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Modeling Habitat of Freshwater Mussels (Bivalvia:Unionidae) in the Lower Great Lakes 25 Years after the Dreissena Invasion

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Modeling habitat of freshwater mussels (Bivalvia:Unionidae) in the lower Great Lakes 25 years after the *Dreissena* invasion

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Abstract: Finding remnant populations of species that are of conservation concern can be difficult, particularly in aquatic habitats. Models of ecological niches can aid in the discovery of refuges. Remnant populations of native freshwater mussels (unionids) have been found in Lakes Erie and St Clair. Our goals were to predict undiscovered refuges in Lake Ontario based on habitat analysis from Lake Erie and to conduct surveys to test those predictions. We built a presence-only model on environmental data including attributes of the benthic zone and shoreline where mussels occurred in Lake Erie. We found a link between small- and large-scale variables related to unionid persistence. Bathymetry, fetch, and shoreline geomorphology contributed most to the model. These variables correspond to local-scale environmental factors important for unionid survival, including presence of vegetation and substrate composition, which explained ~22% of the variance in presence, abundance, and richness. The model predicted that 0.8% of the near-shore area of Lake Ontario should be habitat for unionids. In surveys at 34 locations on the USA shore of Lake Ontario, we found 1800 unionids of 11 species and showed that areas <500 m from predicted good habitat contained significantly more individuals than near-shore areas not identified as good habitat. We were able to predict new refuges in Lake Ontario successfully even though mussel assemblages differed between Lakes Erie and Ontario, a result signifying generality of our model for conservation approaches to freshwater mussels.

Key words: lake, distribution, MaxEnt, modeling, invertebrates, alien species

Ecological niche or habitat models are being used increasingly to aid in the conservation of rare species because they apply computer algorithms to predict the distribution of a species or assemblage in geographic space (Guisan et al. 2013). Unionid mussels are among the most-imperiled faunal groups in North America (Lydeard et al. 2004). Anthropogenic modification of aquatic systems profoundly reduces potential habitat of mussels and their host fish required for reproduction (Schwalb et al. 2013) through the combination of channel modification and cultural eutrophication (Strayer

2008). The invasion of dreissenid mussels in the Laurentian Great Lakes increased the strain on unionid mussel assemblages because the invader fouled and smothered all historically monitored mussel beds in Lakes Erie (Strayer and Malcom 2007, McGoldrick et al. 2009, Lucy et al. 2014) and Ontario (Burlakova et al. 2014). Despite the environmental changes in the lower Great Lakes, refuges persist (Zanatta et al. 2002, McGoldrick et al. 2009, Crail et al. 2011), and their locations can be used to describe an ecological space where unionid mussels could survive in other

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Great Lakes (Zanatta et al. 2015). Unionid refuges have been found in large drowned river mouths, shallow embayments, and coastal wetlands with soft substrates (Zanatta et al. 2015).

The important habitat variables associated with refuges probably are those that inhibit dreissenid establishment (e.g., water-level fluctuations, access by zebra mussel predators) or enable unionids to remove attached dreissenids (Lucy et al. 2014). Unionids can remove attached zebra mussels or reduce zebra mussel settlement in substrates soft enough to permit them to burrow (Nichols and Wilcox 1997, Schloesser et al. 1997, Burlakova et al. 2000, Sherman et al. 2013). Such substrates occur more often in large areas of shallow waters (protected bayous) with low flow and warmer temperatures than elsewhere (Nichols and Wilcox 1997). Additional factors that inhibit establishment of stable zebra mussel populations include wave action, water-level fluctuations, ice scour (Nichols and Wilcox 1997, Karatayev et al. 1998, Bowers and de Szalay 2004, 2005, Sherman et al. 2013), remoteness from a source of dreissenid veligers (Zanatta et al. 2002, McGoldrick et al. 2009), dense reed beds that lower the rate of veliger dispersal (Bodamer and Bossenbroek 2008, Nelson et al. 2009), predation on *Dreissena* attached to unionids (Bowers and de Szalay 2007), warm thermal plumes from power plants that limit *Dreissena* presence (Bryan et al. 2013, 2014), and lower Ca^{2+} concentration in the water (Hollandsworth and Lowe 2011). Many of the specific ecological factors that create refuges apply at limited spatial scales, and most are related to small-scale variables like depth and substrate type. However, large-scale variables (e.g., hydrological regime) may determine sediment type and stability, thereby creating habitat where unionids persist. Incorporation of data on multiple habitat characteristics at known unionid

refuges into models can lead to identification of landscape-scale predictors that define conditions favorable for taxon persistence (Guisan and Thuiller 2005, Elith et al. 2006, Elith and Graham 2009).

Our primary goal was to predict the habitat in which unionid refuges in Lake Ontario should occur because this large lake had been minimally studied. Our specific objectives were to: 1) use regional-scale geographical information system (GIS) data related to the environmental characteristics at sites in Lake Erie with unionid populations (Crail et al. 2011, Zanatta et al. 2015) to develop a MaxEnt (version 3.3.3k; Phillips et al. 2006) model to predict the presence of unionids at sites in other large lakes infested with dreissenid mussels, and 2) verify model predictions by extensively sampling assemblages in Lake Ontario. We then compared the local-scale characteristics at new sites to those at refuge sites in Lakes Erie and St Clair (Zanatta et al. 2015) to understand how links among small- and large-scale variables may define a refuge for an imperiled freshwater mussel assemblage.

