The introduction and establishment of populations of *Dreissena polymorpha* (zebra mussel) in North American lakes, rivers, and reservoirs have been documented over the last 5 yr (Hebert et al. 1989; Nalepa and Schloesser 1993). There has been much discussion of the potential economic and biological impacts of the spread of zebra mussel among the Laurentian Great Lakes (Griffiths et al. 1991; Mackie 1991; Nalepa and Schloesser 1993, and references therein). Also, Carlton (1992) noted that the Great Lakes need to be considered as a source of *Dreissena* for spread to inland lakes. However, less attention has been focused on the questions of how and where *Dreissena* will spread among inland lakes and where they might have important ecological and environmental impacts. For example, with intense development along the shores of many inland lakes, the relative impact on individual property owners could be quite substantial. Also, major power plants are located along larger inland water courses, where biofouling (e.g., clogging of water intake pipes by attaching *Dreissena*) can be a concern. Armor et al. (1993) described four major power plants along rivers in Wisconsin that could be affected, and there are dozens of hydro-power dams located along smaller water courses in Wisconsin and other states and provinces surrounding the Great Lakes. The displacement of native species by *Dreissena*, particularly in protected areas such as the St. Crois River, is an additional concern. The St. Crois River is a rare example of a relatively pristine river in the U.S. upper midwest; invasion of zebra mussel will undoubtedly place rare native species, such as unionid clams, at risk.

The opportunity to examine the potential spread of zebra mussel to inland lakes is timely. *Dreissena* are found in all of the Great Lakes. In Wisconsin, *Dreissena* have been
found along the western shore of Lake Michigan, including the southern half of Green Bay, locally along the southern shore of Lake Superior, as well as in the Mississippi River. However, to date, no Wisconsin inland lake has been found to contain Dreissena (Wisconsin Sea Grant 1992). Similarly, only a few inland lakes in North America that do not have inflowing hydrologic connections to known Dreissena sources have established populations of zebra mussel. These exceptions include Lake Hargus, a reservoir in Ohio (Wisconsin Sea Grant 1992), Lake Wawasee, Indiana (personal observation, 1992), and Eagle Lake, Michigan (Ladd Johnson, personal communication). Dreissena populations have also been reported in New York State (New York Sea Grant 1991), but these lakes (Conesus, Seneca, and Cayuga) are likely to have been invaded via waterways connecting to canals from the Great Lakes.

Our study consisted of two parts: (1) we made predictions of potential zebra mussel abundance in a number of Wisconsin lakes (assuming they were invaded) using previously developed models and (2) we used a geographical information system (GIS) to examine landscape-scale characteristics associated with predicted population density levels of zebra mussel in 194 Wisconsin lakes. First, we used three models developed by Ramcharan et al. (1992), based on data from European lakes, to predict Dreissena occurrence and abundance in individual lakes. These models are (i) an absence/presence model using discriminant function analysis (DFA), (ii) a categorical density model (absent, low, high population density), also using DFA, and (iii) a numerical, regression-based density model (number per square meter). Hereafter, we refer to these models as the occurrence, density, and abundance models, respectively. We modeled a sample of inland lakes, mapped the spatial distribution of those lakes, and characterized each lake by predicted density class or range, as appropriate for each model. We also compared the results of the three models. Then we associated the population density prediction for each lake with various landscape-scale variables.

Overview of a GIS and Its Application

GIS’s are increasingly being used by a broad range of researchers. To date, most GIS usage in aquatic ecology has involved either building geographically referenced databases of ecological data or producing computer-generated maps. These capabilities allow researchers to visualize the spatial relationships among ecological variables and easily perform logical spatial operations. Meanwhile, recent releases of packaged GIS software have taken advantage of window-oriented user interfaces and reductions in hardware costs to make increasingly sophisticated spatial analytical power accessible to the ecological researcher.

