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Geographic information system (GIS) analysis of ecosystem invasion: Exotic mussels in Lake Erie

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Abstract

Geographic information system (GIS) analysis with bathymetric, substrate, and side scan sonar (SSS) data was used to assess both spatial and temporal expansion of exotic dreissenid mussels onto sedimentary habitats in Lake Erie. These data were used for developing multiple regression models with substrate types and SSS data to interpret the expansion of *Dreissena* assemblages across the central and western basins of Lake Erie from 1994 to 1998. The 1994–1996 GIS model predicted the 1997 SSS measurements of *Dreissena* coverage correctly in 84% of the cases ($n = 50$). Similarly, the 1994–1997 GIS model predicted the 1998 SSS measurements of *Dreissena* coverage correctly in 80% of the cases ($n = 20$). These models indicated that *Dreissena* coverage ranged from $<1\%$ on muds in 1994 to 67% on sands and gravels in 1997. Based on all of the substrates, the 1994–1997 model indicates that *Dreissena* beds have been expanding since 1994 at $1{,}000 \pm 6$ km^2 yr^{-1} and presently occupy $5{,}484 \pm 32$ km^2 of the 25,734 km^2 sedimentary bottom of Lake Erie. Our observations indicate that expanding *Dreissena* beds are altering soft-substrate habitats and influencing the ecosystem dynamics throughout Lake Erie. Furthermore, this study demonstrates that the distribution, abundance, and ecosystem impacts of invasive species in other watersheds can be accurately described and interpreted over diverse spatial and temporal scales using GIS models.

Invasion by nonindigenous species has been one of the most damaging anthropogenic impacts in ecosystems (Elton 1958). These invaders have ecological effects worldwide, many of which are poorly known (Vitousek 1986). Invasive, introduced species have been defined as ‘‘successfully reproducing organisms transported by humans into regions where they did not previously exist’’ (Mills et al. 1993) with their success dependant upon survival in unfavorable conditions, adaptability to new environments, high reproductive capacity, and the ability to disperse. Successful exotics often readily exploit their new habitat and outcompete native species. Populations can increase explosively and, once established, are rarely eliminated from the invaded ecosystem. These factors, which describe the general nature of species invasions, lead to problems assessing how exotic species invade and impact ecosystems.

Invading species have impacted Lake Erie since the beginning of the twentieth century. One of the most well-studied species introductions, the zebra mussel (*Dreissena polymorpha*), was discovered in Lake St. Clair in 1988 (Herbert et al. 1989; Griffiths et al. 1991). *Dreissena polymorpha* is well known to inhabit hard substrates (Dermott et al. 1993), although there have been coincidental observations on sedimentary habitats usually explained in relation to hard substrate nuclei. Shortly after the zebra mussel invasion from the Caspian Sea region of Europe, its congener the quagga mussel (*Dreissena bugensis*) was also introduced to the Great Lakes (May and Marsden 1992; Spidle et al. 1994). *Dreissena bugensis* typically occurs on soft substrates in colder, deeper water than *D. polymorpha* (Mills et al. 1996).

Following *Dreissena*’s initial introduction into Lake Erie, populations on hard substrates grew explosively, with mussel densities approaching 30,000 m^{-2} on all hard surfaces (Griffiths et al. 1991) with maximum mussel densities exceeding 300,000 m^{-2} (Leach 1993). The mussels’ success on hard substrates led to significant economic and ecological impacts, for example, fouling of water intakes (Mackie 1991; Herbert et al. 1991) and displacement of natural benthic populations (Mackie 1991). During the initial colonization of Lake Erie, Bij de Vaate (1991) concluded that solid substrates would ultimately limit the distribution and density of the mussels in Lake Erie.

Previous studies have identified the occurrence of both *D. bugensis* and *D. polymorpha* on soft substrates in Lake Erie (Dermott and Munawar 1993). Studies using remotely operated vehicles (ROVs) and SCUBA have documented invading mussel assemblages directly colonizing sand, silt, and clay substrates (Coakley et al. 1997; Berkman et al. 1998). This colonization of sedimentary habitats by dreissenid mussels raises new concerns regarding ecosystem impacts in Lake Erie, where 85% of the lake bottom is composed of

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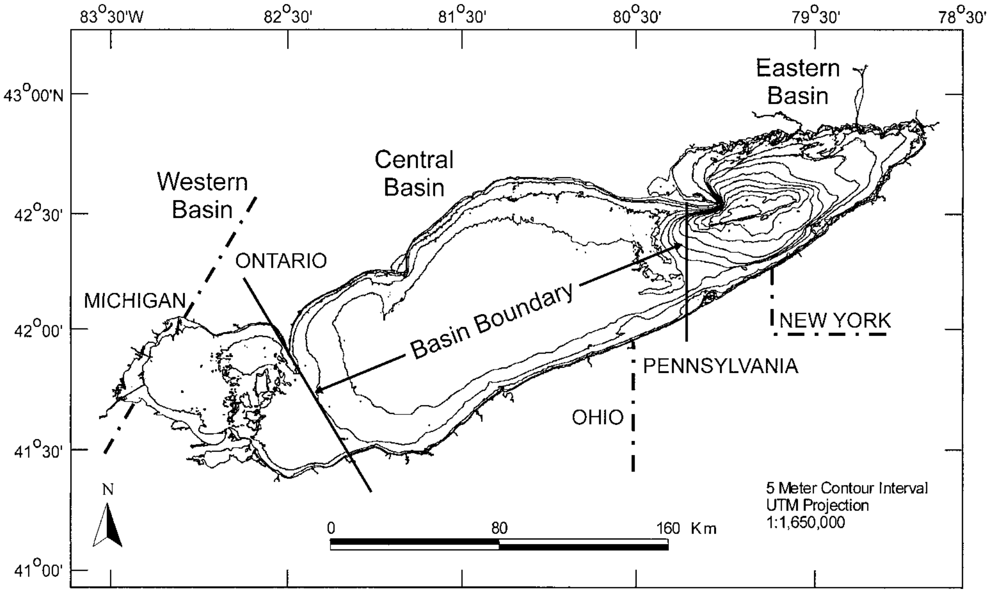

Fig. 1. Lake Erie bathymetry.

soft substrates (Lewis 1966; Bolsenga and Herdendorf 1993; Haltuch 1998). A single 200 km transect surveyed by side scan sonar (SSS) in 1995 provided an estimate that *Dreissena* assemblages covered 2.5–14% of soft sediments in Lake Erie (Berkman et al. 1998). These preliminary studies indicated that Lake Erie sediments are being transformed and benthic habitats modified by mussel beds covering hundreds to thousands of square kilometers. Future analysis of ecosystem variability would benefit from the incorporation of *Dreissena* distribution and abundance information that is more closely linked to soft substrates and the offshore regions in Lake Erie (Madenjian et al. 1998). The purpose of this study is to create a geospatial framework for assessing the ecosystem impacts associated with the rapidly expanding mussel populations across the soft-substrate habitats in Lake Erie, in areas that traditionally have been assessed solely in relation to their sedimentary characteristics without invading mussel beds.

