Forecasting the Spread of Invasive Rainbow Smelt in the Laurentian Great Lakes Region of North America

NORMAN MERCADO-SILVA,*‡ JULIAN D. OLDEN,* JEFFREY T. MAXTED,* THOMAS R. HRABIK,† AND M. JAKE VANDER ZANDEN*

*Center for Limnology, University of Wisconsin-Madison, 680 N. Park Street, Madison, WI 53706, U.S.A.
†Biology Department, University of Minnesota Duluth, 211 Life Science, University of Minnesota Duluth, 1110 Kirby Drive, Duluth, MN 55812, U.S.A.

Abstract: *Rainbow smelt (*Osmerus mordax*) have invaded many North American lakes, often resulting in the extirpation of native fish populations. Yet, their invasion is incipient and provides the rationale for identifying ecosystems likely to be invaded and where management and prevention efforts should be focused. To predict smelt presence and absence, we constructed a classification-tree model based on habitat data from 354 lakes in the native range for smelt in southern Maine. Maximum lake depth, lake area, and Secchi depth (surrogate measure of lake productivity) were the most important predictors. We then used our model to identify lakes vulnerable to invasion in three regions outside the smelt's native range: northern Maine (52 of 244 lakes in the non-native range), Ontario (4447 of 8110), and Wisconsin (553 of 5164). We further identified a subset of lakes with a strong potential for impact (potential-impact lakes) based on the presence of fish species that are affected by rainbow smelt. Ninety-four percent of vulnerable lakes in the non-native range in Maine are also potential-impact lakes, as are 94% and 58% of Ontario and Wisconsin's vulnerable lakes, respectively. Our modeling approach can be applied to other invaders and regions to identify invasion-prone ecosystems, thus aiding in the management of invasive species and the efficient allocation of invasive species mitigation and prevention resources.*

Keywords: classification trees, inland lakes, invasive species, nonindigenous species, *Osmerus mordax*, prediction

Pronóstico de la Dispersión de la Especie Invasora *Osmerus mordax* en la Región de los Grandes Lagos de Norteamérica

Resumen: Osmerus mordax *ha invadido muchos lagos de Norteamérica, a menudo provocando la extirpación de poblaciones de peces nativos. No obstante, su invasión es incipiente y proporciona fundamentos para identificar los ecosistemas que pueden ser invadidos y hacia donde se deben enfocar los esfuerzos de gestión y prevención. Para pronosticar la presencia y ausencia de* O. mordax*, construimos un modelo de árbol de clasificación basado en datos de hábitat de 354 lagos en el rango de distribución nativo de* O. mordax *en el sur de Maine. Los predictores más importantes fueron la profundidad máxima del lago, la superficie, y la profundidad Secchi (medida sustituta de la productividad del lago). Posteriormente utilizamos nuestro modelo para identificar lagos vulnerables a la invasión en tres regiones fuera del rango nativo: norte de Maine (52 de 244 lagos en el rango no nativo), Ontario (4,447 de 8,110) y Wisconsin (553 de 5,164). Luego identificamos un subconjunto de lagos con un fuerte potencial de impacto (lagos de impacto potencial) con base en la presencia de especies de peces que son afectadas por* O. mordax. *Noventa y nueve por ciento de los lagos vulnerables en el rango no nativo en Maine también fueron lagos de impacto potencial, como lo fueron 94% y 58% de los lagos vulnerables de Ontario y Wisconsin, respectivamente. Nuestro método de modelaje puede ser aplicado a otros invasores y regiones para identificar ecosistemas propensos a la invasión, ayudando por lo*

‡*email mercadosilva@wisc.edu*
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tanto a la gestión de especies invasoras y a la asignación eficiente de recursos para la mitigación y prevención de especies invasoras.

Palabras Clave: árboles de clasificación, especies invasoras, especies no nativas, lagos interiores, *Osmerus mordax*, pronóstico

Introduction

The introduction of nonindigenous species is a major threat to freshwater ecosystems and biodiversity (Richter et al. 1997; Claudi & Leach 1999), and the effects on ecosystem services and associated economic impacts can be substantial (Pimentel et al. 2000; Leung et al. 2002). The freshwaters of North America are vulnerable to nonindigenous species introductions, which pose serious threats to native biodiversity through competition, predation, habitat modification, and hybridization (e.g., Lodge et al. 1998; Vander Zanden et al. 1999; Perry et al. 2002). Managing aquatic ecosystems in an age of invaders will require new tools for forecasting invader spread. Success in predicting spread and vulnerability will allow allocation of resources for invasive species prevention to be spent where the funds will achieve the greatest benefit (Vander Zanden et al. 2004).

