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Forecasting dispersal of nonindigenous species

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Forecasting dispersal of nonindigenous species

By

James R. Muirhead

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Abstract

A leading conceptual model of the invasion process suggests that nonindigenous species (NIS) must pass through a series of 'filters' when dispersing from colonized to non-colonized regions. These steps include the initial dispersal of propagules, survival of these propagules upon encountering the new physicochemical environment, and biological integration into the new community.

Here, I forecast invasions for two aquatic NIS, the spiny waterflea *Bythotrephes longimanus* and zebra mussel *Dreissena polymorpha* based on the entire invasion sequence using gravity models to assess movement of propagules, data on lake morphometry and physicochemistry, and data on fish community composition. The gravity models included information on movement patterns of recreationalists and life-history characteristics of the NIS that may facilitate invasions. I also contrast the abilities of a hierarchical approach to a single 'all-in-one' model that considered all variables simultaneously in detecting actual invasions versus false alarms. Here, the 'all-in-one' model was better at predicting invasions if they had, in fact, occurred.

Next, I compare predictions of *Bythotrephes* invasions for three types of gravity models: total-flow-, production- and doubly-constrained. These models differ in the type of information required to parameterize the model. The Production-constrained model was most likely to detect actual invasions relative to false alarms, and the total-flow-constrained model was least likely to predict false positives.

I also compare backcast patterns of propagule pressure for two groups of related species: one group comprising the spiny waterflea and the fishhook waterflea *Cercopagis pengoi;* and the other, the zebra mussel and quagga mussel *Dreissena rostriformis bugensis*. Differences in species' life-histories may interact with various transport mechanisms to produce highly dissimilar levels of propagule pressure to inland lakes. Species with the broadest distribution had the highest propagule pressure scores.

Finally, I examine the attributes of an invasion network formed by lakes invaded by spiny waterfleas connected by recreational traffic. I was interested in whether specific lakes served as 'hubs', and whether the network of lakes exhibited a scale-free topology. Management implications for a scale-free invasion network include a potential decrease in the overall rate of NIS spread if propagule flow from 'hubs' is reduced.

Co-authorship Statement

This thesis includes materials reprinted from co-authored articles. In all cases, the contribution of co-authors was primarily in an advisory capacity or through the provision of facilities and materials to complete the research. The primary contributions, experimental designs, data collection and interpretation as well as the preparation of all manuscripts were performed by the author.

Chapter 2 published as:

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I dedicate this work to my parents,

who have supported me in so many ways

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There is an acronym in the world of computer programming, GIGO, which stands for Garbage In, Garbage Out. As a modeller whose quality of models is critically dependent on other people's data, I gratefully acknowledge the following: Dr. Norman Yan (York University); Dr. Nick Mandrak (Department of Fisheries and Oceans, DFO); Dr. Dean Jeffries, Dr. Russ Weeber, Dr. Don

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Chapter 1: General introduction

Nonindigenous species (NIS) are one of the leading causes of global homogenization of biodiversity, in part due to the rate and extent of spread of common species, but also because of their adverse consequence on native biota (Ruiz et al. 1997, Sala et al. 2000, Crooks 2002, Rahel 2002, Olden et al. 2004). The interchange of species among continents is occurring at unprecedented rates (Ricciardi 2007) and leaving virtually no habitat unaffected, including remote locations such as the Antarctic and the Southern Ocean (Clarke et al. 2005). A key component in managing NIS is the ability to accurately forecast dispersal. This aspect of risk assessment is critical, as prevention of invasions is usually more cost effective than mitigation of impacts once the invasion has occurred (Leung et al. 2002, Keller et al. 2007).

One of the leading conceptual models in understanding the process of invasions is the multistage invasion sequence, in which propagules must pass through a series of 'filters' that can prevent propagule establishment in novel habitats (Richardson et al. 2000, Kolar and Lodge 2001, Sakai et al. 2001, Heger and Trepl 2003, Theoharides and Dukes 2007). After each 'filter' in the invasion sequence, propagule composition consists of only a subset of that from the previous stage (e.g. Williamson and Fitter 1996). In first stage of the sequence, propagules must survive transport from the source to the recipient habitat (Figure 1). Considering that the number of propagules that survive each stage of the invasion process tends to decline, it would seem that large inocula would favour invasion success. Indeed, propagule pressure - which is comprised of the

combination of the number of introduction events, the number of propagules transported per event, and quality of propagules upon arrival – has been suggested as an important aspect of invasion success (Williamson and Fitter 1996, Lockwood et al. 2005). Indeed propagule pressure has been established as a consistent predictor of invasion success for taxa including birds (Veltman et al. 1996, Cassey et al. 2005), fish (Marchetti et al. 2004), ants (Hee et al. 2000), beetles (Grevstad 1999), mammals (Forsyth et al. 2004) and plants (Jongejans et al. 2007).

Upon arrival in the novel habitat, propagules must be able to tolerate the ambient environment. Life-history characteristics of successful NIS have been proposed, including phenotypic plasticity, as propagules must be able to withstand environmental conditions across the introduced range, which may differ from the source region (Baker 1965, Lodge 1993, Morton 1996). Other factors, including asexuality or hermaphroditic reproduction may allow small, founding populations to avoid problems finding mates (e.g. Allee effect) and maintain positive population growth. As well, species with high intrinsic rates of population increase may be favoured as invaders owing to their propensity to rapidly increase from small (colonizing) population size (Crawley et al. 1986). Evidence for specific life-history factors that consistently favour invasiveness is, however, lacking.

Finally, many workers have attempted to identify specific community properties that influence integration success of the NIS into the recipient community (Elton 1958, Lodge 1993, Kolar and Lodge 2001). These studies

have proven increasingly controversial, as both the magnitude and the direction of these patterns may vary among systems. For example, Elton's (1958) classical view that diversity of NIS would be inversely related to native species diversity has been upheld at local scales with plant communities, but rejected at larger scales (e.g. Stohlgren et al. 2003). In many cases, it appears that factors beneficial to enhancement of native species diversity also promote diversity of NIS.

It has recently been proposed that it is unlikely that single factors govern complex interactions of NIS invading an established community. Rather it may well be the case that multiple factors acting additively, synergistically or antagonistically, determine the eventual success of an invading species. For example, Blumenthal (2006) proposed that success of introduced plants was affected by an interaction between a release from natural enemies and soil nutrient availability in new habitats. Species adapted to living in high nutrient environments would benefit most from a reduction in natural enemies that often accompanies invasions.

Many of the early models of invasion describe spread of the colonizing population as a simple wave moving at constant velocity from the origin (e.g. basic diffusion model, Skellam 1951). Propagules that survive initial colonization become the 'source' propagules in subsequent iterations of the invasion sequence (i.e. secondary spread). Although the terms are often used interchangeably, here I define 'dispersal' as the process that describes the movement or redistribution of individuals from one place to another, and 'spread'

as the change in population density as a function of space and time. One of the simplest forms is a reaction-diffusion model that predicts population density, or gene flow as a function of space and time based on exponential or logistic population growth (i.e. Stage 3 of invasion sequence, biotic integration)(Fisher 1937). These models assume that dispersal distances of particles from their sources are normally distributed, and that diffusion occurs across homogenous space (i.e. Stage 1, transportation)(Okubo 1980). Although simplistic, these models have been successfully applied in describing population spread for a number of species including muskrats, *Ondatra zibethicus* (Skellam 1951), and the small cabbage white butterfly, *Pieris rapae* (Andow et al. 1990). Diffusion models for NIS spread can be modified to include a term for advective transport (Shigesada and Kawasaki 1997), if the species is subjected to strong prevailing winds or for populations of zooplankton in river currents, for example. The downstream spread of zebra mussels (*Dreissena polymorpha*), for example, occurred much more rapidly than upstream spread in the Great Lakes during the initial colonization period (Griffiths et al. 1991).

For many NIS, however, predicted rates of spread are often seriously underestimated from reaction-diffusion models. Forecast rates of spread of the cereal leaf beetle (*Oulema melanopus*), for example, were underestimated by at least 2 orders of magnitude (Andow et al. 1990). Observed patterns of spread for this beetle are consistent with "stratified diffusion", in which spread occurs through a combination of local and long-distance dispersal events (Hengeveld 1989). To forecast population spread adjusting for rare, long-distance dispersal

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events, models have been developed using integrodifference equations and leptokurtic, or "fat-tailed" dispersal kernels (Kot et al. 1996). These models of spread estimate dispersal at discrete time intervals, and are flexible in their use of non-Gaussian (non-normal) distribution kernels (e.g., Kot et al. 1996, Veit and Lewis 1996). Like their reaction-diffusion counterparts, integrodifference models assume a homogenous landscape and are better suited to aerial, terrestrial or marine invasions.

Dispersal of aquatic NIS among lakes or streams is best described with models that recognize the patchiness of suitable habitat in a heterogeneous landscape. One example is the use of gravity models that estimate propagule flow (i.e. Stage 1) from spatially-discrete 'sources' to 'destinations' proportional to destination attractiveness and inversely weighted by the distance between them (Haynes and Fotheringham 1984). Gravity models provide a flexible modelling framework, especially for human-mediated dispersal, because they incorporate the cognitive process of humans in making decisions about where they travel. A number of types of gravity models are available for use, depending on the type of information available. Total-flow-constrained models are used when information only on the total flow within the system is available. Production- and attraction-constrained models require information about outflows from sources and inflows from destinations, respectively. Doubly-constrained models require information about outflows and inflows from sources and destinations. Gravity models have been developed to forecast dispersal of the zebra mussel (Schneider et al. 1988,

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Bossenbroek et al. 2001) and spiny waterflea (*Bythotrephes longimanus*)
(MacIsaac et al 2004).

In this thesis, I explore several aspects of the multistage invasion
sequence for terrestrial and aquatic NIS. In Chapter 2, I focus on the first stage
of the invasion sequence in demonstrating that movement of the emerald ash
borer (*Agrilus planipennis*), a destructive beetle that colonized the Great Lakes
region in recent years, is consistent with patterns of stratified dispersal. Here,
stratified dispersal is comprised of a combination of local diffusive dispersal of
the emerald ash borer in conjunction with human-mediated transportation of the
beetle in firewood and other ash products. I also illustrate how quarantine efforts
have had mixed results depending on the timing of their application. This chapter
has been published in the journal, Diversity and Distributions.

In Chapter 3, I implement all three stages of the invasion sequence in a
multistage, hierarchical model for two aquatic NIS, the spiny waterflea and the
zebra mussel. The multistage model relates measures of propagule pressure
based on gravity models, data on lake morphometry and physicochemistry, and
fish community composition to species presence/absence. I also contrast the
abilities of the hierarchical approach vs. a single 'all-in-one' model to correctly
detect invasions, and explore interactions between the stages of the invasion
sequence on predicted NIS occurrence.

In Chapter 4, I compare predictions of spiny waterflea invasions for three
types of gravity models: Total-flow-constrained, production-constrained and
doubly-constrained. The three gravity models differ in the type of information

required to parameterize the model and the model constraints under which propagule pressure from sources to destinations is modeled. Based on the models' abilities to detect actual invasions relative to false alarms and the amount of data required to parameterize the model, I make recommendations on use of specific gravity models for future studies.

In Chapter 5, I compare backcast patterns of propagule pressure for two groups of related species, one group comprising the spiny waterflea and the fishhook waterflea, *Cercopagis pengoi;* and the other, the zebra mussel and quagga mussel, *Dreissena rostriformis bugensis*. Differences in species' life-histories may interact with various transport mechanisms to produce highly dissimilar levels of propagule pressure to inland lakes for these species. This is the first study to utilize a comparative approach to assess relative spread of different NIS.

Finally, in Chapter 6, I examine the attributes of an invasion network formed by lakes invaded by spiny waterfleas connected by recreational traffic. I was particularly interested in assessing whether specific lakes served as 'hubs', and whether the network of lakes exhibited scale-free behaviour. Scale-free networks have been described in other areas, including the structure of the Internet, social and transportation networks (Albert et al. 1999, Watts 2002, Barabási and Bonabeau 2003). This chapter has been published in the Journal of Applied Ecology.

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77:1661-1666.

Source region

Filters

A B C D E F G H

Entrainment in
tranportation
pathway

Survival during
exposure to physico-
chemical environment

Biotic integration into
native community

Establishment
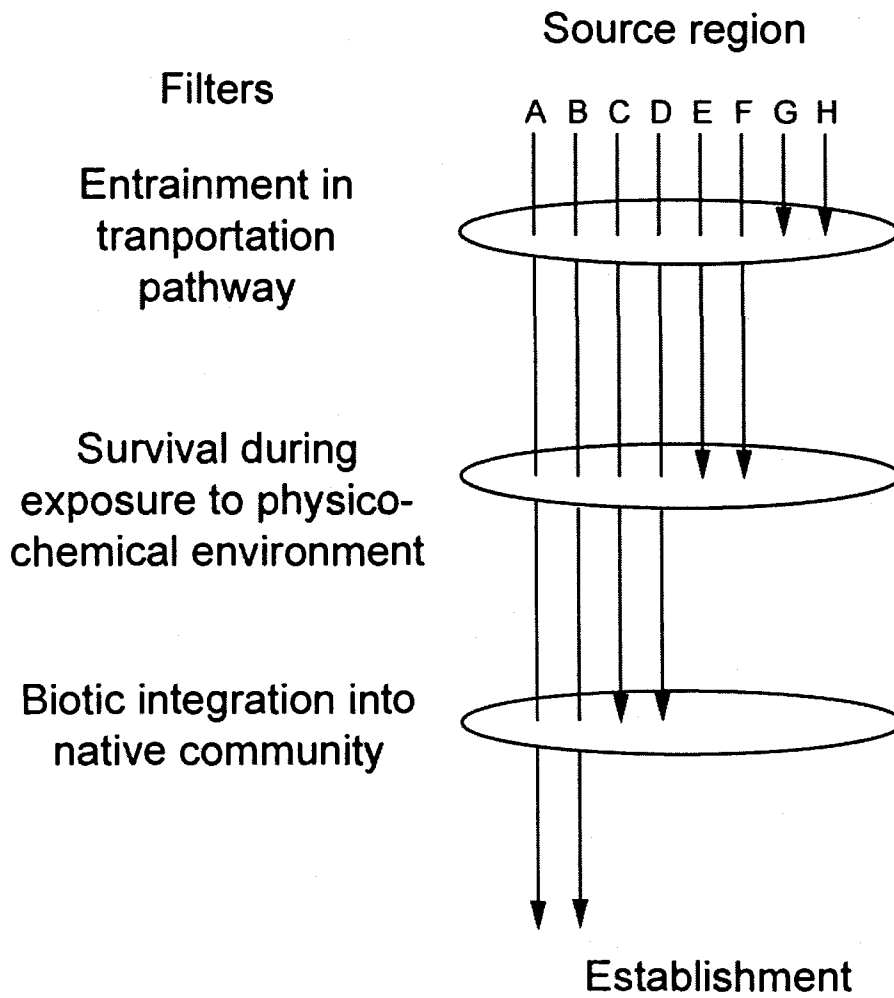
Figure 1. Conceptual model of filters in the invasion sequence.

Chapter 2. Modeling local and long-distance dispersal of invasive emerald ash borer *Agrilus planipennis* (Coleoptera) in North America

Summary

Limiting damage by nonindigenous species requires rapid determination of current and potential distributions, vectors of dispersal, and development of appropriate management measures. The emerald ash borer (*Agrilus planipennis*), a wood-boring beetle native to Southeast Asia, was first reported in the Great Lakes region during summer 2002. The beetle poses an enormous threat to native ash (*Fraxinus*) species of North America, as untreated trees in infested areas of Ontario, Michigan and Ohio suffer high mortality. We demonstrate that the borer has spread in North America through a combination of diffusive range extension, associated with local flights, and by long-distance 'jump' dispersal associated with human movement of infested sapling or contaminated firewood. Probability of infestation was inversely related to distance from borer epicenters but positively related to the size of human population centers. At least 9 of 39 populations that were first reported in Michigan during 2004 cannot be accounted for by local diffusion, raising the possibility that other unidentified mechanisms may be contributing to dispersal of the beetle. Absent quarantine, by 2005 all of Michigan's lower peninsula was contained within the boundaries of potential diffusive range expansion. Infested ash saplings also were introduced from Michigan to Maryland during 2003, and subsequently transplanted to five sites in Maryland and Virginia. Quarantine and eradication

measures have had mixed results: in the south-central USA, the species appears

on the brink of eradication, whereas its distribution has continued to spread

during 2005 in the Great Lakes region despite extensive containment and

quarantine measures. Quarantine success in the Great Lakes region is

encumbered by multiple dispersal vectors, larger borer population sizes and by

the more extensive geographic distribution that was achieved prior to

implementation of control measures.

Introduction

Dispersal is fundamental to species' distributions and ecology. With a

history that dates back to Darwin, dispersal remains one of the most intensively

studied fields in ecology (e.g. Bullock *et al.,* 2002; Clobert *et al.,* 2002; Nathan,

2005). In recent years, attention has focused on the relative contributions of local

and long-distance dispersal and its consequences for species' ranges, patterns

of dispersal, and population persistence (e.g. Lewis, 1997; Higgins & Richardson,

1999; Levin *et al.,* 2003; Green & Figuerola, 2005; Trakhtenbrot *et al.,* 2005).

Biological invasions by nonindigenous species represent an important applied

extension of dispersal ecology since, in many cases, human-mediated dispersal

transports a significant number of individuals to distances farther from the source

than they could disperse naturally (e.g. Hebert & Cristescu, 2002). As with their

counterparts in basic ecology, invasion biologists have focused on the relative

importance of local- versus long-distance dispersal (With, 2002, 2004; Neubert &

Parker, 2004; Hastings *et al.,* 2005; Puth & Post, 2005). Long-distance

dispersants provide opportunities for 'nascent foci' to develop, from which new populations or coalescing nodes can be founded (Moody & Mack, 1988; Lewis, 1997; Muirhead & MacIsaac, 2005). The choice of control strategies (e.g. suppression, containment, eradication) is, in turn, affected by the dispersal characteristics and geographic distribution of the species in relation to funding available for management (Moody & Mack, 1988; Sharov, 2004; Taylor & Hastings, 2004).

The International Union for Conservation of Nature and Natural Resources' Global Invasive Species Database compilation of the world's 100 most harmful, nonindigenous species includes 14 insects (Lowe *et al.*, 2000). Considering that insect invasions can have profound consequences to human, animal, plant, and ecosystem and economic health, it is not surprising that their dispersal characteristics and population ecology have been well studied (e.g. Gilbert *et al.*, 2003, 2004; Krushelnycky *et al.*, 2004; Morrison *et al.*, 2004; Smith *et al.*, 2004; Juliano & Lounibos, 2005). The emerald ash borer (borer) is a beetle native to Southeast Asia, including parts of China, Korea, Japan, Russia Mongolia, and Taiwan (Liu *et al.*, 2003). The borer was first observed in Southeastern Michigan and Southwestern Ontario (Figure 1A) in summer 2002 following investigations of dieback and epicormic branching in native ash species. The borer likely entered North America in infested ash strapping, pallets or dunnage more than ten years ago (Herms *et al.*, 2004). Adults lay eggs under tree bark, and feeding larvae kill trees by disrupting nutrient transport in the phloem (Liu *et al.*, 2003). Affected species include green ash (*Fraxinus*

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pennsylvanica), white ash (*F. americana*), black ash (*F. nigra*) and blue ash (*F. quadrangulata*) (Liu *et al.*, 2003). Collectively these species are a dominant component of the eastern deciduous forest of North America, a status now threatened by spread of the borer. The borer also threatens about $300 billion of timberlands in the United States (Nowak, 2003).

