Predicting the Likelihood of Eurasian Watermilfoil Presence in Lakes, a Macrophyte Monitoring Tool

Lucy A. J. Buchan; Dianna K. Padilla

Ecological Applications, Vol. 10, No. 5. (Oct., 2000), pp. 1442-1455.

Ecological Applications, 10(5), 2000, pp. 1442–1455

PREDICTING THE LIKELIHOOD OF EURASIAN WATERMILFOIL PRESENCE IN LAKES, A MACROPHYTE MONITORING TOOL

LUCY A. J. BUCHAN[1,3] AND DIANNA K. PADILLA[2]

[1]*Department of Zoology, 430 Lincoln Drive, University of Wisconsin, Madison, Wisconsin 53706 USA*
[2]*Department of Ecology and Evolution, State University of New York, Stony Brook, New York 11794 USA*

Abstract. In regions with abundant and diverse freshwater resources, it is difficult and costly to survey all lakes at the level required to detect invasive plants. Effective allocation of monitoring resources requires tools that identify waterbodies where exotic species are most likely to invade. We developed and tested models that predict conditions in which Eurasian watermilfoil, *Myriophyllum spicatum,* is most likely to survive and successfully colonize. We used logistic regression to model the likelihood of *M. spicatum* presence or absence using a suite of biological, chemical, and physical lake characteristics which are easily obtainable from public databases. We evaluated model fit by the Aikake criterion and model performance by the percentage of misclassification errors as well as the costs associated with acquiring data for variables modeled. Several models fit our data well, misclassifying only 1.3–11.0% of the lakes where *M. spicatum* was observed, and used relatively inexpensive landscape variables (percent forest cover in a drainage basin, presence and type of public boat launch, and bedrock type) that typically exist as information layers in geographic information systems (GISs) or recreational atlases. We found that the most important factors affecting the presence or absence of *M. spicatum* were those that influence water quality factors known to impact *M. spicatum* growth, rather than factors associated with human activity and dispersal potential. In particular, the amount of forest cover in the lake watershed was consistently important and could control the level of dissolved inorganic carbon in lakes, one of the factors known to affect *M. spicatum* growth rates. Factors such as the number of game fish species and number and types of boat ramps or proximity to roads were generally less important lake characteristics. Our models can be useful tools for developing management strategies to prevent or slow the spread of *M. spicatum* and aquatic invaders, such as the zebra mussel, that can attach to it and thus be dispersed. Our models also exemplify a general approach for slowing or stopping the spread of other invading species.

Key words: aquatic macrophytes; habitat suitability; invasive species; logistic regression; monitoring invasive species in lakes; Myriophyllum spicatum.

INTRODUCTION

Invasions by exotic species are unfortunately becoming a common occurrence, and are often linked to a decrease in the relative abundance and richness of native species in communities. In most regions of the world, 10–30% of the flora consists of exotic species (Heywood 1989, U.S. Congress, Office of Technology Assessment 1993). Once established, exotics are often impossible to eradicate. It may be possible, however, to slow their invasions and protect areas of concern by predicting where they are most likely to spread. Accurately predicting patterns of spread requires knowledge of physiological and ecological limitations to the successful colonization, establishment, and growth of exotic species. Because it is difficult to monitor for invasive species across large geographic areas, we developed models that identify suitability of habitats, using existing, accessible data. The models provide a basis for prioritizing often-limited resources for monitoring and managing invasions. Similar models have been effectively used to predict and monitor the invasion of the zebra mussel, *Dreissena polymorpha* (Ramcharan et al. 1992, Koutnik and Padilla 1994).

Eurasian watermilfoil, *Myriophyllum spicatum* L., (hereafter referred to as milfoil) exists on every continent except Antarctica, and is native to Europe, Asia, and Northern Africa (Couch and Nelson 1985). The earliest confirmed voucher specimen in North America was collected in 1942 in Washington, D.C. (Couch and Nelson 1985). In subsequent decades its range increased to include most of the eastern part of the continent as far north as Ontario and Quebec provinces of Canada, and most of the western part of the continent of North America as far north as Vancouver Island and the Okanagan Valley in the province of British Columbia. The earliest milfoil voucher specimens in Wisconsin were recorded in 1967 (Pewaukee Lake, Waukesha County), and in 1968 (Fish Lake, Dane County).

Manuscript received 23 April 1998; revised 5 August 1999; accepted 21 August 1999; final version received 14 September 1999.

[3] Present address: EOA, Inc., 699 Town & Country Village, Sunnyvale, California 94086 USA.
E-mail: buchan@eoainc.com

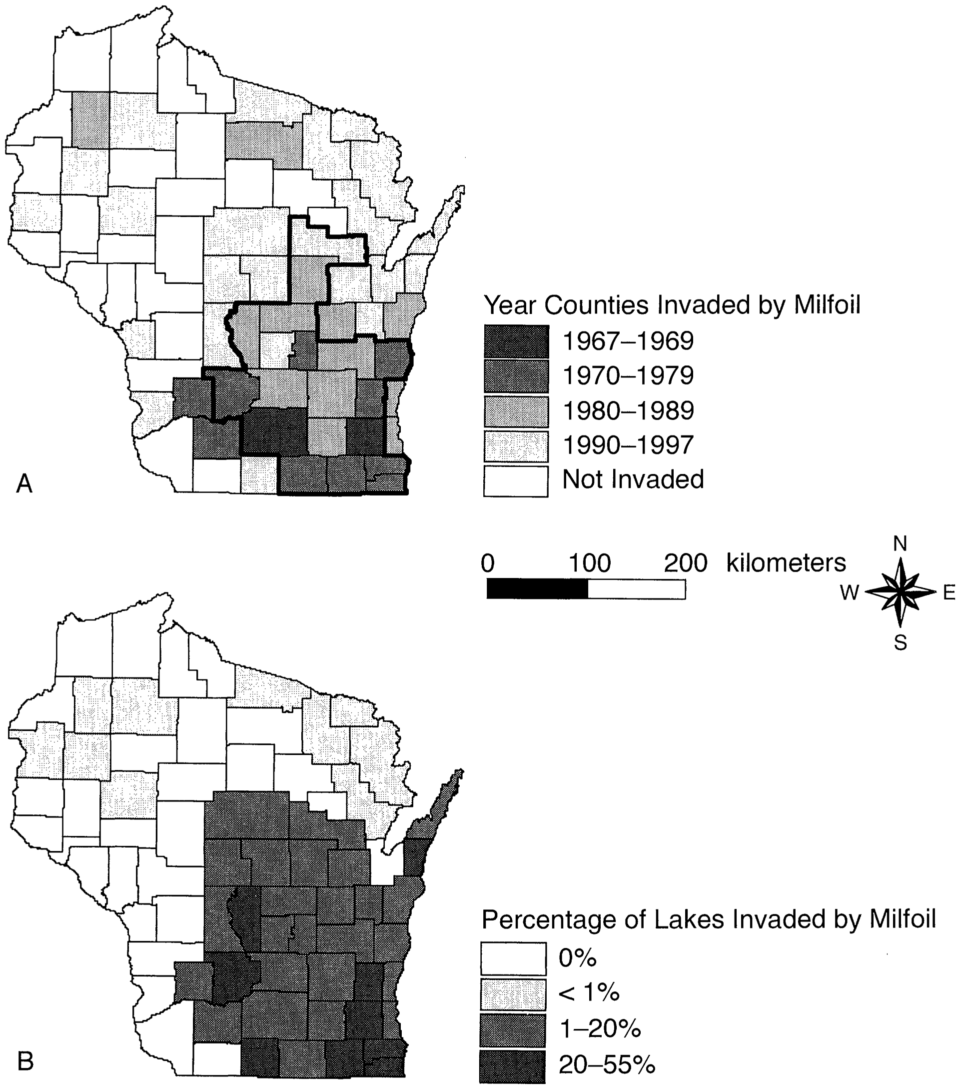

FIG. 1. Invasion of Wisconsin counties by Eurasian watermilfoil (*Myriophyllum spicatum*). Invasion is shown (A) by year (source: Engels 1997), and (B) as the percentage of lakes invaded in counties (source: Buchan 1997). Counties within the bold outline in (A) are those in which authors surveyed lakes for milfoil presence/absence.

