Lampsilis siliquoidea*	1	48.0	0.0	
St. Clair delta, site 2	13-Jul-10	6	*Anodontoides ferussacianus*	1	40.0	0.0	
	13-Jul-10		*Elliptio dilatata*	1	59.0	17.0	
	13-Jul-10		*Fusconaia flava*	2	43.8 (8)	4.5 (3.5)	1–8
	13-Jul-10		*Lampsilis siliquoidea*	7	54.6 (4)	12.9 (4.1)	1–35
	13-Jul-10		*Potamilus alatus*	2	63 (7)	4 (4)	0–8
	13-Jul-10		*Strophitus undulatus*	1	39.0	6.0	
St. Clair delta, site 3	13-Jul-10	1	*Elliptio dilatata*	1	60.0	1.0	
N. Maumee Bay, site 1	20-Jul-10	1	*Leptodea fragilis*	3	72 (4.6)	1.7 (1.7)	0–5
N. Maumee Bay, site 3	21-Jul-10	1	*Pyganodon grandis*	1	96.0	1.0	

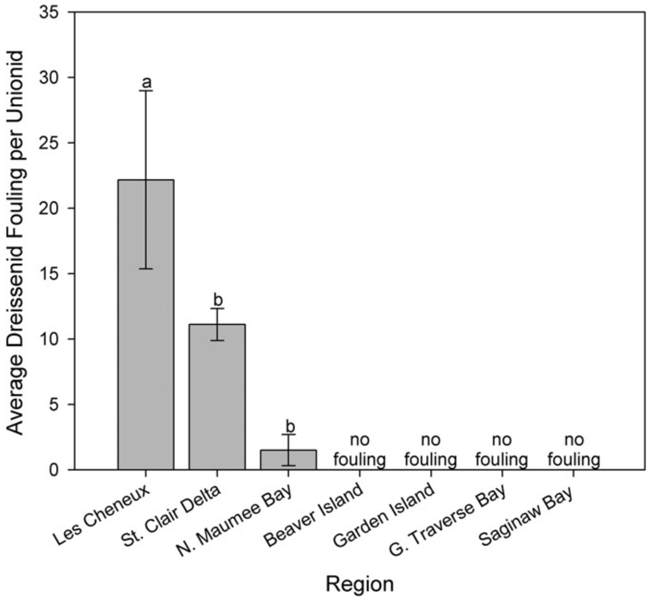

Fig. 2. Mean number of dreissenids fouling unionids at each study region. Error bars denote standard error, letters represent significantly different fouling means ($\alpha = 0.05$). No live unionids were found at Beaver Island, Garden Island, Grand Traverse Bay, or Saginaw Bay sites.

Schalie, 1932). One shell of *Potamilus ohiensis* was found posterior end out of the substrate (i.e., filter up) with little weathering to the periostracum, suggesting that the specimen had not been dead for a long period of time and that either the species could still be present upon increased investigation of the region, or that unionids have only recently been extirpated from the area.

In the Les Cheneaux Islands, two of six sites (Sheppard Bay and Government Bay) contained only one unionid species, *Elliptio complanata*, with an average density of 0.015 ± 0 (S.E.) mussels m^{-2} at each site. No live unionids were observed in the other four of the six sampling sites in this area. Dreissenids fouling the unionids within the Les Cheneaux Island sites were large, mature adults and there was no evidence of juvenile dreissenids on the unionids.

Unionids were found at all three sites surveyed in the Lake St. Clair delta at varying densities and species compositions. Big Muscamoot Bay (site 1) had the highest species richness of unionids (seven) (Table 2) and the highest average density with 0.056 ± 0.009 m^{-2}. Goose Bay (site 2) had similar species richness (six), but a lower average density (0.022 ± 0.003 m^{-2}), while Anchor Bay (site 3) only contained one species at an average density of 0.015 m^{-2}. Dreissenid fouling rates were significantly lower in the Lake St. Clair delta compared to the Les Cheneaux Islands ($F_{2,76} = 4.97$, $p = 0.0095$), and fouling dreissenids consisted of small juveniles but no large adult dreissenids. Evidence of past dreissenid fouling was noted in the form of byssal threads on many of the unionids surveyed in the Lake St. Clair delta.