The rainbow smelt (*Osmerus mordax* Mitchill) is an anadromous fish species that is indigenous to coastal freshwater and estuarine environments of northeastern North America. Beginning in the early part of the twentieth century, however, its freshwater range has increased dramatically through both intentional and accidental introductions (Nellbring 1989), resulting in widespread invasion of the Laurentian Great Lakes by the 1940s and secondary spread into smaller, inland lakes throughout the Great Lakes, Mississippi, and Hudson Bay watersheds during the past three decades (e.g., Evans & Loftus 1987; Franzin et al. 1994; Hrabik & Magnuson 1999). The main mechanisms of dispersal for these pelagic, carnivorous, cool-water fish are legal and illegal introductions, accidental bait-bucket transfers, and dispersal through drainage networks (Evans & Loftus 1987). Smelt are also introduced as forage fish for top carnivore game fishes (Johnson & Goettl 1999). Negative effects of rainbow smelt on native fauna include predation and competition with native species (e.g., Loftus & Hulsman 1986; Evans & Loftus 1987; Hrabik et al. 2001). Moreover, some native piscivores appear to exhibit strong preferences for rainbow smelt over native forage species (Krueger & Hrabik 2005), and there are indications that changing to a diet of rainbow smelt biomagnifies contaminants such as mercury and organochlorines (Vander Zanden & Rasmussen 1996; Swanson et al. 2003).

In light of the well-documented negative effects, the ongoing spread of rainbow smelt, and the immense number of inland lakes in North America, it is imperative that lakes most prone to invasion and impact by *O. mordax* be identified. This would help optimize the use of the scarce resources dedicated to invasive species prevention, the conservation of native and endemic species, and the protection of ecological services that lakes provide (Kolar & Lodge 2001). Early identification of invasion suitability is particularly important because once fish species invade and establish self-sustaining populations, eradication is nearly impossible and negative effects on native fish communities are common (Lodge 1993). In aquatic ecosystems, predictive models of species invasions have been used for smallmouth bass (*Micropterus dolomieu*) in Ontario lakes (Vander Zanden et al. 2004) and zebra mussels (*Dreissena polymorpha*) (Koutnik & Padilla 1994), rainbow smelt (*O. mordax*) (Drake & Lodge 2006), and spiny waterfleas (*Bythotrephes longimanus*) in North American inland lakes (MacIsaac et al. 2004), but only a few have identified specific water bodies that could be invaded. Hrabik and Magnuson (1999) modeled the dispersal of rainbow smelt in a single watershed in Vilas County, Wisconsin, based on three previously published variables (pH, minimum lake depth, and lake surface area) that appear to limit smelt distributions (Evans & Loftus 1987).

Our objectives were to develop a model for rainbow smelt presence and absence based on their distribution in their native range in coastal regions of Maine (U.S.A.) and to apply model predictions in other geographic areas to forecast future invasion potential. We worked explicitly within the theoretical framework of ecological niche modeling by assuming that species will be able to establish populations in areas that match the ecological conditions within their native range (Peterson 2003). Based on the stenothermic nature of smelt, we expected lake size and depth to be important predictors of smelt occurrence, in addition to pH and shoreline perimeter. We validated our model with data from areas outside the smelt's native range in Maine and applied it to lakes of Ontario (Canada) and Wisconsin (U.S.A.) to identify those lakes that are vulnerable to invasion and to identify lakes with the greatest potential to experience negative ecological effects on native fish communities. To achieve these objectives, we used large data sets containing information on fish species composition and lake characteristics compiled by state and federal agencies in Maine, Ontario, and Wisconsin.

Methods

Study Systems

Rainbow smelt are native as glacial relict populations in lakes of southern and southeastern Maine but have established in lakes throughout other areas of the state because of legal and illegal introductions (D. Halliwell and P. Vaux, personal communication; Halliwell et al. 2001; Halliwell 2003). Smelt occur naturally in 200 lakes and have been introduced into approximately 221 lakes throughout Maine. (A list of lakes invaded or prone to invasion by rainbow smelt in Maine, Ontario, and Wisconsin is available from N.M.S.) Many of these introductions were deliberately made by fisheries managers to provide forage fish for landlocked Atlantic salmon stocks, but others were illegal or accidental. In Maine non-native smelt have negatively affected brook trout (*Salvelinus fontinalis*) and lake whitefish populations (*Coregonus clupeaformis*) (Halliwell 2003).

Indigenous populations of rainbow smelt occurred in a small number of eastern Ontario lakes (Evans & Loftus 1987). From these populations and from nonnative populations in the Great Lakes, rainbow smelt have spread to new lakes as a result of human transport and dispersal through connected waterways (Evans & Loftus 1987). In the late 1980s, rainbow smelt were present in 194 Ontario lakes, but the number of invaded lakes increased as smelt continued to spread into northwestern Ontario and eastern Manitoba (Franzin, et al. 1994; Swanson et al. 2003). Our data sets include information on 126 Ontario lakes where smelt are currently present. In Ontario smelt introductions have had adverse effects on pelagic fishes, including lake whitefish (*C. clupeaformis*), cisco (*Coregonus artedi*), walleye (*Sander vitreus*), and lake trout (*Salvelinus namaycush*) (Evans & Loftus 1987).