GIS will be used most effectively if one takes advantage of what a GIS is designed to do. Lillesand and Kiefer (1987) described a GIS as “a system designed to store, manipulate, and display [geographic] data”. A GIS “must be capable of handling both locational data and attribute or descriptive data about features” (italics are the original authors’). A GIS can be differentiated from simple automated mapping by the logical operations that can be performed on sets of spatial features. A set of features is often referred to as a layer. A layer consists of the logical combination of the locational and attribute data about like features in an area of study.

<table>
<thead>
<tr>
<th></th>
<th>pH</th>
<th>Calcium</th>
<th>Nitrate</th>
<th>Phosphate</th>
</tr>
</thead>
<tbody>
<tr>
<td>Minimum</td>
<td>5.0</td>
<td>1.0</td>
<td>0.007</td>
<td>0.002</td>
</tr>
<tr>
<td>Maximum</td>
<td>9.1</td>
<td>76.2</td>
<td>3.400</td>
<td>0.182</td>
</tr>
<tr>
<td>Median</td>
<td>8.0</td>
<td>25.8</td>
<td>0.070</td>
<td>0.005</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>mm</td>
<td>16.9</td>
<td>0.398</td>
<td>0.029</td>
</tr>
</tbody>
</table>

One such layer might be a set of polygons that represent lake shorelines (locational data), along with their respective limnological data (attribute data). An example of a logical operation is an overlay, which is a logical intersection or union of two or more layers. An example of an overlay process would be a logical union of a wetland layer and a linear road network that might impact the water quality of the wetlands. The resulting GIS dataset could be used to easily analyze the proximity of each wetland to a road. Such an analysis could also easily take into account weighting factors (e.g., traffic level) to account for variance in potential pollutant runoff from a given road. GIS’s offer great potential for ecological research, particularly for ecological modeling.

In the second part of this study, we used a GIS to perform spatial analysis of the model results from part one, relating them to landscape features associated with a given lake’s watershed. Much is known about the relationship between lakes and the characteristics of the watersheds surrounding them (Wetzel 1983). Yet there appear to have been relatively few attempts made to predict water quality variables on such a large scale.

Lake water quality influences can be expected to relate to processes occurring within the entire watershed of a lake. We simplified our study by exploring associations between selected landscape features directly underlying subject lakes, e.g., surficial geology, and the projected Dreissena population density of those lakes. We tested the null hypothesis of no association between the predicted density category from the DLA-based density model and two landscape feature attributes for a given lake. We used model-based Dreissena predictions and tested for association of predicted lake Dreissena status with landscape-scale features.

Additionally, we tested for association between the predicted population densities and ecoregions defined based on lake characteristics. The ecoregions used (Omernik et al. 1988) were developed specifically for lake management purposes. This test was intended to test whether broad ecoregions, refined by lake type clustering, would correlate with predicted patterns of Dreissena density. The results of this test could have management implications.

**Methods**

Modeling Dreissena in Individual Lakes

Lake water quality data were obtained from the Wisconsin Department of Natural Resources (WDNR). The source database was the EPA STORET database (U.S. Environmental Protection Agency, Office of Water 1990), which is maintained on a cooperative basis for the state of Wisconsin by WDNR. From this dataset of more than 3000 sampling sites,
TABLE 2. Comparison of *Dreissena* absence and presence predictions among the three models used. For the categorical density model the low- and high-density classes were combined to obtain the present category. For the numerical abundance model, all predictions less than or equal to zero were placed in the absent category, and all predictions greater than zero were placed into the present category. Predictions of abundance less than zero result from absent lakes not being included in the Ramacharan et al. (1992) regression-based abundance model (this model was not forced through the origin).