In North Maumee Bay, unionids were found at site 1 and site 3, but no live unionids were found at site 2 (Table 2). At site 1, three individuals of a single species (*Leptodea fragilis*) were found (each in a separate circle-plot) whereas only one individual (*Pyganodon grandis*) was found at site 3, all at a density of 0.015 m^{-2}. Fouling rates in North Maumee Bay were significantly lower than in the Les Cheneaux Islands ($F_{2,76} = 4.97$, $p = 0.0095$) and fouling dreissenids were exclusively recently settled juveniles with no evidence of adult dreissenids.

Unionid densities were positively correlated with pH ($r = 0.483$, $p = 0.003$) and nitrate ($r = 0.479$, $p = 0.003$). Sampling areas where unionids occurred had an average daytime pH of 8.48 ± 0.02 (Les Cheneaux Islands), 8.53 ± 0.04 (Lake St. Clair delta), and 8.82 ± 0.03 (North Maumee Bay) as opposed to sampling areas without unionids which had an average daytime pH of 8.40 ± 0.05. The average nitrate levels for sampling areas with unionids were 0.08 ± 0.01 mg/L (Les Cheneaux Islands), 0.27 ± 0.01 mg/L (Lake St. Clair), and 0.40 ± 0.05 mg/L (North Maumee Bay) compared to 0.14 ± 0.02 mg/L for sampling areas without unionids. Though the positive correlation between unionids and nitrate may seem counter-intuitive, the concentrations of nitrate that we observed were relatively low and we generally see a bimodal response between disturbance surrounding wetlands and nitrate levels (Uzarski et al., 2005). Unionid densities were not correlated with dreissenid colonization densities on the artificial substrates ($r = -0.088$, $p = 0.654$). Dreissenid fouling rates were not significantly different among unionid species ($F_{11,65} = 1.27$, $p = 0.264$) (Fig. 3) and there was no significant relationship between unionid length and the number of attached dreissenids ($r = 0.205$, $p = 0.073$).

Dreissenid colonization

Dreissenids colonized artificial substrates in Saginaw Bay and North Maumee Bay, but we found little or no colonization of tiles deployed in Grand Traverse Bay, Beaver Island, Garden Island, the Les Cheneaux Islands, or the Lake St. Clair delta. One individual *D. polymorpha* was documented on one tile in both the Lake St. Clair delta and Grand Traverse Bay. Dreissenid presence, however, was observed in the open water regions of all study sites and in some of the wetlands in the Les Cheneaux islands during informal visual surveys before, during, or after sampling.

The discriminant model identified three parameters that strongly differentiated sites where dreissenid colonization densities on artificial substrates were present versus absent: specific conductance ($F_{1,58} = 73.92$, $p \leq 0.001$), turbidity ($F_{1,58} = 18.19$, $p \leq 0.001$), and water level fluctuation ($F_{1,58} = 13.46$, $p \leq 0.001$) (Fig. 4). The two sites where a single dreissenid colonized one artificial substrate (Lake St. Clair delta and Grand Traverse Bay) were assigned to the 'absent' group for the discriminant analysis. Dreissenids did not colonize substrates from sites with low turbidity (<2.0 ± 0.3 NTU), low specific conductance (<244 ± 3.7 mS/cm), or water level fluctuations greater than 0.56 ± 0.02 m. The discriminant model was 95% accurate and correctly assigned 19 of the 20 sites used in the model