Adult dispersal by flight is strongly gender-biased, with a mode of 0.8 km in 24 hours per individual female, and only 1% travel farther than 4 km (Taylor *et al.*, 2004). Larval beetles can be transported over long distances in contaminated nursery stock, firewood, or raw logs. The combination of local, natural dispersal of adults and human-mediated long-distance transport of larvae is consistent with stratified diffusion (see Hengeveld, 1989). Other nonindigenous species spread *via* stratified dispersal include mollusks (Bossenbroek *et al.*, 2002), other insects (Sharov *et al.* 2002, Gilbert *et al.*, 2003) and plants (Higgins *et al.*, 2003). Establishment of satellite colonies rapidly increases the overall rate of spread and area infested (Mooney & Mack, 1988; Lewis, 1997) and increases the complexity of management decisions. In this paper, we explore dispersal patterns of the borer from its first detection through to spring 2005. We develop a stratified diffusion model that incorporates local and long-distance transport to project dispersal of the species.

Methods

We obtained records of first reporting of the borer for the United States and Canada from the Michigan, Ohio, Indiana and Maryland Departments of

Agriculture and the Canadian Food Inspection Agency. We used three approaches to predict local and long-distance dispersal of the borer. First, we modeled local diffusion based upon changes in the reported distribution of the infested subcounties (i.e. township or municipality) using a standard exponential decay function relating the probability of dispersers stopping at a given destination and distance from the epicenter to the centroids of infested and noninfested areas in 2002, and from 2002 sources to sites reported invaded during 2003 (see Lewis, 1997). This function was used to predict occurrence in 2004 and the same function was then used to predict the 2005 distribution from 2002-2004 infestations. This model is phenomenological in that it makes no assumptions about flight capabilities of the borer, although it implicitly assumes dispersal occurs *via* adult flights.

The probability (p_j) of a destination remaining noninfested is given by the joint probability that the borer fails to disperse from all infested subcounties i to destination j:

$$p_j = \prod_i \left[1 - \frac{\exp\left(-bx_{ij}\right)}{d_i} \right] \tag{1}$$

where b is the estimated coefficient of the exponential slope, and x_{ij} is the Euclidean distance from source (i) to noninfested destination (j), estimated as the center of each subcounty. d_i is a normalizing constant given by:

$$d_i = \sum \exp\left(-bx_{ij}\right) \tag{2}$$

where d_i scales for all potential destinations, such that p_j ranges from 0 to 1, and we obtain the relative risk of invasion. The slope of the exponential kernel, b, is solved by finding the minimum value of the likelihood function, L, where:

$$L = \begin{cases} -\sum_{j=1}^{m} \log(1 - p_j), & j \text{ is invaded} \\ -\sum_{j=1}^{m} \log(p_j), & \text{otherwise} \end{cases} \qquad (3)$$

Slopes of the exponential decay functions were calculated separately for the U.S.A. and Ontario, Canada owing to the smaller spatial scale of township divisions in the former. Predicted areas of local dispersal were mapped in an Albers-Equal Area Conic projection to maintain the shape and distance between infested areas using ArcGIS (Desktop v. 8.3, ESRI, Redmonds, CA, U.S.).

Second, we predicted long-distance dispersal of the borer under two scenarios of human-mediated transport. First, long-distance dispersal of the borer was modeled based on human population size at the subcounty level using the U.S. 2000 Census and beetle invasion status. Models based on population size at this spatial scale were constructed only for Michigan, Indiana and Ohio. We used population size of townships and municipalities as surrogates of human activities (e.g. horticultural ash trees) that may result in transfer of ash products from infested sources to noninfested destinations. Previously, human population density was found to provide the best estimate of spread of the chestnut leafminer moth *Cameraria ohridella* in Europe (Gilbert *et* al., 2004). Comparable predictions of long-distance dispersal based on population size in Ontario were

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not possible, because required data from outlying centers is lacking. Data on invasion status, population size and distance from the epicenter for the three states were randomly divided into two 80:20 training/model validation subsets. A spatial "null" logistic regression model based on invasion status as a function of the log-transformed distance from the epicenter was constructed since reports of the borer are highly concentrated at the epicenter of the invasion, and the borer may not have had sufficient time to disperse throughout the three states. A second logistic regression model predicted the probability of invasion with a term added for log-transformed population size of the recipient area, and differences in fit between the two models were thus attributed to human population size. Validation of the second model was assessed by comparing the predictions of the test data subset fitted with the training model parameters to the observed invasion status of the testing data set. We used the Generalized Linear Models in Statistica (Version 7, Statsoft Inc.) for model construction and validation.

Third, we developed a gravity model that utilized data pertaining to human-dispersed firewood to predict long-distance dispersal in Michigan, Ohio, Indiana and Ontario. Gravity models relate the interaction strength between a discrete, invaded source and a non-invaded destination, weighted by the distance between them, in a manner analogous to Newton's Law of Gravitation (Bossenbroek et al., 2001, Muirhead & MacIsaac 2005). In summer 2003, provincial and national parks throughout Ontario initiated a surveillance program to intercept firewood bundles brought by campers from within the quarantine

zone. The number of wood bundles intercepted was related to the number of campsites as an independent measure of attractiveness giving:

$$w = \alpha c d^{-\beta} \tag{4}$$

where w is the number of wood bundles, c is the number of campsites, and d is the shortest road distance from the park to Windsor, Ontario, the invasion's Canadian epicenter. The unknown variables α and β were simulated by fitting a nonlinear model using least-squares regression in Statistica (version 6, StatSoft Inc. Tulsa, U.S.). Road distance is preferable to straight-line distance from the parks to the quarantine zones as it reflects the actual distance covered by vehicles. We assume that the relationship among transported wood bundles and attractiveness to recreational parks developed for Ontario also holds for traffic to state parks in the United States. Ash trees are floristic dominants in both Canadian and American epicenters, and we assume the likelihood of transfer outside of quarantine areas was the same in both countries. The predicted number of wood bundles transported outside state and Ontario parks was interpolated by fitting an inversely distance-weighted surface to point data from the gravity model.

Results

Emerald Ash Borer Spread and Quarantine

The beetle's invasion epicenter in North America encompasses the immediate area around Detroit, Michigan and Windsor, Ontario (Figure 1A). Quarantine zones were established in 2002 in both Michigan (6 counties) and

Ontario (1 county) in an attempt to prevent long-distance dispersal of the borer (Figure 1B).

During 2003, the borer was reported in 13 townships in Michigan contiguous to sites reported infested during 2002 (Figure 1A). These sites were all located within the quarantine zone, which had now expanded to thirteen counties. The borer was reported at an additional 6 sites in Michigan outside of the newly established quarantine region. One of these sites, St. Joseph, located in Michigan's southwest corner, is almost 200 km from the nearest population identified in 2002. In Michigan, quarantine consisted of cutting healthy ash trees in the area immediately surrounding infestations, and banning export of ash products to noninfested regions. In Ohio, the borer was reported from 6 sites in three areas, with the farthest, Columbus, located 250km from the nearest site reported invaded during 2002. Quarantine was established for all invaded sites in Ohio in 2003. In Ontario, the borer expanded its distribution to contiguous sites in Essex County (Figure 1B), which was then placed under quarantine during summer 2003. In addition, a 10-km wide 'firewall' was created during winter 2003/2004 by cutting all healthy ash trees on public and private lands along the eastern boundary of the quarantine zone, between Lakes Erie and St. Clair, followed by chipping or burning of the cuttings (see Figure 1B). This procedure was implemented to create a host-free (i.e. ash-free) region to slow spread to uninfested areas by flying adults. The borer also dispersed to Maryland and Virginia during 2003 (Figure 1B). A tree nursery in Maryland received an illegal shipment of 121 infested samplings from within the quarantine zone in Michigan

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during April 2003, of which some were subsequently planted at one site in Virginia and four sites in Maryland.

The borer's distribution expanded dramatically in 2004. In Michigan, the borer was reported at 1 site inside the 2003 quarantine zone, 8 sites outside but proximate (<25km) to it, and at 20 sites distal to the zone, including one location ~225km from the nearest known population (Figure 1C). Seven new locations were reported invaded in Ohio during 2004, all in close (< 50km) proximity to populations reported during 2003. New populations all were located in the NW part of the state, adjacent to infested areas in Michigan. The borer also spread to four locations in Indiana, all of which were ≥100km from known infested sites. All newly discovered populations in the Great Lakes states were quarantined during 2004. Also, individual borers were reported at four sites in Maryland, which implemented quarantine efforts in spring 2004. These efforts consisted of destruction of all ash trees in the infested nursery, and on public and private lands in a surrounding 0.5-mile buffer zone. In total, almost 1000 infested or potentially infested trees were destroyed. The four new infestations were also eradicated (Figure 1C). In Ontario, 23 new sites were reported invaded, all located within two foci on the distal side of the firewall. These trees were removed, and the quarantine zone expanded to nearly double its previous size (Figure 1D).

Thus far, four new sites have been reported invaded during 2005. Three sites are located in Michigan, one straddling the 2004 quarantine perimeter, the other two along the northeastern coast of Lake Michigan (Figure 1D). The single

report of invasion in Ohio during 2005 occurred at a site contiguous to one reported invaded during 2004, and is consistent with diffusive spread.

Dispersal Models

Distribution changes between 2002 and 2003 were used to develop a local, diffusion-based dispersal model. The area covered by the most expansive model, which considered invasion probabilities as low as 0.05, encompassed 77% of all sites reported invaded during 2004 in the Great Lakes states, though this value fell to 23% when the least inclusive model was used (i.e. 0.76-1.00 probability of invasion) (Table 1). If control efforts were not implemented, or if they prove unsuccessful, the range vulnerable to invasion by the borer in 2005 includes all of Michigan's lower peninsula. While the 23 occurrences observed east of the firewall in Ontario during 2004 are consistent with diffusive spread from across the firewall (i.e. probability of ≥0.26), they are likely the result of firewood and saw logs transported prior to establishment of the firewall (K. Marchant, unpubl. data). Likewise, dispersal of the borer within Maryland during 2004, although consistent with diffusive spread (probability of ≥0.51), was the result of movement of infested saplings within the state.

The logistic regression model predicted dispersal based upon distance from the epicenter and human population in the recipient area (Figure 2A). The addition of the human population term improved the model fit significantly over the null model based only on distance from the epicenter (χ^2 = 16.52, d.f. = 1, P<0.0001), implying that human population size (in recipient areas) and activity is

a major factor in the spread of the borer. The long-distance invasion probability

for Michigan, Ohio and Indiana was estimated as:

$$p(\text{infestation}) = \frac{\exp\left(7.95 - 2.92d + 0.37n\right)}{1 + \exp\left(7.95 - 2.92d + 0.37n\right)} \tag{5}$$

where d is the log-transformed distance (km) and n is the log-transformed

population size. This model correctly classified 64.6% of the invaded sites and

97.5% of all sites overall with regard to their invasion status based upon these

two parameters (Table 2). Distance from the epicenter was the most important

determinant of this relationship, and thus invasion probabilities form concentric

circles from Detroit (Figure 2A). The ability of the model to correctly classify

invaded sites declined with distance from the epicenter, and was poor with

respect to invaded sites in the northern end of Michigan's lower peninsula. The

only two sites correctly classified as invaded in these outlying areas were

Greenbush and Oscoda townships (Alcona and Iosco counties) and Grand

Traverse (Figure 2A). The model suggests that the areas of Gary and Fort

Wayne, Indiana, and Bay City, Michigan, are at moderate risk of invasion

(probability of 0.01-0.04), while risk is slightly lower in Indianapolis, Indiana, and

Cincinnati and Dayton, Ohio (Figure 2A).

A 'gravity' model was developed to predict dispersal across spatial scales

using information on the quantity of firewood transported between the epicenter

of Windsor, Ontario and provincial parks in the province that were frequented by

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campers, the number of campsites at each park frequented, and distance between the epicenter and park (Figure 2B). Although the model was developed for Ontario, we also applied it to Great Lakes states. Areas at highest risk of firewood-vectored dispersal form an ellipse bordered by the southeastern edge of Lake Huron in Michigan and Ontario and the southwestern edge of Lake Erie in Michigan and Ohio (Figure 2B). The latter areas already support some borer populations, and are also highly vulnerable to diffusive dispersal, while vulnerable areas in Ontario lie well outside of the current quarantine zone, are distal to the firewall, and are currently borer-free.

Discussion

Introduced beetles are often associated with significant damage to forests, caused either directly through their boring or feeding activities or indirectly by serving as vectors for pathogen transmission (e.g., see Allen & Humble, 2002; Haack, 2003). A number of introduced boring beetles currently threaten North American forests, including the pine shoot beetle *Tomicus piniperda* in the greater Great Lakes region (Haack & Poland, 2002), the Asian longhorned beetle *Anoplophora glabripennis* in New York, Chicago and Toronto (e.g., Auclair *et al.*, 2005), and the Brown spruce longhorn beetle *Tetropium fuscum* in Nova Scotia (Smith & Hurley, 2000). Emerald ash borers were discovered in the Great Lakes region during summer 2002, and pose an enormous threat to native ash forests in eastern North America. By 2004, ash mortality rate in infested areas in southwestern Michigan was positively correlated with proximity to the epicenter

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of the invasion, and highest (61%) in Wayne County, the focal point of the invasion (Witter & Storer, 2004).

As with all invasions, an important determinant of invasion success is introduction effort (see Memmott *et al.*, 2005; Colautti *et al.*, 2005). It is imperative that we collect comprehensive data pertaining to the density and geographic distribution of imported propagules to predict identities of possible invaders and the locales where invasions may occur. This requirement is typically met by national screening programs which allow identification of species intercepted as they enter the country (see case studies in Ruiz & Carlton, 2003). Haack (2003) provided one such example for scolytid beetles entering ports in the USA, based upon the Animal and Plant Health Inspection Service's (APHIS) inspection records.

Once nonindigenous species have established, additional models are needed to predict spread based upon patterns and density of propagule dispersal. Models developed here address dispersal patterns of the emerald ash borer in North America by both local diffusion and long-distance transport. New reports of the beetle increased very rapidly between its first description in 2002 and 2005. A high proportion (77%) of invasions reported in 2004 conceivably resulted from diffusive spread (probability ≥0.05), although a much lower percentage (23%) of these can be ascribed to diffusion with higher certainty (probability ≥0.76; Figure 1C; Table 1). Virtually all of the reports that could not be explained by diffusive spread occurred in the upper regions of the lower peninsula of Michigan, distal to the primary invasion front. All of the invasions

reported thus far in 2005 are in areas with high probability of diffusive spread

(Figure 1D). Some of the new populations that cannot be accounted for *via*

diffusive spread are consistent with the logistic regression model based upon

distance from the epicenter and human population size in the recipient area

(Figure 2A). Nevertheless, even this model was unable to account for 17 of the

48 new populations in the Great Lakes states during 2004 (Table 2). Many of

these populations were located in the same region of Michigan that could not be

explained by diffusive spread. Some of these populations were found in areas

where humans transport firewood, albeit at low frequency (Figure 2B).

The logistic regression model had a greater error rate in predicting

invaded sites as noninvaded (17 of 48 =35%) than noninvaded sites as invaded

(5 of 36 = 16%). This finding supports the concept that diffusive dispersal from

the epicenter occurs with much greater predictability than long-distance dispersal

to peripheral areas (Table 2). This pattern is also consistent with theoretical

models that suggest predicting location of invasions in peripheral areas can be

very difficult (e.g. Lewis, 1997). Nevertheless, knowledge of current distribution

can be used to formulate risk assessment and management strategies. For

example, 'trap' or sentinel trees are now used in the USA to detect and provide a

semi-quantitative measure of migrating emerald ash borers in areas where

dispersal is anticipated. This approach has been used for other introduced pest

species. For example, pheromone traps have been successfully deployed to

detect early spread of the gypsy moth, *Lymantria dispar* in Michigan (Gage *et al.*,

1990).

An alternative to the vector-based approach is provided by ecological niche modeling, in which a nonindigenous species' ecological requirements are characterized for its native range and then applied to the landscape in the actual or potentially invaded region (e.g., Peterson, 2003; With, 2004). Peterson & Vieglais (2001) utilized this approach to determine the possible range of Asian longhorned beetles in North America. Ecological niche modeling allows identification of areas vulnerable to establishment of the nonindigenous species, with the implicit assumption that propagules are available to transport the species to these locations. The most promising possibility to predict future ranges of nonindigenous species is to marry vector-based and ecological niche modeling approaches. This methodology would allow identification of vulnerable sites based upon vector and pathway studies, following which the model could be refined based upon the match between the species' ecological needs and the habitat's characteristics. A simple application of this approach was provided by Peterson (2003), who noted that although areas in California should be vulnerable to Asian longhorned beetles - based upon shipping traffic inbound from Asian source ports - available habitats in most port areas would be inhospitable to the beetle's needs. MacLeod *et al.* (2002) concluded that Asian longhorned beetles pose a significant threat of establishment, spread and economic damage in southern Europe based upon a CLIMEX niche model. A CLIMEX model that incorporated both temperature and moisture was used to evaluate possible establishment and spread of the red imported fire ant *Solenopsis invicta* in New Zealand and Australia (Sutherst & Maywald, 2005).

Before similar niche modeling can be applied to the emerald ash borer across North America, information must be obtained on key aspects of its biology, including its thermal limits in Asia. Nevertheless, approximately 9 billion ash trees inhabit and are potentially at risk in the USA and Ontario (Nowak, 2003; K. Marchant, unpubl. data). As the beetle is already present in areas with large numbers of vulnerable hosts in the Great Lakes region, this area remains highly susceptible to additional spread and harm.

