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PREDICTING OCCURRENCES AND IMPACTS OF SMALLMOUTH BASS INTRODUCTIONS IN NORTH TEMPERATE LAKES

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Abstract. Smallmouth bass and other warmwater littoral piscivores are presently expanding their geographic range northward into lakes across southern Canada. Smallmouth bass introduction can dramatically reduce minnow abundances, causing native lake trout to shift to low quality, invertebrate-based diets. Here we develop models to predict future occurrences and impacts of smallmouth bass in central Ontario, with the goal of identifying ''vulnerable'' lakes in order to better guide prevention efforts. Using local and regional environmental variables for 3046 central Ontario lakes, an artificial neural network was used to predict lakes that are likely to be invaded by bass. Smallmouth bass can significantly influence the occurrence and abundance of small-bodied fishes (mainly minnows), and stable isotope analysis of food webs in 18 lakes revealed that lake trout are buffered from impacts of bass on minnows in lakes containing pelagic prey fishes. In the absence of pelagic prey fishes, the trophic niche of lake trout depends on the presence of bass; lake trout feed primarily on zooplankton in the presence of bass, and minnows in the absence of bass. Of the 3046 lakes, the 788 lake trout lakes in central Ontario were classified according to their vulnerability to bass invasion based on the predictability of bass occurrence and their subsequent impacts, and mapped in a Geographic Information System (GIS). Only 48 lake trout lakes (6%) were classified as ''high vulnerability''—predicted to be invaded *and* impacted by bass. Another 301 lakes had a sensitive food web structure but were not predicted to support a bass population. Based on this information, efforts to prevent further impacts can be optimized by focusing on this vulnerable subset of lakes.

Key words: artificial neural networks; exotic species; food webs; GIS; lake classification; lakes; Ontario, Canada; smallmouth bass; species introduction; stable isotopes.

Introduction

Invasions by nonnative species are a leading threat to biodiversity worldwide (Coblentz 1990, Soulé 1990, Wilcove and Bean 1994). Furthermore, they have caused tremendous economic impacts, annually exceeding U.S. $137 billion in the United States alone (Pimentel et al. 2000). While some exotic species invasions have no observable impacts on native species and ecosystems, others have had catastrophic impacts ranging from extinction of native species to alteration of ecosystem processes (Spencer et al. 1991, Lodge 1993, Vitousek et al. 1996, Strayer et al. 1999). In light of the magnitude of this global problem, a synthetic, predictive, proactive approach for managing species invasions is badly needed (Peterson and Vieglais 2001). Such an approach would integrate understanding of invader dynamics and the ecological interactions between the invader and natural ecosystems, ultimately yielding models that would identify areas or ecosystems that are most vulnerable to invaders. These models would serve as the basis for specific strategies to prevent the further invasion and adverse impacts of exotics. Indeed, prevention is the most effective invasive management strategy, because once an aquatic invader becomes established, range expansion is almost inevitable and elimination is rarely a viable option (Lodge 1993).

This study focuses on the ongoing invasions of smallmouth bass (*Micropterus dolomieu*) into lakes in central Ontario, a region at the northern edge of their geographical range. The ranges of many game fishes such as smallmouth bass, rock bass (*Ambloplites rupestris*), northern pike (*Esox lucius*), and largemouth bass (*Micropterus salmoides*) have expanded dramatically during the past century, and their expansion continues at a rapid pace. While stocking of nonnative game fishes by resource management agencies is no longer a common practice, littoral (inshore) predators continue to expand their range as a result of unauthorized introduction by anglers, accidental bait bucket transfers, and dispersal through drainage networks. The

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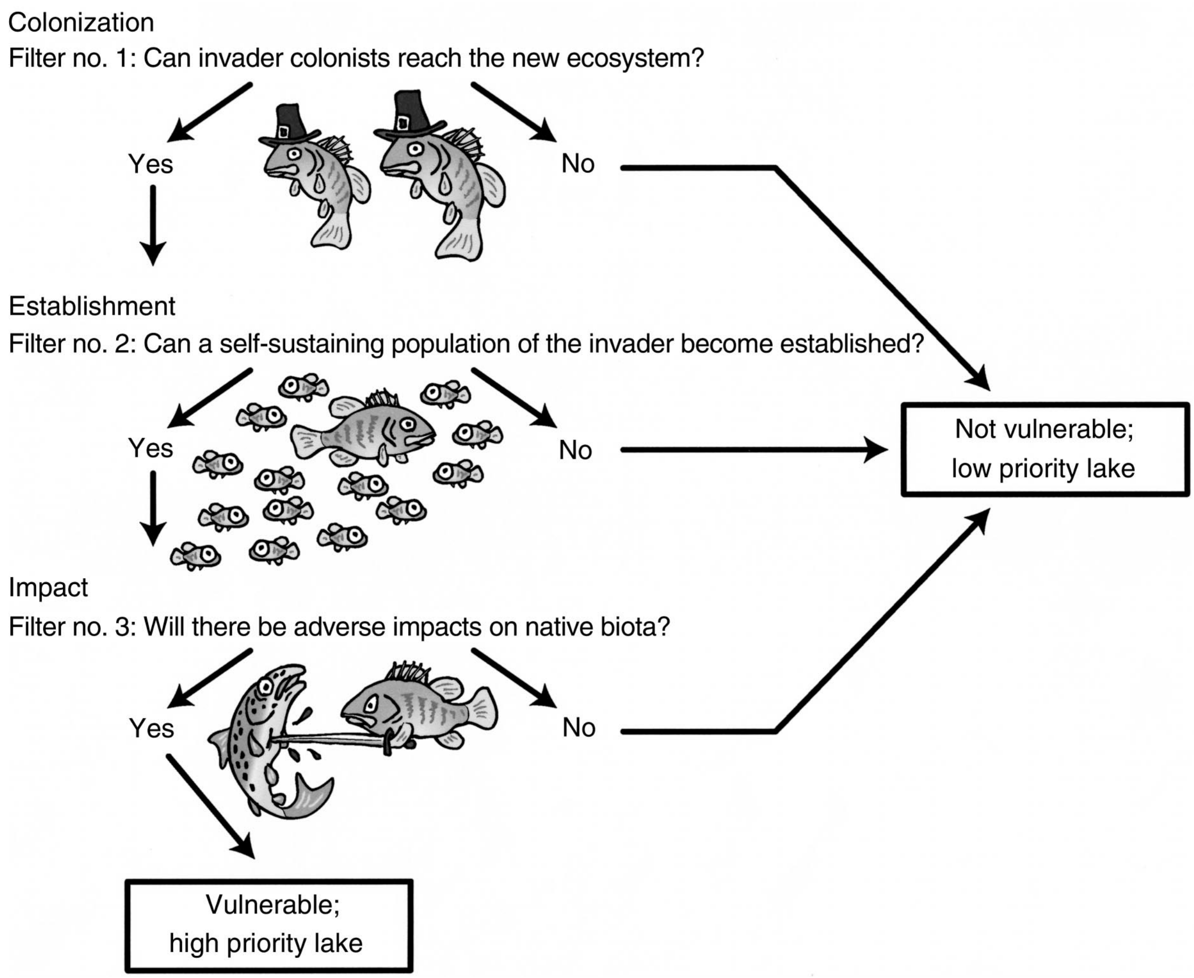

FIG. 1. The conceptual model used for characterizing the vulnerability of Ontario lakes to bass introductions. Based on Vander Zanden et al. 2004.

baitfish trade is not closely regulated in many U.S. states and Canadian provinces (Litvak and Mandrak 1993), and juvenile rock bass, smallmouth bass, and largemouth bass are just a few of the species reported from commercial bait dealerships (Litvak and Mandrak 1993). In addition, the projected warming of many lakes due to global climate warming is predicted to benefit warmwater fish species and hasten the northward spread of species such as smallmouth bass (Mandrak 1989, Stefan et al. 2001), with major impacts on prey fish biodiversity anticipated on a regional scale (Jackson and Mandrak 2002).

There is ample evidence that establishment of nonnative bass can adversely impact littoral prey fish abundance and diversity in north-temperate lakes (Chapleau et al. 1997, Whittier et al. 1997, Vander Zanden et al. 1999*a*, Whittier and Kincaid 1999, Findlay et al. 2000, MacRae and Jackson 2001, Jackson 2002). Reductions in prey fish populations can have adverse impacts on populations of native top predators such as lake trout (*Salvelinus namaycush*) and brook trout (*Salvelinus fontinalis*) (Olver et al. 1991, Vander Zanden et al. 1999*a*). Considering these adverse impacts on native biodiversity and fisheries, management plans should be designed to minimize ecological impacts of bass introductions. Unfortunately, with almost a quarter of a million lakes in the province of Ontario alone (Olver et al. 1991), this is a daunting task, particularly if it were to involve on-the-ground surveys. Consequently, identifying specific lakes that are vulnerable to bass invasion using existing information would be an important advancement.