By 1980 milfoil had spread to 11 other counties in southeastern Wisconsin. It currently exists in surface waters in two-thirds of Wisconsin's counties (Fig. 1A).

Milfoil is a submersed, perennial aquatic herb that typically grows where water is one to four meters deep (Nichols and Shaw 1986) but is found in water up to 10 m in depth (Grace and Wetzel 1978). It obtains most of its nutrients from the sediment through an adventitious root system (Barko and Smart 1980, Carignan and Kalff 1980). Reproduction is both sexual and asexual, but dispersal occurs primarily by fragments (Madsen et al. 1988, Hartleb et al. 1993). Milfoil fragments are created both by autofragmentation after flowering, and by disturbances such as water turbulence and human activities. Interlake fragment transport may be caused by several dispersal mechanisms, including wind, waterfowl, water flow between connected waterbodies, and human-related activities. Motorboats and boat trailers, however, are the dispersal mechanisms most often cited for interlake transport of milfoil fragments (Scales and Bryan 1979, Johnstone et al. 1985, Smith and Barko 1990, Johnson and Carlton 1996).

Several characteristics have enabled milfoil to dominate the macrophyte communities that they invade. These include maintaining a large biomass throughout the winter, rapid and early seasonal growth that outcompetes neighboring macrophytes for light and sediment nutrients (Madsen et al. 1991), and production of phenolic compounds that deter herbivores and inhibit algal growth (Gross and Sutfeld 1994, Gross et al. 1996). By forming monotypic beds, milfoil has also negatively impacted the richness, diversity, and distribution of benthic invertebrate species (Gibbons et al. 1987) and fish (Keast 1984, Truelson 1985, Frodge et al. 1990, 1991).

In addition to changing ecosystem function, milfoil becomes a human nuisance by forming dense mats on water surfaces that reduce open area in littoral zones and wash up on shorelines, thereby reducing aesthetic appeal of lakes and areas available for swimming and boating. Depending on the size and location of milfoil populations in surface waters, water flow and discharge may be altered, resulting in flooding or interference with municipal or industrial operations (Bates et al. 1985).

Several factors may limit the growth and distribution of milfoil, including light availability, temperature, inorganic carbon, and sediment composition. Milfoil grows under a range of trophic conditions, preferring productive lakes (Smith and Barko 1990). In productive lakes milfoil is more likely to be limited by the supply rate of dissolved inorganic carbon than by the pool of other nutrients (Adams et al. 1978, Titus and Stone 1982, Maberly and Spence 1983, Smart and Barko 1986, Smith and Barko 1990). Milfoil mobilizes nutrients from both ambient water and sediment, preferring fine-textured sediments with 10–25% organic matter content (Nichols and Mori 1971, Madsen 1982). Substrate texture that is either coarse (sand or gravel) or flocculent may impede milfoil root anchorage (Nichols and Shaw 1986). Efforts to mechanically control milfoil may promote and sustain milfoil establishment by increasing fragmentation (Carpenter 1980).

Because freshwater habitats are disjunct, and can be numerous, as in the Laurentian Great Lakes region, it can be difficult for resource managers to monitor all lakes to detect the presence of invasive species. Applying a model that predicts the likelihood of milfoil establishment provides a mechanism for prioritizing the allocation of limited resources toward detection efforts. Indeed, such prioritization of management efforts may result in slowing the further invasion of habitats by enabling resource managers to eliminate nascent colonies that act as new invasion sources or stepping stones for further spread (Moody and Mack 1988, Buchan 1997, Buchan and Padilla 1998). The goals of this study were to identify important parameters that predict the likelihood of milfoil invasion into lakes using data that usually exist in publicly available databases and to provide a useful tool to enhance milfoil detection efforts. We were able to well document spatial and temporal patterns of milfoil presence/absence among Wisconsin lakes due to monitoring efforts by the state for the past 30 years. Thus, we used logistic regression analysis to test whether a suite of biological, physical, and chemical lake characteristics are likely to measure or correlate with factors influencing milfoil growth and/or dispersal. The characteristics we used are available in public databases and could predict lakes in which milfoil was most likely to occur.

While many data can be retrieved from existing databases, there may be instances in which data are either unavailable or too costly to obtain. Therefore, to determine how sensitive model results were to specific variables, variables were individually eliminated and the analysis was repeated. We evaluated models by comparing the cost of included variables versus predictive accuracy.

Methods

Data

Data on milfoil presence/absence was collected in the field (Fig. 1A) and from records maintained by the Wisconsin Department of Natural Resources (WDNR), the Wisconsin Geological and Natural History Survey (WGNHS), and three herbaria located at the University of Wisconsin–Madison, University of Wisconsin–Oshkosh, and the Milwaukee Public Museum. Although 668 records of milfoil presence/absence were compiled, we used only 404 records because for 264 records data were missing for some of the independent variables. The total sample size for our analysis ($N = 404$) consisted of 106 of our field survey records, 294 records from the WDNR (Engels 1997 and WDNR, *unpublished data*), and one and three records, respectively, from the UW–Oshkosh herbarium and the museum (University of Wisconsin–Oshkosh, herbarium curators, *unpublished data*) respectively. To increase the probability of including lakes where milfoil could not survive rather than lakes that could support milfoil but have not been invaded yet, we limited our field survey to lakes in southeastern Wisconsin, the region first invaded by milfoil, and where exposure to milfoil was most likely. Since most existing records in southeastern Wisconsin came from lakes with public boat access, we surveyed all lakes without public boat launches ($N = 38$) in this region (18 counties) (Fig. 1A) that were accessible either by public property or at the permission of private landowners. Where lake density was greatest in the most northern county in this region we sampled, in addition, a random selection of 10 lakes without public boat launches. The remaining 58 samples in our field survey were collected from lakes with public boat launches.

To assess presence/absence of milfoil in the field we used the milfoil sampling protocol established by the WDNR after 1992: shoreline and shallow littoral areas around boat launches were sampled first, followed by a transect paralleling the entire lake shoreline. We sampled transects every 100–200 m by tossing a rake 4–6 times, allowing it to sink to the lake bottom, and examining and identifying the retrieved submersed species.

To develop predictive models, we compiled existing information from publicly accessible data sources

(Wisconsin Surface Water Inventory [SWI] and U.S. Environmental Protection Agency Storage and Retrieval database [STORET], both accessible by contacting C. Tiegs [WDNR Bureau of Fisheries Management and Habitat Protection, Monitoring Section, Madison Wisconsin, USA]; and GIS coverages maintained by the WDNR, accessible by contacting L. Perry [WDNR Bureau of Enterprise Information Technology and Applications, Geographic Services Section, Madison, Wisconsin, USA]), and collected data in the field where necessary (Table 1). During model development and validation we included parameters for chemical, physical, biological, morphological, and anthropogenic variables likely to influence milfoil growth (Nichols and Mori 1971, Adams et al. 1978, Carpenter 1980, Madsen 1982, Titus and Stone 1982, Maberly and Spence 1983, Smart and Barko 1986, Smith and Barko 1990) and dispersal (Scales and Bryan 1979, Johnstone et al. 1985, Smith and Barko 1990, Johnson and Carlton 1996) (Table 1). These variables may be categorized as follows: (1) those affecting human lake access, and potentially milfoil dispersal (distance of lakes from highways, type of public boat launch, and number of residences and boat launches on lakes); (2) those influencing milfoil growth conditions, including data measured in individual lakes (fine spatial resolution)—alkalinity, pH, Secchi depth, water color, substrate type, and water source—and across landscapes (coarse spatial resolution)—phosphorus (1:2 000 000), bedrock type (1:250 000), and land use in drainage basin; and (3) those that may attract human lake activity and could affect milfoil growth (lake maximum depth, lake area, littoral zone area, and relative abundance of game fish species). The two fish species included in our analysis, smallmouth bass (*Micropterus dolomieui* Lacepede), and walleye (*Stizostedion vitreum* (Mitchill)), were chosen because they were game species and, therefore, their measured relative abundance was likely correlated with human fishing activity, a potential milfoil dispersal vector; the relative abundance of the two species was relatively uncorrelated ($r < 0.5$); and their geographic distribution covered the milfoil sample area (Becker 1983).