Our models are based upon observed ash borer distributions between 2002 and 2005, and surveys of campers entering provincial parks in Ontario. A number of uncertainties are implicit to our models. First, our diffusion model is based on changes in reported distribution between 2002 and 2003, and assumes that diffusion rate is invariant over time. Second, because of the threat posed by this beetle, manpower devoted to its study and control has increased through time, decreasing the likelihood of missing established populations (reduced type II error). This could be particularly important for populations distal to the epicenter, which may have been underreported in earlier years. If so, our diffusion model would underestimate early and overestimate later spread. Third, current eradication efforts, especially in outlying 'nascent foci' (Moody & Mack, 1988), could dramatically reduce the size of borer populations available to disperse to adjacent areas. These suppression efforts could effectively lower the probability of dispersal and increase the area less vulnerable to diffusive spread (Figures 1C,D). Fourth, our firewood model was developed using data for parks in Ontario, but applied to both Ontario and the Great Lakes states, assuming that

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behavior of campers is similar in both countries. Differential success of public education campaigns – including the deployment of quarantine notification signs on major highways – between the USA and Canada, would affect spatial patterns of firewood transport and thus the vulnerability of long-range dispersal. At present, we are unable to test this possibility. Finally, there are a number of sites that have been invaded that cannot be accounted for by any known vectors. It is possible that other, unidentified vectors may transport beetles to these sites, or that predictor variables may have been incorrectly parameterized. For example, both distance from the epicenter and human population size of the recipient area were $\log_e$-transformed in the logistic regression model. It is possible that some outlying areas that were expected to have very low visitation rates of individuals arriving from the epicenter may, in fact, have had a much higher rate owing to site attractiveness or some other measure not considered in our model. This would create a 'fat-tail' in the dispersal kernel of human vectors (Lewis, 1997), and increase the probability of invasion at greater distances. For example, one of the outlying areas invaded in our study was near Traverse City, Michigan, which is a very popular tourist destination for individuals from metropolitan Detroit.

Quarantine efforts may be willfully disregarded by some members of the public. For example, illegal transportation of infected ash saplings was responsible for the introduction of emerald ash borers to Maryland. During 2004, four new sites were discovered infested in Maryland. The rapid implementation of eradication procedures, combined with intensive follow-up surveys, indicate

that borer has been controlled and possibly extirpated from the region. Only a single larva was found at each of four sites of outplanted trees during 2004 (Figure 2A). Likewise, no new invasions have been reported in Virginia following implementation of quarantine measures there. Intensive surveys should be repeated in future years in both states to confirm that the species has in fact been extirpated.

Quarantine in Michigan and Ontario is a far more arduous task than in Maryland and Virginia, as new infestations could result from many different source populations. Most new reports of borer invasions in Michigan during 2004 occurred outside of the quarantine zone, and all of the sites reported thus far in 2005 have been outside but contiguous to quarantine zones. Unless local dispersal from these currently isolated colonies can be curtailed, infilling of the distribution may be expected (Figure 1D). The 23 infestations reported in Ontario during 2004 (Figure 1 C) were located in close proximity to one another, and all were outside the eastern boundary of the ash-free zone. Moody & Mack (1988) stressed the importance of focusing on satellite populations in controlling spread of invading plants. Taylor & Hastings (2004) also suggested eradication prioritization for isolated, low-density *Spartina* colonies as opposed to high-density core populations owing to faster spread capabilities of the former. Sharov (2004) explored the different treatment options available and the conditions under which each would be the optimal management strategy for a harmful, introduced species. He showed that the optimal strategy changes from "eradication" to "slow-the-spread" and then to "do-nothing" as the distribution of

the target species increases. In this context, the eradication programs in Maryland and Virginia seem appropriate, as does the "control-the-spread" program using the ash-free zone in Ontario. Furthermore, local eradication programs directed toward satellite colonies in each of the political jurisdictions surrounding the Great Lakes can also reduce spread of the emerald ash borer. A "slow-the-spread" management strategy that targeted isolated satellite colonies along the invasion front dramatically reduced the overall rate of spread of the gypsy moth in North America (Sharov *et al.*, 2002).

In summary, the emerald ash borer is a very destructive species that has colonized North America and is spreading quickly. The beetle is currently spreading via stratified diffusion through a number of natural and human-mediated mechanisms. Management based upon the eradication of isolated colonies in Maryland and Virginia appears to have been successful, whereas range expansion in the Great Lakes region has continued despite deployment of an array of management strategies.

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Tables

Table 1. Cumulative number of infested townships and municipalities inside (or contiguous to) and outside of zones categorized by probability of local diffusion for the Great Lake states. The probability model is based on range expansion that occurred from 2002 to 2003 (for 2004 predictions) and 2002 through 2004 (for 2005 predictions).

	Year			
	2004		2005	
Probability of dispersal	Number of new invasions inside the probability zone	Number of new invasions outside the probability zone	Number of new invasions inside the probability zone	Number of new invasions outside the probability zone
0.05 – 0.25	30	9	4	0
0.26 – 0.50	21	18	4	0
0.51 – 0.75	10	29	4	0
0.76 – 1.00	9	30	4	0

Table 2. Cross-validation of the logistic regression model that incorporated both log-transformed human population size and log-transformed distance from epicenter to predict invasions by emerald ash borers in the three Great Lakes states (MI, OH, IN) based upon 2004 data. N = 867 townships and municipalities.

Observed	Predicted Invaded	Predicted Noninvaded	Total	% Correct
Invaded	31	17	48	64.6
Noninvaded	5	814	819	99.4
Total	36	831	867	97.5

Figure 1. Sightings of the emerald ash borer from 2002 (A), 2003 (B), 2004 (C)

and 2005 (D) in the USA and Canada, and predicted local dispersal of the

beetle *via* adult beetle flights from infested areas in 2002-2003 (C) and

2002-2004 (D). Local dispersal is based upon an exponential decay

function (probability of spread = e^{-x*D} where x is 0.038 for the U.S.A. and

0.050 for Ontario, and D is distance from the center of the invasion source

in km). An ash-free 'firewall' (light green) was cut in Ontario during winter

2003/2004 to reduce the probability of locally dispersing beetles settling in

areas with uninfested ash hosts. The epicenter of the invasion in SE

Michigan and SW Ontario is shown in red and quarantine zones are

outlined with a dashed black and white line.

Legend
- ■ Epicenter
- ▦ Infested Areas
- --- Quarantine Zones
- ☐ Ontario Ash-Free Zone

0 50 100 200 kilometers

Figure 1 A, B.

Legend

■ Epicenter

Years Infested
■ 2002-2003
▨ 2004

--- Quarantine Zones

▨ Ontario Ash-Free Zone

Probability of local dispersal
< 0.05 not shown
☐ 0.05 - 0.25
☐ 0.26 - 0.50
■ 0.51 - 0.75
■ 0.76 - 1.00

Years Infested
■ 2002-2004
★ 2005

0 50 100   200 kilometers

Figure 1 C, D.

45
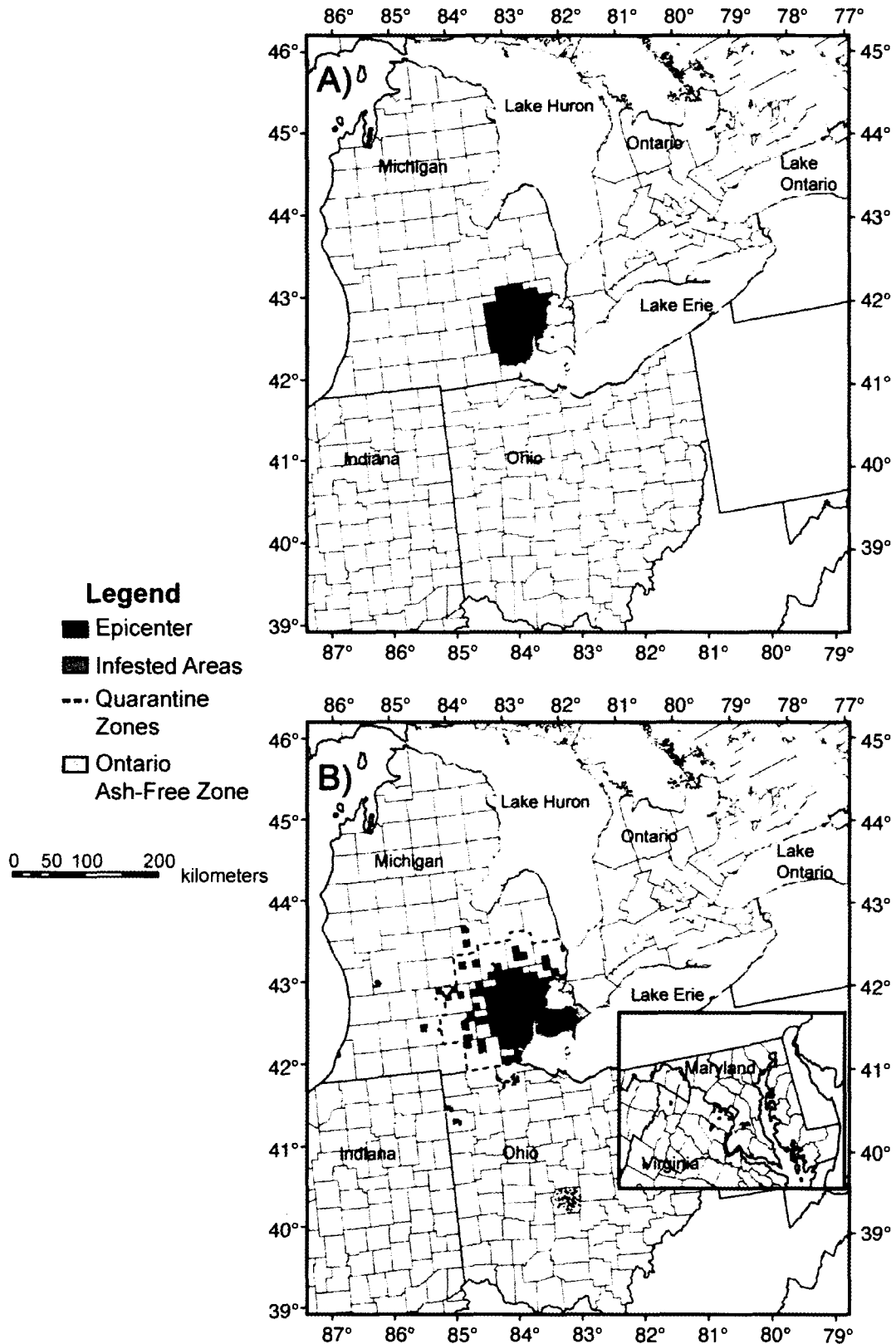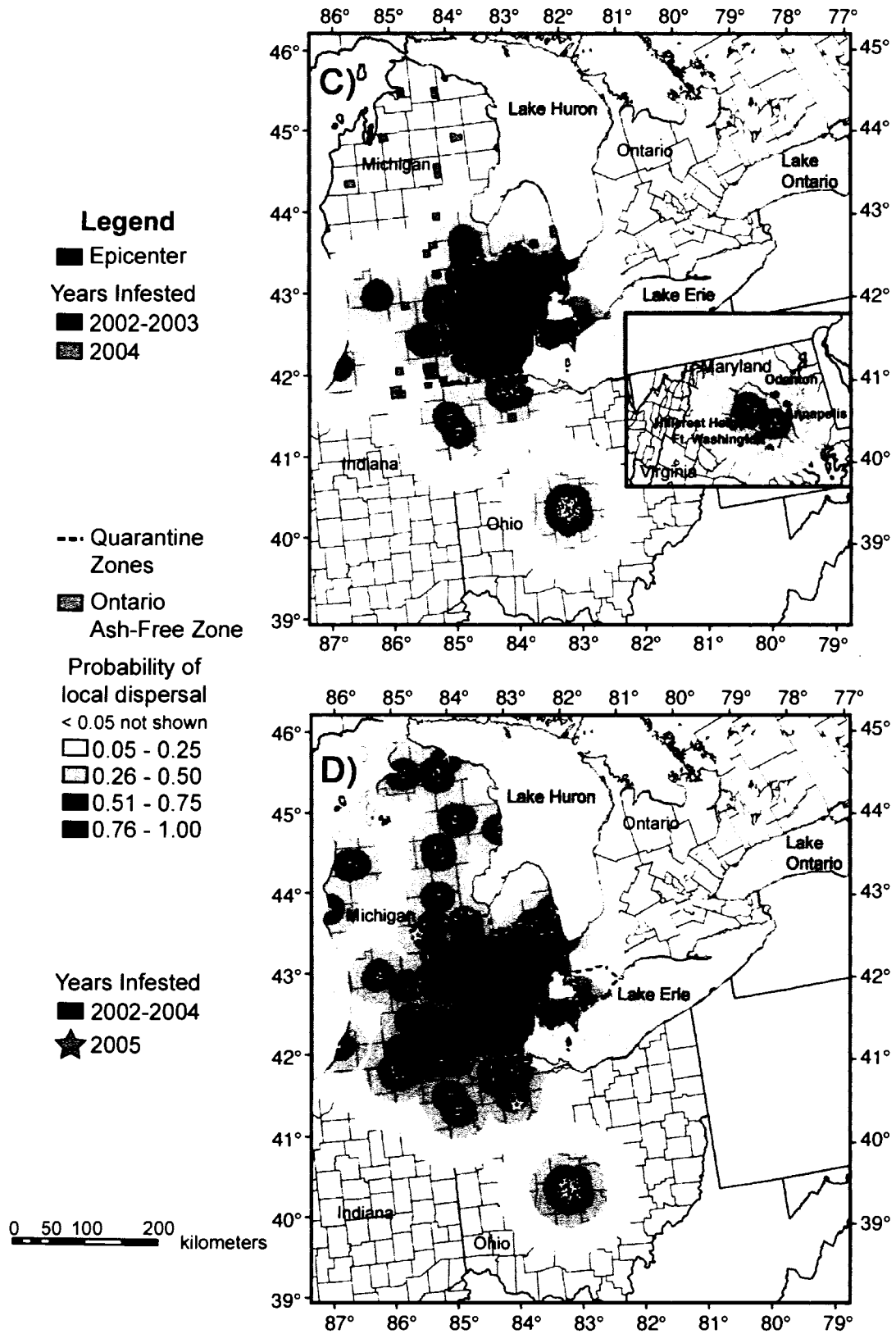
Figure 2. Probability of invasion based on township/municipality population size

and distance from the epicenter (A). Both population size and distance

were log-transformed. Also shown are areas at risk of infestation in

Michigan, Ohio, Indiana and Ontario based on long-distance transport of

firewood (B).

Legend

■ Epicenter

■ Infested Areas

Probability of infestation
< 0.004 not shown
☐ 0.004 - 0.010
■ 0.011 - 0.017
■ 0.018 - 0.030
■ 0.031 - 0.040
■ 0.05 - 0.06
■ 0.07 - 0.09
■ 0.10 - 0.14
■ 0.15 - 0.20
■ 0.21 - 0.30
☐ 0.31 - 0.43
☐ 0.44 - 0.57
■ 0.58 - 0.72
■ 0.73 - 0.89
■ 0.90 - 1.00

Number of Wood Bundles Transported
■ 3 - 4
■ 5 - 6
■ 7 - 11
■ 12 - 22
■ 23 - 46
▨ 47 - 98
☐ 99 - 211
■ 212 - 455
■ 456 - 983

0   100   200
kilometers

Figure 2.

47
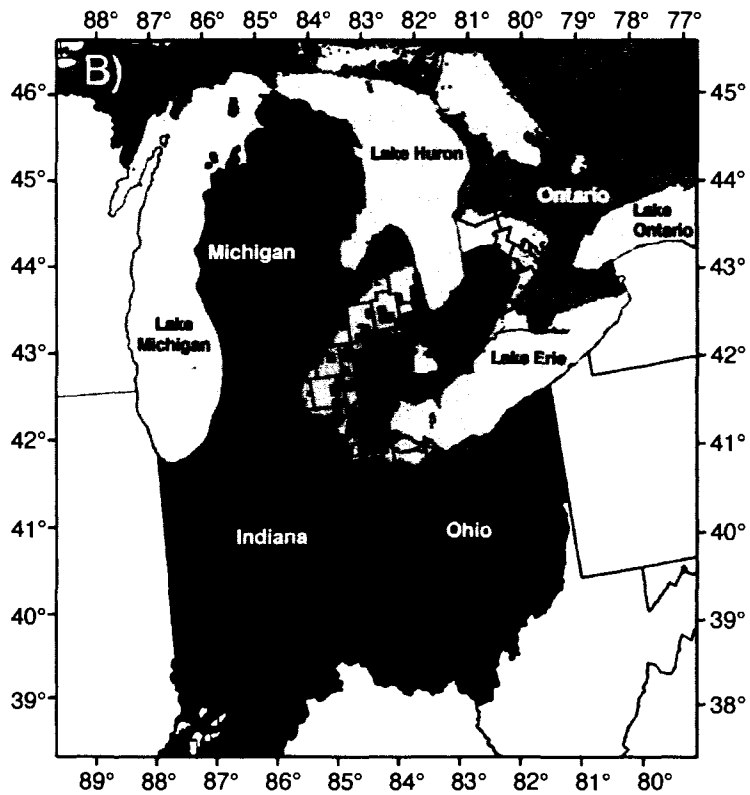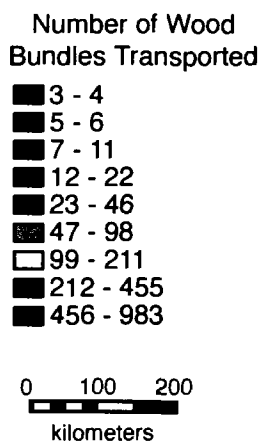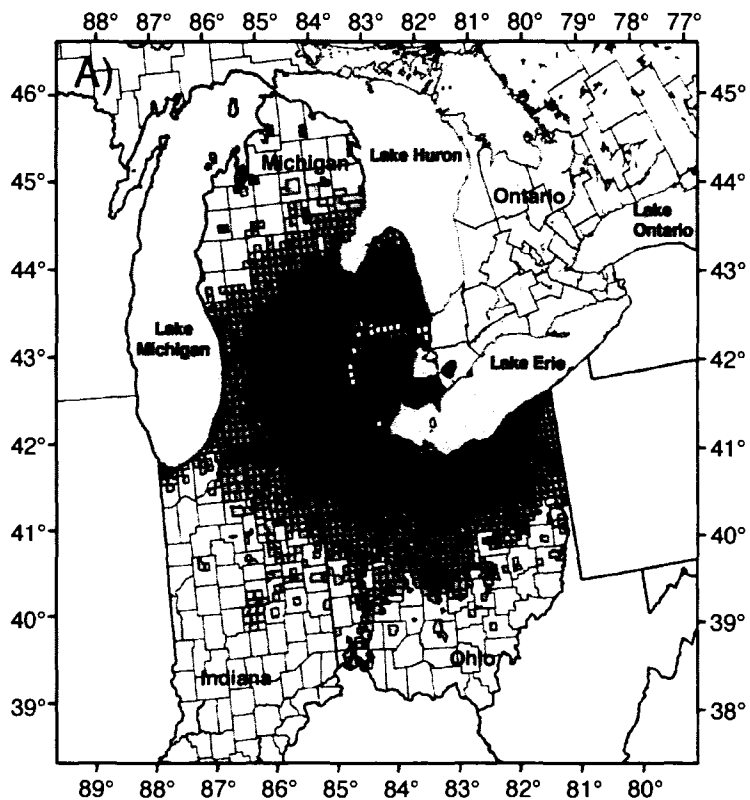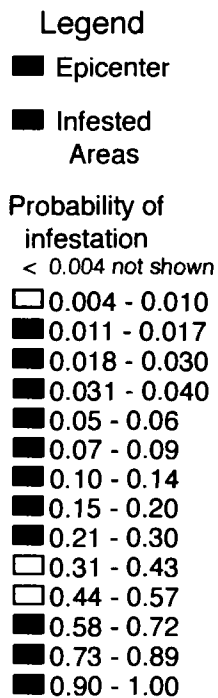
Chapter 3: Comparative stage-based hierarchical modeling of invasion success of two invasive, aquatic invertebrates

Summary

Nonindigenous species (NIS) must pass through a series of 'filters' when dispersing from a colonized to non-colonized region. These steps include introduction effort (i.e. number of introduction events and propagules introduced per event), survival in physical and chemical characteristics of the novel habitat, and biological integration into the existing community. Testing of hypotheses regarding invasibility should follow this sequence, and structured in a hierarchical approach such that relationships at latter stages of the invasion sequence do not confound relationships at earlier stages. In this study, I forecast the comparative spread of the spiny waterflea *Bythotrephes longimanus* and zebra mussel *Dreissena polymorpha* using hierarchical models that sequentially tested the importance of introduction effort (propagule pressure), lake physicochemistry, and fish community composition. Hierarchical modeling revealed that spiny waterfleas were more likely to be found in lakes with higher levels of propagule pressure, larger surface area, greater maximum depth, higher NO_3 concentration, absence of northern pike, and presence of walleye. Models developed for zebra mussels indicated that they were more likely to be found in lakes with high levels of propagule pressure, larger surface area, shallower maximum depth and lower NO_3 concentrations, though fish community composition did not influence occurrence patterns. The hierarchical approach was able correctly predict 88% and 84% of invaded and noninvaded lakes for the

spiny waterflea and zebra mussel, respectively. This approach provides a refined hazard assessment of lakes most susceptible to invasion by NIS.