To identify vulnerable lakes, we use a conceptual framework for modeling invader occurrences and impacts presented by Vander Zanden et al. (2004). The species invasion process is composed of three steps or filters (Fig. 1). The first filter identifies which lakes are accessible to invader colonists, the second filter identifies which lakes are capable of supporting an invader population, and the third filter identifies which lakes would be adversely impacted if an invader were to establish. Lakes predicted to be invaded *and* adversely impacted are considered *vulnerable* and would be the focus of management efforts aimed at slowing or halting further bass introductions (Vander Zanden et al. 2004). Based on this conceptual approach and using a data set composed of 3046 lakes in central and northern Ontario, we develop two separate lake classification models: the first model predicts the location of future bass invasions based on environmental suitability, and the second identifies lakes in which bass will have negative impacts on lake trout populations based on known food web interactions derived from extensive stable isotope and gut content-based food web studies (Vander Zanden and Rasmussen 1996, 2002, Vander Zanden et al. 1999*a*, *b*). By combining the predictions of these two models, along with information about lake remoteness (e.g., in or out of the Algonquin Park roadless area), we identify a subset of lakes in the region that are considered vulnerable to smallmouth bass invasion.

Study Systems

The present study examines potential smallmouth bass introductions into lakes of central Ontario. Lake trout are the top pelagic predator in many lakes of this region, and support a highly prized sport fishery. Nearly all of the suitable lakes (>20 m in depth and generally >50 ha in surface area) of central Ontario historically supported lake trout populations (Olver et al. 1991). Lake trout are highly sensitive to anthropogenic impacts, and their populations are often used as a sentinel of ecosystem health in northern lakes (Olver et al. 1991). Most recent estimates indicate that 5% of native lake trout populations have been extirpated as a result of overexploitation, habitat degradation, lake acidification, eutrophication, and fisheries stocking practices (Olver et al. 1991). Lakes of central Ontario are experiencing rapid cottage development because of the proximity to the major population centers of Toronto and Ottawa, and impacts on lake trout populations in this region are particularly evident.

Community composition of the pelagic/profundal (offshore and deepwater) zone of north-temperate lakes is remarkably variable, having been shaped by events during the retreat of the Wisconsonian continental ice sheet (commencing ~14 000 yr BP). Following the glacial retreat, massive glacial lakes extending beyond the current extent of the Great Lakes inundated low-lying regions of central Ontario. These glacial lakes acted as dispersal corridors for aquatic organisms colonizing lakes newly formed by the glacial meltwaters. Present-day lakes that fall within the boundaries of these former glacial lakes contain a characteristic assemblage of pelagic and profundal prey fishes: lake herring or cisco (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*), and round whitefish (*Prosopium cylindraceum*), as well as relict invertebrates, such as *Mysis relicta* and *Diporeia hoyi* (Dadswell 1974). Of the non-glacial lakes, only a subset contain pelagic prey fish species, although rainbow smelt (*Osmerus mordax*) are rapidly spreading as a result of human introductions (Evans and Loftus 1987, Hrabik and Magnuson 1999).

Variation in prey community composition is the basis for differences in pelagic food chain structure and lake trout diet (Martin 1970, Martin and Fry 1972, Trippel and Beamish 1993, Vander Zanden and Rasmussen 1996). If pelagic prey fish are present in a lake, they comprise the majority of lake trout diets, whereas in lakes lacking pelagic prey fish, lake trout subsist on a mix of invertebrates and littoral prey fish. More recent work indicates that the relative contribution of invertebrates and littoral prey fish is mediated by the presence/absence of smallmouth bass and rock bass (Vander Zanden et al. 1999*a*). While lake trout predation appears not to impact littoral prey fish populations, bass are a more efficient littoral predator, and dramatically reduce littoral prey fish abundance and diversity (Vander Zanden et al. 1999*a*, Whittier and Kincaid 1999, Findlay et al. 2000). Given these feeding preferences, lake trout from lakes containing bass are relegated to consuming mostly invertebrates due to the predation efficiency of bass in the littoral zone. With smallmouth bass and other littoral piscivores presently invading lakes of this region, there is concern over potential impacts on both native minnows and lake trout populations (Vander Zanden et al. 1999*a*, Jackson 2002).

Methods

Data

Patterns of lake trout and smallmouth bass occurrences and bass–habitat relationships were examined in 3046 lakes located in central Ontario (all lakes south of 48° N). The primary source of the fish distribution data was the Fish Species Distribution Data System (FSDDS) of the Ontario Ministry of Natural Resources (OMNR). This database was extensively supplemented with additional data obtained through extensive fish sampling in central Ontario, particularly the Algonquin Park region, 1989–1999 (N. E. Mandrak, *unpublished data*). The fish community of each lake was further characterized by: number of cyprinid species; number of piscivorous species (based on Scott and Crossman 1973); number of prey species with adult size <15 cm, and >15 cm based on Scott and Crossman (1973); and, number of warm, cool, and cold water species.

Glacial history and climate variables were also used as independent variables. The extent of fish colonization of Ontario lakes is directly related to events occurring after the retreat of the Wisconsonian continental ice sheet (Hinch et al. 1991, Mandrak 1995). Colonization potential was measured as the number of years each lake was uncovered by the ice sheet and the number of years, if any, covered by glacial lakes. These values were calculated by overlaying the location of each lake onto a series of maps depicting the location of the Wisconsonian ice sheet and glacial waterbodies in eastern North America between 14 000 and 5000

TABLE 1. Summary statistics for the 20 environmental variables used in modeling smallmouth bass presence/absence in central Ontario, Canada lakes.

Variable	Code	Min.	1st Q	Med.	3rd Q	Max.
Glacial history						
No. yr with glacial water (×10^3)	# WATER	0	0	0	0	4
No. yr uncovered by ice (×10^3)	# NO ICE	2	3	4	5	7
Climate						
Mean temperature (°C)	TEMP	1.1	3.4	4.2	5.0	14.3
SD temperature (°C)	SD TEMP	5.6	10.8	11.1	11.6	12.9
Precipitation (mm)	PPT	609.3	699.6	727.2	821.9	1063.8
SD precipitation (mm)	SD PPT	91.2	149.8	175.2	187.4	336.7
Local habitat						
Lake area (ha)	AREA	1.0	12.0	34.0	107.0	29 484.0
Shoreline perimeter (km)	SH.PER	1.0	2.0	4.0	9.0	511.0
Maximum depth (m)	MAX.D	1.0	8.0	14.0	22.0	214.0
Elevation (m)	ELEV	42.0	264.5	335.0	396.0	595.0
pH	PH	4.0	6.6	7.1	7.8	9.8
Total dissolved solids (mg/L)	TDS	3.3	23.5	33.4	67.7	488.2
Secchi disc depth (m)	SDD	0.2	2.6	3.7	5.0	22.0
Local biotic						
No. cyprinid spp.	# CYPR	1	1	2	3	9
No. piscivorous spp.	# PISC	0	1	2	3	9
No. prey spp. <15 cm	# PREY L	0	2	3	4	9
No. prey spp. ≥15 cm	# PREY G	0	1	2	2	15
No. warm spp.	# WARM	0	2	3	4	9
No. cool spp.	# COOL	0	0	1	2	12
No. cold spp.	# COLD	0	0	1	2	6

Note: Reported values are minimum (Min.), first quartile (1st Q), median (Med.), third quartile (3rd Q) and maximum (Max.) for the training data set.

years ago (Dyke 1996). Climate data were obtained from the Digital Archive of Canadian Climatological Data (Atmospheric Environment Service of Environment Canada).[5] These data represented total monthly precipitation and mean monthly temperature collected between 1960 and 1989 at 1836 recording stations. Average values for total monthly precipitation and mean monthly temperature over the 30-year recording period were calculated for each station with a minimum sampling record of five consecutive years. Total annual precipitation and mean annual temperature at each station was calculated as the total or mean of the 12 total monthly precipitation and mean monthly temperature averages. Trend surfaces for mean annual temperature and total annual precipitation were interpolated using Inverse Distance Weighting Interpolation (12 nearest neighbors) in ArcView GIS 3.2 (ESRI Institute 1999).