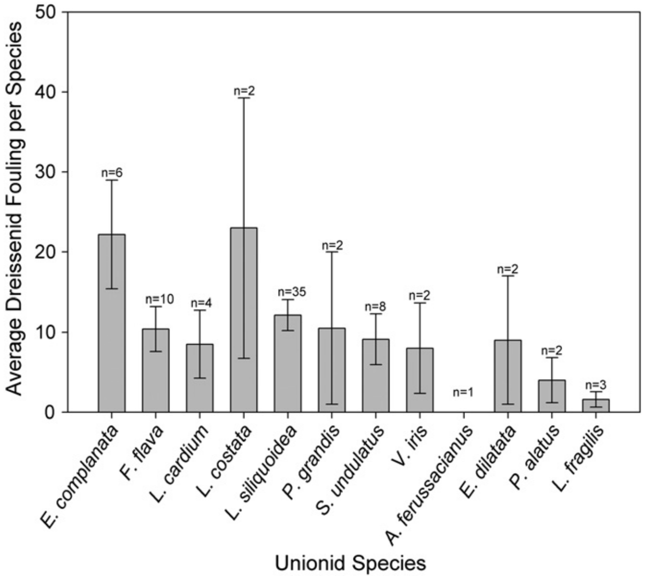

Fig. 3. Mean number of fouling dreissenids on unionid species surveyed during this study. Error bars represent standard error. Number above each bar denotes the number of unionids of that species surveyed in this project. *Anodontoides ferussacianus* (n = 1) did not have any attached dreissenids when surveyed.

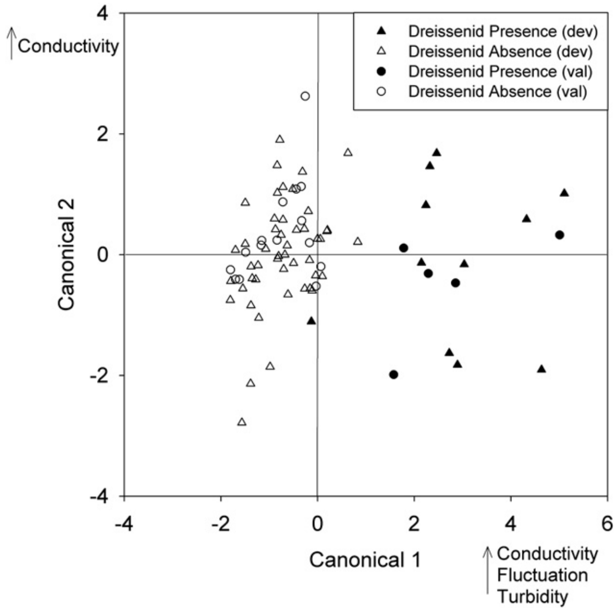

Fig. 4. The distribution of study sites in the discriminate analysis which represents dreissenid presence (filled shapes) and absence (unfilled shapes) on artificial substrates. Sites used in the model development (dev) are signified by triangles ($n = 60$) while sites used in model validation (val) are represented by circles ($n = 20$). Dominant factors for this model include conductivity, turbidity, and water level fluctuation.

validation. The North Maumee site 1 (outer wetland) did not have dreissenid colonization, though our model predicted this to occur.

At the two sampling areas where colonization on artificial substrates occurred (Saginaw Bay and North Maumee Bay), dreissenid densities were highly variable among sites (Table 3). North Maumee Bay had a higher average density compared to Saginaw Bay ($5636 \pm 2095\ \mathrm{m}^{-2}$ versus $2327 \pm 1004\ \mathrm{m}^{-2}$, respectively). The single highest colonization rate measured in this area occurred at site 2 of North Maumee Bay at $31{,}007 \pm 3513\ \mathrm{m}^{-2}$.

Dreissenid colonization in Saginaw Bay consisted of 7% adults (111 individuals) and 93% juveniles (measured as <7 mm) (1497 individuals). Of the adults, 88% were *D. polymorpha* (98 individuals) and 12% were *D. rostriformis bugensis* (13 individuals). In contrast, at the North Maumee Bay sites, 18% of the colonizing dreissenids were adults (478 individuals) and 82% were juveniles (2119 individuals) and the adults were all *D. polymorpha*.

Table 3
Mean (SEM) dreissenid colonization densities (m^{-2}) calculated from the artificial substrates set in the inner and outer zones of the wetlands. Colonization was not observed on artificial substrates in the Les Cheneaux Islands, Beaver Island, or Garden Island. The Lake St. Clair delta and Grand Traverse Bay each had one site where one dreissenid colonized the artificial substrates (listed below).