Introduction

Invasions of aquatic ecosystems by nonindigenous species (NIS) are occurring at increasing rates globally (Ruiz et al. 1997, Cohen and Carlton 1998, MacIsaac et al. 2004, Gollasch 2006, Ricciardi 2006). Proactive efforts to reduce invasions are the most cost-effective management option (Leung et al. 2002), although some invasions may be managed post-establishment (Simberloff 2003). However, a major challenge exists with respect to forecasting dispersal and establishment of NIS.

An extensive literature exists of both theoretical and empirical approaches to forecast invasions (e.g. Sakai et al. 2001). Much of the research on forecasting invasions has focused on attributes intrinsic to the NIS (Thuiller et al. 2006). For example, in California nonindigenous fish that were able to establish populations in novel habitats were characterized by parental care of young, broad physiological tolerance, and large maximum adult size (Marchetti et al. 2004). The identification of species traits that may facilitate invasion is not always straightforward, however, as traits that may confer an advantage at the initial stage(s) of invasion may not be applicable at later stages (Kolar and Lodge 2002).

Another approach to predict invasions has sought to link factors extrinsic to the NIS - such as environmental suitability and native species diversity of the

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invaded community - to invasion success. Environmental suitability in novel regions is most often forecast by matching correlates of species occurrence or abundance with environmental data from the native range with those in the new region. For example, Herborg et al. (2007) used an environmental niche modeling procedure called Genetic Algorithms for Rule-Set Prediction (GARP) to forecast suitable habitat in North America for the Chinese mitten crab *Eriocheir sinensis* based upon its current distribution in Asia and Europe. Air temperature and wetness index were the strongest contributors to models that were able to distinguish colonized from uncolonized sites.

Biotic interactions and resource availability may influence the integration of NIS into novel habitats, although disentangling the roles of these and other ecological factors are not always straightforward and often scale-dependent (Davies et al. 2005, Romanuk and Kolasa 2005; Fridley et al. 2007, Melbourne et al. 2007). Competition from native species tends to reduce invasion success at local spatial scales, though a positive relationship often exits between introduced and native biodiversity at regional spatial scales (Shea and Chesson 2002; Davies et al. 2005). Competition may be less important at high resource levels, but this is not always the case (Davis et al. 2000). For example, establishment of the waterflea *Daphnia lumholtzi* was not affected by nutrient supply, but was negatively related to native zooplankton biomass and biodiversity (Dzialowski et al. 2007).

The relationship between establishment success and predation can vary depending on whether the predator preys on the invading species or on

community residents. Direct predation on NIS by members of the native community may greatly reduce the likelihood of establishment (Miller et al. 2002). Conversely, a positive relationship between establishment success and predation may occur through indirect effects, where the predator either reduces competition from native species at similar trophic levels to the invader, or preys on the predators of the NIS (Holt 1977).

An invasion sequence - characterized by a series of 'filters' the NIS must pass through to become successfully established - provides a logical framework in which to assess NIS establishment with both intrinsic and extrinsic drivers considered. These steps include introduction effort (i.e. number of introduction events and number of individuals introduced per event) following transport, survival during exposure to (or exploitation of) physical and chemical characteristics of the new habitat, and integration into the existing community (Richardson et al. 2000, Kolar and Lodge 2001; Melbourne et al. 2007). Colautti et al. (2006) proposed that hypothesis testing follow this sequence, as characteristics of the NIS or the recipient community that may facilitate or hinder invasion may be applicable only at certain stages of the sequence (Figure 1).

Dispersal of the spiny waterflea *Bythotrephes longimanus* (Leydig) and the zebra mussel *Dreissena polymorpha* Pallas in Ontario present ideal cases for examining the relationship between establishment success and sequential invasion 'filters' for NIS with different life histories. The spiny waterflea is an invading, predatory cladoceran that was reported in Lake Ontario in 1982 and has since spread to the other Great Lakes, and up to 119 inland lakes (Ontario

Federation of Anglers and Hunters, unpublished data). Predicting patterns of spread of the species is important as it has been shown to reduce zooplankton species richness (Yan et al. 2002). The presence of a caudal appendage (i.e. spine) deters predation by juvenile life stages of planktivorous fish, thus allowing *Bythotrephes* to survive and compete with smaller size classes of fish for zooplankton. A key life-history characteristic of the spiny waterflea that facilitates its spread is its seasonal production of resistant "resting" eggs that remain viable even though the parent has died, and thus serve as propagules capable of overland transport to novel systems. Accumulation of a 'resting' egg seed bank serves to replenish populations after adverse weather conditions kill off planktonic individuals.

Invasion success by the zebra mussel has been linked to high fecundity, production of planktonic larvae, and byssal-pelagic drifting by juveniles in river systems (Griffiths et al. 1991). Zebra mussels likely established in the Great Lakes in 1986 (Hebert et al. 1989), though it has since spread widely in temperate, eastern North America, including to at least 128 lakes in Ontario (Ontario Federation of Anglers and Hunters, unpublished data). Zebra mussel veliger larvae may be transported overland in all forms of water carried by boats (Johnson et al. 2001). Adults disperse overland fouled to boats or to aquatic vegetation that subsequently becomes snagged on boat trailers, and are able to survive brief aerial exposure (Ricciardi et al. 1995). In their role as "ecosystem engineers" (*sensu* Crooks 2002), zebra mussels have altered aquatic systems by increasing light penetration in the water column, fouling and competing with

native unionid species (Martel et al. 2001), as well as by enhancing benthic invertebrate diversity and abundance (e.g. Ward and Ricciardi 2007).

Modeling efforts have been used for both *Bythotrephes* and *Dreissena* to assess dispersal and environmental suitability. Like many NIS, dispersal of these species follows a pattern of stratified diffusion, in which processes responsible for local diffusion operate in concert with mechanisms that transport propagules over long-distances (e.g. Kraft et al. 2002). Diffusion models have been used to assess local dispersal, while gravity models were used for combined local and long-distance dispersal (e.g. Schneider et al. 1998; Buchan and Padilla 1999). The latter approach provides information on the relative strength of vector movement among sources and destinations (Schneider et al. 1998, MacIsaac et al. 2004, Leung et al. 2006, Bossenbroek et al. 2007). Assessments of habitat suitability in the introduced range have been accomplished using environmental matching in the native range with discriminant function analysis and environmental niche models (e.g. Ramcharan et al. 1992, MacIsaac et al. 2000; Drake and Bossenbroek 2004).

The objective of this study was to develop and validate models forecasting the comparative dispersal and establishment of *Bythotrephes* and *Dreissena* throughout Ontario based on the three-stage hierarchical model. Specifically, I modeled establishment probability of both species using boosted regression trees relating NIS presence/absence to introduction effort, lake physicochemistry, and fish community composition. Sequential model development and evaluation provides an unbiased assessment of each invasion 'filter' in influencing

establishment success. In addition, use of a hierarchical approach in which lakes are removed from the dataset at each stage of the invasion sequence if the species are predicted not to establish reduces confounding effects among stages. This approach allows the testing of the following hypotheses: 1) Are lakes with high inbound propagule pressure more likely to be invaded than those with low or no propagule pressure? 2) For lakes with high propagule pressure, are systems with environmental conditions similar to those in the native range more likely to be invaded than those with dissimilar conditions? and 3) Of the of lakes with high propagule pressure and suitable environmental conditions, does the presence or absence of specific fish facilitate or prevent invasion? Models were validated by comparing lakes predicted to be invaded, based on 2004 data, to reported invasions occurring in 2005 and 2006.

Methods

Implementation of the invasion pathway concept

The relationship between the invasion status of lakes (NIS presence or absence) and each of the components of the invasion sequence was developed using a hierarchical approach. At each of the three levels of the invasion sequence, lakes are divided into two subsets based on whether they are predicted to be invaded or noninvaded, with lakes predicted as invaded directed down the right branches of the hierarchical classification tree (Figure 2). At the first stage of the invasion pathway, inbound propagule pressure to invaded and noninvaded lakes was modelled using doubly-constrained gravity models (see

below). The doubly-constrained gravity model was chosen as it is suitable for modeling the flow of propagules among spatially-discrete habitats (MacIsaac et al. 2004). Analysis is continued on the subset of lakes predicted to be invaded or noninvaded based on inbound propagule pressure where invasion status is related to lake physical characteristics and water chemistry. Predicted presence or absence of NIS in lakes with suitable water chemistry and physical conditions was further classified in relation to fish community composition. In this hierarchical approach, NIS presence in lakes is based on the species' ability to successfully bypass all three filters of the invasion sequence (i.e. the right-most branch in the classification tree, Figure 2). The main advantage of the hierarchical approach over a single model combining all filters simultaneously is that it allows independent testing of each filter in the invasion sequence. Lakes predicted as noninvaded based on low propagule pressure or unsuitable environmental characteristics are identified and "removed" from the data set prior to an assessment of the importance of fish community. Thus, their influence on models later in the invasion sequence is also removed. For completeness, all branches of the hierarchical classification tree were modeled.

Gravity model of propagule pressure

Gravity models allow for the calculation of flow from spatially discrete origins to destinations. They provide an ideal method for forecasting overland dispersal of aquatic NIS, and testing in the hierarchical model the importance of propagule pressure.

To collect data on recreationalist movement among Ontario lakes, 10,000 surveys were mailed to owners of fishing licences registered with the Ontario Ministry of Natural Resources in July 2004. Approximately 218 surveys were sent to households in each of 46 zones within Ontario as identified by the first two digits of their postal code to minimize bias due to differences in population density across the province. A χ^2 test was used to assess whether equal numbers of surveys were returned from each area.

Doubly-constrained gravity model

The doubly-constrained gravity model allows for the most accurate prediction of the interaction flow between origin and destination since both the predicted total outflows for each origin and total inflows for each destination are constrained to match observed values (Haynes and Fotheringham 1984).

In the doubly-constrained model, the interaction flow T_{ij} is calculated as:

$$T_{ij} = \frac{A_i O_i B_j D_j}{\alpha \exp(\beta d_{ij})} \tag{1}$$

where O_i is the outflow from origin i, D_j is the inflow to destination j, d_{ij} is the distance between origin i and destination j, α and β are the scale and slope parameters of the distance decay function. The parameters A_i and B_j are balancing factors and are added to the model to ensure that the propagule flow arriving at a lake is equal to the flow leaving the lake.

The parameters A_i and B_j are solved iteratively using a constrained least-squares algorithm as:

$$A_i = \frac{1}{\sum B_j D_j \left[\alpha \exp(-\beta d_{ij}) \right]}$$

(2)

and

$$B_j = \frac{1}{\sum A_i O_i \left[\alpha \exp(-\beta d_{ij}) \right]},$$

(3)

respectively.

Distance Decay function

To capture the likelihood of a recreationalist - the main dispersal agent - travelling a specified distance after visiting an invaded lake, the proportion of recreationalists was calculated based on the road distance traveled in 50 km increments. A two-parameter exponential function, $p = \alpha \exp\left(-\beta d_{ij}\right)$, was fitted to the midpoints of the frequency histogram using a maximum likelihood approach since residuals around the fitted proportion of boaters are not normally distributed. The relationship between the proportion of recreationalists and the distance they travel is assumed to be similar for each of the origin/destination lake pairs in the gravity model. This assumption was not specifically tested due to insufficient data on numbers of boaters leaving particular sources required for rigorous comparisons.

A measure of propagule flow among lakes contributed by each survey respondent was developed by combining an index of risk associated with various activities associated with recreational boating and fishing. In addition, life-history characteristics of the NIS, such as the timing of the production of 'resting' stages

and seasonal peaks in population size, were also included in the gravity model.

For each survey respondent, their contribution to propagule flow among lakes

(pp) is represented by:

$$pp = \left[a * b * c * \left(d + e + f + g + h + i \right) \right]$$ (4)

where

a = seasonal NIS population risk due to NIS abundance in lakes; b = proportion

of resting stages in NIS population during the corresponding time period; c =

correction for bias in response rate due to differential population sizes; d = risk

from using bait buckets; e = risk associated with transporting NIS on boat exterior

and fishing/downrigger lines; f = risk due to recreational activities; g = risk of

transporting viable propagules after leaving lake; h = risk associated with

transporting NIS via macrophytes; i = risk associated with water-based

mechanisms

These components are the dominant mechanisms by which aquatic

species may be transported through recreational boat use. Propagule pressure

contributed by each of these sub-vectors is further divided into the probability of

that sub-vector in use, as measured by the proportion of recreationalists at risk of

transporting propagules by that sub-vector, multiplied by the associated

propagule load (Table 1).

Estimates of propagule loads

Life-history attributes of *Bythotrephes* and *Dreissena* are represented in

the model by several terms, and interact with the timing and type of recreation.

The seasonal population risk (term a, eqn. 4) is the proportion of the NIS

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population in lakes during three time periods multiplied by the number of days the survey respondent's boat was used in those periods (Table 1). Values for *Bythotrephes* and *Dreissena* relative abundance were derived from literature values, summed over each time period and converted into proportions of annual abundance estimates (Dermott et al. 1993, Fraleigh et al. 1993, Nalepa et al. 1995, Yan and Pawson 1998, Yan et al. 2001). For *Dreissena*, the relative abundance of larvae and adults for each time period was converted to proportions of annual abundance separately and then averaged in lieu of creating separate models for each life stage.

The production of resting eggs is an important life-history attribute that may facilitate *Bythotrephes'* invasion success, as the eggs are able to withstand desiccation and may remain viable even though the parent has died (Ketalaars and Gille 1994). The proportion of *Bythotrephes* populations that produce resting stages increases from July to a maximum in September and coincides with popular times for recreational activity (term *b*, eqn. 4, Table 1). Values for the proportion of resting stages in *Bythotrephes* populations were extracted from Yan et al. (2001). Since *Dreissena* does not produce resting stages, this term remained constant in the model.

Survival of propagules once a boat is trailered out of the source lake was also incorporated into the model. Survival of *Bythotrephes'* resting stages is assumed to be invariant over short time periods (Table 1). Survival of *Dreissena* propagules, in particular the adult stages, decrease rapidly once they are subject to aerial exposure. The relationship between propagule survival and time period

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elapsed since the boat was removed from the water was derived from Ricciardi (1995), and scaled to a maximum of 5.

Field collections of *Bythotrephes* were conducted on weekends from July 25, 2005 to August 17, 2005 to estimate relative loads for some of the subvectors (Table 1). Lake Ontario and five inland lakes were sampled with replicated vertical zooplankton net hauls (500 μm mesh size, 43.7 cm diameter) 10-L bait buckets, and weighted (2 oz) fishing line. When leaving each lake, water from the transom well was filtered and contents preserved in 95% ethanol. Propagule loads for 100-L live wells were estimated assuming similar density of propagules as per bait buckets and transom wells. Propagule loads were averaged across replicates and lakes for use in models. Estimates for *Dreissena* propagule loads associated with different subvectors were extracted from Johnson et al. (2001).

In addition to parameterizing propagule load based on specific mechanisms, risks associated with general recreational activities were also considered (eqn. 4, term *f*, Table 1). Propagule loads for general recreational use of lakes, such as whether the survey respondent used the lake primarily for fishing or swimming, were given lower weights than for specific mechanisms.

Parameterization of the model was corrected for bias in the survey return rate from each of the postal zone strata (term *c*, eqn. 4). For each survey respondent, the corresponding gravity flow was multiplied by a correction factor of the total number of surveys divided by the number returned from that postal zone. Thus, trips made by survey respondents were given a greater weight if the number of surveys returned from that area was low. This correction for spatial

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bias ensures that differences in propagule pressure to different areas in the province are a result of differences in the attractiveness of those lakes and not artifacts of differential survey response rates.

The flow of propagules between each origin and destination was calculated as the sum of the trips made by the survey respondents between those lakes (T_{ij}). Since the model is doubly-constrained, the sum of the interaction flow, T_{ij}, for each origin is equal to the total outflow, O_i, for each origin. Likewise, the sum of the interaction flow for each destination is equal to the total inflow for each destination, D_j.

Water chemistry and lake physical characteristics

Data on lake physicochemistry was obtained through the Ontario Ministry of the Environment Lake Partnership program (http://www.ene.gov.on.ca/envision/water/lake_partner/index.htm) and from the 2004 Ontario Lake Assessment program (Dean Jeffries, Environment Canada). Data were averaged over multiple samples and multiple years for a given lake if required. For lakes for which water chemistry data were not available, values were interpolated from nearby lakes using kriging corrected for spatial trend and autocorrelation (Oliver and Webster 1990). Summary statistics of lake characteristics for lakes invaded by *Bythotrephes* and *Dreissena* are presented in Table 2. Lake chemical and physical characteristics were $\log_{10}(x+1)$ transformed except pH and Secchi depth prior to analysis, since they were already normally

distributed with values of similar magnitude to those of the log-transformed variables.