Other independent variables were obtained from the OMNR Lake Inventory database (Dodge et al. 1985). Water chemistry variables included pH and total dissolved solids (milligrams per liter). For each lake, the data were partitioned by month of record and mean annual values for each measurement were calculated as the mean of the average monthly values. Lake morphometry variables included lake area, shoreline perimeter, maximum depth, and elevation.

[5] URL: ⟨http://climate.weatheroffice.ec.gc.ca/climateData/canada_e.html⟩

Predicting smallmouth bass presence/absence

An artificial neural network was used to model the presence/absence of smallmouth bass as a function of 20 regional and local environmental variables (Table 1). We used a one hidden-layer, feedforward neural network trained by the back-propagation algorithm (Rumelhart 1986), which is considered to be a universal approximator of any continuous function (Hornik et al. 1989, Bishop 1995). The neural network architecture included an input layer containing 20 neurons (a neuron representing each environmental variable), a five-neuron hidden layer and a single neuron output layer (representing the predicted probability of smallmouth bass occurrence). The number of neurons in the hidden layer (optimal referring to minimizing the trade-off between network bias and variance) was determined empirically by comparing the performances of different cross-validated networks, with 1–25 hidden neurons, and choosing the number that produced the greatest predictive performance. Learning rate (η) and momentum (α) parameters (varying as a function of network error) were included during network training to ensure a high probability of global network convergence and a maximum of 1000 iterations for the backpropagation algorithm to determine the optimal axon weights. Prior to training the network, the environmental variables were converted to z scores to standardize the measurement scales of the inputs into the network. We refer the reader to

Bishop (1995) and Olden and Jackson (2001) for more details regarding the neural network methodology.

The explanatory importance of each environmental variable was quantified by calculating the product of the connection weights between its input neuron and the output neuron and then summing the products across all hidden neurons. This procedure is repeated for each environmental variable, and the relative contributions of the variables were calculated by dividing the absolute value of each variable contribution by the grand mean (sum of all absolute variable contributions). This method provides a measure of the explanatory importance of each environmental variable, which were subsequently assessed for their statistical significance using a randomization test. We refer the reader to Olden and Jackson (2002*a*) for more details on calculating variable contributions and testing their significance using the randomization approach.

A neural network approach was chosen to model smallmouth bass occurrence over other traditional parametric approaches because artificial neural networks are capable of modeling nonlinear associations with a variety of data types (an important consideration given the discrete and continuous nature of the data), require no specific assumptions concerning the distributional characteristics of the independent variables (eliminating the need to make subjective data transformations), can accommodate interactions among predictor variables without any a priori specification (Bishop 1995), and have been shown to exhibit substantially higher predictive power (based on empirical and simulated data) when modeling nonlinear relationships compared to logistic regression analysis and linear discriminant analysis (Olden and Jackson 2002*b*).

To evaluate predictability of smallmouth bass occurrence the neural network was validated using two approaches. First, *n*-fold or ''leave-one-out'' cross validation was used to assess model performance using 2615 Ontario lakes (i.e., training data). This technique was employed as it provides a nearly unbiased estimate of model performance. Second, we conducted external validation by applying the above network to an additional set of 431 lakes. The test set contained lakes in central Ontario in areas where lake trout were originally present and smallmouth bass were largely absent but have been introduced within the last 150 years. This analysis provides an opportunity to assess the transferability or generality of the model to other lakes of Ontario. For both analyses we partitioned the overall classification success of the network by deriving confusion matrices (Fielding and Bell 1997). A confusion matrix tabulates the observed and predicted presence/absence patterns, and thus provides a summary of the number and direction of correct and incorrect classifications produced by the model. Using these matrices we examined three metrics of prediction success. First, we quantified the overall classification performance of the model as the percentage of lakes where the model correctly predicts the presence/absence of the species. Second, we examined the ability of the model to accurately predict species presence, termed model sensitivity. Third, we examined the ability of the model to accurately predict species absence, termed model specificity. Rather than following the conventional decision threshold of 0.5 (the cut-off at which a species is predicted to be present), we constructed a receiver-operating characteristic (ROC) plot to estimate the predictive ability of the network over all decision thresholds (Fielding and Bell 1997). An ROC graph is a plot of the sensitivity/specificity pairs resulting from continuously varying the decision threshold over the entire range of results observed. The optimal decision threshold was chosen to maximize overall classification performance of the model, given equal costs of misclassifying the species as present or absent. The optimal decision threshold was then used to calculate correct classification, sensitivity, and specificity. Cohen's kappa statistic (Titus et al. 1984) was used to assess whether model performance differed from expectations based on chance alone. Correct and incorrect classification of bass presence/absence from the neural network model was tabulated: predicted, observed (true presence); not predicted, not observed (true absence); predicted, not observed (false presence); not predicted, observed (false absence). Lakes in which bass were predicted, not observed are considered candidates for bass invasion. The lake classification was displayed using a Geographic Information System (GIS).

Food web vulnerability

In this study, we used stable isotopes to characterize the food web structure of 18 central Ontario lakes. All study lakes contained lake trout and spanned a broad range of community composition and lake size. Carbon and nitrogen stable isotope ratios ($\delta^{13}C$ and $\delta^{15}N$) provide valuable information about aquatic food webs (Peterson and Fry 1987). There is a 3–4‰ increase in $\delta^{15}N$ from prey to predator, such that $\delta^{15}N$ can be used to estimate consumer trophic position (DeNiro and Epstein 1981, Minagawa and Wada 1984, Cabana and Rasmussen 1994, 1996, Vander Zanden and Rasmussen 2001). Benthic algae are enriched in ^{13}C relative to phytoplankton owing to differential fractionation over dissolved inorganic carbon (DIC). These isotopic differences are retained at higher trophic levels and serve as a basis for estimating the energetic contributions of littoral and pelagic prey (Hecky and Hesslein 1995, Vander Zanden and Rasmussen 2001).

Fish and invertebrates were collected for isotope analysis during summers from 1995 through 1997. Details of the sample collection and isotope analysis are presented elsewhere (Vander Zanden et al. 1999*a b*, Vander Zanden and Rasmussen 1999). Stable isotope ratios (*R*) are expressed in delta (δ) notation, defined as the parts per thousand (‰) deviation from a standard material; $\delta^{13}C$ or $\delta^{15}N = ([R_{sample}/R_{standard}] - 1) \times 1000$,

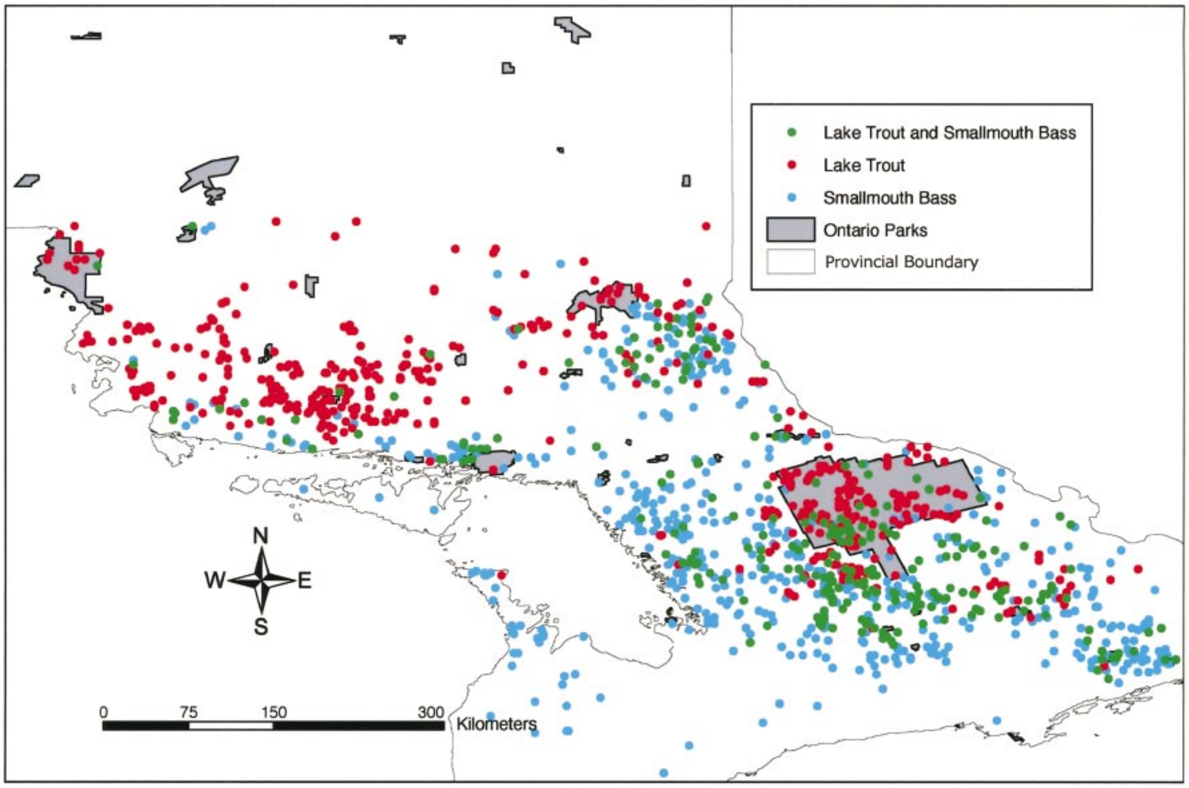

FIG. 2. The geographic distribution of lakes in Ontario containing lake trout alone (508 lakes), smallmouth bass alone (854 lakes), and both lake trout and bass (280 lakes).