Rainbow smelt established in Lake Michigan and Lake Superior in the 1930s, and by 1968 a number of inland lakes in Wisconsin had established non-native populations (Becker 1983). As of 2005, 24 lakes are known to support rainbow smelt (N.M.S., unpublished data). In Wisconsin smelt have caused the extirpation of yellow perch (*Perca flavescens*) and cisco (*C. artedi*) in two well-studied lakes (McLain 1991; Hrabik et al. 1998; Hrabik & Magnuson 1999), led to declines in walleye recruitment (S. Gilbert, personal communication), and have been associated with ecosystem-wide impacts (Beisner et al. 2003).

Predictive Variables

We used five environmental variables as predictors of smelt presence and absence: lake area (mean = 265 ha, SD = 634.78), maximum lake depth (mean = 12.93 m, SD = 9.72), pH (mean 7.19 standard units, 95% CI 6.04–7.34), Secchi depth (mean = 5.17 m, SD = 1.80), and lake shoreline perimeter (mean 11.89 km, SD = 17.31). These variables were available for lakes from the three study regions, and some have been identified as key predictors of smelt presence in Maine (Halliwell et al. 2001), Ontario (Evans & Loftus 1987), and Wisconsin (Hrabik & Magnuson 1999).

The distribution of Coregonids, lake trout, brook trout, walleye, and yellow perch were also examined in each study area. We focused on these taxa because they have thermal and habitat requirements similar to rainbow smelt and are affected by smelt in the Great Lakes region and Maine (Evans & Loftus 1987; Page & Burr 1991; Hrabik et al. 1998; Halliwell et al. 2001). Therefore, we were concerned with the distribution of these five taxa and the degree of co-occurrence with predicted occurrence of rainbow smelt.

Data

Limnological data and fish (rainbow smelt, lake trout, brook trout, walleye, yellow perch, and Coregonids [either *C. clupeaformis* or *Prosopium cylindraecum*]) distribution data for Maine lakes were obtained from databases managed by the Public Educational Access to Environmental Information (PEARL) in Maine. This data repository is maintained by the Senator George J. Mitchell Center for Environmental and Watershed Research and the Department of Spatial Information Science and Engineering, University of Maine. We determined the native range of rainbow smelt in Maine based on data in Halliwell et al. (2001), Halliwell (2003), maps created by the U.S. Geological Survey (USGS 2000), and personal communications with David Halliwell and Peter Vaux (Maine Department of Environmental Protection and University of Maine, respectively). Thus, we estimated that 354 Maine lakes are within the native range of rainbow smelt (Fig. 1a). We assumed the native range of rainbow smelt is saturated (i.e., smelt are present in all suitable lakes and absent from unsuitable lakes and have had the capacity to reach all lakes within this area). For fish distribution data, we considered only lakes that had been sampled and for which at least one species was recorded in the available data sets. Lakes where fishes were not sampled were removed from the analysis.

Lake morphometry and physical-chemistry variables were obtained for 819 lakes from data sets in PEARL (provided by the Maine State Department of Inland Fisheries and Wildlife, Maine Department of Environmental Protection, the Volunteer Lake Monitoring Project, Senator George J. Mitchell Center, U.S. Environmental Protection Agency, and the Acadia National Park Lake Monitoring project of the National Park Service) and from geographic information provided by Maine Department of Environmental Protection. Shoreline perimeter and lake area were calculated with geographic information systems (GIS) (ESRI 2002). Mean Secchi depth (available for 709 lakes) and pH for each lake were calculated from values in several PEARL data sets, prior to which we checked for interannual and seasonal variations before calculating a final mean value per lake.

For species distribution, morphological, and physical–chemical attributes of Ontario lakes, we used a database