Values for parameters of pH and alkalinity were both obtained from the SWI and STORET databases and measured in the field, using a LaMotte alkalinity test kit (LaMotte Company, Chestertown, Maryland, USA) and a Hanna pH probe (Hanna Instruments, Woonsocket, Rhode Island, USA). The STORET database contained multiple records per sample station, reflecting time and depth series data. Because milfoil grows in the epilimnion, we retained epilimnetic records between 27 April and 5 October. We averaged values for pH and alkalinity over this time period because measurements may vary according to diel and temperature changes, and because sampling dates and times were not standardized throughout the data set. We also averaged values when measurements from multiple sources existed. We calculated lake littoral area by subtracting existing values (SWI) for lake area >6 m deep from total lake area. We used a 6 m threshold depth because the SWI database included a value for lake area >20 ft. which we converted (rounded to a whole number) to SI units. This variable was used in our calculation of lake littoral area.

Categorical data were included in regression models as indicator variables, and the most common category was used as the reference category. Water color was coded as clear (reference class), green, brown due to suspended sediment, and brown due to dissolved tannins. Water color was also coded as a dichotomous variable (clear or not clear) to see whether this was a better classification for model development. Lake water supply was classified using the Wisconsin Department of Natural Resources (1995) system, as drainage (lakes have both inlet and outlet and are primarily fed by stream drainage), seepage (lakes lack both inlet and outlet, and are primarily fed by precipitation or runoff, supplemented by groundwater), spring fed (lakes lack inlet but have outlet, and are primarily fed by groundwater), and drained (lakes lack inlet, have a continuously flowing outlet, and are primarily fed by precipitation and runoff). We recognized three categories of lake boat launches: (1) public launches designed for motor boats (the largest category, including lakes without public launches connected by navigable water to lakes with public motorboat launches); (2) public launches where motorboats were not permitted, or lakes without launches that were accessible to boat trailers from a road; and (3) launches or lakes without launches accessible from private property or from a foot trail. As an alternative classification we coded boat launch as a dichotomous variable: with (categories 1 and 2 above) or without (category 3) public access.

Variables measured as percentages (substrate types, littoral area, and land cover type) were arcsine transformed for analysis (Zar 1984). We log transformed ($\log_{10}$) lake size because it exhibited a large range in measurement that could positively bias its significance in a logistic regression analysis.

We used spatial analysis in a GIS (ARC/INFO; ESRI 1992) to determine phosphorous classification, bedrock type, and distance from highways for lakes. For each lake with known milfoil presence/absence, we obtained lake center coordinates from the U.S. Geological Survey Geographic Names Information database (1:24 000)[4] or from USGS 7.5′ topographic maps (1:24 000). We projected coordinates to the Wisconsin Transverse Mercator coordinate system, and created a GIS coverage of lake centroids (1:24 000). Lake phosphorous (total, unfiltered) classification (1:2 000 000) and bedrock type (1:250 000) beneath each lake were determined by intersecting the lake coverage with respective physical feature coverages. Phosphorus clas-

[4] URL = ⟨http://mapping.usgs.gov/www/gnis⟩

TABLE 1. Data included in logistic regression analysis (data are not transformed; N = 404).

Variable	Units	Source	Classification	Mean ± 1 SE, or percentage of lakes: With milfoil	Mean ± 1 SE, or percentage of lakes: Without milfoil
Eurasian watermilfoil	presence or absence	WDNR, Field	categorical	40%	60%
Lake area	km^2	SWI	continuous	2181.3 ± 395.4	1406.4 ± 246.6
Maximum depth	m	SWI, WDNR	continuous	9.8 ± 0.6	8.9 ± 0.4
Littoral area	percentage of total lake area	SWI	continuous	58.7 ± 1.7	59.0 ± 1.6
Alkalinity ($CaCO_3$)	mg/L	STORET, SWI, Field	continuous	162.8 ± 5.0	99.9 ± 4.4
pH		STORET, SWI, Field	continuous	8.3 ± 0.0	7.7 ± 0.1
Phosphorous class	mg/L	WDNR	ordinal		
<5				0.0%	0.0%
5–9				0.0%	0.0%
10–14				5.7%	24.8%
15–19				2.0%	2.2%
20–24				0.7%	10.9%
25–29				21.8%	6.2%
30–50				0.0%	0.0%
>50				9.9%	15.8%
Secchi depth	m	SWI, Field	continfous	2.3 ± 0.1	2.7 ± 0.1
Water color	presence or absence	SWI, Field	categorical		
Clear				24.6%	34.3%
Green				5.3%	4.6%
Brown–sediment				4.3%	7.6%
Brown–stained				6.3%	12.9%
% Substrate	percentage of total lake area	SWI	continuous		
Sand				32.9 ± 2.1	38.9 ± 2.0
Gravel				14.0 ± 1.4	10.8 ± 1.1
Rock				1.4 ± 0.4	4.3 ± 0.7
Organic				50.7 ± 2.3	45.9 ± 2.2
Bedrock type	presence or absence	WDNR	ordinal		
Igneous/volcanic/metamorphic				4.5%	23.0%
Sandstone				10.6%	26.7%
Carbonate				25.0%	10.2%
% Drainage basin in agriculture	m^2	SWI	continuous	50.4 ± 2.5	29.4 ± 2.1
% Drainage basin forested	m^2	SWI	continuous	17.0 ± 2.5	55.4 ± 2.7
Water source	presence or absence	SWI	categorical		
Drainage				21.3%	26.7%
Seepage				2.0%	1.7%
Spring-fed				5.0%	5.7%
Drained				11.9%	25.7%
Fish species: walleye; smallmouth bass	0) absent	SWI	ordinal	14.6%; 3.0%	25.5%; 6.7%
	1) present			2.2%; 3.5%	1.5%; 5.4%
	2) common			3.0%; 5.7%	2.0%; 10.1%
	3) abundant			0.2%; 7.9%	1.0%; 7.7%
Number of residences	no. residences per lake	SWI, Field	continuous	139.7 ± 19.0	24.9 ± 9.3
Public boat launch	presence or absence	WDNR, DeLorme 1992	categorical		
Motorboats				36.4%	48.3%
Nonmotor				2.5%	3.5%
None				1.2%	8.2%
Distance from highway	km	WDNR	ordinal		
<0.25				4.2%	4.7%
0.25–5				7.7%	6.9%
0.5–1				9.9%	10.4%
1–2				17.6%	36.4%
2–3				0.5%	0.0%
3–4				0.3%	0.7%
3–5				0.0%	0.5%
5–6				0.0%	0.0%
6–7				0.0%	0.3%

Notes: SWI = Surface Water Inventory database, STORET = Storage and Retrieval database, WDNR = Wisconsin Department of Natural Resources, Field = data collected in field. Percentage of fish species in each relative abundance class are reported in the same row, with the value for walleye first.

ses followed Omernick et al. (1991) (Table 1). We ranked bedrock type by chemical weathering capacity (Wisconsin Geological and Natural History Survey 1987) with a higher score indicating greater capacity: (1) igneous/metamorphic/volcanic; (5) sandstone; (10) carbonic. To estimate distance between lakes and highways, we buffered highways (1:100 000) at 0.25 km, at 0.5 km, and at 1 km intervals thereafter, and intersected buffer polygons with lake centroids.

Models

We selected data to develop and to test models using a stratified random sampling approach. The data (N = 404) were stratified into two categories: lakes with (162) and lakes without (242) milfoil present. Half of the lakes in each category were selected randomly and served as a learning data set (N = 202), and the other half were used to validate the model. We refer to this stratified-random use of the 404-lake data set as the All Lakes (AL) model.

Since lack of dispersal opportunity may result in models misclassifying lakes with suitable milfoil habitat, we developed a model using a subset (N = 216; learning and validation data sets, N = 108) of lakes that were likely to have had greater exposure to milfoil dispersal opportunity. For this model, hereafter referred to as the Dispersal Exposure (DE) model, we included all lakes where milfoil was detected in the first two-thirds of the milfoil invasion period in Wisconsin (1967–1985), and lakes that were close (<45 km) to invaded lakes but where milfoil was absent. Forty-five kilometers is the mean distance plus one standard error traveled by recreational boaters based on a WDNR survey (Buchan and Padilla 1998).