Fish community composition

Fish presence/absence data for inland lakes in Ontario was provided by Nick Mandrak, Dept. of Fisheries and Oceans, Burlington and supplemented by J. La Rose, Ontario Ministry of Natural Resources and G. Morgan, Ontario Ministry of the Environment. Data on Great Lakes' fish species were obtained from Cudmore-Voker and Crossman (2000). Fish species that are known predators of *Bythotrephes* and *Dreissena*, and species that may facilitate NIS establishment by exhibiting strong top-down control on planktivorous fish (e.g. northern pike, walleye), were included in the models and listed in Table 3.

One of the recent approaches to modeling species distributions is fitting boosted regression trees using presence/absence data and relevant predictor variables. This approach is a strong performer relative to other methods for a variety of species and geographical regions since it is able to take into account nonlinear relationships that are often present in ecological data (Elith et al. 2006). This method is also robust to changes in the spatial scale of samples (Guisan et al. 2007).

Boosted regression, or stochastic gradient boosting, is an iterative procedure that fits a series of regression trees that predict only slightly better than by chance at each iteration. Iterations of fitted regression trees (i.e. weak learners) progresses such that observations that are misclassified by the

regression tree fit in the first iteration are given a greater weight so that the error

is more likely to be fixed in subsequent iterations. To avoid overfitting the model,

model performance is gauged by splitting the observations into subsets for model

training and testing (70-30% split). Model predictions are then based on the

optimum number of iterations that balances the tradeoff between the error in the

fit of the training data and error obtained through 5-fold cross-validation (see

example in Figure 3). With this method, five separate models are fit in order to

calculate the cross-validation error estimate with a final model using all data.

The stopping-rule is based on observations not used in the model training (i.e.

"out-of-bag" observations Breiman 1998) to estimate the improvement in the loss

function of the regression tree. The optimum number of iterations is reached

when the out-of-bag change reaches 0.

The proportion of data used in training/testing subsets is normally set at

0.5 for normally-distributed response variables or from 0.5-0.8 for classification

related problems, such as presence/absence (Friedman 2002). For this study,

the proportion was set at 0.70.

In boosted regression models, the relative influence of each independent

variable on the boosted estimate is based on the average relative influence of the

variable across the optimum number of trees used in the model predictions

(Friedman 2001). Similarly, the associated marginal relationships, or partial

dependency of each independent variable with the boosted estimate, is solved by

integration by the weighted tree traversal method (Friedman 2001). Boosted

regression trees were modeled and evaluated with the R package gbm (Ridgeway 2006).

Lakes were classified as invaded if the estimated probability from the boosted regression models for each stage of the invasion sequence was greater than or equal to a threshold based on the shape of the receiver operator characteristic curve (ROC) (Figure 4). The ROC plots the performance of the model being able to correctly predict an invasion (hit rate) versus incorrectly predicting an invasion when one had not occurred (false alarm rate) at different thresholds (Figure 5) (Liu et al. 2005). The threshold was chosen based on the minimum distance from the upper left corner, with values often comparable to the prevalence of invaded lakes. This procedure was recommended by Liu et al. (2005) over setting a fixed threshold for the analysis. The ROC was calculated with the R package verification (NCAR - Research Application Program 2006). Model performance was evaluated based on the area under the receiver operator characteristic curve (AUC). This criterion is used to test whether the model can predict better than at random, independent of the threshold used. Model performance is acceptable only if the AUC is significantly greater than 0.5 (random).

The use of a hierarchical approach assumes that there is minimal interaction between the levels at each stage of the invasion sequence. The relationship between the composition of the fish community and the presence/absence of NIS may be confounded by the interaction with environmental characteristics from the previous stage of the invasion pathway.

This relation was assessed with redundancy analysis in which the presence/absence of fish species in lakes was constrained by a linear combination of lake characteristics. High factor loadings for fish species that correspond with significant lake characteristics indicate that confounding may occur, especially for fish species and lake characteristics identified as highly influential from the boosted regression models. Similarly, the relationship between fish community composition and gravity inflow to lakes was assessed with redundancy analysis to test for confounding effects. Finally, interactions between propagule pressure and environmental characteristics were assessed with a boosted regression model with gravity inflow as the response. The relationship between environmental characteristics and NIS occurrence may be confounded by the indirect effects of propagule pressure.

Comparison of hierarchical to single boosted regression

In the hierarchical approach, an overall classification table representing all three stages of the invasion sequence was constructed by pooling the number of lakes where the species was predicted absent (top row) following the right-most pathway of the classification tree (i.e., branches B,F; Figure 2). To complete the overall classification table, lakes where the NIS was predicted present were those predicted present in the 2x2 table for fish community branch 4. In the single model approach, all variables and lakes were considered simultaneously (i.e. lakes were not subset based the stages of the invasion sequence). The

overall classification table for this approach is simply the observed vs. predicted presence/absence from the regression model.

The predictive ability of the hierarchical and single boosted regression models was compared using calculated AUC and contingency table analysis on the overall classification tables.

Model validation

Although cross-validation is used in the creation of boosted regression models, data sets independent of those used to develop and calibrate the models or records of new invasions after the models were constructed, are required for a robust assessment. Lakes that were reported noninvaded as of 2004 but predicted as invaded for 2005 and 2006 based on the hierarchical approach were identified at risk for *Bythotrephes* and *Dreissena* establishment.

Results

Spatial results from mailout campaign

Significant differences existed in the response rate of recreationalists surveyed among postal code strata, warranting the correction of bias in return rate (χ^2=63.53, d.f. = 45, p = 0.04). The fewest surveys were returned from major metropolitan areas in Ontario, and thus individual trips from recreationalists outside these areas were given greater weight (Figure 6).

Recreationalist behaviour and propagule loads

The ability to assess the risk of transporting NIS propagules associated with recreational traffic depends on the interactions between the behaviour of the individual recreationalist, the propagule load for each dispersal mechanism, and the life-history of the NIS. Based on the survey results and field studies on potential propagule loads, few recreationalists (< 1%) are likely to transport either *Bythotrephes* or *Dreissena* propagules *via* live wells that can potentially contain large propagule loads based on volume of water (Table 1). For *Bythotrephes*, approximately 80% of recreationalists failed to inspect or remove propagules from fishing line after use, and 70% did not inspect the anchor line. Considering that resting stages may remain viable even though the adult has died, transportation of *Bythotrephes* by these mechanisms is most likely, especially in late summer when *Bythotrephes* populations are at peak abundance and the proportion of these populations producing resting stages is maximal (Table 1).

The proportion of recreationalists at risk of transporting *Dreissena* on macrophytes is relatively low, as fewer than 2% of recreationalists reported that they failed to remove macrophytes from the boat or trailer when towing from a boat launch or marina. Over 80% of boaters planned to use their boat in the next two weeks, and 29% of those surveyed plan to go boating within 3 days of leaving a lake (Figure 7).

Dispersal kernel from recreational traffic

The rapid spread of *Bythotrephes* and *Dreissena* among Ontario lakes is consistent with a pattern of stratified dispersal and is largely influenced by the movement of recreationalists. After visiting a lake invaded by either species, approximately 40% of recreationalists traveled 100 km or less, and the proportion of recreationalists decreased exponentially with respect to maximum distance traveled (Figure 8). Eight out of 332 survey respondents who reported distance travelled, however, traveled 800 km or greater. One boater moved 1800 km.

Propagule pressure

The spatial pattern of lakes receiving high propagule pressure was similar for both species. High propagule loads were concentrated in southern Ontario and corresponded with lakes correctly predicted as invaded based upon gravity scores (Figure 9). At moderate levels of propagule pressure, differences in spatial patterns for both species became apparent. In northern Ontario, lakes receiving low to moderate inflows of *Bythotrephes* propagules were concentrated in the northwestern region (Figure 10), whereas the dominant lake receiving *Dreissena* propagules was Lake Nipigon, located north of Lake Superior (Figure 11).

The relationship between gravity inflow and the probability of occurrence differed between the two species. The probability of *Bythotrephes* establishment increased to a maximum of 0.66 at relatively low propagule inflow and remained constant at higher levels (Figure 9). It should be noted, that for certain lakes, the

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likelihood of occurrence decreased with increasing propagule pressure, a result where the boosted regression fit the regression trees to lakes that were currently noninvaded but had higher gravity inflows than some invaded lakes. Factors other than gravity inflow may account for *Bythotrephes* absence at this stage of the classification hierarchy.

Of the 273 lakes identified in the survey as destinations for *Bythotrephes* propagules, 102 were predicted invaded for an overall classification accuracy of 71% (Table 4). The model was able to correctly forecast 70% of lakes (hit rate) that were observed invaded and 72% of noninvaded lakes. This model predicted the invasion status significantly better than at random (AUC = 0.75, P < 0.0001). Most of the lakes incorrectly predicted to have *Bythotrephes* were located north of Lake Ontario or in the northwest corner of Ontario where there was high propagule pressure. A cluster of lakes in northeastern Ontario that were misclassified as invaded received only low to moderate propagule inflows (Figure 10).

The probability of *Dreissena* establishment also increased rapidly at low propagule inflow, but then leveled off (Figure 9). The model predicting invasion status for *Dreissena* based on propagule inflow was more accurate overall than that for *Bythotrephes* and also produced fewer false alarms. *Dreissena* was predicted to have invaded 74 of 291 lakes identified in the survey. The model correctly predicted 63% of lakes observed invaded, and 87% of noninvaded lakes (Table 4). Model performance for *Dreissena* was similar to that of *Bythotrephes* with an AUC of 0.77 (P < 0.0001). Most of the lakes incorrectly

predicted to have *Dreissena* present occurred north of Lake Huron, and two of these lakes, one north of each of Georgian Bay and Lake Superior, received high levels of propagule pressure (Figure 11).

Lake morphometry and physicochemistry

Only the results from models for lakes predicted invaded based upon gravity scores and suitable lake physicochemistry are presented here (branches B and F). Results for the models of lakes removed from the hierarchical analysis are located in the appendix.

At the second stage of the invasion pathway, *Bythotrephes* presence was strongly related to lake depth, NO_3 concentration, lake area and dissolved organic carbon (DOC) concentration (Figure 2 Branch B; Figure 12). These characteristics accounted for 81% of the reduction in model error and were all positively related to the likelihood of occurrence. Probability of invasion increased for lakes with NO_3 and DOC concentrations of approximately 10 μeq L^{-1} and 5012 μg L^{-1} or greater, respectively (Figure 13). There was a distinct spatial pattern of lakes incorrectly predicted as either invaded or noninvaded. Lakes for which *Bythotrephes* was misclassified as present were located primarily in northwestern and eastern Ontario (Figure 14). These lakes tended to be larger (average 2508 ha), deeper (47 m) and have higher DOC concentration (7925 μg L^{-1}) than those correctly classified as absent (285 ha, 12 m maximum depth and 5208 μg L^{-1} DOC).

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<u>Interaction between gravity inflow and lake physicochemistry on NIS</u>

<u>presence/absence</u>

The relationship between lake physicochemistry and *Bythotrephes*

presence is likely confounded by the influx of propagules with respect to lake

area. Lake area was the most influential variable identified from the boosted

regression of gravity inflow as a function of lake physicochemistry (Figure 15),

The relationship between lake area and *Bythotrephes'* gravity inflow (Figure 16)

is nearly identical to that between lake area and establishment for lakes with low

and high inbound propagule pressure (Figures A1, 13), with gravity inflow

increasing rapidly for lakes with area of 1000 ha or greater. The relationship

between lake depth and gravity inflow is less clear. Although there is an increase

in the odds of *Bythotrephes* occurrence as the maximum depth increases in

lakes with both low and high levels of propagule pressure (Figures A1, 13), the

strongest interaction between lake depth and gravity inflow occurs where the

likelihood of occurrence actually decreases at increasing but moderate gravity

inflow (Figure 9A). Lake depth only accounted for 8% of the error in the boosted

regression of gravity inflow and lake physicochemistry, and therefore is not likely

a confounding factor in predicting *Bythotrephes* presence. The remaining lake

characteristics were responsible for less than 7% in the reduction of error.

Lake depth and area were the two most important predictors of *Dreissena*

presence (91% of error reduction). As with *Bythotrephes*, the likelihood of

Dreissena occurrence decreased as lake depth increased and increased with

increasing lake area. Chemical characteristics accounted for less than a

combined 9% of the reduction in error (Figure 17). The highest likelihood of Dreissena presence occurred at NO_3 concentrations below 9 μeq L^{-1} and NH_4 concentations below 2.2 μeq L^{-1}. The model also predicted thresholds for calcium concentrations of 250 μeq L^{-1} and pH of 7.4, above which Dreissena is more likely to occur (Figure 18).

There was a strong spatial component in the classification of lakes with respect to Dreissena presence given high propagule pressure. The seven lakes incorrectly predicted as invaded were located at the southern and northern edges of the distribution of lakes in this dataset. On average, these lakes were of similar depth, but were larger and had lower NO_3 concentrations than those where Dreissena was correctly predicted as absent. The 13 lakes that were misclassified as noninvaded formed a cluster in southern Ontario with the exception of Lake Superior (Figure 19).

Interaction between gravity inflow and lake physicochemistry on establishment success

Lake area and maximum depth were again the most influential variables in the regression model relating inflow of Dreissena propagules to lake physicochemistry, and accounted for a combined 82% of the reduction in error (Figure 20). Propagule pressure increased rapidly for lakes with increasing surface area, and decreased with increasing lake depth (Figure 21). The relationship between gravity inflow and lake area may confound predictions of Dreissena invasion success based on lake area alone, as lake depth is unlikely a factor in lake attractiveness for recreationalists.

Fish community composition

For lakes with high propagule pressure and suitable lake physicochemistry (Branch F), northern pike (*Esox lucius*) was the dominant predictor and negatively related to *Bythotrephes* establishment, with a relative influence over 63% (Figure 22). Of the 52 lakes that were formally predicted as invaded from the previous stages of the invasion sequence, 8 of these were correctly classified as noninvaded with northern pike present in all lakes.

The other major species – walleye (*Sander vitreus*), cisco (*Coregonus artedi*) and largemouth bass (*Micropterus salmoides*) – were all positively related to *Bythotrephes* occurrence, and accounted for a combined reduction of 26% in residual error. The majority of the 34 lakes that were correctly predicted to contain *Bythotrephes* contained yellow perch (*Perca flavescens*), although perch was not a key indicator of *Bythotrephes* presence/absence overall. In addition, walleye and largemouth bass were present in 68% of the 34 lakes.

This model (Branch F) was able to predict significantly better than at random (AUC=0.74, P=0.00017), and correctly identified 92% of invaded lakes (Table 4, Figure 23). In addition to the Great Lakes, most of the lakes that were correctly predicted as invaded were located primarily in south central Ontario (Figure 24). Lakes in which *Bythotrephes* was incorrectly predicted present were located along the eastern edge of Ontario, and the majority contained smallmouth and rock bass as well as lake trout (*Salvelinus namaycush*), cisco and lake whitefish (*Coregonus clupeaformis*) populations.

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Interaction between gravity inflow, lake physicochemistry and fish community

composition affecting invasion success

The relationship between the presence/absence of key species in the fish

community and *Bythotrephes* occurrence may be confounded by the previous

two levels in the classification hierarchy. In the redundancy analysis of fish

community composition constrained by the inbound propagule pressure, the

gravity inflow accounted for only ~3% of total variation among sites, and thus is

not likely a confounding factor. The relationship between lake physicochemistry

and fish community composition was more pronounced, as 19% of total variation

in fish community composition among sites was accounted for by lake

characteristics (Figure 25A). Lake area and maximum depth were the strongest

correlates among lakes, with lake trout, lake whitefish, cisco, and walleye related

to these characteristics. Since these four species were also among the dominant

predictors of *Bythotrephes* presence, confounding is likely to have occurred with

these species. Northern pike, however, was highly correlated with maximum and

minimum total phosphorus concentration and only weakly to lake area, and thus

its relationship to *Bythotrephes* presence is not likely confounded by lake

physicochemistry. The negative relationship between northern pike and

Bythotrephes presence indicated by the four regression models (Appendix,

Figure A5) suggests direct predation by pike, or indirect effects of pike on a third

species whose presence benefits *Bythotrephes*.

In lakes with high propagule pressure and suitable lake characteristics (Branch F), there was no significant relationship between the fish community composition and *Dreissena* presence. The model at this stage of the invasion sequence did not predict significantly better than random (AUC=0.64, P = 0.13) and was only able to correctly classify 61% of currently invaded lakes (Table 4, Figure 26). There was no analysis on the spatial pattern of the final boosted regression model since it was nonsignificant.

Interaction between gravity inflow, lake physicochemistry and fish community composition affecting invasion success

Although there was no significant relationship between fish community composition and *Dreissena* presence, there are likely confounding effects from lake physicochemistry. Lake physicochemistry accounted for 22% of the total variation in fish community composition among sites (Figure 25B). Spottail shiners (*Notropis hudsonius*), the species that was most strongly related to *Dreissena* presence (Appendix, Figure A6, Panel D), was also correlated with lake area and minimum total phosphorus concentration. The other species were correlated to lake characteristics that had only little to moderate influence in the regression models (Appendix, Figure A6). Thus, lake area likely confounds the relationship between *Dreissena* presence/absence and fish community composition.

Overall classification from hierarchical approach

In summary, the hierarchical approach was able to accurately classify 88% of the lakes with respect to occurrence of *Bythotrephes*, with a 57% hit rate, and 3% false alarm rate (Figure 27). The AUC for the hierarchical approach was highly significant (P<0.0001) at 0.82. Most of the lakes correctly predicted as invaded were located west Lake Huron, as well as Lakes Superior and Nipigon. The majority of lakes that were incorrectly predicted as noninvaded were also concentrated in the region west of Lake Huron (Figure 28).

The hierarchical classification for *Dreissena* performed worse than that for *Bythotrephes* with a only a 45% hit rate, and a 3% false alarm rate. The final classification was based on only two invasions stages since *Dreissena* occurrence was unrelated to fish community composition. The overall predictive power was highly significant (AUC=0.78, P<0.0001) (Figure 27). The range for lakes correctly classified as invaded did not extend north past Georgian Bay (Figure 29). Lakes in which *Dreissena* was incorrectly identified as present were located in northeastern Ontario. Conversely, the hierarchical model incorrectly classified *Dreissena* presence in Lakes Huron and Superior.

Single model approach

In the single model approach, in which gravity score, physiochemistry and fish community were simultaneously considered, the relative importance of the variables predicting *Bythotrephes* occurrence was similar to the hierarchical model with the exception of propagule pressure, which was only the 7th most

influential variable (Figure 30). Lake depth and surface area were the most important predictors for *Bythotrephes* occurrence, accounting for 31% of error reduction. In general, *Bythotrephes* occurrence increased as both lake depth and area increased (Figure 31). Fish community composition was a minor component in predicting invasion success, accounting for less than 7% overall in error reduction. In addition to the Great Lakes, *Bythotrephes* presence was correctly predicted for inland lakes west of Lake Huron as well as two inland lakes north of Lake Superior (Figure 34). Lakes misclassified as having *Bythotrephes* present were located throughout the province, including northern and northwestern Ontario.