METHODS

Habitat model

We selected 35 sites in Lake Erie that had been listed as supporting unionids by Zanatta et al. (2015) (Fig. 1) based on the extent of GIS environmental data available. The environmental variables (Table 1) we used for the habitat model were a subset of a suite of variables developed to assess the near-shore habitats of fish and included: 1) physical attributes of the benthic zone (i.e., lake bathymetry, bottom slope, and aspect) and 2) information about the lake shoreline, such as distances to different types of wetlands, sinuosity, fetch, and landuse category (McKenna and Castiglione 2010). Fetch is the distance traveled by wind

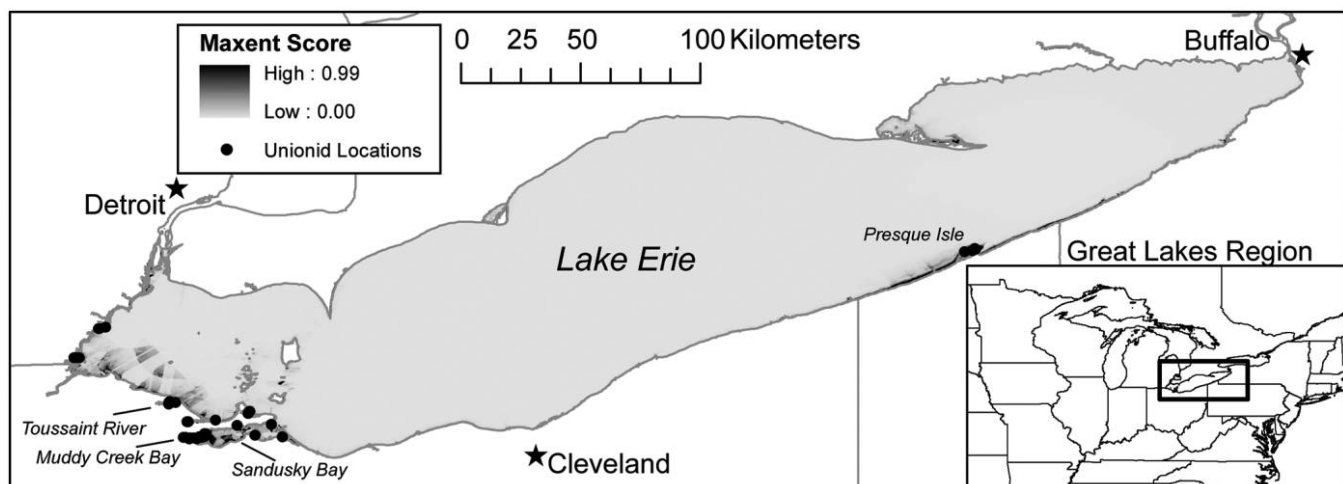


Figure 1. Unionid sites used in MaxEnt modeling. The 35 sites are those sampled by Zanatta et al. (2015) that have unionid assemblages present and are within the extent of the geographic information system layers developed by McKenna and Castiglione (2010). The shading of the map represents the MaxEnt habitat predictions for Lake Erie.

Table 1. Environmental layers used in the MaxEnt analysis, including a brief description and the importance of each layer for explaining presence of unionids. Shoreline categories include: High (>15 m) Bluff, High (>15 m) Bluff with Beach, Low (<15 m) Bluff with Beach, Sandy/Silty Banks, Clay Banks, Sandy Beach/Dunes, Coarse Beaches, Baymouth Barrier Beaches, Bedrock (Resistant), Bedrock (Non resistant), Low Riverine/Coastal Plain, Open Shoreline Wetlands, Semi Protected Wetlands, Composite, US Shore: Unclassified, Canadian Shore: Artificial, US Shore: Artificial, Canadian Shore: Unclassified.

Environmental layer	Description	Importance
Aspect	Compass direction of slope	0.5
Bathymetry	Depth (m)	58.5
Distance to delta-type wetland	Distance (m) to wetlands formed at river mouths	2.1
Distance to open-type wetland	Distance (m) to wetlands that are open to fluctuations in Great Lakes water levels	0.2
Distance to protected-type wetland	Distance (m) to wetlands that are protected and controlled by levees, etc.	5.1
Fetch	Distance along open water over which the wind blows	15.9
Shoreline geomorphology	Shoreline categories projected outward from coastline	15.1
Sinuosity	Sinuosity of coastline (ratio of straight line distance to coastline distance)	1.9
Slope	Submerged bottom slope	0.6
Submerged aquatic vegetation (SAV)	Binary variable – SAV present on $\geq 50\%$ of the raster cell area	0

across open water and, thus, affects wave energy and substrate distribution. The shoreline category data were developed by personnel at the Great Lakes Environmental Research Laboratory of the National Oceanic and Atmospheric Administration to aid in shoreline management (Lee et al. 1998). The extent of the environmental data included the near-shore open water of each Great Lake, i.e., the portion of each lake that is <10 m deep. The resolution of the environmental data was $\sim 110 \text{ m}^2$ (data were distributed in a geographic coordinate system with cell resolution of ~ 0.001 decimal degrees).

Several statistical methods to model ecological niches exist: multivariate analysis (canonical coordinate analysis [CCA] or nonmetric multidimensional scaling [NMDS]), regression-based techniques, and stand-alone modeling systems, such as GARP and MaxEnt (Herborg et al. 2009). To predict potential unionid habitat in Lake Ontario, we used MaxEnt (Phillips et al. 2006), a machine learning method that has been rated highly among similar modeling algorithms (Elith et al. 2006). MaxEnt often enables broader sampling of distributions than other algorithms because presence-only records with background environmental data are sufficient to predict the probability of a species distribution (Doko et al. 2011, Blank and Blaustein 2012, Couce et al. 2012, Matawa et al. 2012). MaxEnt combines: 1) known locations for the organism of interest, and 2) environmental data in the format of a grid of equally sized cells, such that predicted locations fall within the extent of the environmental data. The locations at which a species is present are assumed to provide information on required layers that represent the range of environmental characteristics. MaxEnt identifies the geographical ranges possessing these characteristics (Lozier and Mills 2011). We applied the default settings recommended by Phillips and Dudik (2008) for situations with small sample sizes. We selected 10,000 random

pixels from the environmental layers to represent the range of environmental background conditions, a recommended approach when the environmental layers are large. We used all available presence data from Lake Erie to train the model.