Because some data may be unavailable or too costly to obtain, we developed and tested a series of alternative models to determine how well milfoil presence could be predicted without variables that were selected into the best fit AL model (AL-1). We individually removed variables from the data set, repeated our analysis with all 404 records, and compared results across AL models (AL-2 through AL-7). We also built an AL model without interaction terms (AL-7) for comparison with all other AL models that included them.

Analysis

We used logistic regression, which estimates the probability that a defined suite of characters accurately predicts the class of a dichotomous or categorical dependent variable (Press and Wilson 1978, Trexler and Travis 1993), to test whether milfoil presence/absence could be predicted by a suite of the above factors. Logistic regression is a useful analysis tool both because it enables the use of dichotomous data as dependent variables and because, unlike the commonly used linear regression, it does not require multivariate normality and equal covariance matrices. In logistic regression, a logit transformation is used to convert each dichotomous datum to a linear value (logit), e.g., estimating a conditional mean for the dependent variable given a vector of independent parameters. Like linear regression, slope coefficients for independent parameters represent the change in the logit for a change in one unit in a dependent variable. The difference between logit values (log odds ratio) provides a useful measure of association: it approximates the probability for the outcome of interest (milfoil, for example) to be present or absent given the suite of independent parameters.

To develop and test models we used stepwise forward and backward elimination techniques with the logit link in SAS (SAS Institute Inc. 1990). Variables entered the model if their significance level was at least 0.5 and stayed in the model if their significance level was at least 0.05 when tested by the -2 Log Likelihood statistic. We specified a probability threshold of 0.5 for the classification into present or absent categories. After variables were chosen for models, we included first order interaction terms for all combinations of variables except for public boat launches. Stepwise forward and backward techniques were again used to determine combinations of main effects and first order interaction terms that produced the best fit model. If a variable was included in a model as an interaction but not as a main term, we did not reintroduce the main term into the model. This was done to develop the best predictive model possible. As a result, analogous to standard linear regression, the nonsignificance of such main terms may not be inferred, nor may the functional significance of variables be determined from their P values (Hosmer and Lemeshow 1989).

It is important to note that the logistic regression model biases classification into the larger group defined by the dependent variable (Hosmer and Lemeshow 1989). In this analysis, the set of records in which milfoil was absent was 20% larger than the group in which it was present, so the classification was biased towards the absent group. We opted in favor of retaining the largest sample size rather than reducing the amount of data in the absent group to eliminate this potential bias.

Logistic regression models may be evaluated by a number of statistical criteria, including significance of variables, goodness-of-fit, and rates of misclassification error. We used the Wald Chi-square test to evaluate the significance of variables in the models and evaluated models by goodness-of-fit and misclassification statistics. Goodness-of-fit was assessed with the Akaike Information Criterion (AIC) (Hosmer and Lemeshow 1989) which adjusts the Log Likelihood statistic for the number of terms in a model. A lower AIC score indicates a better model fit. The AIC is similar to an adjusted r^2, taking into account the number of variables included in a model when evaluating its performance. We evaluated model predictive capability by the percentage of cases in which observed data were misclassified, including cases in which milfoil was absent but the model predicted milfoil was present (false positive misclassification), and cases in which milfoil was present but the model predicted milfoil was absent (false negative misclassification). While rates of misclassification error do not consider the number of variables included in a model, they are particularly useful for evaluating predictive models. Therefore, we evaluated model performances using both statistical criteria (AIC, rates of misclassification) and costs of model development and application.

Misclassification statistics can be misleading because they reflect a process that created a dichotomous variable from a continuous linear function (logit values) based on an arbitrary threshold value. Since many logit values may be close to the threshold chosen to classify the logit values into presence/absence categories, the choice of the threshold value could have a large influence on model accuracy. Therefore, we explored model sensitivity to the threshold value (0.50), changing it by ±5% (0.525 and 0.475). We further tested model robustness by treating the validation data set as a new data set for model development.

Data sampled across geographic areas are often spatially autocorrelated, and when included in regression analyses, they violate the assumption that data are independent. In such cases the standard formula used to calculate variance (mean square error) is incorrect, and the effect is to attribute greater significance to variables than exists, and to allow too many significant terms to enter a model (Legendre 1993). Spatial autocorrelation may be detected and removed from some models, e.g., multiple regression; however, it cannot be removed from logistic regression models (Cressie 1993). Nevertheless, by examining whether residuals generated from logistic regression analyses exhibit spatial autocorrelation the potential magnitude of this effect can be quantified and P values for variables included in models can be conservatively interpreted to take the effect of spatial autocorrelation into account. Therefore, we examined Pearson and deviance residuals for spatial autocorrelation by generating correlograms using maximum distances of 25–250 km (Legendre and Fortin 1989).

Results

Correlograms calculated for regression residuals did not exhibit strong spatial autocorrelation ($\rho < 0.3$) when maximum distance was ≥75 km. Residuals from data points located <25 km apart were more correlated ($\rho \leq 0.5$), but no positive or negative trend was observed. Therefore we did not consider the model assumption of data independence to be violated.

Results from model development for the AL models and the DE model are summarized in Table 2. Stepwise forward and backward selection processes converged on very similar models. Therefore, we report only results from stepwise forward regressions. The AL-1 model had the lowest AIC score and provided the best fit to the data based on the function

$$\begin{aligned}\mathrm{Logit}(p) = {} & -4.0618 - 3.9644F + 0.0339AW \\ & + 0.3604FB + 3.3230BL - 0.5883BW \\ & + 0.00917A \qquad (1)\end{aligned}$$

where p is the probability of milfoil occurrence, F is percent forest cover in a drainage basin, AW is alkalinity × walleye abundance, FB is percent forest cover × bedrock type, BL is presence of a public boat launch, BW is bedrock × walleye abundance, and A is alkalinity. Using the parameter estimates reported in Table 2, all other models may be reconstructed as shown in Eq. 1. The probability that a lake will contain milfoil may be calculated using the following equation:

$$p = \frac{e^{\mathrm{logit}(p)}}{1 + e^{\mathrm{logit}(p)}} \qquad (2)$$

and classifying values according to a specified threshold value.

Using the data set of lakes likely to have had the longest exposure to milfoil, stepwise forward logistic regression converged on a model (DE) that included only two terms found in the AL-1 model, percent forest cover, and percent forest cover × bedrock, and of all models, was the only one that did not include presence of a public boat launch (Table 2). Because a different set of data were used to develop the DE model we can compare only model predictive capability (not parameter estimates) to the AL models. For model development (Table 3), the percentage of false positive misclassification for the DE model was an improvement over similar values for the AL models; however the percentage of false negative misclassification was on the high end of the range for the AL models. For model validation, the percentage of false positive misclassification for DE model validation was on the high end of the range, and the percentage of false negative misclassification was almost twice the worst rates for the AL models (Table 3).

In addition to splitting our data for the purpose of model development and validation, we further tested AL model robustness by treating the validation data set as a new data set for model development. The AL robustness test model (detailed results not shown) included three of the same terms (percent forest cover, presence of a public motor boat launch, and percent forest cover × bedrock) as the AL-1 model and included bedrock type as a main effect. Because the rates of false negative (14.0%) and false positive (26.1%) misclassification of the robustness test model fell within the range of the AL models, we considered them to be robust.

Most models were insensitive (<3% change in rates of misclassification errors) to a ±5% change in the threshold value. However, several models (develop-

TABLE 2. Parameter estimates for logistic regression models predicting the presence and absence of Eurasian watermilfoil in Wisconsin lakes.