<table>
<thead>
<tr>
<th>Category</th>
<th>Absent</th>
<th>Present</th>
<th>% present</th>
</tr>
</thead>
<tbody>
<tr>
<td>Occurrence (absence/presence)</td>
<td>101</td>
<td>93</td>
<td>47.9</td>
</tr>
<tr>
<td>Density (categorical density)</td>
<td>31</td>
<td>163</td>
<td>84.0</td>
</tr>
<tr>
<td>Abundance (numerical density)</td>
<td>30</td>
<td>164</td>
<td>84.5</td>
</tr>
</tbody>
</table>

we chose a subset of 194 lakes. Lakes were chosen for the subset when (1) all limnological parameters required by the three *Dreissena* models were available (pH, ionic calcium, nitrate, and phosphate), (2) the size was larger than 8 ha, and (3) the lake was not a reservoir. The 8 ha minimum was chosen because (1) most lakes under 8 ha have not been surveyed and (2) many of these smaller lakes are unnamed, making confirmation of geographic location difficult. For lakes with multiple sampling sites, the site closest to the lake outflow was chosen. From the extensive list of parameters available in the database, only those parameters required to run the three models were extracted.

STORET contains both field and laboratory-processed pH values. When both were available, the values were averaged. Combined nitrate/nitrite, the only available nitrate measure, was used as a surrogate for nitrate alone, since nitrite was expected to be an insignificant contributor to the combined nitrate/nitrite total (Wisconsin State Hygiene Laboratory, personal communication). Similarly, orthophosphate was used as a surrogate for available phosphate, since it was the only measurement available. Sampling history of the lakes varied widely, with samples dating as far back as 1970. Frequency of sampling varied from once every few

**Fig. 1.** (A) Map of absence/presence predictions from the DFA-based occurrence model. Open triangles represent lakes where *Dreissena* are predicted to be absent (101 lakes). Solid circles represent lakes where *Dreissena* are predicted to be present (93 lakes). Note that lakes not predicted to have *Dreissena* tend to dominate the north and lakes where *Dreissena* are predicted to occur tend to dominate the southeast. (B) Map of density category predictions based on the DFA-based density model. Open triangles represent lakes where *Dreissena* are predicted to be absent (31 lakes). Open squares represent lakes where *Dreissena* are predicted to be present in low densities (21 lakes). Solid circles represent lakes where *Dreissena* are predicted to be present in high densities (142 lakes). Lakes without *Dreissena* are congregated in the northern area, consistent with Fig. 1A. (C) Map of predictions based on the regression-based abundance model. Open triangles represent lakes with predicted *Dreissena* density of approximately zero or less (52 lakes). The lakes predicted to have *Dreissena* were divided into three equal-sized categories. Open squares represent lakes predicted to have the lowest density, open circles a medium density, and solid circles the highest density. Note that lakes predicted to have the highest *Dreissena* densities tend toward the southeast.
years to as many as six each year. The majority of lakes
had samples taken at various points along a depth profile
for a given sampling event. Although *Dreissena* are reported
from deep waters, the highest population densities appear
tend toward shallow water. Thus, only data collected at
≤2 m depth were used, as initial colonization is likely to
occur in the littoral zone. Within these restrictions, all
remaining sample values were averaged across available
sampling dates to obtain the final parameters for each lake.
Table 1 presents a summary of the final data values.

It should be noted that there were inherent biases in the
lake sample data, both temporally and spatially. As noted
above, the frequency and timing of the samples varied
widely, with many lakes being sampled in only a few closely
clustered years. Additionally, many lakes were not sampled
as frequently (or at all) in ice-over months. Spatial bias
derived primarily from the jurisdictional impetus (i.e.,
WDNR) for collecting the data. For instance, relatively few
sample lakes were located in national forest areas (approx-
imately 600 000 ha in Wisconsin). Further, many of the
sample lakes are heavily used for recreation. On balance,
this dataset appeared to be the most comprehensive and re-
representative available for Wisconsin, which served the purpose
of our study.