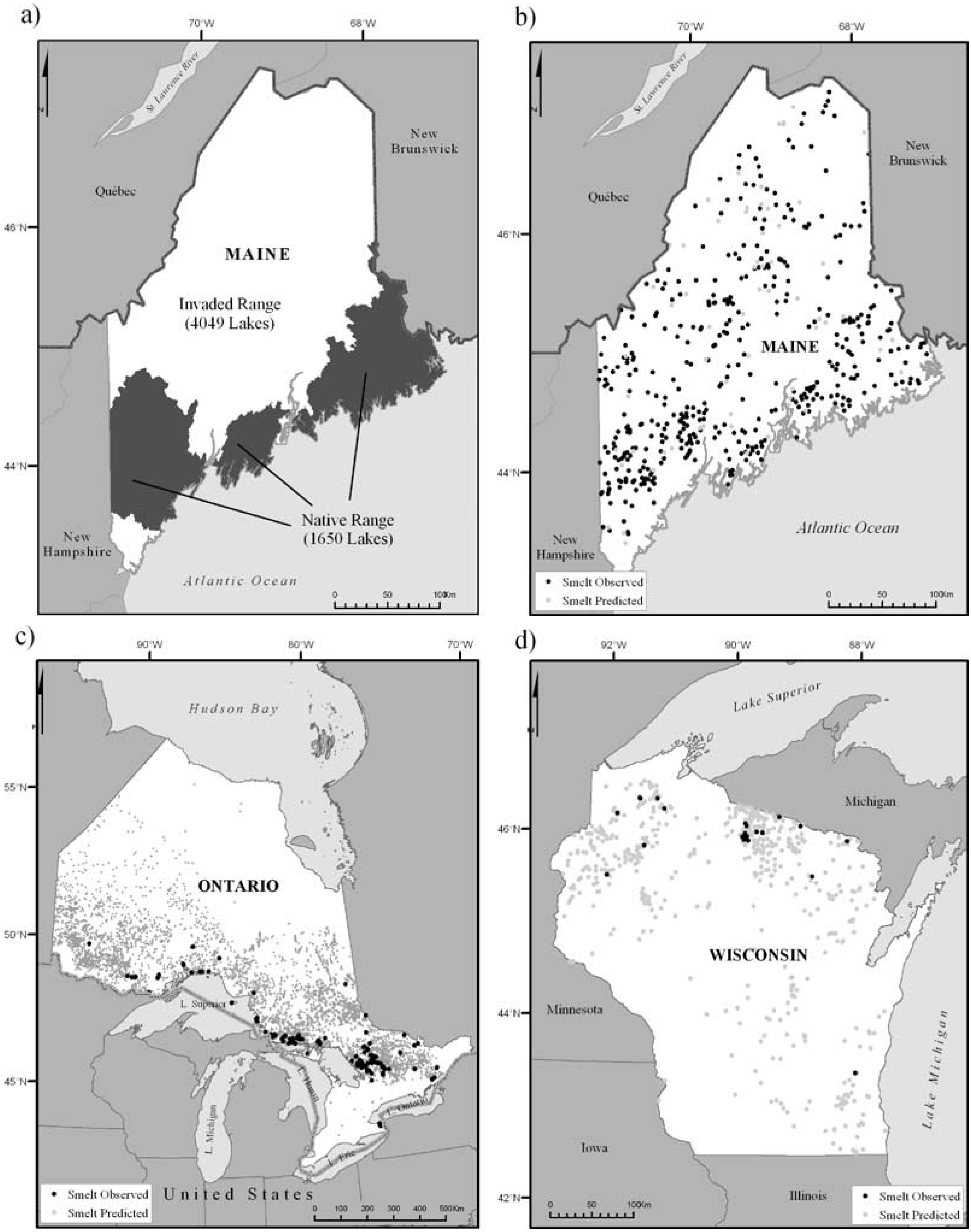

Figure 1. (a) Distribution of rainbow smelt in Maine (U.S.A.). Shaded areas indicate native range. (b) Predicted presences of rainbow smelt for Maine lakes (n = 52 lakes) outside their native distribution. (c) Current and predicted (n = 4447 lakes) rainbow smelt distribution in Ontario, Canada. (d) Current and predicted (n = 553 lakes) rainbow smelt distribution in Wisconsin (U.S.A.).

integrated by Vander Zanden et al. (2004), which we expanded with species distribution and lake information from the Fish Species Distribution Data System of the Ontario Ministry of Natural Resources (OMNR), N. Mandrak (OMNR, unpublished data) and the OMNR Lake Inventory Database. Information was compiled for all variables for 8236 Ontario lakes. From fish presence–absence data, we obtained the distribution of lake trout, brook trout, walleye, yellow perch, and Coregonids. All species in the Coregoninae subfamily that are known for Ontario were used to create this group (*Coregonus* sp., *C. clupeaformis*, *C. artedi*, *C. hoyi*, *C. nipigon*, and *P. cylindraecum*).

We obtained rainbow smelt, lake trout, brook trout, walleye, yellow perch, and Coregonid distributions in Wisconsin by reviewing the published literature (Becker 1983; Colby et al. 1987; Hrabik & Magnuson 1999; Lyons et al. 2000; Krueger & Hrabik 2005), interviews with Wisconsin Department of Natural Resources (WDNR) regional fish managers (see Acknowledgments), data sets in the Wisconsin Aquatic Gap Mapping Application (WDNR) (http://web2.er.usgs.gov/wdnrfish/), and our own unpublished observations.

We compiled information for Wisconsin inland lakes from various sources. Maximum lake depth, area, and Secchi-disk readings were obtained from an extensive lake data set at the WDNR (K. E. Webster, personal communication), pH information was obtained from the STORET database of the U.S. Environmental Protection Agency (STORET-EPA), and shoreline perimeter was calculated with a GIS (ESRI 2002) from data obtained from the WDNR. We obtained information for 5188 lakes in Wisconsin, but data availability was uneven among lakes (lake area = 5188 lakes, Secchi-disk readings = 3891, pH = 1190, maximum depth = 5142, shoreline perimeter = 1190).