Model variables	AL-1 (best fit)	AL-2 {−Alkalinity}	AL-3 {−Public boat launch}	AL-4 {−% Forest}	AL-5 {−Bedrock}	AL-6 {−Walleye}	AL-7 {−Interactions}	DE
Intercept	−4.06 ± 1.19 (0.0006) [0.017]	−2.55 ± 1.05 (0.0148) [0.078]	−0.50 ± 0.33 (0.1267) [0.604]	−4.72 ± 1.11 (0.0001) [0.009]	−4.64 ± 1.20 (0.0001) [0.010]	−3.69 ± 1.11 (0.0009) [0.025]	−4.80 ± 1.22 (0.0001) [0.008]	−0.62 ± 1.10 (0.5754) [0.541]
% Forest	−3.96 ± 0.86 (0.0001) [0.02]	−4.08 ± 0.79 (0.0001) [0.02]	−3.82 ± 0.82 (0.0001) [0.02]	NE	−1.65 ± 0.34 (0.0001) [0.19]	−1.64 ± 0.34 (0.0001) [0.19]	−1.68 ± 0.34 (0.0001) [0.19]	−36.73 ± 11.28 (0.0010) [0.00]
Public boat launch	3.32 ± 1.08 (0.0020) [27.74]	3.26 ± 1.06 (0.0020) [26.03]	NE	3.05 ± 1.08 (0.0047) [21.11]	3.30 ± 1.10 (0.0028) [27.00]	3.35 ± 1.08 (0.0020) [28.37]	3.34 ± 1.11 (0.0026) [28.21]	NS
Alkalinity	0.01 ± 0.00 (0.0050) [1.01]	NE	NS	NS	0.01 ± 0.00 (0.0001) [1.01]	NS	0.01 ± 0.00 (0.0001) [1.01]	NS
% OM	NS	NS	NS	NS	NS	NS	NS	−15.22 ± 4.63 (0.0010) [0.00]
Walleye abundance	NS	NS	NS	NS	NS	NE	0.54 ± 0.25 (0.0288) [1.71]	NS
Smallmouth bass abundance	NS	NS	NS	NS	NS	NS	NS	1.11 ± 0.33 (0.0008) [3.04]
Bedrock type	NS	NS	NS	NS	NS	NS	NS	1.85 ± 0.55 (0.0008) [6.35]
Alkalinity × Bedrock	NS	NE	NS	0.001 ± 0.00 (0.0001) [1.00]	NE	0.001 ± 0.00 (0.0001) [1.00]	NE	−0.01 ± 0.00 (0.0019) [1.00]
% Forest × Bedrock	0.36 ± 0.11 (0.0009) [1.43]	0.40 ± 0.10 (0.0001) [1.49]	0.35 ± 0.10 (0.0004) [1.42]	NE	NE	NS	NE	1.76 ± 0.65 (0.0070) [5.82]
% Forest × Alkalinity	NS	NE	NS	NE	NS	NS	NE	0.09 ± 0.03 (0.0052) [1.10]
Bedrock × Walleye	−0.59 ± 0.19 (0.0020) [0.56]	NS	−0.50 ± 0.18 (0.0041) [0.60]	NS	NE	NE	NE	NS
% OM × Walleye	NS	NS	NS	1.13 ± 0.38 (0.0031) [3.08]	1.05 ± 0.46 (0.0200) [2.87]	NE	NE	NS
Alkalinity × Walleye	0.03 ± 0.01 (0.0003) [1.03]	NE	0.03 ± 0.01 (0.0002) [1.03]	NS	NS	NE	NE	NS
Alkalinity × Smallmouth bass	NS	NE	0.003 ± 0.00 (0.0015) [1.00]	NS	NS	NS	NE	NS
Alkalinity × % OM	NS	NS	NS	NS	NS	NS	NS	0.06 ± 0.02 (0.0040) [1.06]

Notes: For each variable and model, the following are provided: maximum likelihood parameter estimates ± 1 SE (top value in column); Wald chi-square *P* values (a measure of parameter significance, alpha ≤ 0.05) (middle value; in parentheses); and odds ratio (a measure of association that approximates the likelihood of the outcome modeled, e.g., Eurasian watermilfoil presence, given an additional unit of a variable [Hosmer and Lemeshow 1989]) (bottom value; in brackets). First-order interaction terms are noted as the product of two variables. Terms in braces prefaced by a minus sign in column headings indicate removal of respective variables and associated interaction terms from model development. NS = not selected into model, NE = not entered into model. Sample sizes for model development and validation were equal: all-lakes data set (AL models) N = 202; dispersal exposure data set (DE model) N = 108. Abbreviations: % OM = percentage of organic matter in substrate, % Forest = percent forest cover in drainage basin.

TABLE 3. Results of logistic regression model development and validation.

Statistic	AL-1 (best fit)	AL-2 {−Alkalinity}	AL-3 {−Public boat launch}	AL-4 {−%Forest}	AL-5 {−Bedrock}	AL-6 {−Walleye}	AL-7 {−Interactions}	DE
Model development								
Akaike Information Criterion	176.51	197.76	190.27	213.94	194.37	195.13	195.68	84.07
Misclassified (%)								
False positive	28.6	32.4	27.6	25.8	32.3	30.5	33.3	14.7
False negative	10.6	10.3	15.7	23.5	21.3	20.0	22.3	20.0
Change in percentage misclassified								
False positive	−2.8, 0	−1.3, 0	−3.5, +0.8	−3.6, +1.0	−1.6, +0.1	−4.8, +2.1	−1.7, −1.1	+4.7, +6.1
False negative	+0.4, 0	−0.2, 0	−0.8, +0.1	−0.5, −1.4	+1.4, −1.5	+0.3, −0.2	+0.7, −3.2	+4.3, −1.2
Model validation								
Misclassified (%)								
False positive	25.8	29.0	34.4	28.4	29.1	25.6	29.5	33.3
False negative	11.0	5.3	1.3	21.9	20.3	18.5	21.0	40.9
Change in percentage misclassified								
False positive	−1.4, +0.5	−4.6, 0	0, 0	−1.6, −0.4	−0.5, −1.1	−1.6, −0.3	−0.1, +2.9	0, +1.1
False negative	+0.6, −0.7	+6.3, 0	0, 0	+0.2, −0.6	+0.5, −2.0	+0.4, −2.5	+3.6, +3.2	0, +1.2

Notes: Percentage misclassification is included for both model development and validation, but Aikake Information Criteria (AIC) only reflect model development goodness-of-fit. Lower values for AIC represent better model fit; lower percentage misclassification represents better model predictive capacity. Sample sizes for model development and validation were equal: all lakes data set (AL models), $N = 202$; dispersal exposure data set (DE model), $N = 108$. Terms in braces prefaced by a minus sign in column headings indicate removal of respective variables and associated interaction terms from model development. The percentage misclassified refers to misclassifications of records, based on a 0.5 threshold for classifying logit values as Eurasian watermilfoil presence/absence; change in the percentages misclassified are based on changing threshold value ± 5%.

ment data set unless noted) responded more strongly to the increase in the threshold value. Rates of false positive or false negative misclassification changed >3% for models: AL-3 (without data for boat launches), AL-4 (without percent forest cover), AL-6 (without walleye abundance), AL-2 (without alkalinity; validation set), and the DE model. Only the AL-7 model (without interaction terms) and the DE model responded to the decrease in the classification threshold.

The odds ratios for each of the variables were relatively constant across all models (Table 2). Presence of a public boat launch exhibited the largest range in the odds ratio, reflecting predictions that lakes with public boat launches were 21–28 times more likely to have milfoil present than lakes without public boat launches. Odds ratios for percent forest cover in a watershed basin ranged from 0.20–0.02, reflecting a prediction that lakes in watershed basins with one percent more forest cover were 5–50 times less likely to become infested by milfoil than lakes with one percent less forest cover in watershed basins.

DISCUSSION

Invasions of aquatic communities by exotic species can lead to extensive ecological changes in community structure and function (Mooney and Drake 1986, Drake et al. 1989, Lodge 1993, McKnight 1993, Mills et al. 1993, Karatayev et al. 1997). To limit the range or slow the rate of spread of an invasive species such as Eurasian watermilfoil we need to improve our understanding of the parameters affecting its survival and dispersal (Hengeveld 1988, 1994, Kareiva 1990, Reichelt et al. 1990, Buchan and Padilla 1998). This is particularly true in the Great Lakes region where monitoring to detect invasives is a costly and difficult process due to the abundance of lakes and streams, and the high frequency of recreational boating activity. Models such as ours that predict invasion likelihood using readily available data will be valuable tools for increasing efficiency of monitoring for aquatic invasions.

Importance of variables

We found that variables associated with water quality characteristics important for milfoil growth, especially those that affect dissolved carbon, were the most important factors affecting the probability of finding milfoil in a given lake for all of our models. Percent forest cover in a lake's drainage basin was the most important term both because it was highly significant in every model and because when deliberately eliminated, the model had the highest AIC score. Nilsson and Hakanson (1992) also found land cover type to be the most important determinant of water chemistry in Swedish lakes. They concluded that bedrock geology was not an important determinant of water chemistry in their study due to the low weathering rates caused by the

Swedish climate. Other studies investigating lakes in the midwest and northeast United States (Newton et al. 1987, Rapp et al. 1987) have found bedrock and surficial geology to be important factors governing water chemistry, including alkalinity. Local groundwater inputs have also been found important in regulating milfoil growth and distribution (Lillie and Barko 1990).