where R = $^{13}C/^{12}C$ or $^{15}N/^{14}N$. The $\delta^{15}N$ values were converted to a continuous measure of trophic position (TP) in order to correct for variation in $\delta^{15}N$ at the base of the food web:

$$TP_{consumer} = [(\delta^{15}N_{consumer} - \delta^{15}N_{baseline})/3.4] + 2 \quad (1)$$

where 3.4 is the assumed per trophic level enrichment in $\delta^{15}N$ primary producers are trophic level one, primary consumers are trophic level two, and so on. TP was estimated for each fish; population- or lake-specific TP estimates are the mean of all adults from a population. Lake trout piscivory (percentage consumption of fish) was calculated as the difference in trophic position between lake trout and prey fish. Two end-member $\delta^{13}C$ mixing models were used to estimate the fractional reliance of lake trout on littoral and pelagic prey using the following equation:

$$\%\text{littoral} = \frac{\delta^{13}C_{\text{lake trout}} - \delta^{13}C_{\text{pelagic}}}{\delta^{13}C_{\text{littoral}} - \delta^{13}C_{\text{pelagic}}} \times 100. \quad (2)$$

Piscivory and trophic position are summary variables that reflect the trophic niche of lake trout, and were used to examine how the trophic niche of lake trout varies in the presence/absence of smallmouth bass and pelagic prey fish. These relationships form the basis for classifying lakes into one of three categories: pelagic prey fish present (PPF), pelagic prey fish absent and bass present (B), and pelagic prey fish absent and bass absent (NB). Pelagic prey fish (PPF) include the following species: cisco (*Coregonus artedii*), lake whitefish (*Coregonus clupeaformis*), and rainbow smelt (*Osmerus mordax*). Using species lists from our Ontario lakes database, distributions of these three lake types were mapped using ArcView.

The lake classification from the neural networks (four categories) and the food web analysis (three categories) were cross-tabulated, producing 12 potential lake types. This classification was simplified into our final classification composed of four lake types based on bass introductions and the potential for bass–lake trout interactions. One of these four lake types represents lakes that are considered vulnerable: they have the appropriate conditions for bass establishment, and a sensitive food web structure. Distributions of these four lake types were mapped using ArcView (ESRI, Redlands, California).

RESULTS

Distributions of lake trout and bass

Of the 3046 lakes initially included in the data set, 788 lakes contained lake trout, while 854 lakes contained smallmouth bass. Two hundred and eighty lakes were found to contain smallmouth bass *and* lake trout, while 508 lakes contain lake trout and no bass (Fig.

TABLE 2. Performance of the smallmouth bass neural network for predicting presence/absence in the 2615 study lakes (training data) based on *n*-fold cross validation, and applying the training network to predicting presence/absence in an additional 431 lakes (test data).

Data	SP	Correct classification	Sensitivity	Specificity	Kappa	*P*
Training	27.7	89.8	82.1	92.7	0.745	0.000
Test	35.7	76.8	70.8	80.1	0.502	0.000

Note: Reported values are percentage species prevalence in the data sets (SP), percent correct classification, sensitivity, specificity, kappa statistic, and associated *P* value.

2). The geographic ranges of bass and lake trout broadly overlapped, although lake trout tended to have a more northerly distribution, while bass occurrences were centered in the southern portion of the study region.

Modeling bass presence/absence using artificial neural networks

Smallmouth bass occurrence was highly predictable in the 3046 Ontario lakes based on the 20 regional and local environmental variables (Table 1). The cross-validated neural network ($n = 2615$) correctly predicted bass presence/absence in 90% of the study lakes, and exhibited both high sensitivity (correctly predicting presence) and specificity (correctly predicting absence). Similarly, the occurrence of bass was correctly predicted in 77% of the lakes when the network was applied to the additional set of lakes ($n = 431$). The fact that predictions from the network were significantly greater than random and that the network exhibited high levels of sensitivity (71% and 82%) for both sets of lakes emphasizes the utility of the network for making predictions about the potential presence of smallmouth bass (Table 2). The relative importance of the 20 predictor variables in the neural network are shown in Fig. 3, where they have been grouped into four scale-explicit categories related to: glacial history, climatic conditions, morphological and water chemistry characteristics, and community trophic composition. Smallmouth bass are predicted to occur in lakes with wet, warm climates, short time periods since being uncovered by glacial ice, and locally, by large surface area, large shoreline perimeter, and greater numbers of piscivores and small-sized prey species and smaller

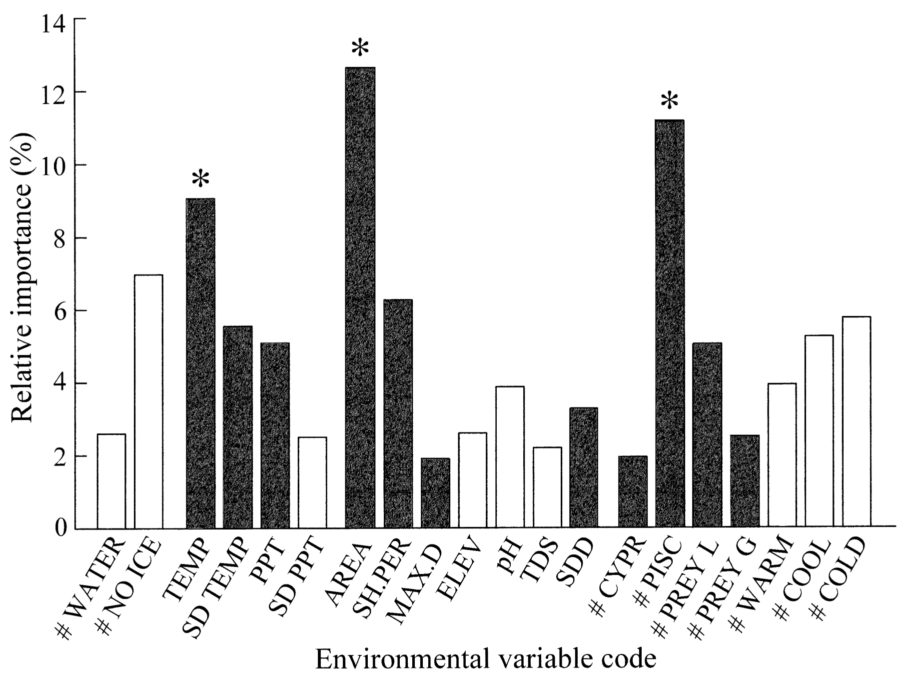

FIG. 3. Relative importance (%) of the 20 environmental variables in the smallmouth bass neural network (see Table 1 for definitions of variable codes). Variables are grouped into four scale-explicit categories related to a lake's glacial history, climatic conditions, morphological and water chemistry characteristics, and community trophic composition. Gray bars indicate variables that have an overall positive influence on predicted smallmouth bass occurrence, and white bars indicate an overall negative influence on predicted smallmouth bass occurrence. Asterisks (*) denote variables that significantly contribute to network predictions based on the randomization test.