Site Name	Mean colonization (m^{-2})
N. Maumee Bay	
Site 2 inner	2236.7 (662.8)
Site 2 outer	19,213 (5540.2)
Site 3 inner	324.1 (105.6)
Site 3 outer	769.7 (175.7)
Saginaw Bay	
Site 1 inner	31.8 (11.4)
Site 1 outer	2546.3 (1962.2)
Site 2 inner	911.5 (330.9)
Site 2 outer	10,425.3 (4654.8)
Site 3 inner	23.1 (13.9)
Site 3 outer	26 (11.6)
Lake St. Clair delta	
Site 2 outer	5.8 (5.8)
Grand Traverse Bay	
Site 1 outer	5.8 (5.8)

Colonization densities on artificial substrates were significantly higher in the outer wetlands ($5497.7 \pm 1668.7\ \mathrm{m}^{-2}$) than in the inner wetlands ($705.4 \pm 207.7\ \mathrm{m}^{-2}$) ($F_{1,65} = 6.78$, $p = 0.011$). Dreissenid colonization density was positively correlated to chlorophyll ($r = 0.619$, $p = <0.001$), turbidity ($r = 0.424$, $p \leq 0.001$), specific conductance ($r = 0.388$, $p \leq 0.001$), total dissolved solids ($r = 0.363$, $p \leq 0.001$), water level fluctuation ($r = 0.324$, $p = 0.003$), alkalinity ($r = 0.264$, $p = 0.015$), and low water levels ($r = 0.226$, $p = 0.033$), and was negatively correlated to oxidation reduction potential ($r = -0.263$, $p = 0.046$).

Physical and chemical habitat characteristics of study areas

The first and second principal components of physical–chemical parameters described 28% and 18.5% of the variation in measured environmental conditions (Fig. 5). PC 1 was positively correlated with dreissenid colonization ($r = 0.26$, $p = 0.022$) and was driven by a gradient contrasting TDS, alkalinity, and specific conductance increasing on the right side of the axis with pH on the left side of the axis (Table 4, Fig. 5). Dreissenid colonization densities on the artificial substrates were negatively correlated to PC 2 ($r = -0.236$, $p = 0.038$) and this axis contrasted increasing turbidity, temperature, and pH on the bottom of the axis versus increasing water depth at the top of the axis, as reflected by the eigenvectors (Table 4). Unionid densities were not correlated to either axis (PC 1 $p = 0.064$, PC 2 $p = 0.321$).

The sampling sites in the Les Cheneaux Islands and the Lake St. Clair delta, although they contained very different unionid densities, species richness, and fouling, were closely grouped in the PCA, suggesting that these sites have similar habitat characteristics. Further analyses of the Les Cheneaux Islands and the Lake St. Clair delta via pairwise comparisons revealed significant differences in water level fluctuation ($T_{25} = -2.28$, $p = 0.03$), turbidity ($T_{52} = -6.63$, $p \leq 0.001$), dissolved oxygen ($T_{52} = 2.40$, $p = 0.02$), temperature ($T_{52} = -4.20$, $p \leq 0.001$), ammonium ($T_{52} = 3.43$, $p = 0.001$), and nitrate ($T_{52} = -10.12$, $p \leq 0.001$).

Maximum water levels were not significantly different across sampling areas ($F_{80,6} = 2.13$, $p = 0.0599$), but minimum water levels differed ($F_{80,6} = 6.56$, $p \leq 0.001$) (Table 5). North Maumee

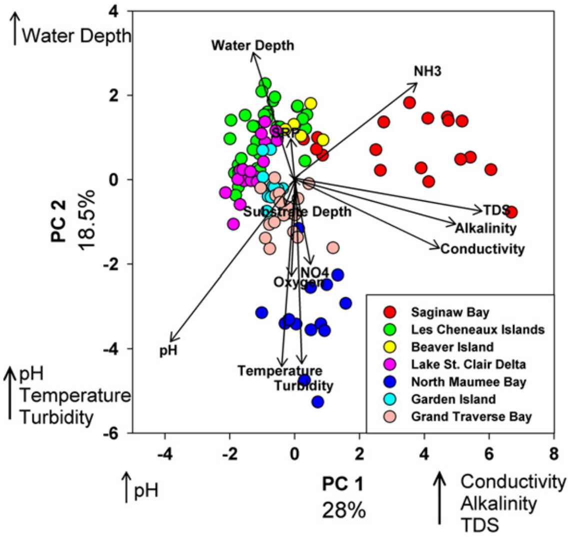

Fig. 5. Principal components analysis of physical and chemical variables measured at each study region.