The potential for the rate of inorganic carbon availability to limit the rate of milfoil growth is well documented (Maberly and Spence 1983, Barko et al. 1986, Smith and Barko 1990). In our analysis, alkalinity was an important variable because it entered all models as either a main term or as an interaction term, and its removal (AL-2 model) had the second greatest effect on the AIC score. The AL-2 was the only model in our analysis in which no new terms were added when alkalinity was eliminated, indicating that coarse resolution landscape variables such as bedrock type, and percent forest cover to a lesser extent, are correlates of ($r = 0.61$ and $r = -0.31$ respectively), and substitute measures of alkalinity. The inclusion of at least two of these variables as either main or interaction terms in our models supports the importance of inorganic carbon as a factor influencing milfoil growth, and demonstrates the ability to represent this factor using both fine resolution lake measurements, and correlated landscape data that are both publicly available and less expensive. The fact that bedrock type was not an important main term but was often included as an interaction term in our models may be more related to its correlation with alkalinity and percent forest cover ($r = -0.40$) than to the data resolution or the classification we used.

Despite studies showing that milfoil is unlikely to be limited by lake phosphorus concentration (Barko and Smart 1980, Carignan and Kalff 1980, Mesner and Narf 1987), we included this variable in our analysis because it reflects trophic conditions known to influence milfoil growth (Nichols and Shaw 1986) and because Omernick et al. (1991) delineated phosphorus regions based on several factors known to influence milfoil growth conditions: surficial and bedrock geology, soils, vegetation, land use, and land-surface form. Similar to other variables of coarse resolution not included in our models, both the relatively coarse resolution of the phosphorus data, and/or the correlation to other variables included in the model may have contributed to the insignificance of this variable.

Percent organic matter in sediment, another variable known to limit milfoil growth (Nichols and Mori 1971, Madsen 1982), was one of the least two important variables in our analysis. Despite lake-level measurement, the lack of significance of this variable relative to others may also be related to data resolution and accuracy.

Although Nichols and Buchan (1997) found that other (nonmilfoil) macrophyte species were useful indicators of milfoil habitat suitability, we found that the best-fit model, using a subset of data including lakes field-surveyed for nonmilfoil macrophyte species, did not include the macrophyte variable, nor any variables different than those included in the AL-1 model. A larger data set may be required to detect the importance of other macrophyte species.

In our analysis, variables indicating human lake access were poorer predictors of milfoil presence/absence than those affecting milfoil growth. Presence of a public boat launch was the only variable in this category included in any of our models. Despite being included in all of the AL models, the public boat launch variable was less significant than either alkalinity or percent forest cover, and its removal had the least impact on model fit. Based on this result it is impossible to evaluate the relative ecological importance of variables affecting milfoil growth versus those affecting human access and thus milfoil dispersal. Nor can we conclude that public boat launch access will be a less important predictor in other studies using data of different resolution and accuracy, or that it is a less ecologically significant variable. The relatively lower statistical significance of public boat launch access in our analysis could have resulted from the accuracy of our data, and/or it may indicate the need to identify a data source(s) and scale(s) that better describe human activities related to milfoil dispersal. For example, we did not have enough data on the number of private boat launches on lakes and thus could not include this variable in our model development, however, such information could contribute to the dispersal aspect of predicting milfoil invasion.

Relative abundance of the two game fish species, walleye and smallmouth bass, were less important than variables that would directly influence milfoil growth conditions, and than those directly indicating human access. Walleye abundance was included as a main term in only one model but appeared in most models an interaction term, most significantly when included with alkalinity. In comparison to other models, the removal of fish variables had a moderately negative effect on the AIC score. Smallmouth bass abundance was one of the least important variables, rarely being included in models. Clearly the relative abundance of game fish species is potentially a useful indicator of human fishing activity. There may be, however, data sets that measure such activity more accurately, e.g., creel surveys, or surveys of fishing derbies and recreational boater activity.

In all cases, statistical significance of variables included in models does not necessarily imply ecological significance or causative factors. Correlations need not imply causation, as model variable selection may be influenced by the spatial and/or temporal resolution of parameter measurement, presence of other correlated variables, and/or absence of other variables that could be powerful predictors. Similarly, the presence of interaction terms in models precludes drawing conclusions about the significance or lack of significance of main factors, analogous to interaction terms in linear regression and analysis of variance.

Since variables included in our analysis were largely based on studies demonstrating their importance for milfoil growth and dispersal from the Laurentian Great Lakes region, North America, and Europe, we expect that our models may be applied in such areas, provided that parameter estimates are adapted to local conditions, and that the relative importance of variables will likely remain similar to the relationships discussed in our analysis. Our modeling approach should certainly be useful in such regions.

Model sensitivity

The value chosen as the classification threshold for logistic regression influences the rates of misclassification error. We found that, with few exceptions (Table 3), most models were not sensitive to a ±5% shift in the classification threshold. Therefore, small errors in data collection and/or estimates will probably not have large impacts on model predictions.

Misclassification error may not be attributed to model fit alone, because a proportion of misclassification errors could have resulted from errors in the milfoil presence/absence data, e.g., surveys might have mistakenly identified milfoil plants, or not observed them in the field. Misidentification, unless biased in one direction, would add noise to the data, but would not bias the results. However, lack of observation would result in a higher rate of false positive misclassification error. Rates of false positive misclassification may also be high because milfoil may not have had the opportunity to disperse to some lakes that provide suitable habitat. It is more likely that errors in our data set resulted from misidentification, and therefore, we do not believe that model misclassification errors are significantly biased. The low rate of false negative misclassification for the model without alkalinity (AL-2) could be explained if the range of alkalinity used in this analysis did not adequately represent the extremes where this variable determines milfoil absence or presence. The low rate of false negative misclassification when validating the model in which boat launch data were eliminated (AL-3) likely reflects the fact that milfoil existed in four of 18 lakes without public boat launches. In each of these cases, fishing was common from private boat launches and/or lake residents had visited other lakes with their boats (lake residents, *personal communication*).

Model evaluation and alternative management strategies

Choosing the best model to predict the likelihood of milfoil invasion depends on management objectives and constraints; managers may need to balance the objective of preventing further invasions with costs involved in monitoring large numbers of lakes. Monitoring costs may be considered both in terms of time involved to monitor a large number of lakes, and the expense of obtaining measurements of variables to include in models. Unless expensive variables substantially improve the accuracy of model predictions, their cost may not be justified. Typically, variables such as bedrock, substrate, and land use type, and public boat launch location exist in publicly available databases, and are therefore inexpensive to include in models. Fish abundance and, to a lesser extent, lake alkalinity data are less likely to be available for all lakes, and because these variables must be measured in individual lakes, they are more expensive.

Decisions about what is the best model or which are the best variables to include will depend on specific management objectives and priorities as well as limitations. Given our information on the relative effectiveness of different models with different variables we can make recommendations of the best models to use given different management objectives or constraints.

Management objective: preventing any further invasions

If a prime concern is to prevent milfoil from invading more lakes, and monitoring cost is less important, a manager should choose a model with a low rate of false negative misclassification. Lowest mean rates of false negative misclassification were achieved by the AL-1 model (11.0%) and by the AL-2 (7.8%) and AL-3 (8.5%) models.

Since mean rates of false positive misclassification error for both development and validation data sets for these three models (24.0–31.4%) did not vary as much as the mean rates of false negative misclassification, choosing any of these models would not incur significantly greater costs in terms of monitoring time. With the exception of the AL-2 model, these models were costly in terms of the fine-resolution input data required to run the models. The AL-2 model was the most parsimonious, including only three terms and three data sources: the percent of the watershed forested, presence and type of public boat launch, and percent forest × bedrock type.