The output for MaxEnt models ranges from 0 to 1, with a higher number indicating a better fit to the modeled ecological niche or habitat of an organism of interest. An importance rating for each environmental variable in the model (Table 1) was calculated based on a jack-knife test (Doko et al. 2011), and the overall model was evaluated with the Area Under the Curve (AUC) of the Receiver Operator Characteristics (ROC). The AUC is the probability that the model will correctly differentiate between a presence location and a random location (Phillips et al. 2006, Razgour et al. 2011). Opinions of model assessment vary, but an AUC value > 0.9 indicates that the model has a high ability to discriminate among locations (Swets 1988, Elith et al. 2006, Phillips et al. 2006).

Lake Ontario surveys

We used predictions from the niche model to guide our choice of locations to sample for new unionid communities in Lake Ontario. We chose 34 locations in the USA on the southern shore of Lake Ontario that included diverse habitats to test niche model predictions. Within these locations, we selected a total of 54 0.5-ha ($50 \times 100 \text{ m}$) sampling sites based on logistical access and spatial coverage (Fig. 2A). Sampling locations stretched from the lower Niagara River to the Thousand Islands archipelago of the St Lawrence River and included areas in the coastal zone of the lake, mouths of tributary rivers, fringing wetlands (extending from the shore into the littoral zone), wetlands near tributary river mouths, and smaller lakes, ponds, and marshes within the coastal zone near the lake. We assigned multiple sites where the predicted area for mussel habitat

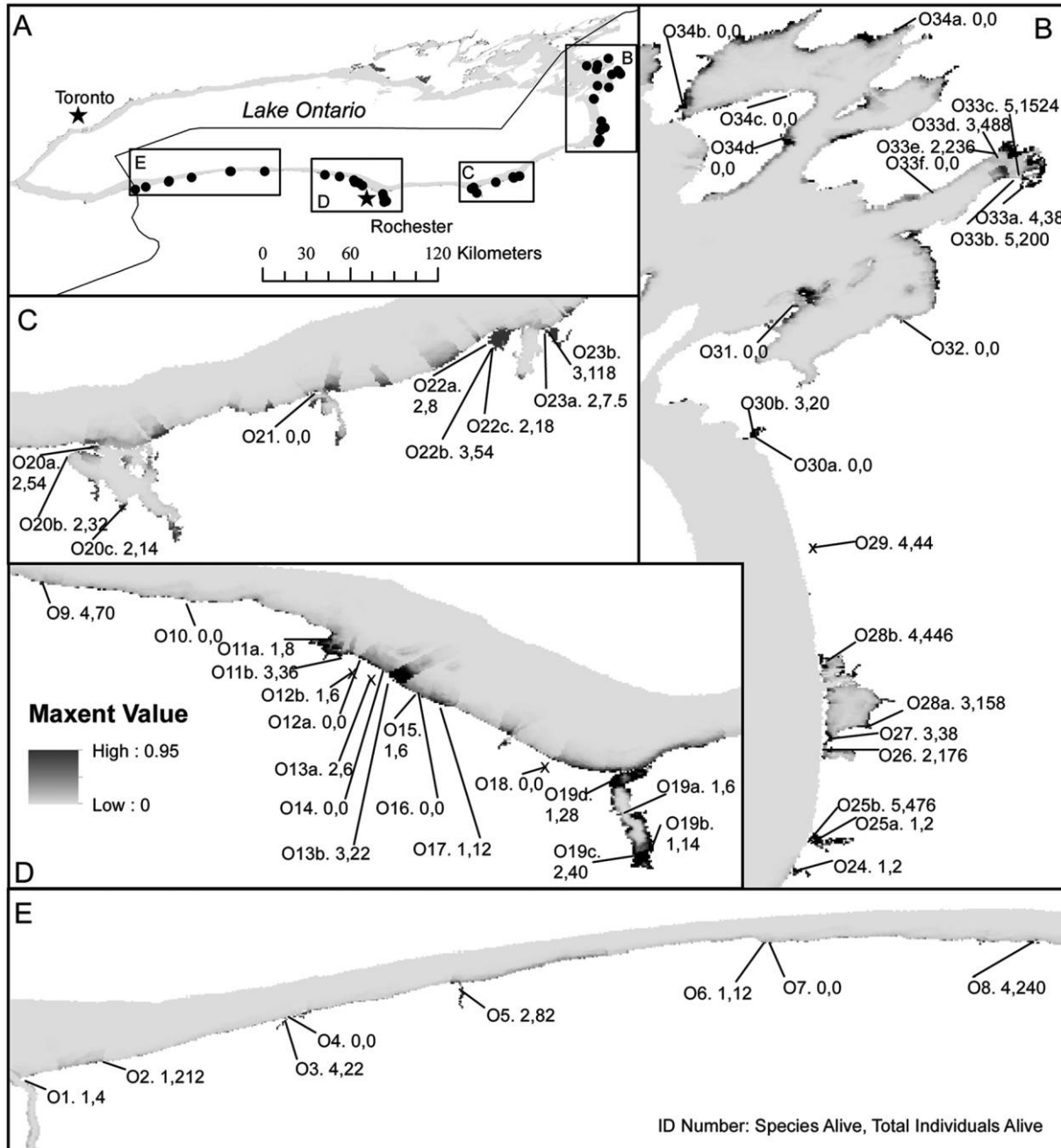


Figure 2. Habitat model predictions of good habitat for unionid assemblages in Lake Ontario based on known occurrences in Lake Erie. A.—Overview of the sampling sites in Lake Ontario used to assess the niche model results. The 4 boxes in panel A are expanded in B–E to show niche model results in gray-scale and the number of species and individuals found alive at each sampling location (identification numbers of sampling locations correspond to Table 2).

was large or heterogeneous in habitat. Where predicted mussel abundances were high, we sampled 1 to 5 sites and included additional sampling sites outside target areas (Fig. 2B–E).