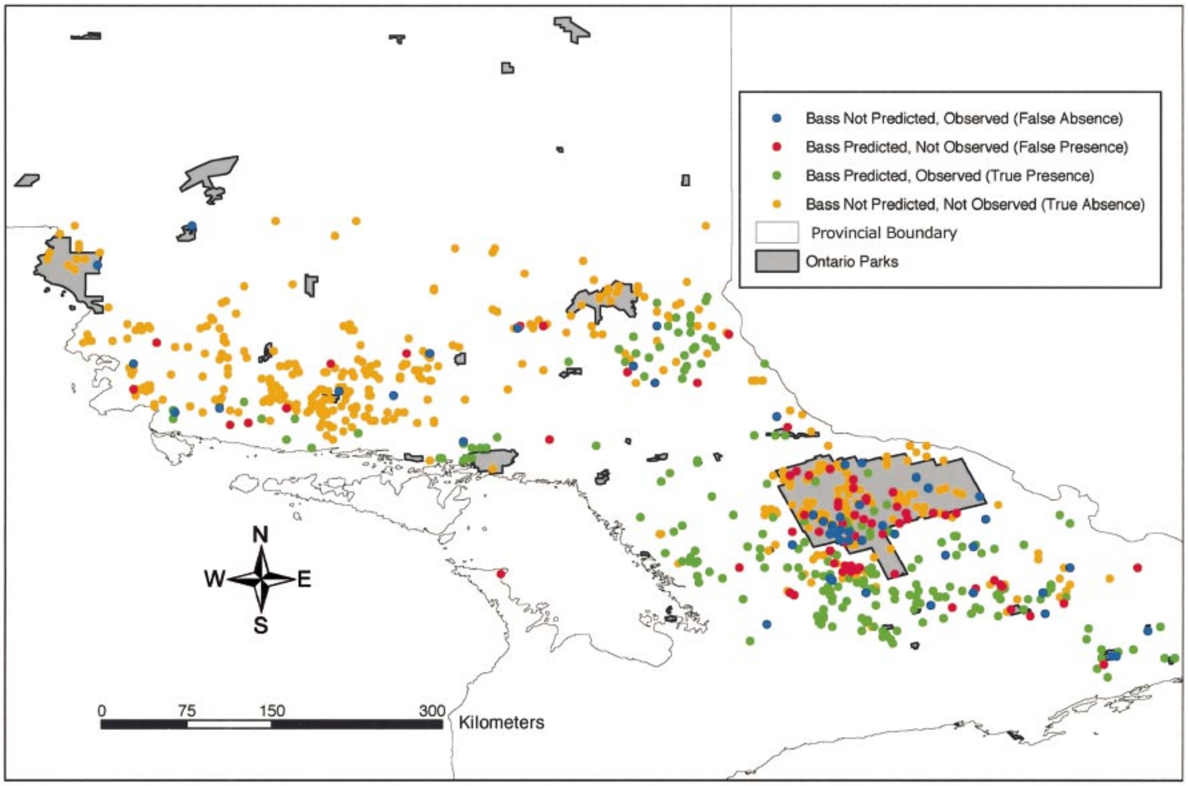

FIG. 4. Correct and incorrect classification of smallmouth bass presence/absence by the neural network. Lakes are classified into the following categories: (1) true presence, bass predicted and observed (229 lakes); (2) true absence, bass not predicted and not observed (438 lakes); (3) false presence, bass predicted and not observed (69 lakes); and (4) false absence, bass not predicted and observed (52 lakes). Lakes classified as ''false presence'' are considered likely to be invaded by bass.

numbers of cool/cold water species (Fig. 3). Of these variables, mean annual temperature, lake surface area, and number of piscivores were statistically significant based on the randomization test.

The correct and incorrect classifications of smallmouth bass presence and absence from the neural network were tabulated for the 788 lake trout lakes in the study area and mapped using ArcView (Fig. 4). The number of lakes in which smallmouth bass presence and absence were correctly and incorrectly classified are shown in Table 3 (right-hand column). In 69 lakes, bass were predicted, but not observed (i.e., false presence). These lakes are considered likely candidates for bass invasion because they have the appropriate environmental conditions, but do not presently support a bass population.

TABLE 3. Number of lakes in each of the 12 lake classes formed by combining the food web classifications, which are indicated as columns (three classes), and the classifications from the neural network model, which are indicated as rows (four classes).

Neural network classification	Food web classification			Total
	PPF	NB	B	
True presence	131	⋯	98	229
True absence	132	306[B]	⋯	438
False presence	21	48[A]	⋯	69
False absence	27	⋯	25	52
Total	311[D]	354	123[C]	788

Note: Superscripts delineate the four final lake types plotted in Fig. 7: A, high vulnerability; B, low vulnerability; C, impacted; D, buffered.

Modeling impacts based on food web structure

Lake trout piscivory was plotted vs. lake trout littoral reliance for the 18 study lakes (Fig. 5). Lake trout from lakes with pelagic prey fish (hereafter referred to as PPF) clustered in the upper left corner, indicating that lake trout are piscivorous, and rely on pelagic prey (Fig. 5). In lakes without pelagic prey fish (B and NB), piscivory and littoral reliance were positively correlated (percentage piscivory = $1.07 \times$ percent littoral $- 9.62$; $r^2 = 0.83$). Lake trout from lakes lacking bass (hereafter NB) were more piscivorous and relied on littoral prey, while lake trout from lakes containing bass (hereafter B) had lower levels of piscivory and relied primarily on pelagic prey. This indicates that bass influence the trophic niche of lake trout, but the effect is apparent only in the absence of pelagic prey fish. Based on these findings, the presence/absence of bass and pelagic prey

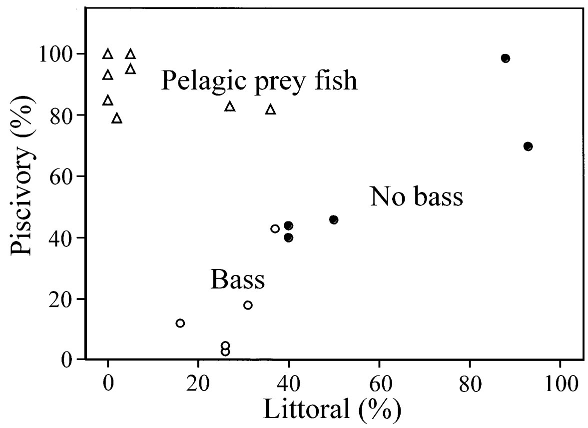

FIG. 5. The trophic niche of lake trout from 18 Ontario lakes, based on carbon and nitrogen stable isotope ratios. In lakes without pelagic prey fish (circles, solid and open), the trophic niche of lake trout is related to the presence/absence of bass. In the absence of bass (solid circles), lake trout tend to be littoral piscivores, while in the presence of bass (open circles), lake trout tend to be pelagic planktivores. In lakes containing pelagic prey fish (open triangles), lake trout are pelagic piscivores, as evidenced by their high piscivory and low reliance on littoral prey.

fish in lakes can be used to classify lakes according to the strength of bass–lake trout interactions (Fig. 6). In NB lakes (no bass, no pelagic prey fish), lake trout rely on littoral prey fish (Fig. 6). In B lakes (bass, no pelagic prey fish) lake trout have a low trophic position and low $\delta^{13}C$ values, indicating zooplanktivory (Fig. 6). In PPF lakes, lake trout and bass are top predators on separate pelagic and littoral food chains, respectively (Fig. 6). The presence of pelagic prey fish, in effect, buffers lake trout from the predatory impacts of bass on littoral prey fish. Based on our food web analysis and lake classification scheme, lakes lacking pelagic prey fish *and* lacking bass (NB lakes) are considered sensitive to bass introductions.

The 788 lake trout lakes from the study area were classified according to the food web classification scheme shown in Fig. 6 and mapped using ArcView (Fig. 7a). Three hundred fifty-four lakes (44%) were NB, 123 lakes (16%) were B, and 311 lakes (40%) were PPF. Although lakes of all three categories occurred throughout the study area, NB lakes were most concentrated in the Algonquin Park region (45°50′ N, 78°20′ W), PPF lakes were concentrated in the surrounding lowland areas, and B lakes were concentrated in the more populated areas located south of Algonquin Park.

Lake classification based on bass occurrences and impacts

Using the predictions from the neural networks and food web classification, we defined 12 lake types based on combinations of predicted smallmouth bass occurrences (i.e., true presence, true absence, false presence, and false absence) and the predicted impacts of a bass introduction, based on food web structure (i.e., lakes containing pelagic prey fish, lakes lacking bass, and lakes containing bass, Table 3). To highlight the lakes that are potentially vulnerable to ecological impacts of bass invasion, we simplified the classification to four lake types (Table 3).