Model Development and Predictions

We used classification trees (Breiman et al. 1984; Salford Systems 2002) to model rainbow smelt presence and absence within their native range in Maine. This methodology uses a recursive partitioning algorithm to repeatedly partition the data set according to the explanatory variables into a nested series of mutually exclusive groups, each as homogeneous as possible with respect to the presence or absence of rainbow smelt (see De'ath & Fabricius 2000). The outcome is a decision tree that represents the numerical relationships in an interpretable, hierarchical model. We used the Gini impurity criterion to determine the optimal variable splits and determined the optimal size of the decision tree by constructing a series of cross-validated trees and selecting the smallest tree based on the 1-SE rule (De'ath & Fabricius 2000). The relative importance of each habitat variable was estimated by summing the changes in misclassification (also called impurity) for each surrogate split across all nodes and was expressed on a 0–100 scale (Breiman et al. 1984). Although there are a number of statistical approaches available to model species presence–absence data, we chose classification trees because they are better able to capture and model the complex, nonlinear patterns found in ecological data than traditional approaches (Olden & Jackson 2002).

We used 10-fold cross validation to assess model predictive performance within rainbow smelt's native range of distribution ($n = 354$ lakes) and applied the final model to information on lakes outside the native range of smelt in Maine ($n = 465$ lakes), Ontario ($n = 8236$ lakes), and Wisconsin ($n = 5188$ lakes). We used Cohen's kappa coefficient of agreement to assess the classification performance of the classification tree compared with the random expectations (Titus et al. 1984). Following Fielding and Bell (1997), we partitioned the overall classification success of the model into a confusion matrix that defines the total number of lakes where smelt were not predicted by the model but observed in our data sets (false absence); the total number of lakes where smelt were predicted by the model and observed (true presence); the total number of lakes where smelt were not predicted and not observed (true absence); and the number of lakes where smelt were predicted by the model but not observed (false presence). Lakes classified as false presence were considered vulnerable to invasion based on environmental suitability according to the lake attributes. Next, we calculated three metrics of model performance: (1) the overall classification performance of the model calculated as the percentage of sites where the model correctly predicted the presence or absence of smelt; (2) the ability of the model to correctly predict smelt presence (i.e., model sensitivity); and (3) the ability of the model to correctly predict smelt absence (i.e., model specificity).

Lakes categorized as false presences in each study area (i.e., lakes environmentally suitable for smelt presence) were considered vulnerable to invasion. For vulnerable lakes in each region, we identified those lakes that contained lake trout, walleye, yellow perch, Coregonids, and/or brook trout. Lakes containing any of these species were considered potential-impact lakes. (A list of lakes classified as vulnerable for each region as well as the potential-impact lakes is available from N.M.S.)

Results

Of 354 lakes used for model development (rainbow smelt native range in Maine) (Fig. 1a), 200 supported rainbow smelt. The model that best explained variability in rainbow smelt distribution within their native range consisted of six splits and seven terminal nodes (Fig. 2). The most important variable in defining the splits in the tree was maximum lake depth (score = 100). Closest competitor variables were Secchi depth (52.26) and lake area (51.41). Shoreline length (44.07) and pH (12.59) were minor

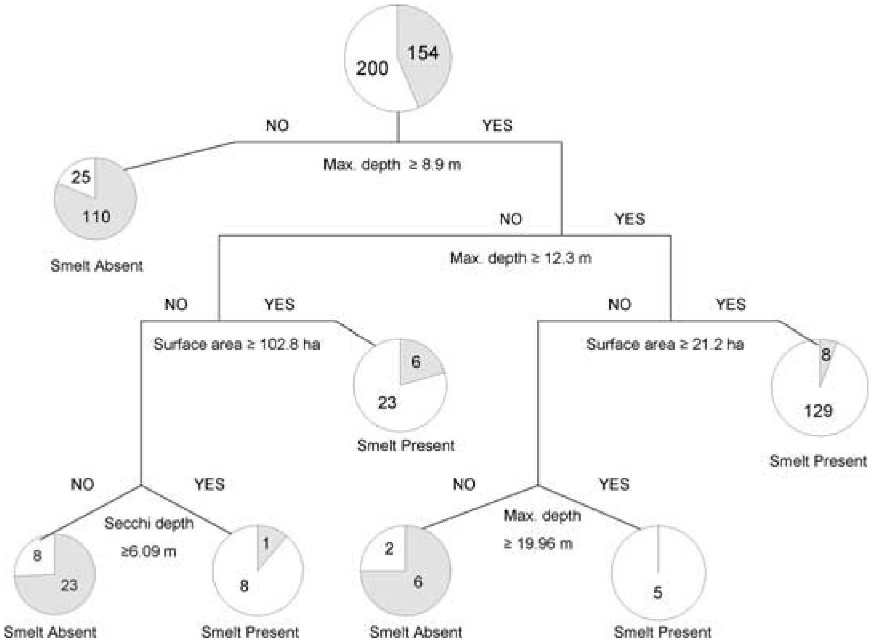

*Figure 2. Classification tree modeling the presence and absence of rainbow smelt (*O. mordax*). Tree constructed from morphological and physical-chemical variables for 354 lakes in the native range of rainbow smelt in Maine (U.S.A.). Each of the six splits is labeled with the variable and values that indicate the split-defining condition. Each of the seven terminal nodes is labeled with the number of lakes grouped in each node that have (unshaded) or lack smelt (shaded) and the model prediction (smelt presence or absence).*