Materials and Methods

Study area—Shallowest of the Laurentian Great Lakes, Lake Erie is divided into three basins (Fig. 1). In this study the western basin was defined as lying west of a line from Point Pelee, Ontario to Lorain, Ohio, an area that encompasses the Sandusky sub-basin. The central basin was defined as extending east of a line between Point Pelee, Ontario and Lorain, Ohio to a north–south line midway between the Ohio–Pennsylvania state line and Erie, Pennsylvania. The eastern basin, which was not investigated in this study, was defined as that portion of Lake Erie east of Erie, Pennsylvania.

Geographic information system analysis—The ongoing expansion of dreissenid mussels in Lake Erie was studied by incorporating bathymetry, sediment types, and SSS surveys into a geographic information system (GIS) (Table 1). GIS approaches have been widely used in ecological modeling applications (e.g., Bian and West 1997) and are appropriate for interpreting the expansion of nonindigenous species, such as *Dreissena* in Lake Erie. In addition, hypsometric and substrate distribution data for Lake Erie were derived from the GIS database.

ARC/INFO was used to manipulate the GIS data, to correct topology errors, and to generate polygon data (ESRI 1994). All data were converted to the Universal Transverse Mercator projection (zone 17, Clarke 1866 spheroid, and NAD 27) to facilitate overlay of sediment distributions, depth contours, and SSS sites. Subsequent query in ArcView allowed sediment distributions to be characterized by depth for each basin and SSS site distance from shore to be measured.

The first GIS layer, Lake Erie bathymetry at 1-m contour intervals, was obtained through the National Oceanic and Atmospheric Administration (NOAA) Geophysical Data Center, Boulder, Colorado (Fig. 1; Table 1). Bathymetric contours on the United States side of the lake were compiled at a 1 : 100,000 scale from digital NOAA National Ocean Service hydrographic soundings. Contours on the Canadian side of Lake Erie were compiled at scales ranging 1 : 2,500 to 1 : 50,000 from Canadian Hydrographic Service analog sounding sheets. Bathymetric data were received from NOAA as digital line data in the ARC/INFO format and were subsequently converted to polygon data (Haltuch 1998). Hypsometry data were derived from the new polygon database using standard query commands in ArcView.

The second GIS layer, composition of Lake Erie substrates, was available as digital data in the ARC/INFO format from the Environment Canada, Burlington, Ontario (Fig. 2; Table 1). Substrates were categorized as mud, sand/mud, sand/gravel, glacial till, and bedrock following Wentworth's particle size classification. The following grain sizes corre-

Table 1. Sources of data used to create the Lake Erie *Dreissena* models.

Data set	Organization	Contact
Bathymetry	Courtesy of the Great Lakes Bathymetry Project, a joint effort of the U.S. National Oceanic and Atmospheric Administration's National Geophysical Data Center and Great Lakes Environmental Research Laboratory; and the Canadian Hydrographic Service. Boulder, Colorado.*	Troy L. Holcombe
Substrates	Courtesy of the Aquatic Ecosystem Restoration Branch, National Water Institute, Canada Centre for Inland Waters, Environment Canada. Burlington, Ontario.	John P. Coakley
1994 side scan sonar	Courtesy of the United States Geological Survey. Ann Arbor, Michigan.	Greg Kennedy
1995 side scan sonar	Courtesy of the United States Geological Survey. Ann Arbor, Michigan.	Greg Kennedy
1996 side scan sonar	Courtesy of the United States Geological Survey. Ann Arbor, Michigan.	Greg Kennedy
1997 side scan sonar	Courtesy of the Ohio Geological Survey. Sandusky, Ohio.	Jonathan Fuller
1998 side scan sonar	Courtesty of the United States Geological Survey. Ann Arbor, Michigan.	Greg Kennedy

* For more information visit the NOAA/NGDC web site: http://www.ngdc.noaa.gov/mgg/.

spond to each sediment class: mud <0.063 mm, sand 0.063–2 mm, gravel 2–256 mm, and glacial till 0.004–256 mm. Lake Erie till is composed of material of all sizes, with clay predominating along with rock fragments reflecting the bedrock of the vicinity. Central and eastern basin sediment types were identified from Lewis (1966) and western basin sediments from Rasul et al. (1997). Substrate data were digitized by the Environment Canada Geomatics unit at a scale of 1 : 50,000 and were received as two polygon layers. Substrate classes in the western basin coverage were modified to match those from the central and eastern basin coverage (Haltuch 1998). Profiles of substrate distributions throughout Lake Erie were derived using standard query commands in ArcView.

Side scan sonar and image analysis—Estimates of the percent coverage of *Dreissena* on soft substrates in Lake Erie were derived from SSS surveys (Table 1) using methodology from Berkman et al. (1998). The SSS system consisted of a towfish, tow cable, processing and display device, and a global positioning system (GPS) (Phaneuf 1997). Acoustic pulses sent out from the towfish are backscattered weakly by soft sediments and strongly by hard substrates (Edsall et al. 1997). Sonar operating at a frequency of 100 kHz is able to resolve particles to 15 mm, serving as a useful proxy for distinguishing coarser sediments from finer sediments (Ryan and Flood 1996). Loran C, with errors <1 km, provided georeferencing for the 1994 SSS cruises, and a Trimble Navigation GPS receiver (errors <30 m) was used for all other years.

Study areas in Lake Erie were distributed throughout the western basin and along the Ohio shoreline of the central basin (Fig. 3; Table 2). SSS surveys were conducted along transects, parallel and perpendicular to shore, throughout the western and central basins from 1994 to 1998. Four areas were surveyed in multiple years to determine temporal trends in *Dreissena* coverage on Lake Erie sediments (Table 2).