There were significant differences in model performance assessed with contingency table analysis and AUC criteria using hierarchical versus single model approaches. Overall, the relationships between observed and expected invasion status as measured by the overall classification was significantly different between the two approaches, driven mostly by the low hit rate from the hierarchical approach (χ^2= 102.2, d.f.=1, P<0.0001). Overall classification accuracy for the single model was nearly as high (85%), though both the hit rate (90%) and false alarm rates (17%) were much higher. Indeed, the false alarm rate was more than 5 times that of the hierarchical approach. The AUC was also highly significant at 0.90 (P<0.0001). Of the 273 lakes included in the model, 218 had identical predicted invasion status in the two model approaches.

In the single model approach for *Dreissena*, lake area was the dominant predictor of species occurrence (74% in error reduction), followed by propagule

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pressure and lake depth (Figure 32). Generally, likelihood of *Dreissena* occurrence decreased with increasing lake area and depth, and increased with increasing propagule pressure (Figure 33). In the single model approach, propagule pressure accounted for 5% of the variability in the model fit and was the second most important predictive variable.

Lakes incorrectly forecast as noninvaded by *Dreissena* were located predominantly north of Lakes Erie and Ontario (Figure 35). Conversely, lakes incorrectly classified as having *Dreissena* ranged along the eastern border of Ontario. For *Dreissena*, the single model approach performed significantly better than the hierarchical model (χ^2=502.3, d.f.=1, P<0.0001). The single model performed well in predicting *Dreissena* presence (AUC=0.99, P<0.0001) (Figure 27) with an overall classification accuracy of 96%, a 96% hit rate, and 0.5% false alarm rate. Predicted invasion status from the hierarchical and single modeling approaches matched for 248 out of 291 lakes.

Validation of hierarchical model forecasts

Bythotrephes was reported to have invaded 8 lakes in 2005 and 24 in 2006 (Norm Yan, pers. comm; Ontario Federation of Anglers and Hunters, unpubl. data). From the hierarchical approach, there were only 7 lakes predicted as invaded from the model constructed on 2004 invasion status. None of these were invaded in 2005 or 2006 (Table 5). Similarly, lakes forecast as invaded by *Dreissena* based on high propagule pressure and suitable lake physicochemistry

did not match any of the 34 lakes invaded in 2005 and 2006 (Ontario Federation of Anglers and Hunters, unpubl. data).

Discussion

The ability to forecast dispersal and establishment of nonindigenous species is an important undertaking, as preventative approaches lead to more desired outcomes in the long-term than post-invasion eradication or control efforts (Lodge et al. 2006, Finnoff et al. 2007). In this study, I developed the first set of comprehensive models that consider and test invasion hypotheses sequentially, and compare model predictions for two aquatic NIS against a model that considers all possible determinants simultaneously. I observed differences between model types with respect to their abilities to correctly identify invaded lakes (hit rate) while protecting against falsely concluding noninvaded lakes were invaded (false alarm). The selection of a hierarchical versus single model to predict invasion depends on the objective. If one seeks to identify invaded lakes, the single model approach is recommended as it was better than the hierarchical model for both *Bythotrephes* (90% versus 57%) and *Dreissena* (96% versus 45%). On the other hand, the hierarchical model tended to be far more conservative in assigning invasion status. Only 3% of lakes that lack *Bythotrephes* were predicted to be invaded by the hierarchical model (false alarm), versus 17% for the single model. The same pattern applied to *Dreissena*, though the difference in false alarm rates was much lower (3% versus 4%, respectively). The hierarchical model developed for *Bythotrephes* performed

better than the single model in terms of correctly identifying invaded lakes (83% versus 60%), though the pattern was reversed for *Dreissena* (83% versus 87%). Thus, the single model offered the highest overall predictive power (i.e. AUC) and sensitivity in detecting invasions at the cost of higher rates of false alarms. These results dovetail with findings of Marchetti et al. (2004), who found that a 'global' model containing all variables related to all stages of an invasion sequence was a better predictor for nonindigenous fish occurrence in California relative to models containing only subsets of variables.

It is surprising that the hierarchical models did not perform consistently better than single models. Because these models focus only on lakes with high introduction effort, lakes with little human vector activity would be excluded from subsequent analysis, as would any influence of their physicochemical and fish community structure. For both *Bythotrephes* and *Dreissena*, models using hierarchical approach were more conservative and detected fewer false alarms than single models. Another possibly related disadvantage of the hierarchical approach is decreasing sample size at each stage of the invasion pathway analysis because observations are sequentially divided into smaller subsets. For multivariate methods, the ability to detect significant relationships for each of the predictors becomes more and more difficult due to increased variability among observations because of low sample size.

The roles of propagule pressure, environmental suitability and biotic integration in determining invasion success.

As the first stage in the invasion sequence, propagule pressure is a key determinant of NIS occurrence and subsequent dispersal. For both *Bythotrephes* and *Dreissena*, the form of this relationship is consistent with the dose-response concept in which the probability of occurrence increases nonlinearly with increasing propagule loads and number of introduction events (Lockwood et al. 2005, Drake and Lodge 2006). Although propagule pressure has been cited as an important component in determining invasion success (Lockwood et al. 2005, Von Holle and Simberloff 2005, Jeschke and Strayer 2006), surprisingly few studies have tried to quantify this relationship. Many studies take a theoretical and parametric approach by assuming a logistical or Weibull function (e.g. Veltman et al. 1996, Leung et al. 2004), although Jerde and Drake (2007) experimentally assessed the relationship between propagule pressure and establishment success for the scentless chamomile *Matricaria perforata*. Our methodology provides a semi-quantitative assessment of propagule pressure and is amenable to other systems in which activities of human vectors can be quantified.

Evaluation of the importance of propagule pressure relative to other factors in determining invasion success requires simultaneous assessment of all variables in a single model. Propagule pressure ranked 7th and 2nd behind measures of lake physicochemistry in the single boosted regression model for *Bythotrephes* and *Dreissena,* respectively. In other studies, however, propagule

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pressure was the most important predictor of invasion success for plants relative to environmental characteristics (Rouget and Richardson 2003), and for bird introductions as compared to life-history characteristics (Veltman et al. 1996). Assessments of introduction effort may be able to identify vulnerability of distant habitats to invasion that other forms of models are highly unlikely to replicate. For example, Bossenbroek et al. (2007) predicted that Lake Mead, Nevada, was the most vulnerable major body of water in the western USA to zebra mussel invasion owing to movement of trailered boats from infected areas in the Great Lakes region. In January 2007, this system was reported colonized by quagga mussels (*D. rostriformis bugensis*), a close relative of the zebra mussel whose closest population occurs some 2500 km away in Lake Michigan. Available evidence, therefore, supports the importance of propagule pressure as an invasion determinant in both terrestrial and aquatic studies.

Relationships between measures of environmental suitability and NIS occurrence were dominated by lake morphometry. Lake depth and area were positively related to *Bythotrephes* presence, a finding similar to results from other studies. For example, European and North American lakes that supported *Bythotrephes* had a significantly greater surface area and maximum depth than those in which *Bythotrephes* was absent (MacIsaac et al. 2000). While the specific effect of lake area and depth are not immediately apparent, both factors could influence habitat diversity, availability of refuge from fish predators and, consequently, population size of the NIS. MacIsaac et al. (2000) also found that Secchi disc transparency was an important predictor of *Bythotrephes* occurrence

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in European lakes. The relationship between water clarity and *Bythotrephes* presence was less clear in this study, as it only weakly corresponded with *Bythotrephes* presence.

Lake area and depth were also significant predictors for *Dreissena* occurrence (Figure 17). Lakes predicted to contain *Dreissena* tended to be shallower, and had greater surface area than lakes without the mussel, likely the result in greater littoral habitat. Ramcharan et al. (1992) found that lakes with zebra mussels had larger surface area than those without, though lakes did not differ with respect to either maximum or mean depth. It is possible that high surface area corresponds with high availability of littoral substrates, which is the preferred habitat of *Dreissena* (Griffiths et al. 1991). In some instances, despite high propagule pressure, lakes may remain noninvaded by established *Dreissena* populations. For example, many of the Illinois reservoirs that were recipients of high propagule pressure contained only *Dreissena* veligers (Schneider et al. 1998). For many mollusks, low calcium levels limit shell production of adults. As a surrogate for measures of water chemistry, surficial or bedrock geology is frequently used with success. Drake and Bossenbroek (2004) suggested that continental areas of the USA with igneous and metamorphic bedrock were unlikely to be invaded by *Dreissena* owing to calcium limitation.

The presence of native predators has historically been viewed as one of the most important deterrents to invasion success (Elton 1958). Indeed, studies of plants (Levine et al. 2004), mollusks (Reusch 1998), and fish (Baltz and Moyle 1993) have illustrated the importance of biotic resistance in retarding invasions.

The distribution of nonindigenous invertebrates in relation to key fish species in this study must be interpreted with caution, as confounding by lake physicochemistry is highly likely. For example, in lakes with high propagule pressure and suitable water chemistry, *Bythotrephes* was positively related to known planktivores such as cisco and piscivores such as walleye and largemouth bass, and negatively related to northern pike presence. These relationships are confounded by lake area and depth, however, with the possible exception of the correlation between *Bythotrephes* and northern pike presence. The presence of planktivorous fish in lakes does not necessary imply that predation is not a limiting factor in *Bythotrephes* establishment. Lakes that are deeper may provide a thermal and light refuge for *Bythotrephes* from coldwater stenotherms, such as cisco, and allow for coexistence providing that the hypolimnion lies below the euphotic zone (Coulas et al. 1998, Palmer et al. 2001, Branstrator et al. 2006, Yan and Pawson 1998). *Bythotrephes* is highly conspicuous relative to other zooplankton, due to its large body size and medial eye, and is consequently an important food item for planktivores in large lakes. For example, *Bythotrephes* made up 10-27% of large alewife (*Alosa pseudoharengus*) diet by biomass in Lake Michigan and 62% in Lake Ontario (Mills et al. 1992, Pothoven et al. 2007). In Harp Lake, Ontario, the percentage of *Bythotrephes* in lake herring (*Coregonus artedi*) diet ranged between 1 and 64% (Coulas et al. 1998).

Ability of models to forecast invaded lakes

For both species, noninvaded lakes that were forecast as invaded from 2004 did not match those reported invaded in 2005 and 2006, presumably as lakes highly susceptible to invasion in the early stages of spread have already been invaded. In this scenario, forecasting ability to detect new invasions is greatly reduced as invasions are typically rare occurrences, highly stochastic events, and the complexity of the network of invaded lakes interconnected by recreational traffic increases geometrically. For example, in 1999 there were only 35 lakes that could serve as potential sources for *Bythotrephes* invasions in 2000 and 2001, and only half of the 11 lakes forecast as invaded had relatively high propagule pressure (MacIsaac et al. 2004). In this study, there were 60 invaded lakes visited by recreationalists, with seven forecast incorrectly as invaded due to relatively high propagule pressure. It is possible that some false alarms may ultimately prove correct, as they simply indicate lakes expected to be invaded. Given a longer time period, noninvaded lakes with substantial propagule pressure and suitable chemistry may, indeed become invaded.

In conclusion, the models developed here are the first attempt to implement a stage-based assessment of the invasion process. Surprisingly, single models that considered biotic and abiotic criteria simultaneously were better able to predict invaded lakes than hierarchical models for both *Bythotrephes* and *Dreissena*. Hierarchical models performed more conservatively, with a lower rate of false alarms. This study highlights the relative importance of propagule pressure and suitable environmental conditions,

especially lake area and depth, in predicting NIS occurrence. Biotic integration was seemingly important for one (*Bythotrephes*) species. Models to predict spread of aquatic AIS require comprehensive information on introduction effort, lake chemistry and morphometry, and community composition. This information may be used to develop single models to predict the most vulnerable lakes to future invasion. While I focus on aquatic NIS, the same approach could be used to assess spread of terrestrial species.

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Table 1. Proportion of recreationalists at risk of transporting *Bythotrephes* and *Dreissena* propagules with associated propagule loads for each mechanism. Propagule loads are on an index from 0-5 individuals unless indicated.

Risk factor	Proportion of recreationalists	*Bythotrephes*	*Dreissena*
Date risk[1,2]		0.001*# days in Nov-Mar + 0.14*# days in Apr-May + 0.86*# days in Jun-Oct	0.37*# days in Nov-Mar + 0.04*# days in Apr-May+ 0.59*# days in Jun-Oct)
Proportion of resting stages in population[1]		Jan 1-Jul 3: 0 Jul 4-9: 0.05 Jul 10-16: 0.03 Jul 17-24: 0.49 Jul 25-31: 0.72 Aug 1-6: 0.44 Aug 7-14: 0.40 Aug 15-21:0.67 Aug 22-Sep 30: 0.71 Sep 31-Dec 30: 0	1

Bait buckets	0.389	6[3]	31[5]
Anchor	0.704	1	2
Downrigger	0.220	10[4]	1
Fishing line	0.797	10[4]	1
Recreational activities			
Boating	0.714	1	2
Fishing	0.881	1	2
Swimming	0.624	0	0
SCUBA	0.066	1	1
Water skiing	0.325	1	1
Propagule viability after leaving lake		5	$v_{load} = \begin{cases} 4.5, \#\,days \leq 1 \\ 0.5, 1 < \#\,days \leq 4 \\ 0, \#\,days > 4 \end{cases}$ [6]
Macrophytes	0.016	1	2[5]
Water-based			
Live well	0.005	60[4]	1230[5]
Engine cooling	0.184	1	16[5]
Bilge water	0.139	1	12[5]
Transom well	0.087	1[3]	12[5]

[1] Estimated from data extracted from Yan et al. (2001)

[2] Estimated from data extracted from Dermott et al.(1993), Fraleigh et al. (1993), Nalepa et al. (1995).

[3] Measured from field surveys

[4] Estimated based on average *Bythotrephes* abundance of 6.9 ind. m^{-3} from field surveys and relative volume of each mechanism.

[5] Estimated adult or veliger abundance from Johnson et al (2001)

[6] Estimated from data extracted from Ricciardi (1995).

Table 2. Mean (± 1 SD) values of physical and chemical characteristics for invaded and noninvaded lakes.

Lake physical and chemical measure	*Bythotrephes* present	*Bythotrephes* absent	*Dreissena* present	*Dreissena* absent
SO$_4$ (µeq L^{-1})	101.9 (33.8)	97.0 (33.3)	100.8 (35.6)	93.8 (31.8)
pH	6.8 (0.6)	6.7 (0.9)	6.9 (0.7)	6.6 (0.8)
Total N (µg L^{-1})	427.0 (11.8)	387.8 (93.45)	419.7 (121.6)	389.5 (91.4)
NO$_3$ (µeq L^{-1})	12.6 (7.4)	6.3 (8.0)	10 (8.5)	6.3 (7.2)
NH$_4$ (µeq L^{-1})	2.2 (1.0)	2.0 (1.1)	2.2 (1.2)	1.9 (1.0)
Ca (µeq L^{-1})	308.9 (298.5)	317.3 (493.0)	439.8 (452.7)	305.4 (545.8)
Conductivity (µS cm^{-2})	66.7 (51.0)	59.7 (84.5)	65.8 (55.9)	60.8 (85.7)
DOC (µg L^{-1})	6198.7 (1470.6)	5944.8 (2197.62)	6092.8 (1252.7)	5926.1 (2091.6)
Minimum Total Phosphorus (µg L^{-1})	9.2 (2.5)	8.5 (2.9)	9.6 (2.6)	8.5 (2.8)

Maximum Total Phosphorus ($\mu g\ L^{-1}$)	12.7 (4.8)	11.5 (11.9)	14.0 (7.0)	11.3 (11.6)
Secchi Depth (m)	4.2 (0.7)	3.99 (0.7)	4.1 (0.5)	4.0 (0.7)
Lake Area (ha)	325263 (1356010.8)	3204 (19536.8)	253048 (1218237.9)	4602 (32478.3)
Maximum Lake Depth (m)	58.9 (69.5)	28.7 (33.2)	38.5 (64.2)	31.8 (25.3)

Table 3. Ontario fish community composition for establishment models

NIS	Species	Common name	Abbreviation	Reference
Bythotrephes				
	Dorosoma cepedianum	gizzard shad	gshd	Branstrator and Lehman (1996)
	Salvelinus fontinalis	brook trout	bt	
	Salvelinus namaycush	lake trout	lt	
	Coregonus artedi	cisco	ci	
	Coregonus clupeaformis	lake whitefish	lwf	
	Coregonus zenithicus	shortjaw cisco	sjci	
	Prosopium cylindraceum	round whitefish	rwf	
	Esox lucius	northern pike	np	
	Esox masqinongy	muskellunge	mu	
	Notropis atherinoides	emerald shiner	es	Hartman et al. (1992)

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Notropis hudsonius	spottail shiner	sts	Hartman et al. (1992)
Morone chrysops	white bass	wbs	Bur and Klarer (1991)
Ambloplites rupestris	rock bass	rbs	
Micropterus dolomieu	smallmouth bass	smbs	
Micropterus salmoides	largemouth bass	lmbs	Ferry and Wright (2002)
Pomoxis nigromaculatus	black crappie	bcr	
Perca flavescens	yellow perch	yp	Bur and Klarer (1991)
Sander canadensis	sauger	sa	Bur and Klarer (1991)
Sander vitreus	walleye	we	Bur and Klarer (1991)

Dreissena

Acipenser fulvescens	lake sturgeon	stu	www.fishbase.net

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Dorosoma cepedianum	gizzard shad	gshd	
Hiodon tergisus	mooneye	me	
Salvelinus fontinalis	brook trout	bt	
Salvelinus namaycush	lake trout	lt	
Coregonus artedi	cisco	ci	
Coregonus clupeaformis	lake whitefish	lwf	
Coregonus zenithicus	shortjaw cisco	sjci	
Prosopium cylindraceum	round whitefish	rwf	
Esox lucius	northern pike	np	
Esox masqinongy	muskellunge	mu	
Umbra limi	central mudminnow	cmud	
Notropis atherinoides	emerald shiner	es	Hartman et al. (1992)
Notropis heterolepis	blacknose shiner	bns	

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Notropis hudsonius	spottail shiner	sts	Hartman et al. (1992)
Notropis volucellus	mimic shiner	mis	
Culea inconstans	brook stickleback	bst	
Pungitius pungitius	ninespine stickleback	nsst	
Morone chrysops	white bass	wbs	
Ambloplites rupestris	rock bass	rbs	
Micropterus dolomieu	smallmouth bass	smbs	
Micropterus salmoides	largemouth bass	lmbs	Ferry and Wright (2002)
Pomoxis nigromaculatus	black crappie	bcr	
Perca flavescens	yellow perch	yp	
Sander canadensis	sauger	sa	Bur and Klarer (1991)
Sander vitreus	walleye	we	Bur and Klarer (1991)

Table 4. Threshold derived from the receiving operator characteristic curve (ROC), hit rate, false alarm rate, overall classification rate and area under the receiving operator characteristic curve (AUC) for branches in the classification tree. Branch names correspond to Figure 2.