We used these data (pH, ionic calcium, nitrate and phos-
phate levels) in the three models of Ramcharan et al. (1992)
to predict zebra mussel populations in each lake. One record
for each lake was imported from our database, with the
STORET station number as a unique identifier. The records
included locational coordinates (latitude/longitude) of the
lake’s sampling station that were used in GIS processes.
Each record contained the averaged values for the physical/
chemical parameters required by the three models. The final
results for the three models were then exported in an appro-
riate format for importing into the GIS.

*Dreissena* Density – Landscape Feature Association

Part two of the study explored whether landscape fea-
tures underlying and surrounding lakes could be used as
predictors of *Dreissena* population density. We tested for
associations between predicted *Dreissena* density (from the
DFA-based density model) and various attributes of the
landscape around and underlying lakes: (1) surficial (qua-
ternary) deposits, (2) bedrock type, and (3) U.S. Environ-
mental Protection Agency (USEPA) ecoregions. We used
the categorical density model results, since they allowed
straightforward classification of lakes and provided more
information than simply absence versus presence.

The landscape feature datasets (layers) were also obtained
from WDNR, along with a layer containing the Wisconsin
state border (used to produce maps). The landscape features
were represented spatially by polygons, along with an
attribute that characterized the polygon. The landscape fea-
ture attribute data required aggregation from more detailed
source data for surficial deposits and bedrock type. We used
aggregate classifications that were developed as part of a
state-wide groundwater contamination susceptibility analy-
sis (Schmidt 1987). The purpose of these classifications
was to determine the ability of surface contaminants to reach
the water table. However, using data presented by Todd
(1980), one can rank the bedrock and surficial deposits
classes by calcium content. Since lake water calcium con-
centration is a factor in each of the models, and since it is
expected that groundwater will generally have a significant
impact on lake water chemistry, one could infer that poten-
tial colonization by zebra mussel is associated with the geo-
logic structure surrounding a lake.

The ecoregion layer was originally derived by Omernik
(1987). These continental-scale ecoregions are areas within
which landscape ecology and other characteristics, such as
weather, are thought to be similar. Omernik based his map
of the coterminous 48 U.S. states on regional submaps of
(1) land surface form, (2) potential natural vegetation, (3) land
use, and (4) soils. Other maps were used to verify classifi-
cation of land areas. Omernik et al. (1988) refined these
ecoregions for the purposes of lake management based on
soils, quaternary geology, bedrock, and phosphorus con-
centrations for inland lakes in Michigan, Minnesota, and
Wisconsin. Omernik et al. (1991) then further refined the
earlier mapping in a particularly problematic area, the nor-
thern west-central portion of Wisconsin. This final version
was used in this study.

The model results from part one were first imported into
the PC ARC/INFO GIS (version 3.4D, Environmental Systems
Research Institute). Each layer within the GIS contained
locational as well as attribute information. The lakes were
located relative to their respective sampling stations’s latitude/longitude coordinates and were considered as point
locations for GIS analyses. These point coordinates were
converted to the Wisconsin Transverse Mercator projection
(a locally used alteration of the Universal Transverse Mercator
coordinate system) so that overlays could be made with the
other landscape layers that use this coordinate system. The
attribute information for each lake included the result for
each model.

The GIS analysis process consisted of performing a point-
in-polygon overlay. In this procedure, the GIS overlaid the
lakes, represented by their respective sampling location
points, onto the landscape features, represented by poly-
gons. A new attribute was then added to each lake that
represented which landscape feature polygon the point (lake)