For the purpose of predicting where milfoil is most likely to establish, the significance of variables in a model is not as great a concern as the rates of misclassification error. However, if managers are interested in determining the strength of the relationship between individual variables and the likelihood of milfoil establishment, it is important for them to examine goodness-of-fit scores and individual P values. The AL-1 model had the lowest goodness-of-fit score, indicating that, collectively, variables included in this model had the greatest significance. The AL-3 model had the second lowest AIC score, whereas the score for the AL-2 model was on the upper end of the range for all models, indicating a weaker relationship between the parameter estimates and the likelihood of milfoil establishment.

Management objective: reducing monitoring costs

If resource managers want to reduce the amount of time spent monitoring lakes and can accept a higher risk of undetected invasions occurring, then it is appropriate to use a model with lower rates of false positive misclassification and higher rates of false negative misclassification. Choosing a better model on this basis alone was not as clear an objective to meet, because mean rates of false positive misclassification did not vary as much as mean rates of false negative misclassification. However the AL-1, AL-4, AL-6, and DE models, had the lowest mean rates of false positive misclassification. The least expensive model to use would be the AL-2; which included percent of watershed forested, public boat launch presence, and bedrock type; followed by the AL-6 which included additionally alkalinity. The AL-2 would also be the preferable to the AL-6 model due to its lower rate of false negative misclassification, and only slightly higher AIC score.

Management objective: preventing most invasions and keeping monitoring costs at a moderate level

An alternative strategy that balances the costs and benefits of each type of misclassification error is to choose a model with moderate rates of false positive and negative misclassification errors and few expensive landscape variables. The AL-2 model again fulfills this management criteria because it includes few, inexpensive variables, has relatively low rates of false negative misclassification, and its mean rate of false positive misclassification, though on the upper end of the range for all models, does not greatly differ from other models.

Conclusions

We developed and compared alternative models to predict habitats that are most likely to support milfoil growth and to indicate which variables have the greatest predictive power. Our research shows that inexpensive landscape data, typically available in databases managed by state resource management agencies, can be used to develop predictions of habitat suitability for an invasive species like milfoil. By using a logistic regression model, we were able to establish likelihoods that individual lakes will support milfoil growth. Factors associated with water quality known to affect milfoil growth, especially the percent forest cover in lake watersheds, were more important predictors than factors primarily associated with human activity and dispersal potential. Because these factors are generally important for milfoil growth, our results should be generalizable across similar landscapes throughout the Laurentian Great Lakes region and other parts of the world with similar habitats. Application of our logistic regression models may be used to prioritize which lakes need to be monitored most intensively and frequently. The model converged on by stepwise forward logistic regression provided the best fit to the data. However, the model without alkalinity (AL-2) included fewer variables that were both relatively inexpensive and easy to obtain, and also resulted in low rates of misclassification. For each management objective, using the AL-2 model as a management tool in Wisconsin would result in the lowest risk of undetected invasions at the lowest cost. The same may not be true, however, when the regression models are applied in other regions; resource managers may have to choose between models depending on the prioritization of monitoring budget versus invasion risk.

If used in conjunction with interlake dispersal dynamics, the AL-2 model would be an even more powerful management tool. Patterns of milfoil habitat suitability among lakes can serve as a backdrop on which patterns of dispersal dynamics are mapped or they can be directly incorporated into models as factors influencing dispersal success (Buchan 1997). Lakes with the greatest risk of being invaded will be those with the highest likelihood of both providing suitable milfoil habitat and being recipients of the greatest frequency of recreational boater traffic (Buchan 1997).

Acknowledgments

We gratefully thank S. Nichols for his help identifying field specimens, and his useful discussion; S. Nichols, M. Clayton, J. Magnuson, M. Turner, and S. Ventura for comments on a previous version of this manuscript; J. Bode for helping obtain field equipment and support from the WDNR; the UW–Madison Limnology Center for providing field equipment; M. Clayton for helpful statistical advice; C. Tiegs for her assistance in retrieving data from the STORET and SWI databases; and J. Myers for facilitating L. A. J. Buchan's visit to the University of British Columbia. We express our appreciation to the many landowners in Wisconsin who allowed us to access lakes through their property. We also thank D. Lodge and several anonymous reviewers for their constructive comments on this manuscript. Fieldwork was partially funded by grants to L. A. J. Buchan from the Anna Grant Birge Foundation and the Wisconsin Department of Natural Resources. D. K. Padilla would like to thank the director and staff of the Friday Harbor Laboratories for support during the writing of this manuscript. This research was supported by grants from WARF to D. K. Padilla and the University of Wisconsin Sea Grant Institute under grants from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, and from the State of Wisconsin. Federal grants NA90AA-D-SG469, NA46RG048, NA116RG0531-01 and R/LR65 to D. K. Padilla.

Literature Cited

Adams, M. S., P. Guilizzoni, and S. Adams. 1978. Relationship of dissolved inorganic carbon to macrophyte photosynthesis in some Italian lakes. Limnology and Oceanography **23**:912–919.

Barko, J. W., M. S. Adams, and N. L. Clesceri. 1986. Environmental factors and their consideration in the management of submersed aquatic vegetation: a review. Journal of Aquatic Plant Management **24**:1–10.

Barko, J. W., and R. M. Smart. 1980. Mobilization of sediment phosphorus by submersed freshwater macrophytes. Freshwater Biology **10**:229–235.

Bates, A. L., E. R. Burns, and D. H. Webb. 1985. Eurasian watermilfoil (*Myriophyllum spicatum* L.) in the Tennessee valley: an update on biology and control. Pages 104–115 *in* L. W. J. Anderson, editor. Proceedings, first international symposium on watermilfoil (*Myriophyllum spicatum*) and related Haloragaceae species. Aquatic Plant Management Society, Washington D.C., USA.

Becker, G. C. 1983. Fishes of Wisconsin. University of Wisconsin Press, Madison, Wisconsin, USA.

Buchan, L. A. J. 1997. Predicting invasion patterns of nonindigenous aquatic species. Dissertation. University of Wisconsin-Madison, Madison, Wisconsin, USA.

Buchan, L. A. J., and D. K. Padilla. 1998. Estimating the probability of long distance dispersal of invading aquatic species. Ecological Applications **9**:254–265.

Carignan, R., and J. Kalff. 1980. Phosphorus sources for aquatic weeds: water or sediment. Science **207**:987–989.

Carpenter, S. R. 1980. The decline of *Myriophyllum spicatum* in a eutrophic Wisconsin lake. Canadian Journal of Botany **58**:527–534.

Couch, R., and E. Nelson. 1985. *Myriophyllum spicatum* in North America. Pages 8–18 *in* L. W. J. Anderson, editor. Proceedings, first international symposium on watermilfoil (*Myriophyllum spicatum*) and related Haloragaceae species. Aquatic Plant Management Society, Washington District of Columbia, USA.

Cressie, N. A. C. 1993. Statistics for spatial data, revised edition. John Wiley and Sons, New York, New York, USA.

DeLorme, M. 1992. Wisconsin atlas and gazetteer. DeLorme Mapping, Freeport, Maine, USA.

Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. 1989. Biological invasions. A global perspective. John Wiley and Sons, Chichester, UK.

Engels, S. 1997. Status of Eurasian watermilfoil in Wisconsin. Wisconsin Department of Natural Resources, Madison, Wisconsin, USA.

ESRI (Environmental Systems Research Institute). ARC/INFO. Version 7.0. Environmental Systems Research Institute, Redlands, California, USA.

Frodge, J. D., G. L. Thomas, and G. B. Pauley. 1990. Effects of canopy formation by floating and submergent aquatic macrophytes on the water quality of two shallow Pacific Northwest lakes. Aquatic Botany **38**:231–248.

Frodge, J. D., G. L. Thomas, and G. B. Pauley. 1991. Sediment phosphorus loading beneath dense canopies of aquatic macrophytes. Lake and Reservoir Management **1**:61–71.

Gibbons, M. V., H. L. Gibbons, Jr., and R. E. Pine. 1987. An evaluation of a floating mechanical rototiller for Eurasian water milfoil control. Washington State Department of Ecology, Water Quality Program, Olympia, Washington, USA.

Grace, J. B., and R. G. Wetzel. 1978. The production biology of Eurasian watermilfoil (*Myriophyllum spicatum* L.) : a review. Journal of Aquatic Plant Management **16**:1–11.

Gross, E. M., H. Meyer, and G. Schiling. 1996. Release and ecological impact of algicidal hydrolysable polyphenols in *Myriophyllum spicatum.* Phytochemistry **41**:133–138.