SSS lines covered an area with extensive historical sediment sampling, which was used as preground truth data for interpretation of backscatter patterns. When areas of known sediment characteristics were surveyed, hard reflectors over soft substrates were randomly verified as *Dreissena* populations using SCUBA as well as ROV and towed-video cameras (Berkman et al. 1998, 2000). From 1994 to 1998 an average of 11.7 ± 8.9 min of ground truth video per each kilometer of SSS survey ($n = 21$) was collected at a boat speed of 1.5 knots. Independent ROV surveys conducted in the 1990s support the interpretation that hard reflectors over known soft substrates represent dreissenid mussels (McQuest Marine Sciences 1991; Coakley et al. 1997)

Two hundred sections of SSS records were randomly selected from surveys conducted 1994–1997, 50 from each year (Fig. 3; Table 2). Twenty sections of SSS records were selected randomly from the 1998 cruise (Fig. 3; Table 2). Each section of hard copy sonograph, 20 cm by 28 cm, ranging in area from 0.03 km^2 to 0.1 km^2, was scanned into a computer. Percent cover of hard reflectors, determined to be *Dreissena* on soft substrates was quantified using thresholding methods with ERDAS Imagine software (Fig. 4) (ERDAS 1991; Haltuch 1998). Validity of this thresholding technique was confirmed by independent image analyses with ERDAS Imagine and NIH Image algorithms that generated the same spatial coverage results (Berkman et al. 1998).

Statistical analysis and modeling—Multiple regression analysis of ecosystem data (depth, substrate type, survey year, and SSS) were used to predict percent cover of *Dreissena*. Variance of the response variable (percent cover of *Dreissena*) was normalized using the arcsine square root transformation, a method used for percentage data. Substrate types were treated as categorical variables with all other independent variables being continuous.

Dreissena coverage predictions were generated from two regression models, constructed with 1994–1996 and 1994–1997 data, which were tested with subsequent SSS measurements from 1997 and 1998, respectively. The 1994–

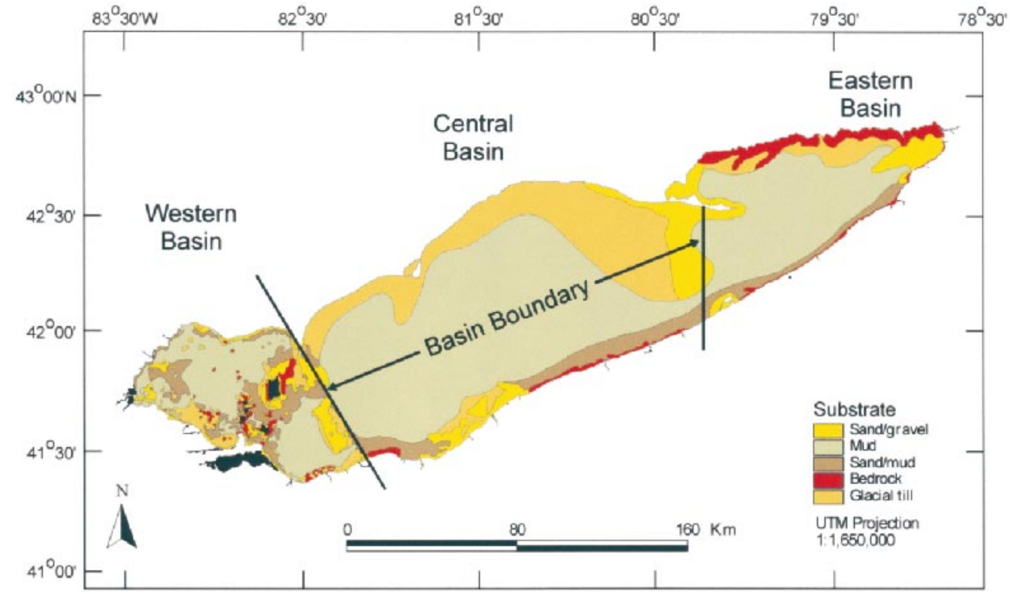

Fig. 2. Lake Erie substrate types.

1997 model was then used to predict *Dreissena* percent cover through the year 2000. All of the model results were generated as new layers in the GIS database to produce digital maps of *Dreissena* coverage over time. Linear and log-linear regressions of *Dreissena* coverage versus time were compared to interpret the expansion profile of the invading mussel assemblages across the soft substrates in Lake Erie.

Results

GIS analysis—GIS analysis of Lake Erie bathymetry revealed that the western, central, and eastern basins, respectively, had areas of 4,837 km^2, 15,061 km^2, and 5,836 km^2, yielding a total area for the Lake Erie ecosystem of 25,734 km^2 (Fig. 5). Maximum depths for each basin were 21, 39,

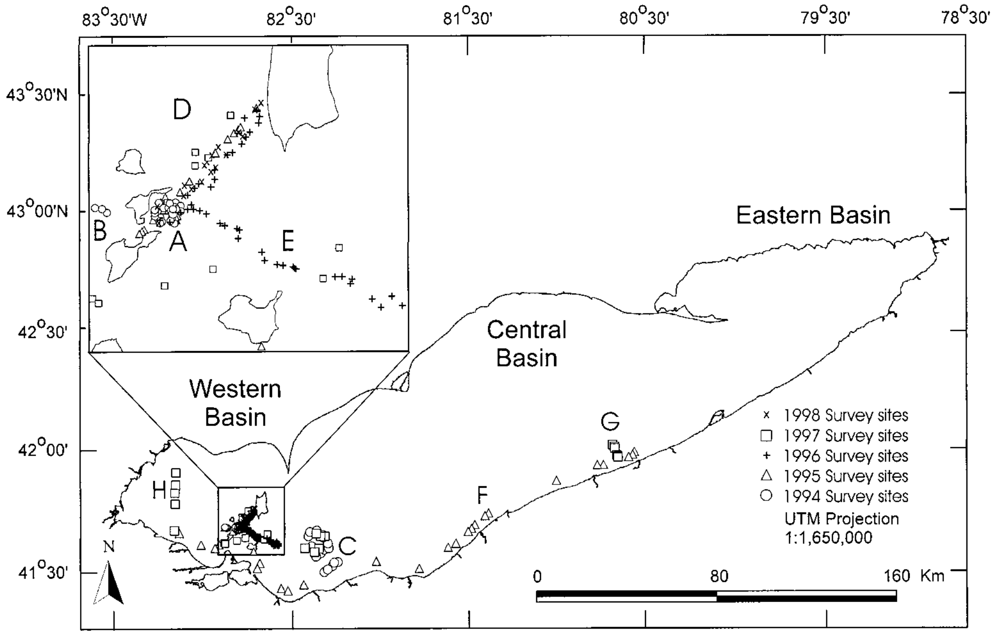

Fig. 3. Side scan sonar survey sites in the western and central basins of Lake Erie for 1994–1998. Each point represents an area of 0.032 km^2 to 0.101 km^2 where side scan sonar was analyzed to derive percent cover of *Dreissena.* Survey sites all lie within 2–21-m depth and cover all substrates. Survey zones A to H correspond to map locations in Table 2.

Table 2. Regions within the western and central basins of Lake Erie surveyed for mussels with side scan sonar from 1994 to 1998.