Species	Branch Node of classification tree	Threshold from ROC	Hit rate	False alarm rate	Overall classification rate	AUC (probability)
Bythotrephes	Propagule Pressure	0.34	0.70	0.28	0.71	0.75 (< 0.0001)
	Chem. Branch 1	0.23	0.72	0.16	0.83	0.82 (< 0.0001)
	Chem. Branch 2	0.49	0.88	0.25	0.80	0.88 (< 0.0001)
	Fish Branch 1	0.05	0.20	0.06	0.91	0.63 (1.6e-1) NS
	Fish Branch 2	0.50	0.46	0.08	0.76	0.70 (2.2e-2)
	Fish Branch 3	0.17	0.80	0.07	0.98	0.94 (7.6e-4)
	Fish Branch 4	0.86	0.92	0.47	0.81	0.82 (1.7e-4)

Species	Branch Node of classification tree	Threshold from ROC	Hit rate	False alarm rate	Overall classification rate	AUC (probability)
Dreissena	Propagule Pressure	0.39	0.63	0.13	0.81	0.77 (< 0.0001)
	Chem. Branch 1	0.17	0.93	0.11	0.90	0.96 (< 0.0001)
	Chem. Branch 2	0.75	0.72	0.26	0.73	0.77 (< 0.0001)
	Fish Branch 1	0.29	1.00	0.00	1.00	1.00 (< 0.0001)
	Fish Branch 2	0.74	0.73	0.25	0.74	0.70 (1.1e-2)
	Fish Branch 3	0.40	1.00	0.00	1.00	1.00 (< 0.0001)
	Fish Branch 4	0.91	0.61	0.29	0.63	0.64 (1.3e-1) NS

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Table 5. Noninvaded lakes predicted to be invaded by *Bythotrephes* and

Dreissena from the hierarchical model.

NIS	Lake
Bythotrephes	Pollywog Lake; Frontenac Co.
	St. Peter Lake; Hastings Co.
	Manitou Lake; Nipissing Dist.
	Big Rideau Lake; Leeds Co., Lanark Co.
	Lady Evelyn Lake; Timiskaming Dist.
	Howard Lake; Timiskaming Dist.
	Minnitaki Lake; Kenora Dist.
Dreissena	Varty Lake; Lennox and Addington Co.
	St. Francis Lake; Glengarry Co.
	Star Lake; Cochrane Dist.
	Silver Lake; Bruce Co.
	Otonabee Reservoir; Peterborough Co.
	Pigeon Bay (Lake Superior)
	Mary Lake; Cochrane Dist.

Source region

Filters

Model components

A B C D E F G H

Entrainment in
tranportation
pathway

Propagule
pressure

Survival during
exposure to physi-
cal and chemical
environment

Lake physical
and chemical
characteristics

Biotic integration into
native community

Fish community

Establishment
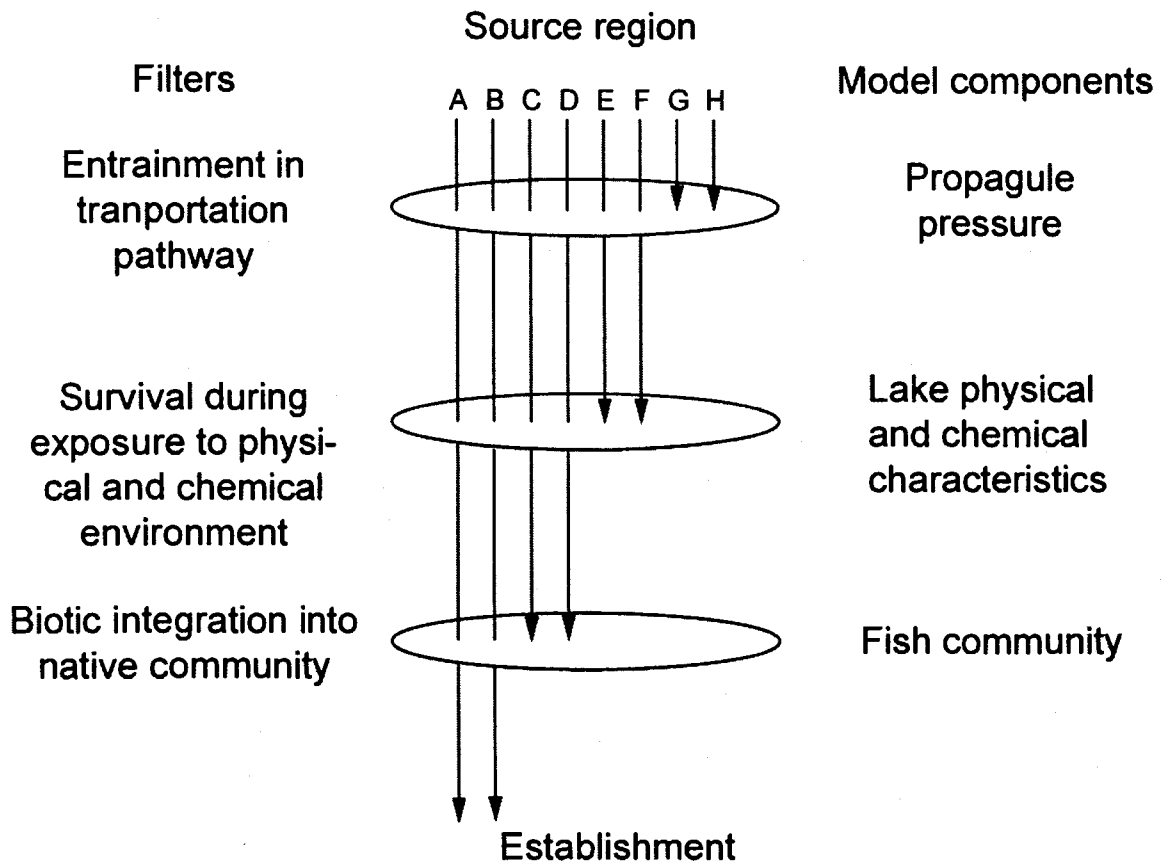
Figure 1. Conceptual model of filters in the invasion sequence with

corresponding model components. Arrows indicate where individuals were

unable to bypass the filters. Modified from Kolar and Lodge 2001.

Predicted
Presence/Absence

Gravity Inflow

Low propagule pressure (0)

High propagule pressure (1)

[A] Lake physicochemistry branch 1

[B] Lake physicochemistry branch 2

Unsuitable (0)   Suitable (1)   Unsuitable (0)   Suitable (1)

[C] Fish assemblage branch 1

[D] Fish assemblage branch 2

[E] Fish assemblage branch 3

[F] Fish assemblage branch 4

0   1   0   1   0   1   0   1
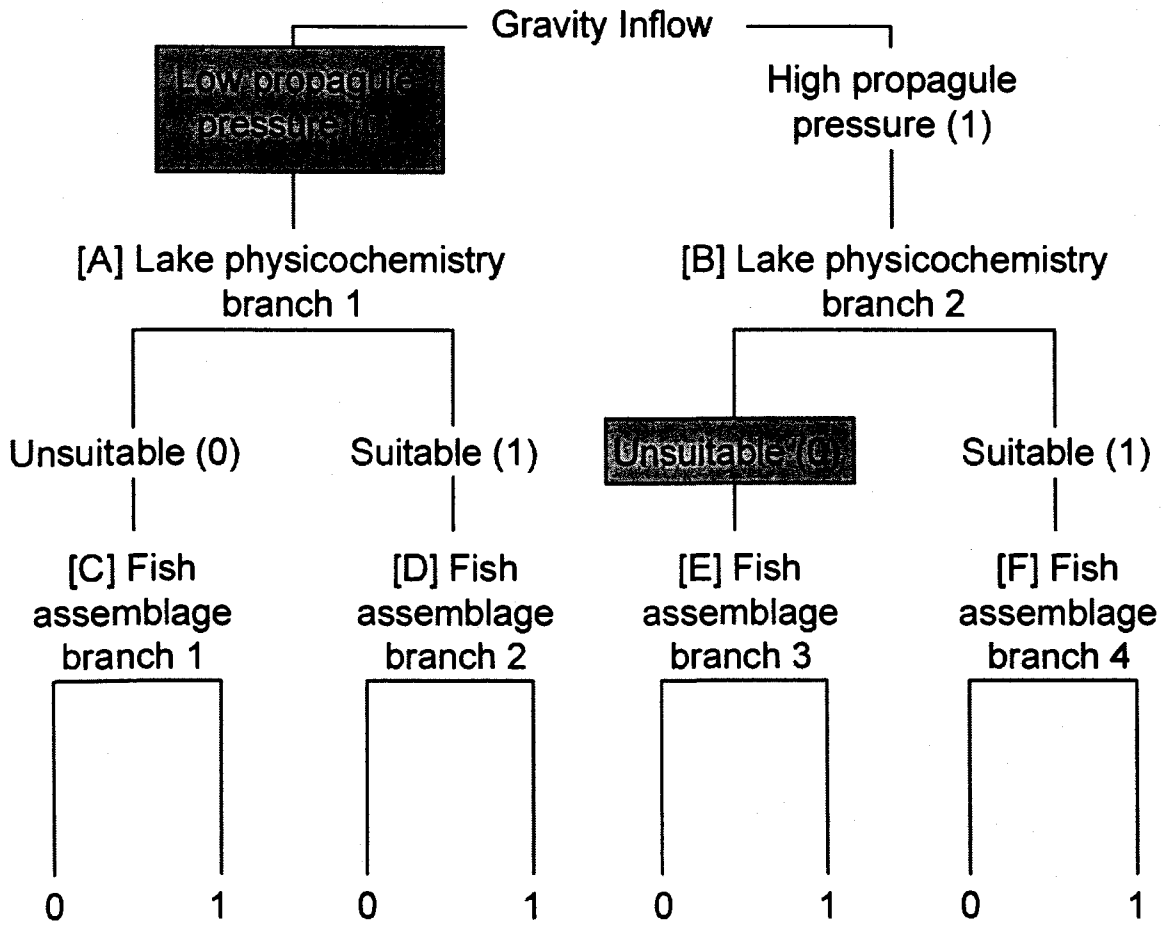
Figure 2. Conceptual model for hierarchical hypothesis testing. Lakes predicted to be invaded follow the right branch of each split. Grey boxes indicate lakes where NIS absence in lakes may be explained by the successful filter in the invasion sequence.
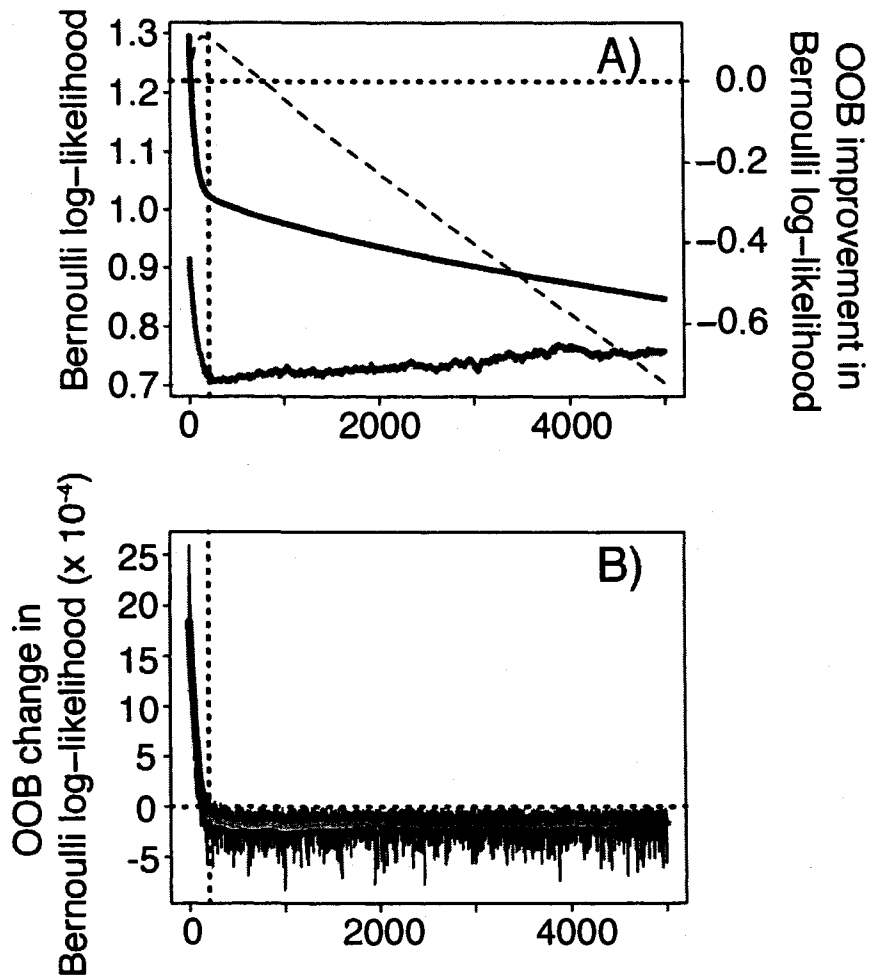
Figure 3. Boosted regression performance for fitting *Dreissena*

presence/absence to inbound gravity flow to find the optimal number of

iterations. Panel A is the log-likelihood loss function and out-of-bag (OOB)

improvement in reducing the loss function and Panel B is the cumulative

improvement in the loss function. The solid black curve in panel A is the

error from the training data set and the light gray line indicates cross-

validation error. The optimal number of iterations for the model is indicated

in both panels by the dotted line where the out-of-bag improvement is

zero.
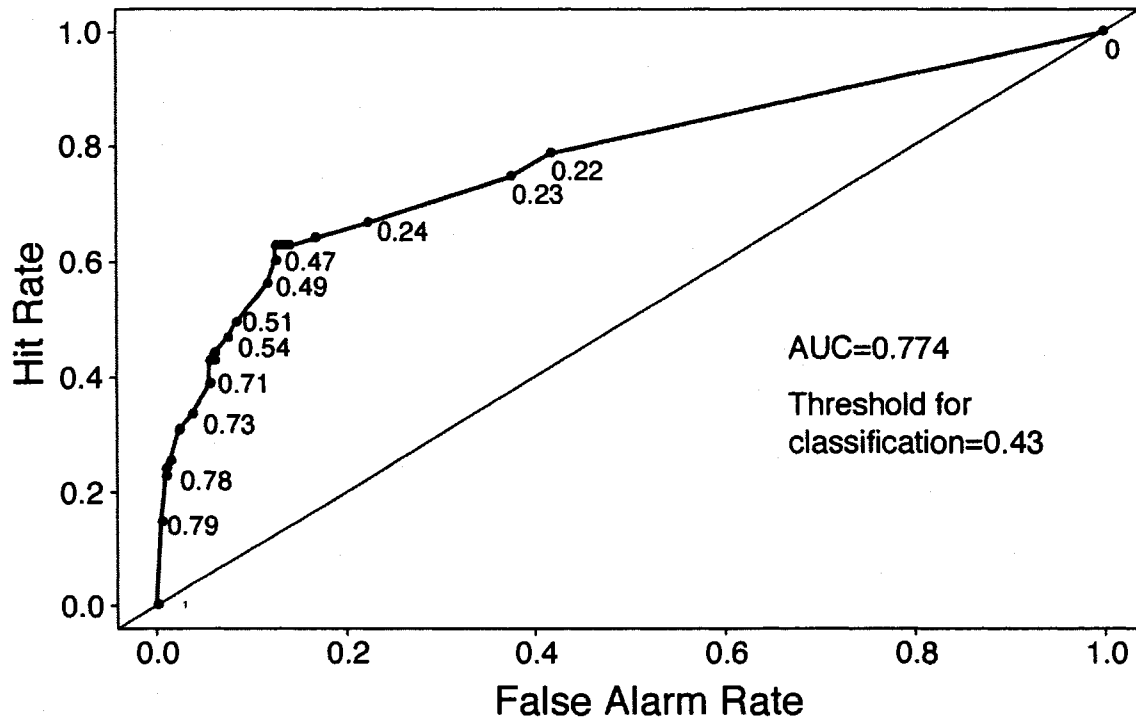
Figure 4. Receiver Operating Characteristic (ROC) plot of *Dreissena* gravity flow
model at various probability thresholds. The AUC, or area under the curve is a
measure of model accuracy, and threshold chosen for classification is the point
nearest to top-left corner.