We did not expect to find a tight correlation between model predictions and unionid species number or abundance because unionid assemblages have patchy spatial distributions, and the grain size (i.e., scale) of our environ-

mental data probably was of a lower resolution than that needed to predict variations in sediment stability precisely. Therefore, we calculated correlations between model predictions and survey results first and then used ArcGIS (version 10.1; Environmental Systems Research Institute, Redlands, California) to compare sampling locations inside or close to areas of good habitat (see definition below). We arbitrarily defined ‘close’ as the area <500 m from predicted

good habitat. Therefore, some shallow-water locations with low predicted values also were chosen to assess the model. Four locations selected were not within the extent of our habitat predictions (sites O12b, O13a, O18, and O29; Fig. 2B, D), but these types of connected wetlands are frequent refuges for unionids in the Lake Erie basin (Bowers and de Szalay 2004, 2005). Therefore, we sampled them to meet the secondary project objective, which was to find as many unionid refuges as possible with limited time and resources.

We searched each site for unionids for 2 person-hours (e.g., 4 searchers for 30 min) using tactile searches while wading and snorkeling. These searches followed the methods used by Zanatta et al. (2015) for Lakes Erie and St Clair. We calculated the mean (\pm SE, unless noted otherwise) number of unionids/site by averaging data from multiple sites sampled in each location. Species richness was the cumulative number of unionid species present across sites within a location. We calculated unionid diversity based on the Shannon diversity index (H') and converted H' to effective number of species, which is the number of species in an assemblage if all species present were equally abundant ($e^{H'}$; Jost 2006). At 4 sites where we found abundant or diverse mussel assemblages, we conducted quantitative area searches (30–60 randomly placed 0.25-m² quadrats) for better assessments of density.

Local-scale variation

We measured local-scale habitat characteristics following the procedure used by Zanatta et al. (appendices 1, 2 by Zanatta et al. 2015). We collected measurements from each site in triplicate, typically at the center and 2 opposite corners of the site. We estimated proportional composition of sediments (bedrock, boulder, cobble, gravel, sand, silt, and clay) qualitatively to a maximum depth of 12 cm. We used a multiparameter water-quality sonde (model 6600 V2; Yellow Springs International, Yellow Springs, Ohio) to measure turbidity, specific conductivity, pH, chlorophyll *a* (Chl *a*), and temperature. At each site, we estimated density of dreissenids qualitatively as absent (none found), low (few aggregations), medium (many aggregations), or high (all hard substrates covered); % emergent and submerged macrophyte cover; and habitat threats, such as visible sediment disturbance, pollution, and nearby watershed development.

We assessed quantitative relationships among local-scale environmental variables for 3 aspects of community composition, total abundance, species richness, and presence/absence of unionids based on combined data across Lakes Erie/St Clair and Ontario (Appendix S1). For a few sites where complete environmental data were not collected during surveys, we estimated missing data with the aid of the *Multivariate Imputation by Chained Equations* package for R (version 3.2.3; R Project for Statistical Computing, Vienna,

Austria; van Buuren and Groothuis-Oudshoorn 2011). To find a best-fit model and estimate model coefficients we used the R package *glmulti*, which automates model selection with generalized linear models (GLMs) based on a genetic algorithm and uses Akaike's Information Criterion (AIC) to assess model fit (Calcagno 2013). For each model selection routine we used *glmulti* to identify those models < 2 AIC units from the best-fit model, calculate model-averaged coefficient estimates and significance values of each variable, and estimate the r^2 value of the best-fit model.

RESULTS

The model selected by MaxEnt for the habitat of unionids in Lake Erie included 10 predictor variables (Table 1) and had an AUC of 0.988. Shoreline geomorphology, bathymetry or depth, and fetch contributed the most to this model, as determined by the jackknife routine (Fig. 3A–C). The most important shoreline category was semi-protected wetlands, which were areas defined as having protection from wave action via natural features, such as Baymouth barriers (EC and USEPA 2009).

The distribution of MaxEnt values at the 35 Lake Erie/St Clair sites used to develop the model was bimodal, and all but 9 sites had values > 0.4 . Therefore, we defined 0.4 as a threshold value to indicate good mussel habitat. The 9 sites with a MaxEnt value < 0.4 were < 500 m from an area defined as good habitat. For Lake Erie, the model predicted that only 65.5 km² (0.2%) of near-shore area is good habitat for mussels. For Lake Ontario, the model predicted that 55 km² (0.8%) of the near-shore habitat is good for unionids. Thus, the total area of predicted good habitat was similar between lakes, but the proportion of good habitat was greater in smaller Lake Ontario. For the Lake Erie localities from which the model was developed, model predictions (i.e., likelihood of occurrence or suitable habitat) were positively related to the number of species found (adj. $R^2 = 0.09$, $p = 0.007$) and the number of individuals within a survey site (adj. $R^2 = 0.08$, $p = 0.009$). In Lake Ontario, the relationships between model predictions and number of species and number of individuals were not significant. However, the number of individuals at sites < 500 m from areas the model predicted to be good (Fig. 2B–E) was greater (44.7 ± 13.9) than in areas farther from predicted good habitat (11.2 ± 3.9 ; Student's *t*-test, $p < 0.01$; Table 2).