Survey region	Map location*	Number of images analyzed				
		1994	1995	1996	1997	1998
Ballast Island	A	16	9	8		
Rattlesnake Island	B	3				
Lorain–Vermilion morain	C	31			12	
Ballast Island to Pelee Island	D		16	20	4	20
South Bass Island to Kelley's Island	E			22	6	
Pennsylvania–Ohio State Line to Little Cedar Point	F		25			
Offshore from Ashtabula Harbor	G				23	
Offshore from Magee Marsh	H				5	

* *See Fig. 2.*

and 64 m for the western, central, and eastern basins respectively. Sediment distributions for the western, central, and eastern basins, respectively, were mud (51%, 61%, 60%), mud/sand (19%, 6%, 6%), sand/gravel (14%, 7%, 13%), glacial sediments (12%, 25%, 9%), and bedrock (4%, 1%, 12%) (Fig. 6). The distribution of sediment types at different depths in each basin was revealed by overlaying the bathymetry and sediment GIS layers (Figs. 1 and 2).

Figure 5 shows that the western, central, and eastern basins represent 18.8%, 58.5%, and 22.7% of the lake area, respectively. Data on substrate types across the lake indicated that mud was the most prevalent substrate and bedrock the least (Fig. 6). Across the whole lake, sand and gravel were the most common substrates in the 1- to 3-m depth zone, whereas either muds or glacial till dominated benthic habitats in the deeper regions (Fig. 7).

Owing to the two different data sources, National Oceanic and Atmospheric Administration and Environment Canada (Table 1), the scale of the bathymetry–sediment map produced was 1 : 100,000. Polygon errors due to differences in the shoreline profiles of the bathymetry and sediment layers covered 62 km^2, with discrepancies falling in the 0 to 10-m

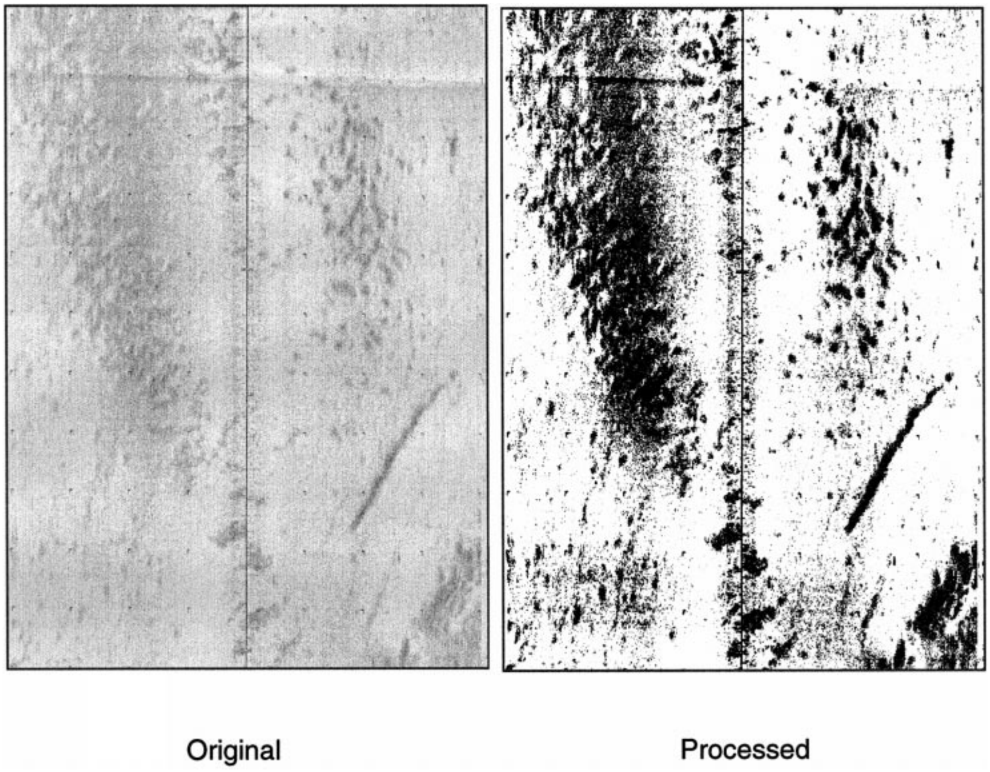
Original
Processed

Fig. 4. Side scan sonar images from the 1998 Ballast Island to Pelee Island transect (*see Fig. 3*). The central line in each image represents the boat path. Compare the original image to the one processed using ERDAS Imagine. In the processed image, a thresholding function has been used to determine the optimum gray shade of 256, it then classified pixels as either black or white depending upon which side of the threshold they fall. Black pixels represent hard reflectors (*Dreissena*) larger than 15 mm (Ryan and Flood 1996), whereas white pixels represent soft substrates.

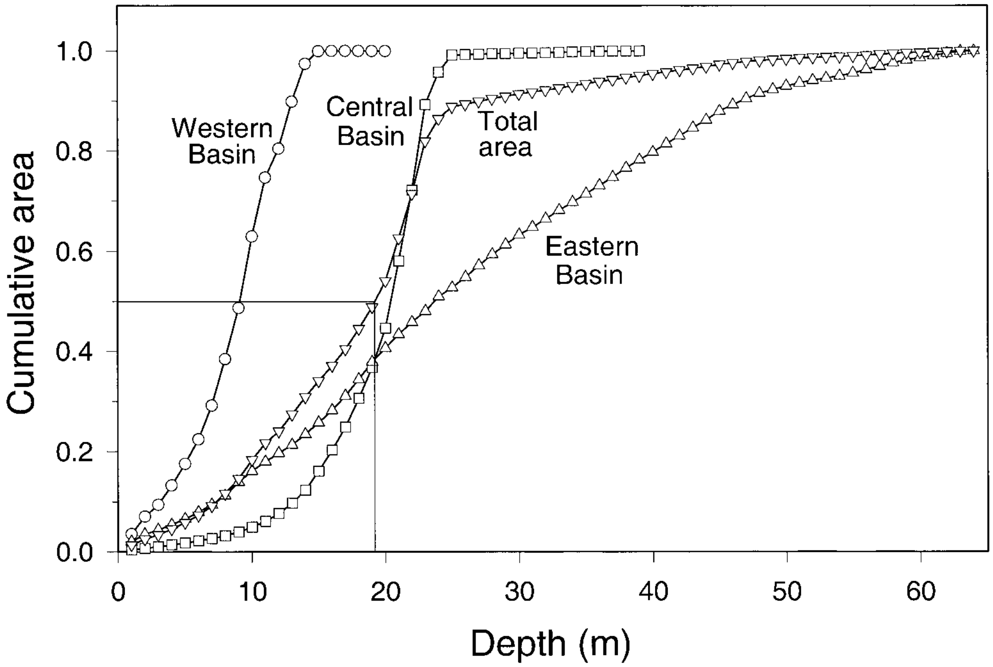

Fig. 5. Lake Erie percentage hypsometric curve broken down by basin and the whole lake. The box drawn in the graph shows that 50% of the total lake area is located at depths ≥19 m. Data were derived from the modified bathymetry coverage using standard spatial query commands in ArcView. This map was in the polygon format to facilitate spatial query.

range. Owing to these different shorelines, the area of the lake derived from the sediment layer was less than that of the bathymetry layer and analysis of substrates by depth was limited to the sediment layer area. Maps of *Dreissena* model estimates are reliable for spatial analysis at a scale of 1 : 50,000.