variables in defining tree architecture. The tree had a low misclassification rate of 14%. The model correctly predicted smelt presence in 165 of 200 lakes (sensitivity = 82.5%) and smelt absence in 139 of 154 lakes (specificity = 90.3%). Smelt presence was predicted for lakes deeper than 12.3 m and a lake surface area ≥21 ha, and for lakes with a maximum depth between 8.9 and 12.3 m and a lake surface area ≥102.8 ha or a Secchi depth ≥6.1 m. For lakes with area <21.2 ha, smelt were predicted present if lakes were deeper than 20 m. Smelt absence was predicted for lakes with maximum depth shallower than 9 m, an area <102.8 ha, and Secchi depth <6.1 m. However, smelt would also be absent if lake area was ≥12.3 ha, but smaller than 21.2 ha and shallower than 19.9 m (Fig. 2).

Predicted Distributions of Rainbow Smelt

The misclassification rate of the model was 20% when applied to Maine lakes outside the native range of rainbow smelt (unshaded area of Fig. 1a). The model accurately predicted smelt occurrences in 79% of the lakes where they were present and 80% of lakes where they were absent (sensitivity = 80%; specificity = 79%). Fifty-two lakes were categorized as false presences (Table 1) (Fig. 1b).

Our Ontario data set contained 126 lakes in which smelt are present currently (Table 1) (Fig. 1c). For lakes in Ontario, the model predicted smelt presence in 87% of the smelt lakes (sensitivity = 87.30%). Specificity of the model was only 45%. In Ontario the model identified 4447 new lakes capable of being invaded by smelt (false presences).

For Wisconsin lakes, the model had a misclassification rate of 11%. The model correctly predicted presence and absence of smelt (sensitivity = 87.5%; specificity = 89%). The model identified 553 new lakes with the potential to be invaded by smelt (Table 1) (Fig. 1d).

In both regions of Maine and in Ontario, roughly 55–60% of lakes currently contain or were predicted to support smelt. In contrast, only 10% of Wisconsin lakes contain or were predicted to support smelt (Table 2). In both native and non-native regions of Maine, the landscape is saturated with smelt: the majority of lakes that could potentially support smelt presently do (Table 2). In Wisconsin and Ontario, <5% of lakes capable of supporting smelt currently do, indicating vast potential for future spread in both areas (Table 2).

Potential for Effects on Native Species

Of 4447 Ontario lakes where smelt were predicted to occur (false presences), 94% had at least one of the fish taxa known to be affected by rainbow smelt (Coregonids, lake trout, walleye, yellow perch, and brook trout) and were classified as potential-impact lakes. A total of 49 of the 52 (94%) predicted lakes in the non-native range of Maine and all 15 lakes in the smelt's native range were potential-impact lakes. In Wisconsin 58% of 553 vulnerable lakes ($n = 323$) contained at least one of these species (Table 3). In Maine the most widely distributed vulnerable taxa in predicted lakes was brook trout. In Ontario yellow perch were the most widely distributed vulnerable species (in 3118 of 4447 predicted lakes), followed by Coregonids (2337 lakes), and walleye (1607). In Wisconsin most of the vulnerable lakes had yellow perch ($n = 310$) and walleye (232), whereas Coregonids, brook trout, and lake trout were present in 41, 26, and 9 lakes, respectively (Table 3).

Table 1. Model results and predictions of lakes suitable for rainbow smelt invasion for Maine lakes outside of the smelt's native range.

Region[a]	*No. of lakes*[b]	*Performance*[c]
Maine (non-native range)		
false absence	45	
		sensitivity = 80% total N = 221 lakes
true presence	176	
false presence	52	
		specificity = 79% total N = 244 lakes
true absence	192	
Ontario		
false absence	16	
		sensitivity = 87.3% total N = 126 lakes
true presence	110	
false presence	4447	
		specificity = 45% total N = 8810 lakes
true absence	3663	
Wisconsin		
false absence	3	
		sensitivity = 87.5% total N = 24 lakes
true presence	21	
false presence	553	
		specificity = 89% total N = 5164 lakes
true absence	4611	

[a] *False absence, smelt not predicted, smelt observed; true presence, smelt predicted, smelt observed; false presence, smelt predicted, smelt not observed (considered vulnerable based on environmental suitability); true absence, smelt not predicted, smelt not observed.*
[b] *Number of lakes in each group.*
[c] *Total* N, *total number of lakes where smelt were actually observed or not observed; sensitivity, model correctly predicted presence of smelt; specificity, model correctly predicted absence.*

Discussion

A critical area of research in the field of invasion biology is the development of predictive models that can assist in the prognosis of invasive species spread and impact on native species and ecosystems (e.g., Williamson 1996; Kolar & Lodge 2001; Peterson 2003). In aquatic ecosystems, the management and control of invasive species hinges on the ability of managers to accurately identify areas and specific water bodies that are vulnerable to invasion. The ecological forecasting of biological invasions is essential for the efficient allocation of prevention and restoration efforts (Vander Zanden et al. 2004). In lake-rich regions such as our study area, invasion-prone systems could become the target of focused management efforts for preventing future introductions (i.e., invasive species advisories at boat landings) or limiting the negative effects of smelt if they are already established (i.e., stocking top carnivores in invaded lakes).