We collected 1800 unionids representing 11 species across the 54 sites at 34 different locations in Lake Ontario (Table 3). These sites included open and cutoff bays, mouths of tributaries, and nearby wetlands, where the most dispersed and abundant species were *Pyganodon grandis* (65% of sampled locations), *Elliptio complanata* (47% of locations), and *Lampsilis radiata* (38% of locations) (Table 3). We combined specimens of *P. grandis* and *P. cataracta* and specimens of *L. radiata* and *Lampsilis siliquoidea* in species counts because of taxonomic ambiguity and poten-

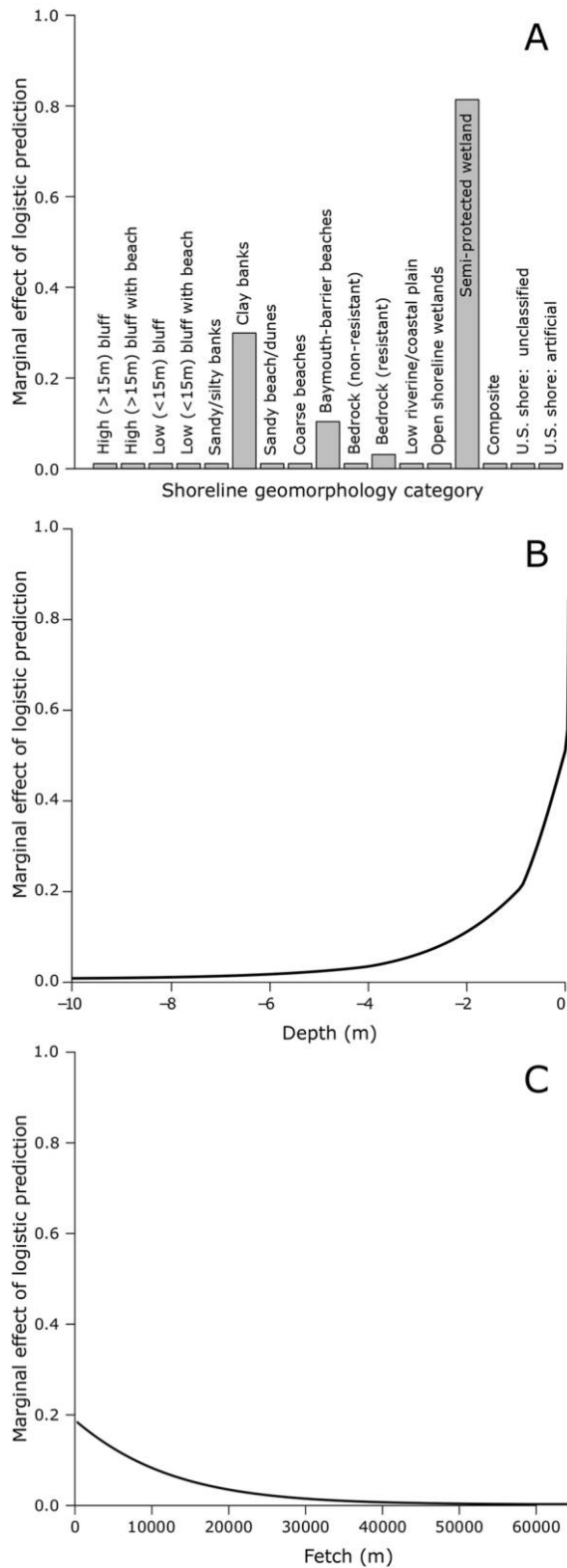


Figure 3. Marginal effect of shoreline geomorphology (A), depth (B), and fetch (C), the 3 predictor variables in the final MaxEnt model on the prediction of suitable habitat for unionid mussels in Lake Erie.

tial for hybridization in the Lake Ontario drainage (e.g., Kat 1986), but we did confirm their presence. The other 6 species were less abundant and were observed at only 2 to 9% of sites. The most species-rich refuges were in the eastern part of the lake. We identified 7 species in Black River Bay (site O33), and we found 239 live individuals belonging to 5 species during timed searches and an additional 71 mussels in quadrat searches in the mouth of Salmon River (site O25) where density was estimated at 4.7 ind/m².

More than 3700 individuals of 25 unionid species were documented in combined surveys of Lakes Ontario, St Clair, and Erie and the Detroit River (Appendix S1). Sites with live unionids had a significantly higher coverage of emergent (Mann–Whitney *U* test, $p = 0.017$) and submerged vegetation ($p = 0.002$), a larger proportion of silt substrates ($p = 0.009$), and deeper soft substrates ($p < 0.0001$) than other sites. Our best-fit model for the total number of live individuals (Table 4) included temperature, and % bedrock, boulder, clay, cobble, mud, and sand as important variables ($R^2 = 0.15$, $p < 0.01$). Location (either in Lakes St Clair/Erie or Ontario), submerged vegetation, temperature, and % mud best explained species richness ($R^2 = 0.12$, $p < 0.01$). The variables that explained 25% of the variance in the presence or absence of unionids at any particular site included % submerged and emergent macrophytes, dreissenid density, mean temperature, pH, and % gravel and mud ($R^2 = 0.25$, $p < 0.01$) (Table 4).

DISCUSSION

The MaxEnt model based on Lake Erie habitat successfully predicted the locations of extant mussel assemblages in Lake Ontario even though <1% of the near-shore areas of both lakes were predicted as good habitat. Our predictions were successful even though assemblages of Lakes Erie and Ontario were very different in the species present. Species richness in Lake Ontario ($n = 11$) currently is only ½ of that of refuges in Lakes Erie and St Clair (Zanatta et al. 2015), but all of these lakes once supported many more species than at present (Strayer and Jirka 1997, Graf 2002). The results, given so much change through time, suggest transferability of the model across species in the Unionidae (Wenger and Olden 2012). In support, models developed for individual species yielded predictions similar to those of our model based on assemblage composition (and therefore were not shown), and together they show how large-scale variables can be used in management to define lake habitat for unionid mussels broadly, whether in dreissenid-infested or dreissenid-free lakes. The ecological character of shore-zone ecosystems is set by the inputs of physical energy, the hydrologic regime, inputs of nutrients, the biota, geologic (or anthropogenic) structure of the shore and its environs, and the climate (reviewed in Strayer and Findlay 2010). Small-scale variables, such as sediment composition

Table 2. Names and codes for 34 locations in coastal areas of Lake Ontario with the number of 0.5-ha sites sampled at a location, mean (\pm SE for locations with multiple sites) number of unionids collected/site, species richness of each location (site[s]), and those sites <500 m from good habitat.