Regression models—The 1994–1996 regression model was significant, explaining 58% of the variability in *Dreissena* coverage (Table 3, Eq. 1a). Among the variables, however, only year, mud, sand/mud, sand/gravel, and bedrock were significant contributors to the estimation of *Dreissena* percent cover (Table 3, Eq. 1a). Insignificant variables were

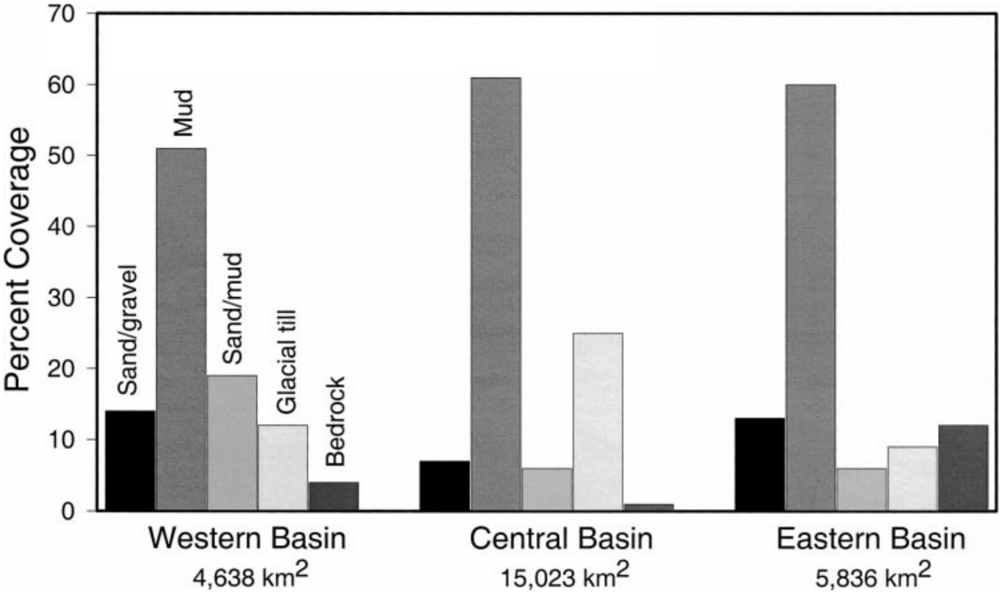

Fig. 6. Distribution of Lake Erie substrates for each basin and the whole lake that was acquired using standard spatial query commands in ArcView geographic information system (GIS).

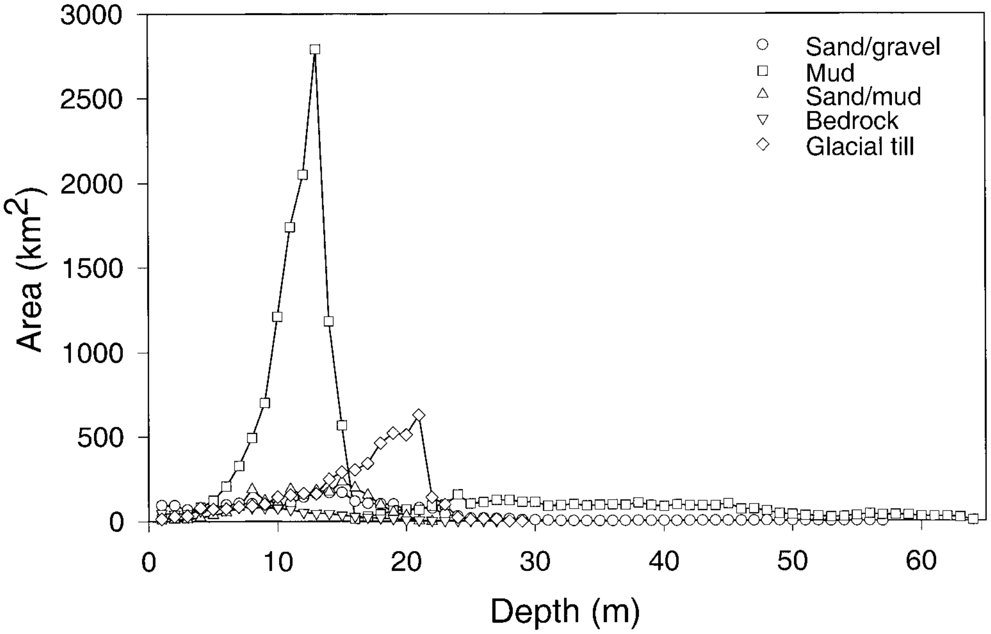

Fig. 7. Areal profiles of Lake Erie substrates by depth range for the whole lake that were acquired by overlaying the polygon format bathymetry with substrates.

omitted from the original model (Table 3, Eq. 1a), with the exception of glacial till, which was an essential sediment category (Table 3, Eq. 1b). Variables in the 1994–1997 models showed similar results to those in the 1994–1996 models (Table 4, Eqs. 2a and 2b). The 1994–1997 reduced model accounted for 56% of the variability (Table 4, Eq. 2b). Residual plots of the models fit the data well, with fitted values showing no trends. Given that substrate types were modeled as categorical variables, and regression modeling omits one category, in this case bedrock; Tables 3 and 4 do not have coefficients for bedrock. The case in which the coefficient for each substrate listed in Tables 3 and 4 is zero represents the predicted value for the omitted bedrock category.

Model tests and trends—Comparison between the 1997 predictions of *Dreissena* coverage (Table 3, Eq. 1b) and observed 1997 SSS measurements were in agreement 84% of the time for bedrock and 93% of the time for all other sub-

Table 3. 1994–1996 regression models from the geographic information system (GIS) analysis of Lake Erie.