Our results show that rainbow smelt presence and absence in their native range is highly predictable as a function of morphological and physical–chemical variables. Our model exhibited very high specificity indicating that environmentally suitable lakes tend to support populations of rainbow smelt, thus supporting the use of native-range data in model development. Likewise, in the other study areas, the model correctly predicted smelt presence for lakes where smelt have been observed and accurately classified smelt absences in lakes that have been sampled and in which smelt have not been collected. A notable exception was the relatively higher misclassification rates for Ontario lakes, a consequence of a large number of lakes in which smelt were predicted to occur but have not (yet) been observed. In contrast to Ontario, the list of lakes with the potential to be invaded in Maine and Wisconsin is low relative to the total number of lakes in each area.

Conservation biologists have increasingly used environmental information to model species distributions in their native range and to predict their potential future distribution (reviewed in Peterson 2003), yet only a few studies have coupled these models with predictions regarding the potential effects of invaders on native communities (e.g., Hrabik & Magnuson 1999; Vander Zanden et al. 2004). Our modeling efforts join these studies in an attempt to identify specific water bodies where invasive species are predicted to occur and affect native species and to provide a multitiered management tool for

Table 2. Summary of lakes currently inhabited or predicted to be inhabited by rainbow smelt for each study region.

Region	*No. of lakes*[a]	*No. of smelt*[b]	*% smelt*[c]	*% vul.*[d]	*% not vul.*[e]	*% sat*[f]
Maine (native)	354	200	56	4	39	93
Maine (non-native)	465	221	48	11	41	81
Ontario	8236	126	2	54	44	3
Wisconsin	5188	24	0.5	11	89	4

[a] *Total number of lakes in study.*
[b] *Lakes currently with smelt.*
[c] *Percentage of lakes with smelt.*
[d] *Percentage of vulnerable lakes.*
[e] *Percentage of invulnerable lakes.*
[f] *Percent saturation (i.e., percentage of smelt-suitable lakes that have a smelt population in each region).*

Table 3. Percentage of lakes in each study area with a strong potential for impact (potential-impact lakes) based on the presence of fish species that are affected by rainbow smelt.*

	Region							
	Maine (native)		*Maine (non-native)*		*Wisconsin*		*Ontario*	
Taxa	%	n	%	n	%	n	%	n
Coregonids	0	0	13	7	7	41	53	2337
Brook trout	47	7	69	36	5	26	16	704
Lake trout	0	0	13	7	2	9	35	1538
Walleye	0	0	0	0	42	232	36	1607
Yellow perch	93	14	56	29	56	310	70	3118
At least 1 taxa	100	15	94	49	58	323	94	4192
All taxa	0	0	0	0	0	2	0	7
Total lakes		15		52		553		4447

**The percentage of lakes predicted by the model and taxa that are most prone to be affected (*n*, number of lakes within each category).*

invasive species prevention efforts. Our use of the literature that documents negative ecological effects of rainbow smelt allowed us to identify lakes that are prone to smelt invasion and where negative effects on valued native fishes are likely to occur. Yellow perch, walleye, lake trout, brook trout, and Coregonids can all be affected by smelt introduction as a result of niche overlap with the invader (Selgeby et al. 1978; Becker 1983; Evans & Loftus 1987; Franzin et al. 1994; Hrabik et al. 1998). Such overlap makes the presence of these species a useful indicator of the potential impact of rainbow smelt.

In Maine and Ontario the majority of lakes identified as suitable for rainbow smelt also contained at least one native species that could be negatively affected by invasion. In Wisconsin our approach identified a reduced number of lakes (323 of 553) where salmonids or percids could be affected if invaded by rainbow smelt. Prevention efforts should focus on these lakes.

The most prevalent species that could be affected by rainbow smelt throughout our study areas was yellow perch. However, given their societal value, vulnerability could be more relevant in lakes with brook trout, walleye, or lake trout populations. Lake trout and walleye support important fisheries in Ontario and Wisconsin, respectively (BIA 2003; Lester et al. 2003) and are present in about half of the lakes vulnerable to smelt invasion in each region. In Maine brook trout support a valuable fishery and most vulnerable lakes have the species. Coregonids are found throughout all the regions but are most prevalent in Ontario lakes. The use of comparative dollar value of fisheries in each region as criteria for the differential allocation of invasion–prevention efforts could further help identify lakes that need such attention.