Location code	Location	County	No. sites	Unionids/site	SE	Richness	Sites <500 m from a location with model value \geq 0.4
O1	Niagara River	Niagara	1	4		1	0
O2	Four Mile Creek	Niagara	1	212		1	0
O3	Twelve Mile Creek	Niagara	1	22		4	0
O4	Roosevelt Beach	Niagara	1	0		0	0
O5	Eighteen Mile Creek	Niagara	1	82		2	1
O6	Golden Hill Creek	Niagara	1	12		1	0
O7	Golden Hill State Park	Niagara	1	0		0	0
O8	Johnson's Creek	Niagara	1	240		4	0
O9	Sandy Creek	Monroe	1	70		4	0
O10	Bush Creek	Monroe	1	0		0	0
O11	Braddock Bay	Monroe	2	22	14	3 (3,1)	1,1
O12	Cranberry Pond	Monroe	2	3	3	1 (0,1)	1,1
O13	Long Pond	Niagara	2	14	8	3 (2,3)	1,1
O14	Grandview Beach	Monroe	1	0	0	0	1
O15	Buck Pond	Monroe	1	6		1	1
O16	Crescent Beach	Monroe	1	0		0	1
O17	Round Pond	Monroe	1	12		1	1
O18	Eastman-Durham Park	Monroe	1	0		0	1
O19	Irondequoit Bay	Monroe	4	22	7.5	2 (1,1,2,1)	1,1,1,1
O20	Sodus Bay	Wayne	3	33	11.6	3 (2,2,2)	0,0,0
O21	Port Bay	Wayne	1	0		0 (0)	1
O22	Blind Sodus Bay	Wayne	3	26.7	14.0	3 (2,3,2)	1,1,1
O23	Fair Haven State Park	Wayne	2	62.8	55.2	3 (2,3)	1,1
O24	Selkirk State Park	Oswego	1	2		1	0
O25	Salmon River	Oswego	2	239	237	5 (1,5)	0,1
O26	South Sandy Pond	Oswego	1	176		2 (1)	1
O27	North Bay	Oswego	1	38		3 (1)	1
O28	North Pond	Oswego	2	302	144	4 (3,4)	1,1
O29	Lake View Pond	Jefferson	1	44		4	0
O30	El Durado Bay	Jefferson	2	10	10	3 (0,3)	1,1
O31	Association Island	Jefferson	1	0		0	0
O32	Henderson Bay	Jefferson	1	0		0	0
O33	Black River Bay	Jefferson	6	414.3	232.9	7 (4,5,3,0,5,0)	1,1,1,1,1,0
O34	Chaumonte Bay	Jefferson	4	0	0	0 (0,0,0,0)	0,1,1,1

and depth and vegetation, have been identified previously as indicative of refuges (Lucy et al. 2014). We expanded this list to include larger-scale variables—depth, fetch, and shoreline geomorphology. These variables also are good predictors for fishes (Chu et al. 2014). In general, more mussels were predicted at shallow depths and where fetch was short (Nichols and Wilcox 1997). Bathymetry and shore elevation control the input of physical energy to shoreline habitats. Therefore, they define substrate stability, sedi-

ment composition, grain size, nutrient and organic content, redox state, inputs of on- and off-site production of organic matter, intensity of predation, presence and zonation of vegetation, and consequently, unionid distributions (Gangloff and Feminella 2007, Strayer 2008, Strayer and Findlay 2010). Depth was the single-most important predictor of unionid habitat. In western Lake Erie and eastern Lake Ontario, shallow areas can have river-like conditions (Haag 2012), modulated by fetch and shoreline geomor-

Table 3. Total numbers of unionids collected/survey location, species richness (SR), Shannon diversity index (H'), and effective number of species ($e^{H'}$; Jost 2006) in Lake Ontario refuges surveyed in 2012. Ten locations where no mussels were found (Table 2) are excluded from this table.

Location	Refuge	<i>Elliptio complanata</i>	<i>Lampsilis radiata</i> + <i>siliquidea</i> ^a	<i>Pygandon grandis</i> + <i>cataracta</i> ^a	<i>Leptodea fragilis</i>	<i>Potamius alatus</i>	<i>Ligumia nasuta</i>	<i>Toxolasma parvum</i>	<i>Utterbackia imbecillis</i>	<i>Truncatella truncata</i>	Total	S_R	H'	$e^{H'}$
O1	Niagara River	2									2	1	0	1
O2	Four Mile Creek			53							53	1	0	1
O3	Twelve Mile Creek	2	1	6					2		11	4	1.17	3
O5	Eighteen Mile Creek		2	39							41	2	0.2	1
O6	Buck Pond			3							3	1	0	1
O8	Johnson's Creek	20	30	8		2					60	4	1.1	3
O9	Sandy Creek	21	11	2	1						35	4	0.94	3
O11	Braddock Bay	6	1	15							22	3	0.76	2
O12	Cranberry Pond			3							3	1	0	1
O13	Long Pond			2	11					1	14	3	0.66	2
O15	Golden Hills			3							3	1	0	1
O17	Round Pond			3							3	1	0	1
O19	Irondequoit Bay			41				3			44	2	0.25	1
O20	Sodus Bay	24	17	1							42	3	0.78	2
O22	Blind Sodus Bay	27	3	10							40	3	0.81	2
O23	Fair Haven State Park	6	25	33							64	3	0.93	3
O24	Selkirk State Park	1									1	1	0	1
O25	Salmon River	220	10	6(2)			3				239	4	0.37	1
O26	South Sandy Pond	79		9							88	2	0.33	1
O27	North Bay	7		12(1)							19	2	0.66	2
O28	North Pond	247	39	13			3				302	4	0.61	2
O29	Lake View Pond	6	8	8(5)							22	3	1.09	3
O30	El Durado Bay	5	4	1							10	3	0.94	3
O33	Black River Bay	486	159	7	5	15	6		1		679	7	0.8	2
	Total	1159	310	278	17	17	12	3	3	1	1800	9 ^a		

^a *Lampsilis radiata* and *siliquidea* cannot be clearly distinguished based on external morphology. Likewise, *P. cataracta* is difficult to differentiate from *P. grandis*. However, 8 *P. cataracta* were field-identified as noted by parentheses, so their numbers and possible hybrids may be greater than indicated.