				Regression ANOVA		
Predictor	SS	*T*	*P*	*DF*	*F*	*P*
1994–1996 full model						
Constant	33.58	−4.86	0.000			
Depth	0.005	−0.52	0.602	142	28.05	0.000
Distance	0.000	−0.14	0.891	*R* squared = 58%		
Year	0.168	4.87	0.000			
Sand/gravel	0.049	3.18	0.002			
Mud	0.053	−5.69	0.000			
Sand/mud	0.039	−6.01	0.000			
Glacial till	0.058	−1.11	0.270			
Equation 1a: Arcsine square root (percent coverage of *Dreissena*) = −163 + 0.0000 distance − 0.0028 depth + 0.0820 year + 0.157 sand/gravel − 0.304 mud − 0.236 sand/mud − 0.0642 glacial till						
1994–1996 reduced model						
Constant	30.91	−5.39	0.000			
Year	0.015	5.40	0.000	144	39.62	0.000
Sand/gravel	0.042	3.38	0.001	*R* squared = 58%		
Mud	0.048	−6.71	0.000			
Sand/mud	0.037	−6.59	0.000			
Glacial till	0.050	−1.61	0.111			
Equation 1b: Arcsine square root (percent coverage of *Dreissena*) = −167 + 0.0837 year + 0.142 sand/gravel − 0.319 mud − 0.243 sand/mud − 0.0806 glacial till						

Table 4. 1994–1997 regression models from the geographic information system (GIS) analysis of Lake Erie.

				Regression ANOVA		
Predictor	SS	*T*	*P*	*DF*	*F*	*P*
1994–1997 full model						
Constant	20.13	−8.41	0.000			
Depth	0.000	0.87	0.383	192	35.96	0.000
Distance	0.003	−1.91	0.058	*R* squared = 57%		
Year	0.010	8.44	0.000			
Sand/gravel	0.046	3.09	0.002			
Mud	0.045	−5.67	0.000			
Sand/mud	0.037	−6.24	0.000			
Glacial till	0.053	−1.40	0.164			
Equation 2a: Arcsine square root (percent coverage of *Dreissena*) = −169 + 0.000 distance − 0.006 depth + 0.085 year + 0.143 sand/gravel − 0.260 mud − 0.235 sand/mud − 0.074 glacial till						
1994–1997 reduced model						
Constant	19.68	−8.29	0.000			
Year	0.009	8.31	0.000	194	49.20	0.000
Sand/gravel	0.040	3.34	0.001	*R* squared = 56%		
Mud	0.042	−6.79	0.000			
Sand/mud	0.036	−7.05	0.000			
Glacial till	0.045	−1.82	0.070			
Equation 2b: Arcsine square root (percent coverage of *Dreissena*) = −163 + 0.082 year + 0.134 sand/gravel − 0.285 mud − 0.255 sand/mud − 0.0836 glacial till						

strates (Table 5). The 1998 predictions of *Dreissena* coverage (Table 4, Eq. 2b) were in agreement with the 1998 SSS measurements 80% of the time for sand/gravel and 98% of the time for sand/mud and bedrock (Table 6).

Western and central basin *Dreissena* coverage increased annually in a linear fashion from 704 to 2,993 km^2 during 1994–1997 (Fig. 8). Linear regression ($F = 124.78$, $p < 0.008$, $DF = 3$, $R^2 = 98\%$) and log-linear regression ($F = 339.35$, $p < 0.003$, $DF = 3$, $R^2 = 99\%$) of the area colonized by *Dreissena* over time were both significant and fitted the data equally well. Based on a linear fit, the average annual increase in the spatial coverage of *Dreissena* between 1994 and 1997 was 1,000 ± 6 km^2 yr^{-1}.

CD-ROM—A CD-ROM consisting of GIS layers, SSS images (.tiff files), and basic spatial analysis of the GIS layers has been created for distribution (*see* http://www.sg.ohio-state.edu). The following GIS layers are included: polygon bathymetry, sediment types, bathymetry-sediment overlay, and percent coverage *Dreissena*-bathymetry-sediment overlay. Side scan sonar images are the scanned originals from 1994 to 1998. Basic spatial analyses are contained in Excel spreadsheet files for the bathymetry, sediment types, and bathymetry-sediment overlays.

Discussion

The GIS approach to assessing invasive species population dynamics across an ecosystem is a powerful tool that incorporates all habitat types, thus providing a framework for ecosystem modeling and predicting changes over spatial and temporal scales. In this study the two principle benthic habitat features forming the basis for the GIS model were bathymetry and substrate distributions, which we determined to be the likely source for most of the variation in the distribution of *Dreissena* in Lake Erie (Dermott et al. 1993; Dermott and Munawar 1993; Mills et al. 1996; Berkman et al. 1998). Lake Erie hypsometric data from this study (Fig. 5) were comparable to prior studies (Gatewood and Herdendorf 1980; Bolsenga and Herdendorf 1993). Areas obtained from GIS bathymetry for the entire lake (Fig. 5) were 25,734 km^2 versus the 25,657 km^2 and 25,758 km^2 identified by Bolsenga and Herdendorf (1993), and Gatewood and Herdendorf (1980), respectively.

Table 5. 1994–1996 model predictions versus 1997 side scan sonar measurements of *Dreissena* coverage.

Substrate	Predicted (% cover *Dreissena*)	1997 observed sonar (% cover *Dreissena*)	Difference
Mud	6.67 ± 0.002	12.8 ± 3.14 (*n* = 16)	−6.13
Sand/mud	10.97 ± 0.001	10.24 ± 1.9 (*n* = 21)	+0.73
Sand/gravel	43.75 ± 0.002	41.49 ± 4.41 (*n* = 7)	+2.26
Glacial till	22.98 ± 0.003	25.08 ± 6.63 (*n* = 5)	−2.10
Bedrock	30.08 ± 0.002	35.2 N/A (*n* = 1)	−5.12

Table 6. 1994–1997 model predictions versus 1998 side scan sonar measurements of *Dreissena* coverage.