High vulnerability lakes (A, 48 lakes) lack pelagic prey fish, and smallmouth bass are predicted to be present but are absent (i.e., false presence). These lakes represent lake trout populations that are susceptible to the ecological effects of bass invasion because they are not buffered by the presence of pelagic prey fish, and have suitable conditions for bass establishment. Low vulnerability lakes (B, 306 lakes) lack pelagic prey fish, and smallmouth bass are predicted to be absent and are reported absent (i.e., true absence). Lake trout populations are potentially susceptible to the ecological effects of bass establishment, although the likelihood of establishment is lower than in the highly vulnerable lakes. Impacted lakes (C, 123 lakes) lack pelagic prey fish, and smallmouth bass are present (classified as either true presence or false absence). In these lakes, lake trout populations may have already been impacted by bass introduction, and should be the focus of efforts to monitor lake trout population health. Finally, buffered lakes (D, 311 lakes) contain pelagic prey fish. Smallmouth bass may be either present or absent. In these lakes, lake trout populations are buffered against the food web impacts of bass since pelagic prey fish are available.

These four lake types were mapped using ArcView (Fig. 7b). There are 48 high vulnerability lake trout lakes (subscript ''A'' in Table 3); those lakes that are predicted to support bass, and vulnerable to food web alterations are individually listed in the Appendix. Of these 48 lakes, 31 lakes are located outside of Algonquin Park. The other 17 lakes are located within Algonquin Park and as such, have limited or no public road access. Lakes outside of Algonquin Park are more accessible and less protected from bass colonists than lakes within Algonquin Park, making bass introduction more likely in these lakes (although we consider all 48 lakes to be potentially vulnerable to bass introductions).

DISCUSSION

Developing a predictive understanding of invasive species and their impacts on native species and ecosystems is an important goal for ecologists (Lodge 1993, Lodge et al. 1998). Previous work in lakes has demonstrated adverse impacts of predator introductions on native species and communities (Zaret and Paine 1973, Vander Zanden et al. 1999*a*). While demonstrating adverse impacts is an important task, efforts to effectively manage invasive species and their impacts will greatly benefit from models that can predict both the potential occurrence and the impact of particular

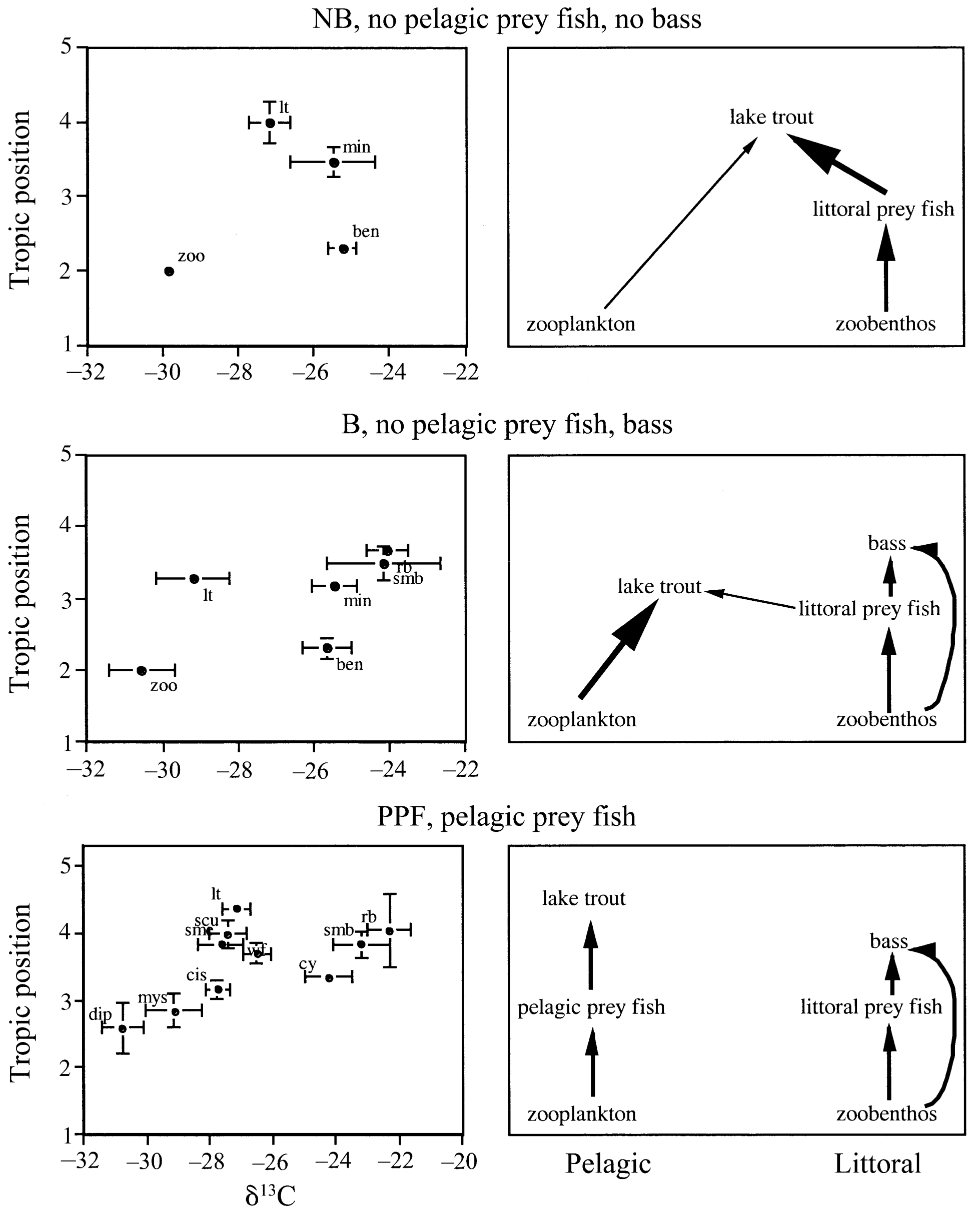

FIG. 6. Average food web structure of the three lake types shown in Fig. 5. The left panels show trophic position–$\delta^{13}C$ food web diagrams of each of the three food web types. The right panels are idealized food web diagrams of the food webs shown on the left. (Top) NB, pelagic prey fish and bass are absent (solid circles in Fig. 5). Lake trout rely primarily on littoral prey fish and are closely coupled with the littoral, inshore food web. (Middle) B, pelagic prey fish are absent, and bass are present (open squares in Fig. 5). The presence of bass reduces littoral prey fish populations, causing lake trout to rely on zooplankton rather than littoral fish. (Bottom) PPF, pelagic prey fish are present (open triangles in Fig. 5). Lake trout are the top predator on the pelagic food chain, while bass are the littoral top predator. Abbreviations are: lt, lake trout; min, minnows; ben, benthic invertebrates; zoo, zooplankton; rb, rock bass; smb, smallmouth bass; dip, diporeia; mys, mysis; cis, cisco; wf, whitefish; sme, rainbow smelt; scu, sculpin; and cy, cyprinids.

invaders. Our study combines results from two separate models: artificial neural networks identified lakes that are suitable for invasion by bass, and analyses of food web structure identified lakes likely to be adversely impacted by a bass introduction. Forty-eight of the 3046 lakes included in the study were classified as both likely to be invaded and likely to be impacted and are individually identified in the Appendix. These lakes should have priority for efforts to minimize further impacts of bass introductions in Ontario.