Other fish species have been negatively affected by rainbow smelt (i.e., burbot [*Lota lota*]; Brandt & Madon 1986). However, we used only species reported to be affected in inland lakes (i.e., not the Laurentian Great Lakes). In addition, it is possible that even if invaded, the fish communities in some lakes would not undergo significant changes. For example, rainbow smelt effects on walleye and coregonids have been reported for a number of lakes in Wisconsin (S. Gilbert, personal communication), but where walleye are heavily stocked, smelt effects on native fish communities appear to be greatly reduced or curtailed (Roth 2005; Krueger & Hrabik 2005). Because it is difficult to forecast the impact of a given smelt invasion, we attempted only to identify lakes with a potential for negative effects of smelt on native fishes.

We limited our invasion predictions to areas for which we were able to obtain extensive data, but our predictions can be applied easily to other areas of the Great Lakes region (e.g., Michigan, Minnesota, Québec) and, in general, to other areas where rainbow smelt could expand in the future (Franzin et al. 1994). Rainbow smelt have been purposefully introduced into reservoirs and lakes in other areas of the United States and Canada (e.g., Colorado, Johnson & Goettl 1999; and Manitoba, W.G. Franzin, personal communication) from which secondary spread could occur.

Our results suggest that the majority of smelt-habitable lakes (81%) have already been invaded in Maine, indicating a high level of saturation in this region. It is possible that smelt occur in some of these lakes at low densities or that local extinctions have resulted from biotic or abiotic conditions. In contrast, few of the vulnerable lakes in Wisconsin and Ontario have been invaded (4% and 3% saturation, respectively), providing a rationale for invasion–prevention efforts (Table 2). Fifty-six percent of all lakes in Ontario are currently invaded or predicted to support smelt. In Wisconsin with 11% of all lakes currently invaded or predicted to support smelt and only 24 lakes invaded thus far, it appears that the time scale for invasions is relatively long and that the number of source populations is still low relative to the number of environmentally suitable lakes (Hrabik & Magnuson 1999).

To aid in further focusing invasion–prevention efforts in both regions, other factors need to be considered. Evans and Loftus (1987) suggest that urban and cottage development is strongly associated with the presence of smelt. Vulnerable lakes identified here could be ranked according to the degree of human impact and accessibility (i.e., road access) or fisheries value to create a subset of lakes where monitoring and prevention efforts can be directed. For example, in Wisconsin the WDNR has walleye population data for 232 of the 553 lakes identified as vulnerable to smelt invasion by our model. Of these 232 lakes, we estimated that 186 (approximately 80%) have public (boat launch) access. (List of Wisconsin lakes vulnerable to rainbow smelt invasion with walleye population estimates [Wisconsin Department of Natural Resources] and with boat-landing access is available from N.M.S.) Considering the important role of humans as a vector of smelt dispersal (Evans & Loftus 1987), a large number of lakes are potentially vulnerable based on access, and smelt invasion–prevention efforts should be prioritized in these systems.

Given the nature of most of our variables, our analysis provides a static scenario for the potential future distribution of smelt. However, two of the predictor variables we considered have the potential to change as a result of anthropogenic influence. Agricultural and urban runoff can cause eutrophic conditions, reduced Secchi depth, and hypolimnetic anoxia in summer months (NRC 1992; Smith et al. 1999), which make lakes inhospitable to rainbow smelt even if the lakes fit some of the depth and area invasion requirements. Similarly, lake pH has changed as a consequence of environmental pollution and subsequent control measures (Mills et al. 2000), and fish communities have responded to these changes (Yan et al. 2003; Larssen et al. 2003). When making assessments of the potential invasion and establishment of rainbow smelt, it will be important to consider temporal changes in ecosystem properties.

Given the approximate timeframe for smelt invasion in each region (1900s, 1930s, and 1960s for Maine, Ontario, and Wisconsin, respectively), the estimates of spread rate are four times higher in Maine compared with Wisconsin (2 invasions/year vs. 0.5 invasions/year, respectively) and approximately 1.2 times higher compared with Ontario (1.7 invasions/year). However, in Ontario, rates could be slightly higher if one considers the total number of invaded lakes in the province (Franzin et al. 1994). The rate of spread will depend on the number and proximity of vulnerable lakes to invaded lakes, patterns of boat traffic, lakeshore development trends, and the effectiveness of efforts to control the spread of invasive species. In a lake district in northern Wisconsin, Hrabik and Magnuson (1999) modeled rainbow smelt dispersal and concluded that with the aid of human intervention (e.g., human vectors) most of the 507 suitable lakes in the district would be invaded in 1000 years, which agrees with past spread rates as estimated above for Wisconsin.

With increasing rates of invasive species introductions and associated negative effects on recipient ecosystems, the protection of unique native faunas will benefit from tools that allow the identification of systems most vulnerable to invasion. Proactive management based on predictions of lakes vulnerable to rainbow smelt will help avoid adverse impacts and costs of invasives. Our modeling approach has identified lakes that could harbor rainbow smelt and lakes that could be affected by this invader, which helps identify systems where monitoring, legislative, and educational efforts should be concentrated to prevent further damage to native fish communities and valuable fisheries.

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