Table 4. Model-averaged estimated coefficients (Est coef) and relative model importance (MI) for the variables included in regression models of the total number of individuals found live, total species richness, and the presence or absence of unionids by local-scale variable across sampling sites in Lakes Ontario, Erie, and St Clair. Model-averages were based on models with an Akaike's Information Criterion (AIC) value <2 AIC units of the best-fit model. Coefficients in bold were contained in the overall best-fit model. The multiple R^2 value for each best-fit model is in parentheses. * = $p < 0.1$, ** = < 0.05 . Blank indicates not significant.

Variables selected	Total alive ($R^2 = 0.15$)		Richness ($R^2 = 0.12$)		Presence/Absence ($R^2 = 0.25$)	
	Est Coef	MI	Est Coef	MI	Est Coef	MI
Intercept	-97.63**	1.00	-2.35	1.00	0.03	1.00
Depth maximum	-0.04	0.06	0.01	0.06	0.00	0.06
Depth minimum	-0.45	0.08			-0.01	0.10
Dressenid low			0.08	0.11	0.21**	1.00
Dressenid med			0.12	0.11	0.26**	1.00
Dressenid high			0.10	0.11	-0.05	1.00
Location	0.16	0.06	-0.86**	1.00	0.00	0.04
% bedrock	10.28**	1.00	0.02	0.08	0.01	0.13
% boulder	10.70**	1.00	0.00	0.06	0.00	0.05
% clay	3.76**	1.00	0.00	0.06	0.00	0.06
% cobble	4.63*	0.92			0.00	0.06
% gravel	-0.16	0.08	-0.02	0.12	-0.05**	1.00
% mud	4.33**	1.00	0.30**	1.00	0.04*	0.94
% organic	-0.40	0.09			0.00	0.05
% sand	6.30**	1.00	0.01	0.10	0.00	0.04
Macrophyte emergent	0.03	0.06	0.02	0.11	0.09**	1.00
Macrophyte submerged	0.29	0.13	0.29**	1.00	0.03*	0.82
Mean pH	0.47	0.08	-0.02	0.08	-0.11*	0.88
Mean temperature	2.79**	1.00	0.12**	1.00	0.05**	1.00
Threats	-0.40	0.11	-0.01	0.07	0.00	0.05

phology, that influence sediment supply. Energy extremes can reduce species richness, and a 'Goldilocks zone' may exist between areas where energy is too high and leads to bed scouring and armoring and areas where energy is too low and fine sediment over-accumulates (Dila and Biddanda 2015).

Peak wave heights offshore and peak wave energy impinging on shoreline are directly related to fetch (Denny 1988). Therefore, fetch was one of the most important larger-scale variables in our model of unionid refuges. Fetch also strongly influences grain size and stability of shore sediment and the presence of vegetation, all of which affect habitat structure (Gangloff and Feminella 2007, Newton et al. 2008, Zigler et al. 2008, Daraio et al. 2010). The distribution of unionid mussels in small inland lakes is strongly influenced by fetch (Cyr 2009) and, in coastal wetlands in Lake Huron, abundances of insects were higher and abundances of crustaceans and gastropods were lower in regions with longer fetch than in other regions (Cooper et al. 2014). The sinuosity (or curvature) of the shoreline can influence fluvial processes by creating breaks in fetch and, therefore, may structure littoral freshwater mussel assemblages (Harris et al. 2011). For example, in Sandusky Bay of Lake Erie, 2 oppo-

site rip-rap-hardened points create a channel through which fetch is unimpeded. Unionid assemblages appear to be restricted to a narrow band along the leeward sides of each point, where heterogeneous substrates accumulate as a response to the interactive effects of depth, fetch, and sinuosity.

Shoreline geomorphology and the distance to different wetland types composed a 2nd set of factors that affected unionid presence. Shoreline geomorphology determines a gradient of shores from reflective (e.g., vertical seawalls that reflect nearly all incident wave energy), to dissipative (e.g., gently sloping beaches that dissipate nearly all incident wave energy). Species richness, abundance and biomass of aquatic macroinvertebrates, and biological interactions increase with the ability of the shore zone to dissipate wave energy, and ecological processes increase from dissipative and ultradissipative shores to tidal flats (Defeo and McLachlan 2005, Strayer and Findlay 2010). By providing protection from strong physical forces, dissipative shallow shores allow establishment of emerged and submerged macrophytes that further absorb wave energy, reduce near-bed shear stress, stabilize shores and flow patterns, and increase local sediment deposition. Unionid abundance and species diversity were

positively related to coverage of emerged and submerged macrophytes across our studied lakes.