Predicting occurrences

Smallmouth bass presence/absence was highly predictable from local environmental variables using an

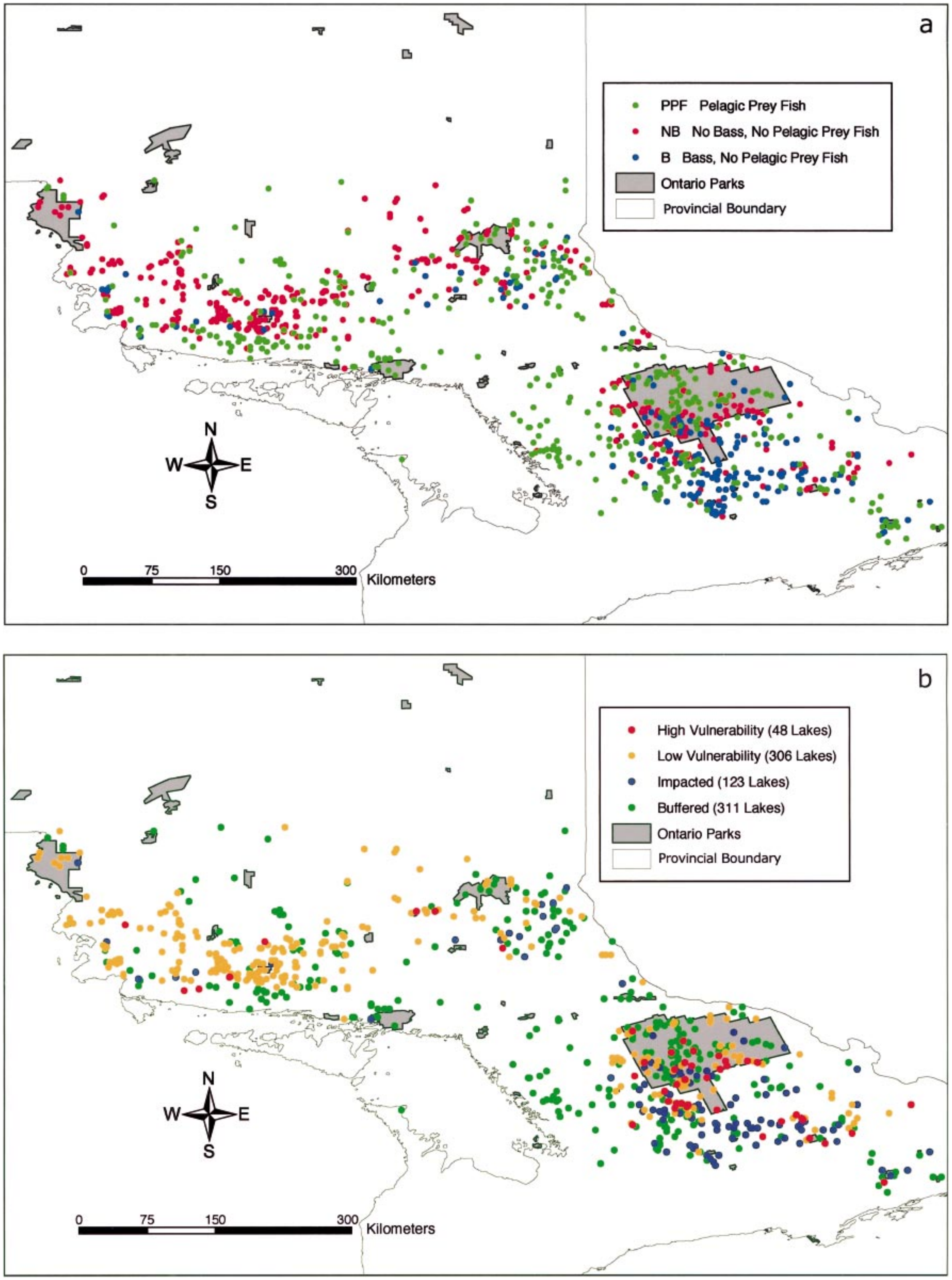

FIG. 7. (a) Geographic distribution of the three lake types from the food web classification: pelagic prey fish present, bass present or absent (PPF, 311 lakes); pelagic prey fish absent and bass absent (NB, 354 lakes); or pelagic prey fish absent and bass present (B, 123 lakes). (b) Occurrences of the final four lake classes based on food web and artificial neural network classifications. Letters (A–D) in the following descriptions refer to superscripts in Table 3: High vulnerability lakes (A, 48

artificial neural network approach. The 69 lake trout lakes in which bass were predicted, but are not presently observed (false presence) are considered to be invasible by bass. These lakes have the appropriate environmental conditions for supporting smallmouth bass populations. The absence of bass in many of these lakes is the result of lack of glacial lake coverage and early isolation, which limited colonization following the retreat of the last glaciation (Hinch et al. 1991). Throughout the last century, humans have introduced bass into many of the historically bassless lakes, with the goal of expanding fishing opportunities. Despite this, there still remain a number of lakes that appear to have the appropriate environmental conditions for bass, but do not presently support a bass population. Presumably, bass have never been introduced into many of these lakes.

Empirical models predicting the occurrence or density of aquatic invaders have been developed for a variety of aquatic invaders, including zebra mussels (Ramcharan et al. 1992, Koutnik and Padilla 1994, Haltuch et al. 2000), Eurasian watermilfoil (Buchan and Padilla 2000), and the invasive spiny water flea, *Bythotrephes longimanus* (MacIsaac et al. 2000). The general approach has been to predict the presence/absence of invaders based on environmental parameters. These studies have not always made specific predictions about which systems or locations are likely to be invaded by particular invaders, information that would be useful for lake managers. MacIsaac et al. (2000) found that many North American lakes with predicted occurrences of the spiny water flea, *Bythotrephes*, do not presently host *Bythotrephes* populations. The authors concluded that many lakes in the Great Lakes basin are vulnerable to *Bythotrephes* invasion. This general approach is similar to ours, in which misclassified lakes (i.e., false presence; bass predicted, not observed) are considered vulnerable to invasion.

Predicting impacts

While some species invasion events have dramatic, adverse impacts on native species and ecosystems, other invaders appear to integrate into the receiving system with little or no observed impacts (Simberloff 1981, Vitousek 1986, 1990, Pimm 1991, Lodge 1993). Clearly, predicting which systems are likely to be impacted is an important management goal, although few studies have been able to make quantitative predictions of aquatic invader impacts (Ricciardi et al. 1998, Parker et al. 1999). While theoretical models have indicated that invader success should be determined by both attributes of the invader and the community (Case 1991, Pimm 1991), there is relatively little evidence indicating that factors such as food web structure determine invader success or impacts on the native biota (Moyle 1986).

Food web structure has rarely been considered in studies of invader impacts or other aspects of lake management. This study demonstrates that the impact of an introduced species can be mediated by food web structure, and that this approach has predictive value. The neglect of food web considerations in most studies stems from the inherent difficulty in measuring food web structure in natural ecosystems. Use of stable isotopes provides an efficient and effective approach for characterizing energy flow pathways through food webs. This approach was used to develop a lake classification scheme that reflected vulnerability to impacts of littoral predators and could be applied to a large number of lakes based on readily available species lists.

Bass are likely to exert competitive impacts on lake trout only in the absence of pelagic prey fish, while in the presence of pelagic prey fish, lake trout forage as a pelagic predator (Figs. 5 and 6). Under this scenario, lake trout are buffered from bass impacts because the two species are partitioned onto separate food chains. Our stable isotope evidence is consistent with dietary studies that show that lake trout feed on pelagic forage fish if present, or a mix of littoral prey fish and invertebrates in their absence (Vander Zanden and Rasmussen 1996). Furthermore, there is emerging field evidence that bass invasions adversely impact lake trout populations in lakes lacking pelagic prey fish. In MacDonald and Clean Lakes, Ontario, both of which lack pelagic prey fish, bass invasion was accompanied by dramatic reductions in lake trout growth rates and fecundity (J. M. Cassleman and D. Brown, *unpublished data*). Meanwhile, in Lake Opeongo, Ontario, a lake that contains cisco and whitefish, bass introduction appears to have had no impact on the native lake trout population.

Predicting invader occurrence and impact: management implications

This study is unique in that it uses quantitative techniques to identify lakes at high risk of bass establishment *and* adverse ecological impacts. Of the 788 lakes included in this analysis, only 48 lakes were classified as both likely to be invaded and impacted (high vulnerability lakes, Table 3; Fig. 7b). Whether these lakes will eventually be invaded by bass depends not only upon the environmental suitability, as modeled here,

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lakes) are false presence, lack bass, and lack pelagic prey fish. Low vulnerability lakes (B, 306 lakes) are true absence, lack bass, and lack pelagic prey fish. Impacted lakes (C, 123 lakes) contain bass and lack pelagic prey fish. Buffered lakes (D, 311 lakes) contain at least one species of pelagic prey fish.

but also on the degree of isolation and the availability of road access, since anglers are a primary vector of bass movement on the landscape (Litvak and Mandrak 1993). Of the 48 vulnerable lakes, 17 are located within the boundaries of Algonquin Park (Appendix). Algonquin Park is the primary protected area in central Ontario and road access to lakes is minimal. While the protected status and limited road access of these lands will likely slow the spread of bass, bass have also been invading within the boundaries of Algonquin Park, and all 48 lakes should be considered vulnerable to bass impacts, regardless of road access. Since a central goal of fisheries management efforts in Ontario has been to protect native inland lake trout populations (Olver et al. 1991), our identification of a relatively small number of vulnerable lakes will help focus efforts to prevent negative impacts of bass invasions. This type of information should be useful for lake managers interested in prioritizing lakes so as to minimize adverse impacts of nonnatives.