Table 4
PCA eigenvector values denoting chemical and physical parameters which characterize gradients along the axes. Values in bold were used for interpretation of axes. The abbreviations in the table represent the following: TDS is total dissolved solids, NH_4^+ is ammonium, SRP is soluble reactive phosphorous, and NO_3^- is nitrate.

Parameter	Axis 1	Axis 2
Temperature	−0.0696	**−0.693**
Conductivity	**0.8902**	−0.2513
Oxygen	0.0211	−0.37
Turbidity	0.0433	**−0.7469**
TDS	**0.9573**	−0.1105
pH	**−0.5974**	**−0.6181**
Alkalinity	**0.9049**	−0.176
Water depth	−0.197	**0.4891**
Substrate depth	0.0138	−0.1157
NH_4^+	0.6292	0.3951
SRP	−0.0422	0.1698
NO_3^-	0.095	−0.3373

Bay sites had the lowest average minimum water level and the Lake St. Clair delta had the highest average minimum water level. Water level fluctuation was significantly different across all sampling areas ($F_{80,6} = 2.72$, $p = 0.0192$). Saginaw Bay, Garden Island, and North Maumee Bay wetlands had the greatest average fluctuation, while Grand Traverse Bay and the Les Cheneaux Islands had the lowest average water level fluctuations (Table 5).

Discussion

This study identified and quantified chemical and physical habitat characteristics in Great Lakes coastal wetlands that are important to remnant unionid assemblages and habitat refugia. We also described factors related to dreissenid presence and absence in these coastal wetlands. Dreissenid fouling has been widely acknowledged as a major source of unionid mortality (Nalepa et al., 1996; Ricciardi et al., 1998; Schloesser et al., 1996) and we observed varying levels of fouling and dreissenid colonization where unionids were documented. The presence of live unionids with attached dreissenids may indicate that co-existence between unionids and dreissenids could occur in certain habitats. This is counter to the initial predictions during dreissenid invasion (Ricciardi et al., 1998). While some wetlands supported some dreissenid colonization, few if any likely support densities of dreissenids found in other habitats (e.g., rocky shoals; Jarvis et al., 2000). We hypothesized that wetlands would provide refuge for unionids from dreissenids because chemical and physical characteristics of these systems deter dreissenid settlement and the soft substrates allow unionids to burrow thus reducing fouling impacts. Other studies have identified strong negative relationships between dreissenid abundance and unionid populations (Ricciardi et al., 1998; Schloesser et al., 1996; Strayer and Malcom, 2007). We did not observe a direct relationship between dreissenids and unionids in wetlands; therefore, this supports our hypothesis that Great Lakes coastal wetlands provide, to some degree, habitat refuge for native unionids.

Table 5
Mean water depth, high and low water levels, and the difference between the high and low measurements for each sampling location in Lakes Michigan, Huron, St. Clair, and Erie. All measurements are in meters. The numbers in parentheses represent the standard error for the mean.

Region	Depth	High water level	Low water level	Difference
Saginaw Bay	0.59 (0.03)	0.84 (0.08)	0.16 (0.03)	0.69 (0.07)
Les Cheneaux Islands	0.74 (0.05)	0.82 (0.05)	0.33 (0.04)	0.49 (0.02)
Beaver Island	0.56 (0.04)	0.76 (0.08)	0.18 (0.04)	0.59 (0.06)
St. Clair delta	0.71 (0.03)	0.99 (0.06)	0.39 (0.03)	0.60 (0.06)
North Maumee Bay	0.56 (0.07)	0.72 (0.09)	0.05 (0.03)	0.67 (0.08)
Garden Island	0.61 (0.05)	0.83 (0.06)	0.16 (0.06)	0.68 (0.03)
Grand Traverse Bay	0.30 (0.03)	0.64 (0.04)	0.13 (0.06)	0.52 (0.05)