Fig. 2. Maps of predicted *Dreissena* density categories overlaid onto bedrock type, surficial deposits, and USEPA ecoregions.
Crosses represent lakes where *Dreissena* are predicted to be absent (31 lakes). Squares represent lakes where *Dreissena* are
predicted to be present in low densities (21 lakes). Triangles represent lakes where *Dreissena* are predicted to be present in high densities.
(142 lakes).
Top: Bedrock types are (1) igneous, metamorphic, and volcanic, (2) sandstone, (3) carbonates, and (4) shale. Note that lakes predicted
to be absent of *Dreissena* tend to be associated with the igneous/metamorphic/volcanic region. (Note that one lake was omitted
due to missing data.) Middle: Surficial deposit types are (1) sand and gravel, (2) sandy, (3) peat, (4) loamy, and (5) clayey. Note that
lakes predicted to be absent of *Dreissena* tend to be associated with gravel/sand and sandy areas. Bottom: Ecoregions are (1) west-
ern corn belt plains, (2) northern lakes and forests, (3) northern central hardwood forests, (4) driftless area, and (5) southeastern
Wisconsin till plains. Note the paucity of lakes in the driftless area, and the near total association of lakes predicted to be absent of
*Dreissena* in the northern lake and forest area.


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Statistical associations between landscape characteristics and population density categories were tested using the $G$ statistic (Legendre and Legendre 1983).

**Results**

The occurrence model produced a spatial concentration of lakes predicted to be absent of *Dreissena* in the northern part of Wisconsin (Fig. 1). Further, the density model indicated a spatial segregation of lakes predicted to have low *Dreissena* densities from those that would lack *Dreissena* (Fig. 1). The abundance model reinforced these patterns by indicating a gradient from lower to higher densities as one moves away from the north-central portion of Wisconsin (Fig. 1). All three models, however, suggest a broad distribution of lakes that are predicted to support *Dreissena* populations. (Note that southwestern Wisconsin was not under represented in the lake sample; this “driftless area” has very few lakes.)

A comparison of model results is shown in Table 2. The occurrence model predicted that *Dreissena* would be present in 47.9% of the lakes. In contrast, the density model predicted presence in 84.0% of the lakes and the abundance model 84.5%.

Part two of our study tested for association between various landscape features underlying lakes and *Dreissena* density class based on the density model. To illustrate the spatial relationship between the landscape features and the lakes, we produced a map for each landscape feature (Fig. 2). Landscape features were significantly associated with *Dreissena* density categories for each of the four landscape layers: (1) bedrock type ($G = 34.9, p < 0.001, df = 6$; Fig. 3), (2) surficial deposits ($G = 18.4, p < 0.02, df = 8$; Fig. 3), and (3) ecoregions ($G = 77.6, p < 0.001, df = 6$; Fig. 3). Low zebra mussel densities were associated mostly with the igneous/metamorphic/volcanic category of bedrock and sand-and-gravel or sandy surficial deposits.

**Discussion**

Our initial attempts to predict the spatial distribution of *Dreissena* among Wisconsin’s inland lakes are encouraging. Earlier work by Neary and Leach (1992) looked at the potential for presence of *Dreissena* among a large sample of inland lakes in Ontario by using a GIS to map the results of threshold-based analysis of pH and calcium in those lakes. The pH and calcium threshold that they used were based on preliminary model results reported by C.W. Ramcharan, D.K. Padilla, and S.I. Dodson (Second International Zebra Mussel Conference). Our work used the three completed statistical models by Ramcharan et al. (1992) and available limnological data to predict absence or presence and population density of *Dreissena*. A GIS was used to test for associations between predicted lake population density classes and driftless area, and southeastern Wisconsin till plains. The western corn belt plains ecoregion contained no sample lakes. The association was statistically significant ($G = 77.5, p < 0.001, df = 6$).
three landscape-scale characteristics. Overall, landscape-scale patterns appeared to be fairly consistent among the models, although they differ in details. Lakes without Dreissena were concentrated in the northern highlands, where forestry and tourism dominate. Calcium availability is probably the limiting factor. The lakes where lower densities of Dreissena were predicted are located mainly in the central and east-central portions of the state, which are dominated by agricultural use and some lesser urban centers. The densest populations of Dreissena were predicted in the south-central, south-eastern, and far western portions of the state. Here, urban/industrial and suburban areas are interlaced with agricultural areas. These areas have higher levels of available calcium from calcareous glacial till, and sandstone and carbonate bedrock. Further, due to agriculture, construction, and urban runoff, nutrient flow into these lakes is higher.