Substrate	Predicted (% cover *Dreissena*)	1998 observed sonar (% cover *Dreissena*)	Difference
Mud	13.53 ± 0.001	No data	No data
Sand/mud	15.65 ± 0.001	14.75 ± 2.74 (*n* = 13)	+0.90
Sand/gravel	51.11 ± 0.001	31.43 ± 1.76 (*n* = 3)	+19.68
Glacial till	29.96 ± 0.002	No data	No data
Bedrock	37.80 ± 0.002	39.15 ± 3.73 (*n* = 4)	−1.35

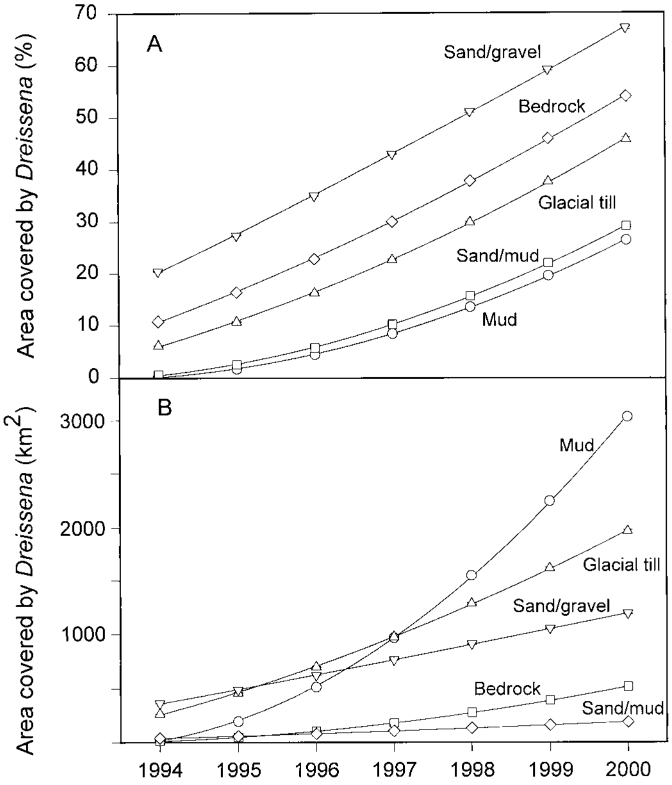

Fig. 8. (A) Model estimates for percent cover of *Dreissena* for 1994–2000. Standard errors for annual estimates of percent cover are smaller than the symbols. (B) Estimated area colonized per year across different substrate types that were derived from the 1994–1997 reduced model and the GIS (*see Table 4*).

Generally, on a lake-wide scale sediment grain size decreases with increasing depth (Fig. 7). However, in Lake Erie the sand/gravel substrate type is found to depths of 57 m, whereas sand/mud distribution is limited to 22 m (Fig. 7). GIS overlay of bathymetry and substrates yielded the first analysis of Lake Erie sediment distributions by depth range (Figs. 1, 2, and 7). These GIS analyses of the bathymetry and sediment distribution in this study were more accurate than past studies due to technological advances in computer mapping. Moreover, instead of qualitative observations concerning the general distribution of sediments, quantitative values can be obtained for any given area by querying the GIS model.

This study enhances earlier observations regarding invading mussels on soft substrates (Berkman et al. 1998) by developing basin-wide geospatial models from more comprehensive SSS surveys. In all cases, hard reflectors on previously described areas of soft sediments represented accumulations of live or dead dreissenid mussels, either *D. polymorpha* or *D. bugensis,* which generated distinct acoustic profiles from previously identified deposits of bedrock, gravel, or anthropogenic debris, such as shipwrecks. All of these hard substrates were interpreted as being covered by dreissenid mussels (Griffiths et al. 1991; Herbert et al. 1991). Moreover, accumulations of live and dead mussel shells provide a positive feedback where additional mussels may colonize these biologically generated hard substrates, creating a dynamic benthic habitat.

Dreissenid mussel percent coverage decreased with sediment grain size (Fig. 8) in the western and central basins, as described by Berkman et al. (1998, 2000). Although insignificant, glacial till was retained in the model because it is the second most common substrate type in Lake Erie (Fig. 6). The high variability of glacial till grain sizes ranging from pebbles and clay to rocks in clay likely leads to highly variable colonization rates by *Dreissena.* Improving the contribution of glacial till to the statistical model would require additional observations in different regions of Lake Erie.

Percent cover of *Dreissena* was interpreted from survey data collected in the western and central basins to 21-m depth, this accounted for 68.3% of the total western and central basin area from which the survey data were collected (Fig. 5). Dreissenid mussel density decreases with depth (Mills et al. 1996), however population densities exceeding 3,000 m^{-2} have been observed in the deepest areas of the eastern basin (Dermott and Munawar 1993). Although insignificant in our models, perhaps as a limitation of the data set, depth should still be considered an important factor when interpreting the distribution of *Dreissena* in large lakes.

Dreissena coverage increased significantly over time (Fig. 8), which allows the statistical model to be used to predict future distributions in the western and central basins of Lake Erie (Tables 5 and 6). Based on the 1994–1997 measurements, *Dreissena* percent coverage was estimated to be increasing at an average rate of 1,000 $\pm$ 6 km^2 yr^{-1} (standard error) in the western and central basins (Fig. 8). This rate is similar to the estimates calculated by Berkman et al (1998). Results from the 1994–1997 model also were used to predict the dreissenid mussel expansion from 1998 to 2000 (Fig. 8). Because the GIS database includes bathymetry and substrate data for the eastern basin of Lake Erie, mussel dreissenid population dynamics in this basin can be easily modeled as SSS or other dreissenid mussel-coverage data become available. Furthermore, this methodology can be adapted to developing similar models to predict *Dreissena* coverage on soft sediments in other large lakes.

Comparisons between the regression model predictions of mussel coverage and subsequent measurements agreed 84% and 80% of the time in 1997 and 1998, respectively (Tables 5 and 6). The difference between the two model predictions was related to the relatively small number of measurements (n = 20) in 1998. Both of these models, however, demonstrate that percent cover of mussels on the soft substrates in Lake Erie can be predicted with reasonable accuracy based solely on sediment type. Additional information on hydrodynamics, nutrient concentrations, thermal and chemical profiles, primary production, predator populations, and other factors would enhance these interpretations about the demographics of the dreissenid mussel invasion in Lake Erie and subsequent ecosystem impacts.

Our study links the distribution and abundance of *Dreissena* assemblages to sediment type and indicates that this invasive species is continuing to spread across soft-substrate habitats in Lake Erie, essentially transforming soft substrates into hard substrate habitats. The dynamic nature of these benthic habitats and the geographic information system results from this study (see http://www.sg.ohio-state.edu) can be incorporated into future assessments of ecosystem variability in Lake Erie. Furthermore, this model provides the framework required for addressing questions regarding the ecological impacts of invasive species, such as coupling invasive species dynamics with energetic models, (e.g., Stoeckmann and Garton 1997) thus providing insights into dynamic changes in energy flow. Such predictive models and maps forecasting the spread of exotic species, such as *Dreissena,* are essential for monitoring and potentially managing their ecosystem impacts. Overall, this study demonstrates the utility of GIS modeling for studying the dynamics and impacts of species invasions across landscapes.