Coastal wetlands contain physical and chemical characteristics that can reduce negative effects of dreissenids, such as soft sediments to allow unionids to burrow and high productivity that could reduce food competition. These two factors could account for the co-existence of unionids and dreissenids that we documented in this study. We identified a previously unreported site in North Maumee Bay, Lake Erie that has these characteristics and supports living unionids. Further investigation of this area is needed to determine whether the habitat is truly acting as a refuge or if the unionids that were located there were simply a remnant population facing extirpation.

Unionid presence

While no single parameter measured predicts unionid presence in coastal wetlands, a host of factors with site-specific importance may account for their continued existence in these habitats despite the impacts from invasive dreissenid mussels and environmental conditions thought to be unfavorable to unionid existence. Sites where live unionids were surveyed often contained substrates composed primarily of sand or silt. Previous habitat studies describe soft benthic substrates as a key to unionid survival because these substrates act as a mechanism for unionids to avoid or remove fouling dreissenids via burrowing (Bowers and de Szalay, 2004; Bowers et al., 2005; Nichols and Wilcox, 1997; Schloesser et al., 1997). Similarly, studies have documented that water level fluctuation (both short term and seasonal) and declining water levels reduce the survival of dreissenid mussels (Balogh et al., 2008; Baumgärtner et al., 2008; Bowers and de Szalay, 2004, 2005). In our study, the lowest fouling was documented at the North Maumee Bay sites which had the lowest water levels and high fluctuations. Conversely, the unionids in the Les Cheneaux Islands had the highest degree of fouling and the greatest water depth and least fluctuation compared to other sites. There was, however, a weak positive correlation between dreissenid colonization on artificial substrates and water level fluctuation ($r = 0.32$, $p = 0.003$). The significance of the correlation is likely due to sample size (n = 96) rather than any meaningful relationship since r is quite small.

The Lake St. Clair delta has a particularly promising remnant unionid assemblage and could possibly be used in the future as a site for unionid recovery or translocation efforts as it contained the highest species richness and densities. The mean number of attached dreissenids documented on individual unionids in the Lake St. Clair delta was 11, which follows a declining trend of fouling noted in this area by Zanatta et al. (2002), in which fouling dropped from 61 to 31 to 17 in 1999, 2000, and 2001, respectively, and down to 15 dreissenids per unionid in 2003 and 2004 (McGoldrick et al., 2009). The cause of the reduced fouling in this sampling area is unknown (Lucy et al., in press), but we speculate post-invasion declines and environmental conditions (i.e., habitat loss from unionid extirpation and vegetation senescence), as described by Hunter and Simons (2004) and Nalepa et al. (2001), as potential reasons.

The Les Cheneaux Islands appear to have similar chemical and physical characteristics to the Lake St. Clair delta (Fig. 5; Table 5), but it is important to note that the PCA is a relative comparison of all of the sites analyzed. Pairwise comparisons between these two sampling areas displayed significant differences in habitat characteristics, including higher water level fluctuation, temperature, nitrate, and turbidity in the Lake St. Clair delta and higher dissolved oxygen and ammonium in the Les Cheneaux Islands. The substrate composition, primarily clay at the Les Cheneaux sites versus primarily sand and silt at the Lake St. Clair sites, is a likely factor to explain why fouling was higher in the Les Cheneaux sites as the firm substrate composition may have inhibited unionids from burying themselves sufficiently to dislodge/suffocate dreissenids.