There was a noted disparity in the proportion of lakes where Dreissena were predicted to be absent versus present between the absence/presence only model and the two density model. For the Ramcharan et al. models, only lakes with known populations of Dreissena were used in development of their density and abundance models. In a test of their model, they found that no lakes with Dreissena were misclassified (as not supporting Dreissena), but there were some lakes without Dreissena that were misclassified as supporting Dreissena. Therefore, for the European dataset, the model seemed conservative. This may explain why there is an apparent difference in the absence/presence predictions using the density and abundance models (84.0% and 84.5% present, respectively) in comparison with the presence model (49.5% present). A more conservative approach would be to apply the presence/absence model first and then apply the density models to those lakes predicted to support Dreissena.

The variance among the models in the proportion of lakes predicted to have Dreissena present also reflects the relative uncertainty in model parameters developed by Ramcharan et al. (1992). In Fig. 4, one can see that many lakes are only marginally classified as absent versus present by the categorical density model. With small adjustments of the discriminant functions, many lakes would be reclassified: 51 lakes are located within ±20% of the absence/presence discrimination line. Further, shifting the focus to the occurrence model (a one-dimensional discriminant factor model), 52 of the lakes are within only ±10% of the absence versus presence discrimination value. Clearly, if parameters are refined the models could move into either lesser or greater agreement, but the potential exists to move them into greater agreement.

In part two of our study, the GIS provided spatial analytical capabilities that would have been impractical to implement manually. The results obtained here suggest that landscape features can potentially be used as a predictor for overall Dreissena distribution. More generally, this study suggests the potential for predicting general patterns of limnological characteristics of lakes across landscapes, based on the characteristics of the landscape itself.

On another level, this study demonstrates the relative ease with which ecological studies can be supplemented by use of a GIS as an analytical tool. Although our study used but a small subset of available GIS functionality, the results underscore the importance of looking beyond the spatial scales typically used in ecological studies. Frost et al. (1988) and Allen and Hoekstra (1992) provided strong arguments for looking at systems at spatial scales both larger and smaller than what experimental expediency might otherwise call for. They suggested that major insight can be gained by examining a system of multiple scales simultaneously.

Summary

We showed that the distribution of Dreissena populations and their densities are not likely to be uniform among Wisconsin inland lakes. We also showed that there is potential for using landscape scale features, associated with lake watersheds, to predict Dreissena density for lakes with less than adequate limnological data. This information will be valuable to resource managers, physical plant managers, and others.

However, this study does not address the timing of invasions for specific lakes or geographical areas (landscapes), nor how a population of zebra mussels in a given lake may be established over time. There are important questions to which future work needs to be directed.

Further research is required to lower the uncertainty in discriminating absence/presence in the Ramcharan et al. (1992) models. Ramcharan et al. used a relatively small set of lakes (76 lakes in the DFA occurrence model, 38 lakes in the DFA density model, and 58 lakes in the regression-based density model). The lake dataset used for their models does not include the complete range of limnetic factors in our Wisconsin lake dataset. A program of proactive study of inland water bodies invaded by Dreissena is needed to refine the Ramcharan et al. models for North American


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lakes. Enhancing the confidence of these models would allow for more robust individual lake predictions, as well as enhance the likelihood that the models could be used for management purposes.

Finally, future work should also look at more comprehensive landscape data. Such work should include (1) variability among landscape features for lake watersheds, (2) additional factors such as land use, and (3) lake inflow contribution volumes, i.e., surface water versus groundwater. It would then also be possible to assess whether these data can drive models to predict Dreissena occurrence in lakes for which inadequate limnological data exist, as the associations between landscape features and Dreissena occurrence demonstrated here suggest.

Acknowledgements

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References