Not all shore geomorphological classification types occur in both Lakes Erie and Ontario, so geomorphic categorizations may have to be modified for applicability to mussels (McKenna and Castiglione 2010, Chu et al. 2014). Nevertheless, these large-scale descriptors still provided predictive power. Unionids were found more often in deep soft substrates and where vegetation coverage was greater, e.g., in the large marshy bay formed by the Black River in eastern Lake Ontario and in the western basin of Lake Erie (Zanatta et al. 2015). These habitats can be described as dissipative or ultradissipative shores with vegetation or in short, semi-protected wetlands. Our model predicted that a combination of shallow dissipative shores with abundant vegetation, i.e., sites categorized as semi-protected wetland, was associated with a higher probability of suitable habitat for unionid mussels. Semi-protected wetlands occur in areas protected by natural barriers, which may reduce dreissenid colonization or create conditions appropriate for ideal sediment composition. Among the lakes in our study, Lake Erie has the highest concentration of coastal marshes (Herdendorf 1992). In this lake, unionids occurred in Muddy Creek Bay, Toussaint Creek, and 5 sites at Presque Isle, all of which are close to semi-protected wetlands. Lake Ontario possesses less shoreline categorized as semi-protected wetland, but the site with the 2nd-highest unionid densities was in an area classified as open shoreline wetland. The other 2 sites with high densities (>200 ind/ha) were categorized as sandy beach/dunes.

Hydrological regime, or the pattern of change in water level over time, strongly influences the composition and activities of the shore-zone biota because it controls many aspects of ecosystem function (Strayer and Findlay 2010) and the shore-zone vegetation (Keddy and Reznicek 1986, Hill et al. 1998). Irregular fluctuations in water level can inhibit establishment of stable populations of dreissenids and can prevent colonization of unionids by dreissenids (Nichols and Wilcox 1997, Karatayev et al. 1998, Bowers and de Szalay 2004, 2005, Sherman et al. 2013). Nevertheless, positive associations between unionid and dreissenid presence are observed (Burlakova et al. 2014), perhaps because where physical forces or other factors extirpate unionids, they also extirpate dreissenids (Nichols and Wilcox 1997, Karatayev et al. 1998, Sherman et al. 2013). We cannot be sure that unionid communities have now equilibrated to the dreissenid invasions, but the number of unionids infested with *Dreissena* has declined dramatically, especially in lakes dominated by *Dreissena r. bugensis* (Burlakova et al. 2014), and some unionid communities in Lake St Clair and western Lake Erie appear to be stable or increasing in densities (Crail et al. 2011, Zanatta et al. 2015).

In Lake Ontario, large declines in species richness were recorded by the 2nd half of the 20th century. The 17 species documented in the Lake Ontario drainage before the 1960s

fell to 11 before the dreissenid invasion (Strayer and Jirka 1997). In this same period, 1/3 of the 33 species present in the St Clair and Lake Erie drainages (Metcalf-Smith et al. 1998) were lost (Zanatta et al. 2015), although the loss was less severe in shallow Lake St Clair (Zanatta et al. 2015). Moreover, the relative abundance of individual species is changing. In Lake Ontario, *E. complanata* was found at almost 1/2 of all locations and made up 64% of all mussels recorded in the survey. Along with its much more common western counterpart, *Elliptio dilatata*, this species appears to be gone from Lake Erie today (Graf 2002). *Lampsilis radiata*, also historically more prevalent in Lake Ontario than its western counterpart, *L. siliquoidea* (Strayer and Jirka 1997), remains abundant and was found at 38% of Lake Ontario locations, whereas *L. siliquoidea* fell from a relative abundance of 60% to <1% in Lake Erie (Zanatta et al. 2015).

The relative abundance of another species in the near-shore mussel assemblages of Lake Erie, *Quadrula quadrula*, has increased, and its distribution in Lake Erie may have expanded in the last few decades (Zanatta et al. 2015). We did not find *Q. quadrula* in our surveys of southern Lake Ontario, but recently it was discovered in abundance in a few coastal embayments and drowned river mouths in western Lake Ontario in Canada (Hoffman et al. 2018). This discovery brings total diversity in the lake to 12 species. A 2nd common species, *P. grandis*, and possible *P. cataracta* hybrids, were present in 16% of the sites sampled in the lower Great Lakes between 1860 and 1960, 45% of sites after 1960 (Metcalf-Smith et al. 1998), 38% of sites sampled in Lakes Erie and St Clair in 2011–2012 (Zanatta et al. 2015), and 64% of sites in Lake Ontario in 2012. These results correspond to its increased relative abundance across the lower Great Lakes (Metcalf-Smith et al. 1998). *Leptodea fragilis* also may be expanding back into the Great Lakes (Bryan et al. 2013, Krebs et al. 2015) and may begin to increase in Lake Ontario.

We did not include host fish in our model. Host-fish distribution is an important dimension of the fundamental niche for freshwater mussels (Haag and Warren 1998) and could be incorporated in future models of lakeshore habitat. In rivers, watershed size is correlated with species richness of fishes and mussels (Bauer et al. 1991, Watters 1992), but relationships in richness between the 2 groups tends to disappear after accounting for area effects (Rashleigh 2008, Krebs et al. 2010) or habitat variation (Inoue et al. 2017). Instead, fish and unionid assemblages may respond independently to the same habitat variables, suggesting that simple models might be transferable between assemblages (Wenger and Olden 2012).

Conclusion

Our habitat model identified large- and small-scale habitat variables that appear to define refuges despite differences in taxonomic composition among mussel assemblages

in these lakes. Depth was the most important predictor and together with fetch and shoreline geomorphology enabled us to predict a high likelihood of finding patches of unionids and small-scale factors like stable substrate (deep, silty sediments) and vegetation. These sites were protected areas with shorter fetch, smaller slope, shallower depth, and higher shoreline sinuosity, which combined as semi-protected wetlands to allow accumulation of organic matter.

Application of this model to Lake Ontario enabled us to discover large assemblages of threatened native unionid species. Dreissenids continue to spread in North America and Europe, and a similar byssate bivalve, *Limnoperna fortunei*, currently spreading in South America (Boltovskoy and Correa 2015), is predicted to invade freshwaters in the near future. Fine-tuning models on a variety of water bodies across continents will aid in defining habitats that can protect native unionid species prior to or after invasion.

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