Dreissenid colonization

Collectively, our results suggest that dreissenid colonization in coastal wetlands is influenced by productivity, anthropogenic disturbance, and fluctuating water levels; conservation efforts can use these parameters to guide unionid population protection. Across all sites, dreissenid colonization on artificial substrates was reliably predicted from wetland specific conductance, turbidity, and water level fluctuation. High specific conductance and turbidity are indicators of anthropogenic disturbance in coastal wetlands (Uzarski et al., 2005), and these parameters in the two regions where dreissenid colonization occurred on artificial substrates (Saginaw Bay and North Maumee Bay) indicated the presence of cultural eutrophication. Water exchange and movement that is typical between the open water and nearshore habitats of fringing systems (Albert et al., 2005) could potentially contribute to the relationships between dreissenid colonization and water level fluctuations, turbidity, and specific conductance. Dreissenid colonization on the artificial substrates had a strong positive correlation with chlorophyll *a* levels as expected since productivity is an important variable in dreissenid colonization. As suspension feeders, dreissenids filter bacteria, algae, and detrital particulates from the water column (McMahon and Bogan, 2001) and high amounts of these particles (which can influence turbidity, chlorophyll *a*, and total dissolved solids) would likely support high colonization rates.

Dreissenids were present in the open water areas adjacent to all sites in this study and on vegetation in the wetlands of the Les Cheneaux Islands, but artificial substrates were only colonized in Saginaw Bay and North Maumee Bay. In addition to anthropogenic disturbance, latitudinal and temporal variations among sites and years may also explain the lack of colonization on artificial substrates in northern sites. We sampled the southern sites first and then sampled the northern sites in an attempt to temporally reduce any latitudinal differences among the sampling areas. Colder water temperatures and reduced productivity at sites in northern lakes Michigan and Huron could cause veliger settlement to occur much later in the year (after the study was finished) than at the warmer, more productive sites in Saginaw Bay and North Maumee Bay (McMahon, 1996).

Dreissenid fouling in the Les Cheneaux Islands was composed of large adults and no juveniles, while the opposite was documented in the Lake St. Clair delta and North Maumee Bay with unionids being fouled by juveniles with no evidence of adult dreissenids. This may imply long-term (years) fouling and a lack of dreissenid recruitment in the Les Cheneaux Islands while the other two areas experience short-term (seasonal) fouling and dreissenid recruitment. Several unionids surveyed in the Lake St. Clair delta displayed evidence of past fouling (remnant byssal threads) which could suggest that dreissenid fouling is being regulated by biotic or abiotic conditions (i.e., unionid burrowing, aerial exposure, predation, etc.).

North Maumee Bay sites had the highest documented dreissenid colonization on the artificial substrates of this study (31,007 m^2; at site 2, outer wetland), but this region also contained a site that had no colonization throughout the duration of this study (site 1). This site, which was the open shoreline site outside of the embayment, appeared to be more affected by seiche events and seasonal water level declines than sites 2 and 3, which were located inside the embayment and had a direct inflow of water from the Maumee River. Low water levels may also explain why the discriminate analysis incorrectly predicted site 1 of North Maumee Bay to have dreissenid presence when dreissenids did not actually colonize tiles at this site.

We believe that the highly variable densities on the colonization plates were due in part to the occurrence of juvenile settlement, natural mortality, predation, and competition. Colonization densities on the artificial substrates were higher in North Maumee Bay at 6 weeks of colonization compared to 12 weeks, whereas the opposite was seen for Saginaw Bay. Competition, natural mortality and predation likely played a part in the declining numbers over time documented in North Maumee Bay during this study (Bowers and de Szalay, 2007; Bowers et al., 2005; Morrison et al., 1997). Higher colonization on the artificial substrates in the outer wetland compared to the inner wetland was likely related to the reduced water flow from dense vegetation in the inner wetland which would restrict transportation of the veligers for settlement.

There was no dreissenid colonization on the artificial substrates in the Lake St. Clair delta, but several of the unionids surveyed in these sites were fouled. Hunter and Simons (2004) suggested that dreissenid abundances in Lake St. Clair were limited by a lack of suitable permanent substrate. The Lake St. Clair delta sites were located between the Saginaw Bay and North Maumee Bay sites, two areas where we documented high dreissenid colonization on the artificial substrates indicating that propagule pressure is likely not limiting. The presence of dense vegetation within the Lake St. Clair delta could have restrict dispersal (from the St. Clair River) of pelagic veligers, which rely on water currents to transport them to settlement areas (Bodamer and Bossenbroek, 2008). Additionally, the turbidity, specific conductance, and total dissolved solids (positively related to dreissenid colonization) were relatively low in comparison to the sites where dreissenid colonization occurred.