References

BERKMAN, P. A., D. W. GARTON, M. A. HALTUCH, G. W. KENNEDY, L. R. FEBO. 2000. Habitat shift in invading species: Zebra and quagga mussel population characteristics on shallow soft substrates. Biol. Invasions. **2:** 1–6.

———, AND OTHERS. 1998. Invading mussel beds in Lake Erie. Nature **393:** 27–28.

BIAN, L., AND E. WEST. 1997. GIS modeling of elk calving habitat in a prairie environment with statistics. Photogramm. Eng. Remote Sens. **63:** 161–167.

BIJ DE VAATE, A. 1991. Distribution and aspects of population dynamics of the zebra mussel, *Dreissena polymorpha* (Pallas 1771), in the Lake Ijsselmeer area (The Netherlands). Oecologia **86:** 40–50.

BOLSENGA, S. J., AND C. E. HERDENDORF. 1993. Lake Erie and Lake Saint Clair handbook. Wayne State Univ. Press.

COAKLEY, J. P., G. R. BROWN, S. E. IOANNOU, AND M. N. CHARLTON. 1997. Colonization patterns and densities of zebra mussel *Dreissena* in muddy offshore sediments of western Lake Erie, Canada. Water Air Soil Pollut. **99:** 623–632.

DERMOTT, R., J. MITCHELL, I. MURRAY, AND E. FEAR. 1993. Biomass and production of zebra mussels (*Dreissena polymorpha*) in shallow waters of northeastern Lake Erie, p. 399–413. *In* T. F. Nalepa and D. W. Schloesser [eds.], Zebra mussels: Biology, impacts, and control. Lewis.

———, AND M. MUNAWAR. 1993. Invasion of Lake Erie offshore sediments by *Dreissena,* and its ecological implications. Can. J. Fish. Aquat. Sci. **50:** 2298–2304.

EDSALL, T. A., T. E. BEHRENDT, G. CHOLWEK, J. W. FREY, G. W. KENNEDY, AND S. B. SMITH. 1997. Use of remote-sensing techniques to survey the physical habitat of large rivers. Great Lakes Science Center Contribution 983.

ELTON, C. S. 1958. The ecology of invasion by plants and animals. Methuen.

ERDAS. 1991. Earth resources digital analysis system field guide. Earth resources digital analysis systems.

ESRI. 1994. PC Arc/Info User Guides. Environmental Systems Research Institute.

GATEWOOD, R. W., AND C. E. HERDENDORF. 1980. Morphometric calculations for Lake Erie. Center for Lake Erie Area Research Technical Report 220. Ohio State Univ.

GRIFFITHS, R. W., D. W. SCHLOESSER, J. H. LEACH, AND W. P. KOVALAK. 1991. Distribution and dispersal of the zebra mussel (*Dreissena polymorpha*) in the Great Lakes region. Can. J. Fish. Aquat. Sci. **48:** 1381–1388.

HALTUCH, M. A. 1998. Modeling expansion of exotic mussels on Lake Erie sediments using geographic information systems (GIS). M.S. thesis. Ohio State Univ.

HERBERT, P. D. N., B. W. MUNCASTER, AND G. L. MACKIE. 1989. Ecological and genetic studies on *Dreissena polymorpha* (Pallas): A new mollusc in the Great Lakes. Can. J. Fish. Aquat. Sci. **46:** 1587–1591.

———, C. C. WILSON, M. H. MURDOCH, AND R. LAZAR. 1991. Demography and ecological impacts of the invading mollusk *Dreissena polymorpha.* Can. J. Zool. **69:** 405–409.

LEACH, J. H. 1993. Impacts of the zebra mussel (*Dreissena polymorpha*) on water quality and fish spawning reefs in western Lake Erie, p. 381–197. *In* T. F. Nalepa and D. W. Schloesser [eds.], Zebra mussels: Biology, impacts, and control. Lewis.

LEWIS, M. 1966. Sedimentation studies of unconsolidated deposits in the Lake Erie basin. Ph.D. thesis. Univ. Toronto.

MACKIE, G. L. 1991. Biology of the exotic zebra mussel, *Dreissena polymorpha,* in relation to native bivalves and its potential impact in Lake St. Clair. Hydrobiologia **219:** 251–268.

MADENJIAN, C. P., D. W. SCHLOESSER, AND K. A. KRIEGER. 1998. Population models of burrowing mayfly recolonization in western Lake Erie. Ecol. App. **8:** 1206–1212.

MAY, B., AND J. E. MARSDEN. 1992. Genetic identification and implications of another invasive species of dreissenid mussel in the Great Lakes. Can. J. Fish. Aquat. Sci. **49:** 1501–1506.

MCQUEST MARINE SCIENCES LTD. 1991. Report on side scan sonar surveys on three sites in Lake Erie: Chicken and Hen Island, East Sister Island, and Chickenolee Reef. Ministry of Natural Resources.

MILLS, E. L., J. H. LEACH, J. T. CARLTON, AND C. L. SECOR. 1993. Exotic species in the Great Lakes: A history of biotic crises and anthropogenic introductions. J. Gt. Lakes Res. **19:** 1–54.

———, G. ROSENBERG, A. P. SPIDLE, M. LUDYANSKIY, Y. PLIGIN, AND B. MAY. 1996. Colonization, ecology, and population structure of the ''quagga'' mussel (Bivalvia: Dreissenidae) in the Lower Great Lakes. Can. J. Fish. Aquat. Sci. **50:** 2305–2314.

PHANEUF, B. 1997. Underwater imaging and GIS integration with side scan sonar. Photogramm. Eng. Remote Sens. **63:** 651–654.

RASUL, N., J. P. COAKLEY, AND R. PIPPERT. 1997. Sedimentary environment of Lake Erie: Geologic setting, sediment distribution, and modern evolutionary trends. Canada National Water Research Institute Contribution 97–114.

RYAN, W. B. F., AND R. D. FLOOD. 1996. Side-looking sonar backscatter response at dual frequencies. Mar. Geophys. Res. **18:** 689–705.

SPIDLE, A. P., J. E. MARSDEN, AND B. MAY. 1994. Identification of the Great Lakes quagga mussel as *Dreissena bugensis* from the Dnieper River, Ukraine, on the basis of alozyme variation. Can. J. Fish. Aquat. Sci. **51:** 1485–1489.

STOECKMANN, A. M., AND D. W. GARTON. 1997. A seasonal energy budget for zebra mussels (*Dreissena polymorpha*) in western Lake Erie. Can. J. Fish. Aquat. Sci. **54:** 2743–2751.

VITOUSEK, P. 1986. Biological invasions and ecosystem properties: Can species make a difference? p. 163–176. *In* H. A. Mooney and J. Drake [eds.], Ecology of biological invasions of North America and Hawaii. Springer-Verlag.

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