Gross, E. M., and R. Sutfeld. 1994. Polyphenols with algicidal activity in the submerged macrophyte *Myriophyllum spicatum* L. Acta Horticulturae **381**:710–716.

Hartleb, C. F., J. D. Madsen, and C. W. Boylen. 1993. Environmental factors affecting seed germination in *Myriophyllum spicatum* L. Aquatic Botany **45**:15–25.

Hengeveld, R. 1988. Mechanisms of biological invasions. Journal of Biogeography **15**:819–828.

Hengeveld, R. 1994. Small-step invasion research. Trends in Ecology and Evolution **9**:339–342.

Heywood, B. H. 1989. Patterns, extents and modes of invasions by terrestrial plants. Pages 31–60 *in* J. A. Drake et al., editors. Biological invasions: a global perspective. John Wiley & Sons, New York, New York, USA.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley & Sons, New York, New York, USA.

Johnson, L. E., and J. T. Carlton. 1996. Post-establishment spread in large-scale invasions: the relative roles of leading natural and human-mediated dispersal mechanisms of the zebra mussel, *Dreissena polymorpha.* Ecology **77**:1686–1690.

Johnstone, I. M., B. T. Coffey, and C. Howard-Williams. 1985. The role of recreational boat traffic in interlake dispersal of macrophytes: A New Zealand case study. Journal of Environmental Management **20**:263–279.

Karatayev, A. Y., L. E. Burlakova, and D. K. Padilla. 1997. The effects of *Dreissena polymorpha* (Pallas) invasion on aquatic communities in eastern Europe. Journal of Shellfish Research **16**:187–203.

Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. Philosophical Transactions of the Royal Society of London B **330**:175–190.

Keast, A. 1984. The introduced aquatic macrophyte, *Myriophyllum spicatum,* as habitat for fish and their invertebrate prey. Canadian Journal of Zoology **62**:1289–1303.

Koutnik, M. A., and D. K. Padilla. 1994. Predicting the spatial distribution of *Dreissena polymorpha* (Zebra Mussel) among inland lakes of Wisconsin: modeling with GIS. Canadian Journal of Fisheries and Aquatic Sciences **51**:1189–1198.

Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? Ecology **74**:1659–1673.

Legendre, P., and M.-J. Fortin. 1989. Spatial pattern and ecological analysis. Vegetatio **80**:107–138.

Lillie, R. A., and J. W. Barko. 1990. Influence of sediment and groundwater on the distribution and biomass of *Myriophyllum spicatum* in Devil's Lake, Wisconsin. Journal of Freshwater Ecology **5**:417–426.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8**:133–137.

Maberly, S. C., and D. H. N. Spence. 1983. Photosynthetic inorganic carbon use by freshwater plants. Journal of Ecology **71**:705–724.

Madsen, J. D. 1982. The aquatic macrophyte communities of two trout streams in Wisconsin. Thesis. University of Wisconsin, Madison, Wisconsin, USA.

Madsen, J. D., L. W. Eichler, and C. W. Boylen. 1988. Vegetative spread of Eurasian watermilfoil in Lake George, New York. Journal of Aquatic Plant Management **26**:47–50.

Madsen, J. W., J. W. Sutherland, J. A. Bloomfield, L. W. Eichler, and C. W. Boylen. 1991. The decline of native vegetation under dense Eurasian watermilfoil canopies. Journal of Aquatic Plant Management **29**:94–99.

McKnight, B. N. 1993. Biological pollution. Indiana Academy of Science, Bloomington, Indiana, USA.

Mesner, N., and R. Narf. 1987. Alum injection into sediments for phosphorus inactivation and macrophyte control. Lake and Reservoir Management 3:256–265.

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. Journal of Great Lakes Research **19**:1–54.

Moody, M. E., and R. N. Mack 1988. The spread of plant invasions: the importance of nascent foci. Journal of Applied Ecology **25**:1009–1021.

Mooney, H. A., and J. A. Drake. 1986. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, New York, USA.

Newton, R. M., J. Weintraub, and R. April. 1987. The relationship between surface water chemistry and geology in the North Branch of the Moose River: Biogeochemistry **3**: 21–35.

Nichols, S. A., and L. A. J. Buchan. 1997. Assessing the use of native submersed macrophytes as indicators of suitable Eurasian watermilfoil (*Myriophyllum spicatum* L.) habitat in Wisconsin lakes. Journal of Aquatic Plant Management **35**:21–24.

Nichols, S. A., and S. Mori. 1971. The littoral macrophyte vegetation of Lake Wingra. Transactions of the Wisconsin Academy of Sciences, Arts and Letters **59**:107–119.

Nichols, S. A., and B. A. Shaw. 1986. Ecological life histories of the three aquatic nuisance plants, *Myriophyllum spicatum, Potamogeton crispus* and *Elodia canadensis.* Hydrobiologia **131**:3–21.

Nilsson, A., and L. Hakanson. 1992. Relationships between drainage area characteristics and lake water quality. Environmental Geology and Water Sciences **19**:75–81.

Omernick, J. M., C. M. Rohm, R. A. Lillie, and N. Mesner. 1991. Usefulness of natural regions for lake management: analysis of variation among lakes in northwestern Wisconsin, USA. Environmental Management **15**:281–293.

Press, J. S., and S. Wilson. 1978. Choosing between logistic regression and discriminant analysis. Journal of the American Statistical Association **73**:699–705.

Ramcharan, C. W., D. K. Padilla, and S. I. Dodson. 1992. Models to predict potential occurrence and density of the zebra mussel, *Dreissena polymorpha.* Canadian Journal of Fisheries and Aquatic Sciences **49**:2611–2620.

Rapp, G., Jr., B. Liukkonen, J. Allert, J. Sorensen, G. Glass, and O. Loucks. 1987. Geologic and atmospheric input factors affecting watershed chemistry in upper Michigan. Environmental Geology and Water Sciences **9**:155–171.

Reichelt, R. E., R. H. Bradbury, and P. J. Moran. 1990. The crown-of-thorns starfish, *Acanthaster planci,* on the Great Barrier Reef. Mathematical Computer Modeling **13**:45–60.

SAS Institute, Incorporated. 1990. SAS/STAT User's Guide, version 6. SAS Institute, Inc., Cary, North Carolina, USA.

Scales, P., and A. Bryan. 1979. Transport of *Myriophyllum spicatum* fragments by boaters and assessment of the 1978 boat quarantine program. Water Investigations Branch, Ministry of Environment, Victoria, British Columbia, Canada.

Smart, R. M., and J. W. Barko. 1986. Effects of water chemistry on aquatic plants: growth and photosynthesis of *Myriophyllum spicatum* L. Environmental Laboratory, U.S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi, USA.

Smith, C. S., and J. W. Barko. 1990. Ecology of Eurasian watermilfoil. Journal of Aquatic Plant Management **28**:55–64.

Titus, J. E., and W. H. Stone. 1982. Photosynthetic response of two submersed macrophytes to dissolved inorganic carbon concentration and pH. Limnology and Oceanography **27**:151–160.

Trexler, J. C., and J. Travis. 1993. Nontraditional regression analyses. Ecology **74**:1629–1637.

Truelson, R. L. 1985. Community and government cooperation in control of Eurasian watermilfoil in Cultus Lake, BC. Pages 154–162 *in* L. W. J. Anderson, editor. Proceedings, first international symposium on watermilfoil (*Myriophyllum spicatum*) and related Haloragaceae Species. Aquatic Plant Management Society, Washington, D.C., USA.

U.S. Congress, Office of Technology Assessment. 1993. Harmful nonindigenous species in the United States. Office of Technology Assessment Report OTA-F-565, U.S. Printing Office, Washington, D.C., USA.

Wisconsin Department of Natural Resources. 1995. Wisconsin Lakes. Publication Publ-FM-800 95Rev. Bureau of Water Resources–Lakes Section, and Bureau of Fisheries Management–Aquatic Education Section, Madison, Wisconsin, USA.

Wisconsin Geological and Natural History Survey. 1987. Groundwater contamination susceptibility in Wisconsin. Wisconsin Department of Natural Resources and the Wisconsin Geological and Natural History Survey, Madison, Wisconsin, USA.

Zar, J. H. 1984. Biostatistical analysis. Second edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.