Interestingly, the vast majority of fouling was by zebra mussels and not quagga mussels and there were noticeable differences in the size and age structure of fouling dreissenids among regions. The implications of this warrant further attention. Several studies have documented the basin-wide movement of quagga mussels into nearshore zones and the changing dominance from zebra to quagga mussels (Mills et al., 1999; Wilson et al., 2006). Our findings are not congruent with these observations as we noted that zebra mussels were more prevalent on the artificial substrates colonized in Saginaw Bay and North Maumee Bay. Further investigation into whether or not nearshore movement and dreissenid dominance will affect fouling rates and unionid mortality in sites with remnant assemblages is needed.

Conclusion and management implications

The significant decline of unionids across the Great Lakes basin underscores the importance of monitoring and conservation efforts to sustain this imperiled fauna. Based on the findings of this study and previous research (McGoldrick et al., 2009; Zanatta et al., 2002), the Lake St. Clair delta and North Maumee Bay act as refuge habitats for unionid assemblages. The observed fouling on unionids in these habitats may indicate a level of co-existence or simply that the fouling threshold for unionid mortality has not been reached.

Live unionids were found in the Les Cheneaux area, but low species richness and density coupled with high dreissenid fouling indicate that this is likely a remnant or sink population that is functionally extirpated and this area does not appear to be functioning as a refuge. This indicates that the Les Cheneaux Islands may need immediate intervention (e.g., reintroduction or augmentation of unionids) to stabilize the populations and prevent extirpation, but the high fouling in this sampling area would not bode well for long term unionid survival without additional strategies. Hallac and Marsden (2001) and Schloesser (1996) suggest in situ removal of dreissenids as a technique to increase survival for unionids in habitats where dreissenids are present. They found that in situ removals were logistically feasible when unionid abundances were small and geographically localized, but due to constraints on burrowing and the relatively high fouling rate, dreissenid removal would be a continuously labor intensive management course.

Michigan's coastal wetlands have historically received little consideration with regard to unionid presence, potential refuge habitats, and interactions with invasive dreissenid mussels, which are strong contributors to unionid mortality (Nalepa et al., 1996; Ricciardi et al., 1998; Schloesser et al., 1996). This study suggests that physical (water fluctuations and potentially vegetation density) and chemical (i.e., turbidity, specific conductance, and total dissolved solids) factors influence dreissenid fouling on unionids and dreissenid colonization on artificial substrates in coastal wetlands. Unionid conservation would benefit from continued efforts to minimize or prevent eutrophication (e.g., regulation and monitoring) while promoting natural water level fluctuations (e.g., preventing water extraction and barriers). Unionid restoration might also be effectively coupled to native macrophyte restoration efforts, especially emergent macrophytes. Further investigations into latitudinal gradient effects on the timing of dreissenid reproduction and juvenile settlement and how riverine landscapes with more lotic characteristics like North Maumee Bay, Saginaw Bay, and the Lake St. Clair delta compare to fringing coastal areas in relation to unionid and dreissenid abundances are needed. Additional studies evaluating coastal wetlands as potential unionid habitat could greatly benefit conservation efforts in the Great Lakes basin and this study provides a framework for future studies to achieve this goal.

Acknowledgments

We would like to thank the following individuals for assistance in data collecting for this study: Thomas Clement, Dave Coulter, Nathan Barton, Neil Schock, Matt Rowe, Erin Fitzpatrick, Dave Schuberg, Eric Calabro, Dave Dortman, Dave Branson, and Sasha Bozimowski. Appreciation goes to Matthew Cooper, Joshua Sherman, and Jerry Droll for contributing to the design of the water level gauges. We would also like to thank Jessica Lapp, Anett Trebitz, and three anonymous reviewers for their helpful comments and suggestions for improving the manuscript. Funding for this study was provided by the Central Michigan University Graduate Student Research and Creative Endeavors Grant, the Daniel E. and Mildred G. Wujek Endowed Scholarship, and a grant from the Michigan Department of Environmental Quality — Coastal Zone Management program.

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