Another 306 lakes were classified as potentially sensitive to bass impacts based on their food web structure, but neural networks did not predict a bass occurrence (thus classified as low vulnerability lakes). While our neural network model does not predict a bass occurrence in these lakes, some of these lakes will be able to support a bass population. Note that bass do occur in lakes in which they are not predicted by the neural network (Table 2: sensitivity is 70.8% for the test data and 82.1% for the training data). Some of these lakes will have been misclassified. Furthermore, global warming and lake eutrophication may increase the vulnerability of these lakes in the future. Considering the significant positive effect of climate-related variables in the neural networks (Fig. 3), temperature increases associated with climate warming would make these lakes more invasible by bass (Jackson and Mandrak 2002). This would, in effect, switch many of the low vulnerability lakes to high vulnerability lakes. Of these 306 lakes, it is expected that the warmer, more southerly lakes would be most likely to become suitable, and could eventually be colonized by bass under global warming-related temperature increases. More northerly lakes would be less likely to be invaded. Consistent with this, cold temperatures are known to limit the geographic distribution of bass, and many warmwater fishes are predicted to further expand their range northward in response to climate warming scenarios (Shuter et al. 1980, Mandrak 1989, Stefan et al. 2001, Jackson and Mandrak 2002).

While the low vulnerability lakes are of less immediate concern, efforts should be made to prevent further bass introductions in both high vulnerability and low vulnerability lakes. Public education efforts will be central to reducing further impacts of bass introductions. While many local residents may welcome new bass fishing opportunities, lake trout fisheries are highly valued and are preferred by anglers. Anglers and residents do not generally perceive bass introductions to have negative consequences for lake trout fisheries. This message must be conveyed to the public. Lake trout and other angling groups may be particularly active and involved in this process. Prohibiting the use of live bait is a second strategy for reducing bass impacts. Not only will this reduce impacts of introduced bass, but more generally it will reduce nonnative fish introductions, as angler's bait buckets are a key vector for the movement of many nonnative fishes (Litvak and Mandrak 1993).

Three hundred and eleven of the lake trout lakes contained at least one species of pelagic prey fish. These lakes are classified as buffered. Even if bass were to be introduced, impacts on lake trout are not anticipated. In effect, the presence of pelagic prey fish protects lake trout from adverse impacts of bass introductions. Bass introduction into these lakes very well may have other consequences, particularly for littoral prey fish populations (Chapleau et al. 1997, Findlay et al. 2000, Jackson and Mandrak 2002),but these impacts are not considered here.

Our findings would suggest that the intentional introduction of pelagic prey fish is a technique for reducing bass–lake trout competition. Prior to the introduction of cisco into Lake Opeongo, Ontario, lake trout fed primarily on littoral prey fish and invertebrates (Martin and Fry 1972). After cisco were introduced, they became the predominant prey item of lake trout. Smallmouth bass were introduced into Opeongo in the late 1800s, and became established as the top predator of the littoral zone. While the introduction of cisco into Lake Opeongo provided trophic separation between lake trout and smallmouth bass, introduction of cisco appears to have altered the growth and life history patterns of lake trout. Adult lake trout now feed on cisco and consequently experience higher growth rates, but juvenile lake trout now compete with cisco, and as a result, grow more slowly. Another factor to consider is that addition of another trophic level to the pelagic food web is likely to lead to increased concentrations of persistent contaminants such as mercury and PCBs in top predators (Rasmussen et al. 1990, Cabana et al. 1994). For these reasons, we argue that the introduction of pelagic prey fishes should not be used as a means of buffering lake trout from bass impacts.

Finally, 123 lakes are classified as impacted; they contain smallmouth bass, but no pelagic prey fish. While some of these lakes may have historically contained bass populations, many of these lakes have been invaded during the last century. As a result of predatory impacts of bass on littoral prey fish communities, lake trout viability in many of these lakes may already be compromised, as recently observed in MacDonald and Clean Lakes, Ontario (J. M. Casselman and D. Brown, *unpublished data*).

Limitations of the available information

Predicting the occurrences and impacts of smallmouth bass introductions at the landscape scale is a difficult task. Our study relied heavily on lake-specific information that was derived from publicly available databases from the Ontario Ministry of Natural Resources and the Ontario Ministry of the Environment. The quality of the Ontario fish database is limited in some regions, particularly as some species lists have not been updated since the 1970s and 1980s. Despite this, we have found the fish distribution database to be quite accurate for the prominent species such as lake trout, smallmouth bass, and pelagic forage fish. Furthermore, the database has been supplemented with additional records, particularly in the Algonquin Park region (N. Mandrak, *unpublished data*), although some recent bass invasions may not have been included. Unfortunately, there exists little historical information about the timing of bass introductions in Ontario. This information would be useful for predicting the location of future invasion, since bass invasions might be expected to be localized in particular areas.

Another limitation of our study was that we did not explicitly model the probability of bass colonists dispersing to a particular lake. Anglers and their bait buckets appear to be a primary vector of bass dispersal in Ontario (Litvak and Mandrak 1993). While we assume that bass can be directly introduced into any lake with road access, the likelihood of a bass introduction will be a function of lake visitation rates, fishing pressure, and lakefront development. Furthermore, bass are capable of dispersing through the drainage network, thereby allowing them to colonize lakes without road access if the drainage patterns allow. We were not able to consider which individual lakes have road access because digital road maps of sufficient resolution were not publicly available for Ontario. However, virtually all lakes in the study area have public road access, with the exception of lakes in the interior of Algonquin Park. Thus, bass dispersal potential can be reasonably characterized by considering whether the lake is located in Algonquin Park (Appendix).

Although introduction of littoral piscivores can have community-wide impacts in lakes (Chapleau et al. 1997, Vander Zanden et al. 1999*a*, Findlay et al. 2000, MacRae and Jackson 2001), we limited our analysis to the 788 lakes that are inhabited by lake trout. Lake trout support an economically and culturally important fishery, which is currently in decline across much of southern Ontario (Olver et al. 1991), and requires the development of regional fisheries management approaches (Shuter et al. 1998). Thus, our emphasis on bass introductions and the consequences for lake trout populations and fisheries greatly increases the relevance of this work to fisheries managers. By focusing on the interactions between bass and lake trout, we neglect other impacts that bass might have on other species and trophic levels. Top-down impacts of bass on littoral prey fish populations are well documented, and appear to occur in a variety of lake types (Chapleau et al. 1997, Whittier et al. 1997, Whittier and Kincaid 1999, Findlay et al. 2000). Nonnative bass introductions may also impact native brook trout and amphibian populations (Oliver et al. 1991, Kiesecker and Blaustein 1998).

Finally, we model occurrences and impacts of a single littoral predator species, smallmouth bass. Other littoral predators such as rock bass, northern pike, and largemouth bass are also invading aquatic systems beyond their native range, including much of central Ontario. These species also have negative impacts on littoral prey fish populations, and their introduction should also be of concern to lake managers. We recommend a similar predictive modeling approach to assess future occurrences and potential impacts of these other littoral predators. Although rock bass and largemouth bass might be predicted to occur in different lakes due to different habitat requirements compared to smallmouth bass, impacts of these predators on littoral prey fishes (minnow) are similar, and our food web-based classification should be applicable to these other littoral piscivores.

Conclusions

As aquatic biotas become increasingly homogenized through nonnative species introductions (Rahel 2000), there is an emerging realization of the importance of protecting the diverse range of food web structures occurring in nature. Degradation of this ''food web diversity'' through biotic homogenization may have unknown consequences. In the case of central Ontario, bass introductions have had adverse impacts on native lake trout populations (J. M. Casselman and D. Brown, *unpublished data*). Furthermore, bassless lakes of the temperate zone harbor unique and diverse fish communities (Chapleau et al. 1997, Whittier and Kincaid 1999, MacRae and Jackson 2001), and support both unique food webs and valuable fisheries (Vander Zanden and Rasmussen 2002). The modeling approach developed here for predicting invader occurrences and impacts is based on an understanding of among-system variability, food web interactions between the invader and the target ecosystem, and the development of quantitative models to classify lakes according to both invader occurrences and impacts. Our models predict specifically which ecosystems will be invaded, and which will be adversely impacted *if* they are invaded. Such analyses can be used to guide educational and legislative efforts to minimize further adverse impacts of nonnative species introductions.

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APPENDIX

A table listing latitude, longitude, and location of vulnerable lakes (in or out of Algonguin Park) is provided in ESA's Electronic Data Archive: *Ecological Archives* A014-001-A1.