Observed

Absent Present

	Absent	Present
Absent	a) Correct Negative	b) Miss
Present	c) False Alarm	d) Hit

Predicted

Overall classification accuracy$=(a+d)/(a+b+c+d)$

Hit rate$=d/(b+d)$

Miss rate$=b/(b+d)$

False alarm rate$=c/(a+c)$

Figure 5. Definitions of overall classification accuracy, hit rate, miss rate and false alarm rates for a 2x2 classification, or 'confusion' table.
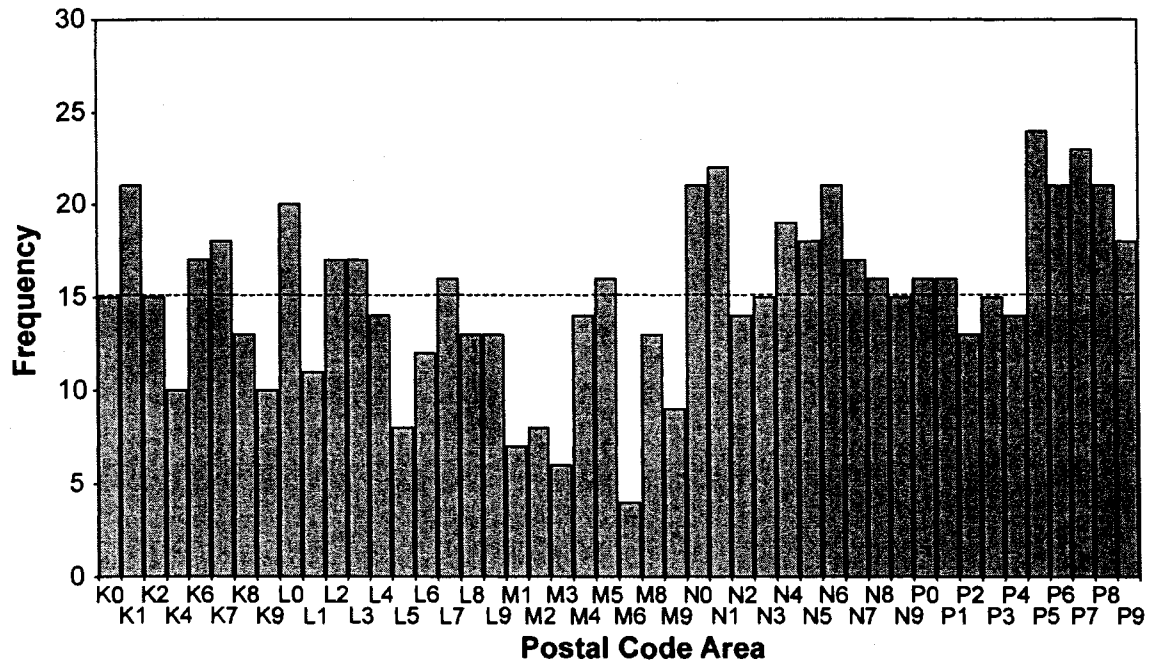
Figure 6. Frequencies of returned surveys from postal code areas. The

horizontal line indicates the expected return rate if equal among areas.
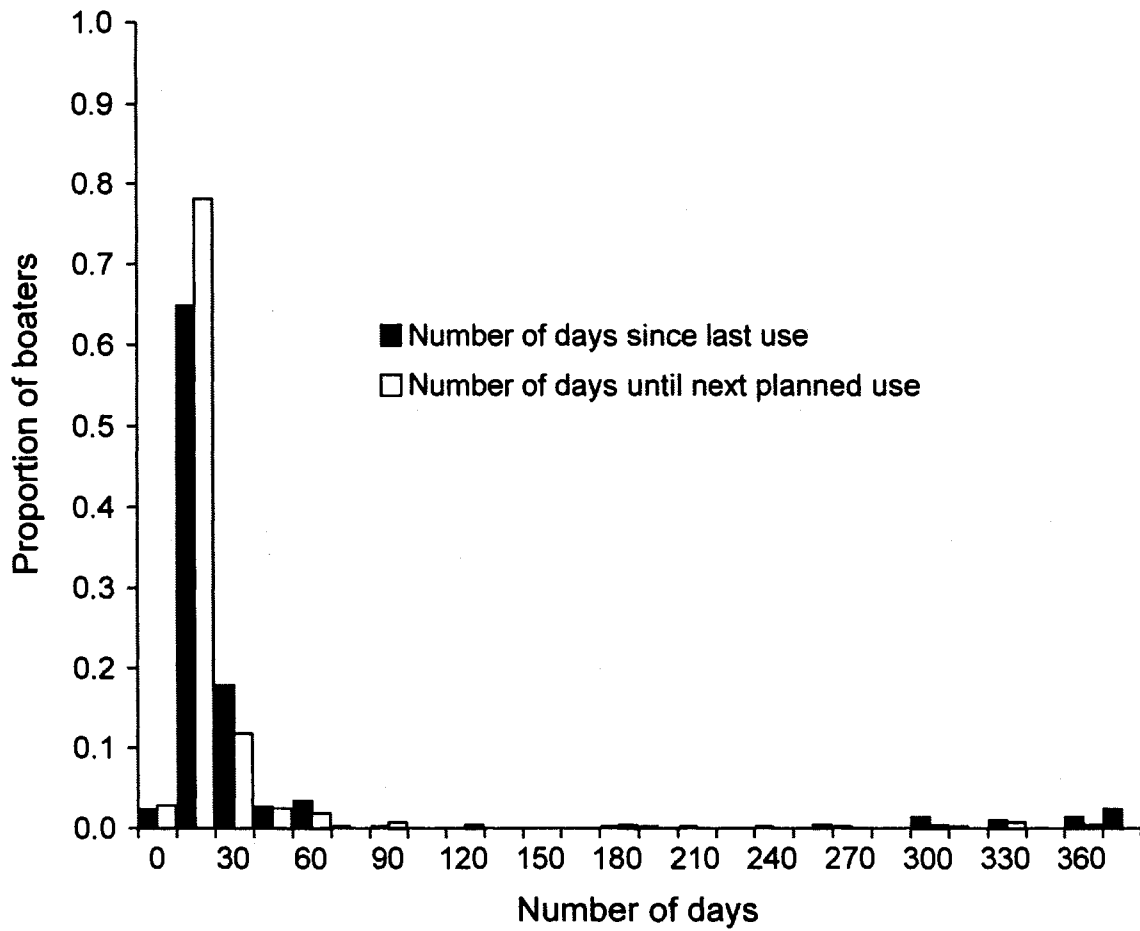
Figure 7. Proportion of recreationalists and the number of days since their boats were last used and the number of days until next planned use.
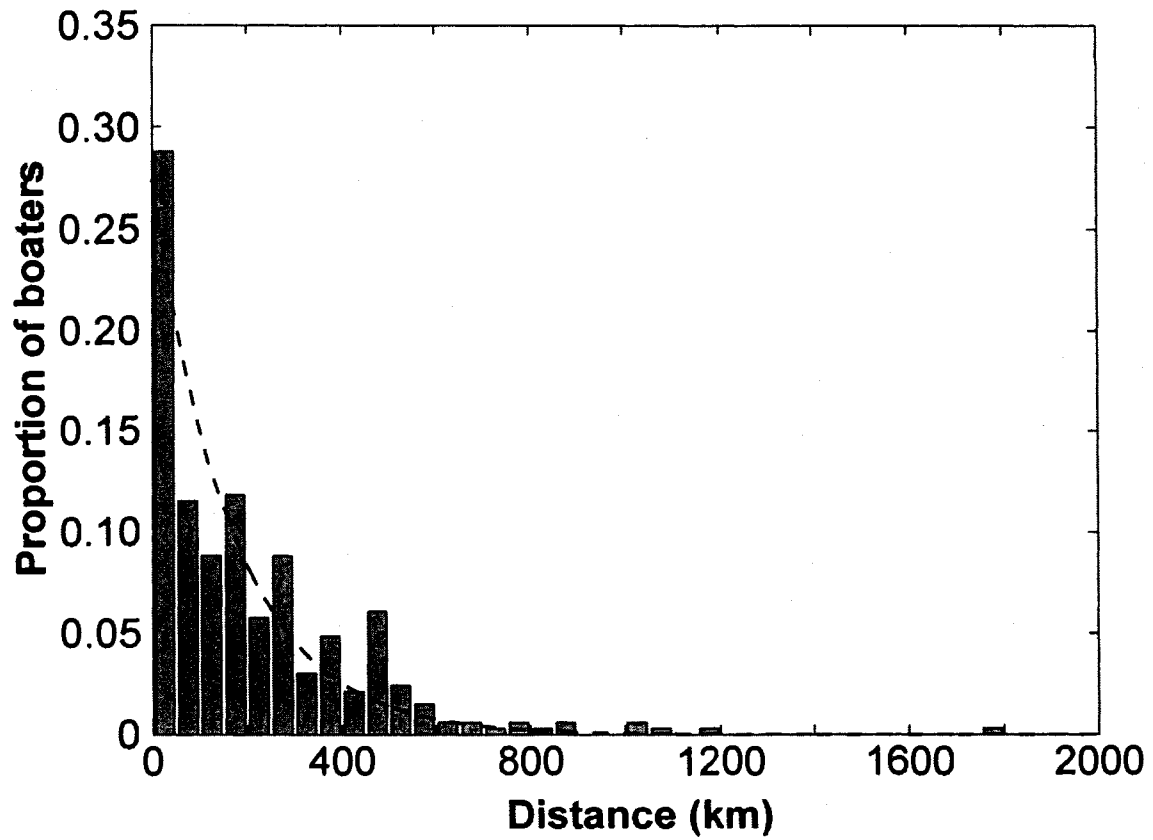
Figure 8. Frequency histogram of the maximum distance recreationalists

traveled after visiting and invaded lake. The exponential decay function,

$y = 0.27\exp(-0.005x)$, was fitted to the midpoint of the distance

categories.
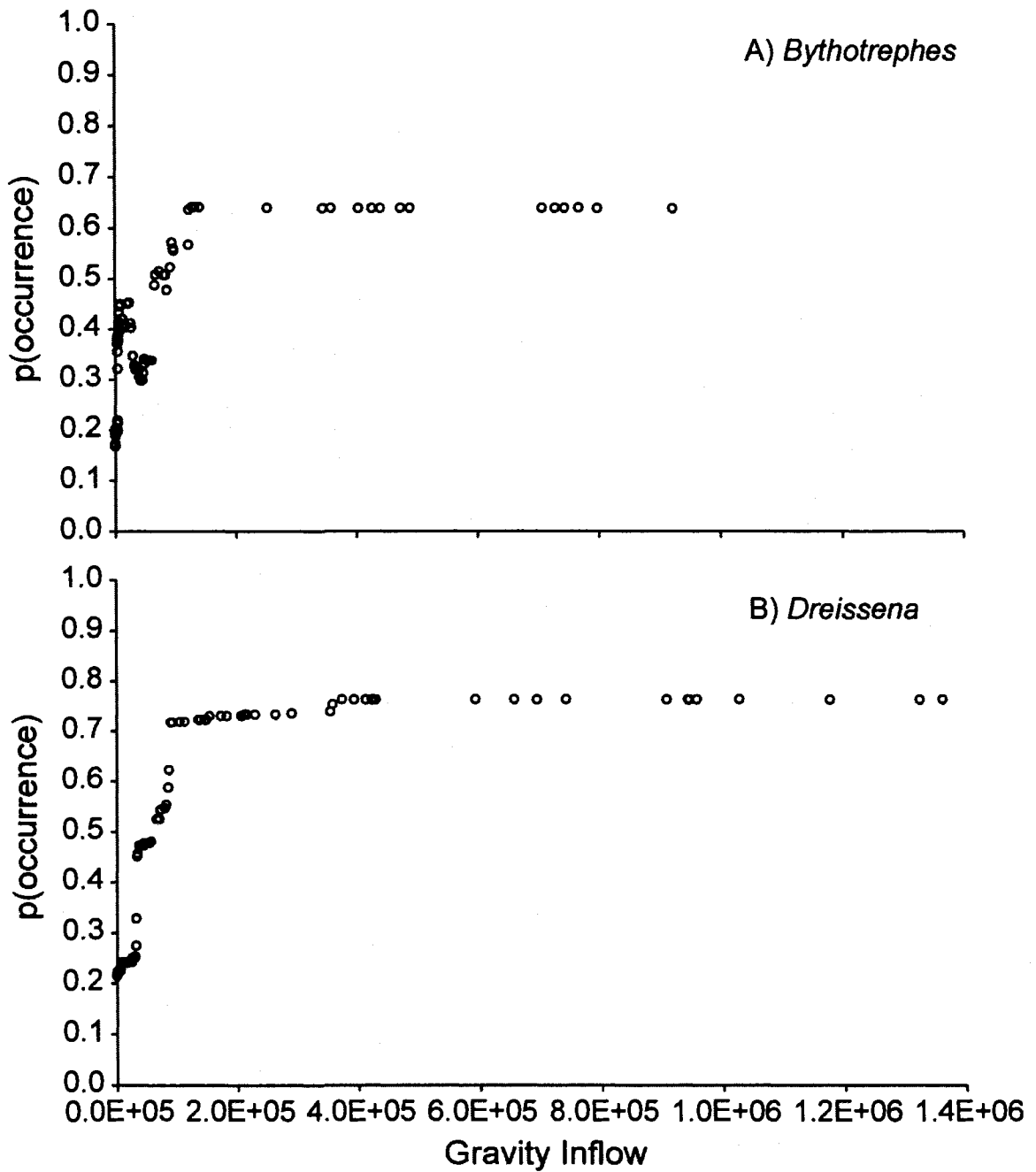
Figure 9. Probability of *Bythotrephes* and *Dreissena* occurrence as a function on inbound propagule pressure estimated from the boosted regression model.
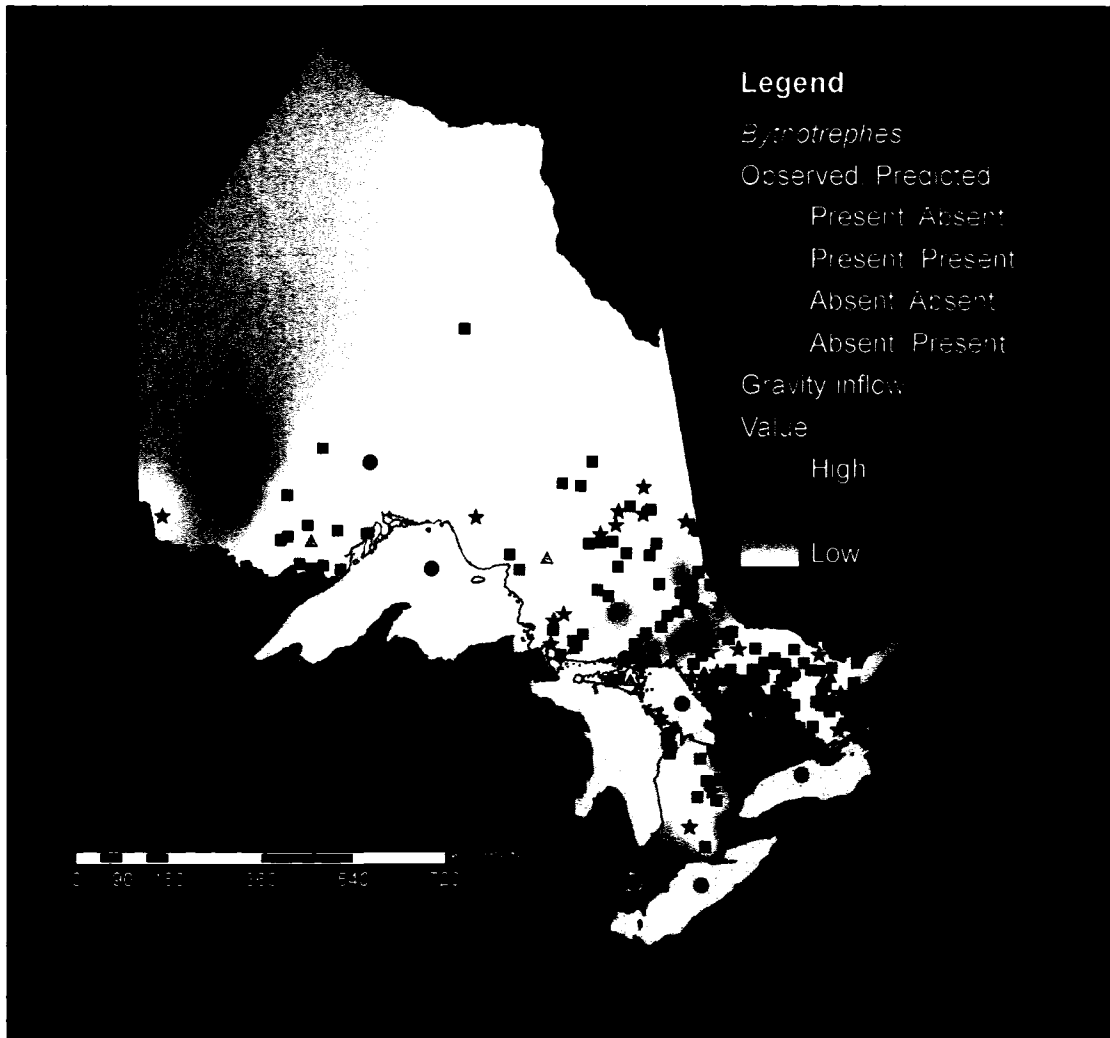
Figure 10. Spatial pattern of inbound propagule pressure with observed and predicted presence of *Bythotrephes* based only on gravity inflow.
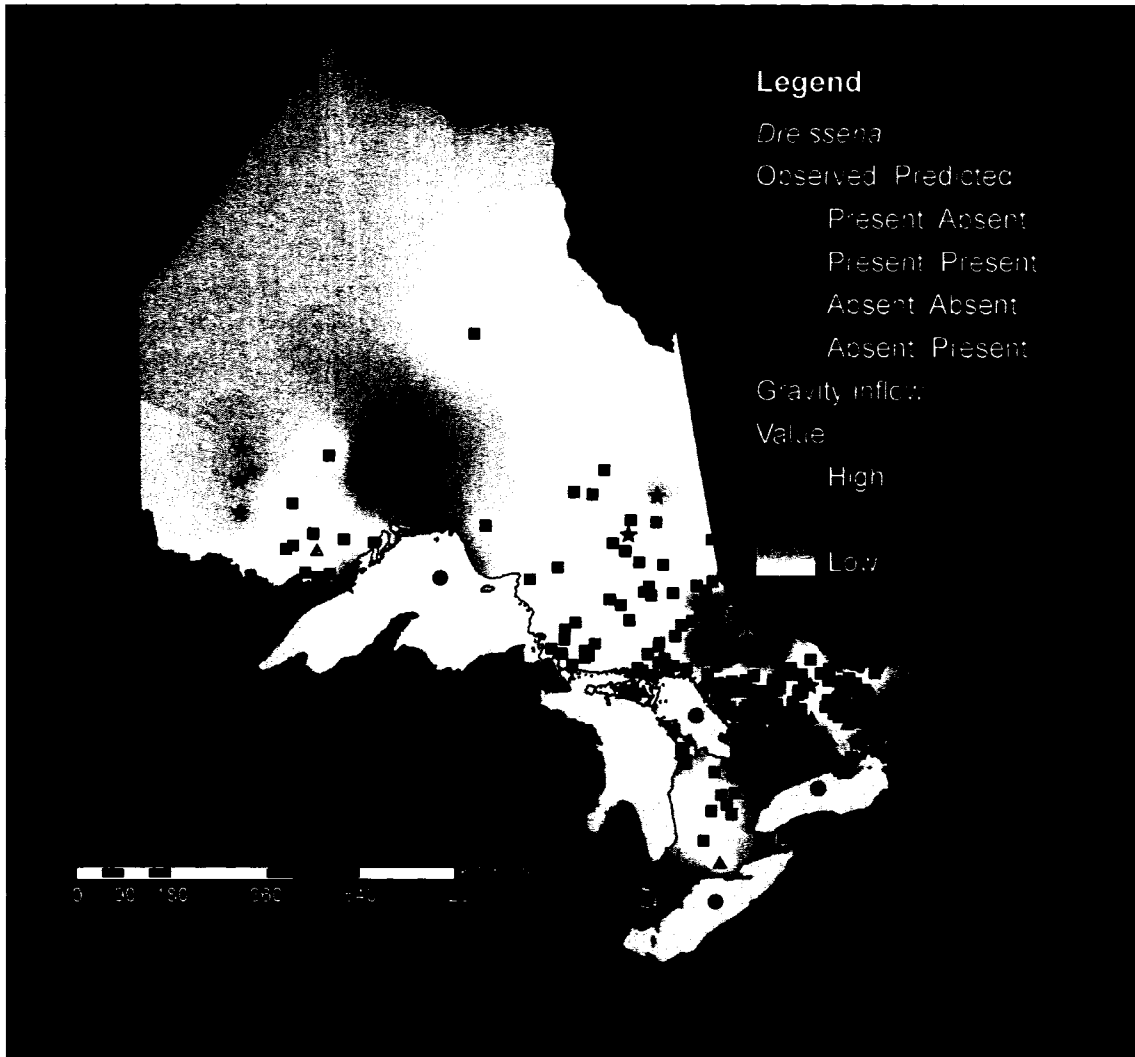
Figure 11. Spatial pattern of inbound propagule pressure with observed and predicted presence of *Dreissena* based only on gravity inflow.
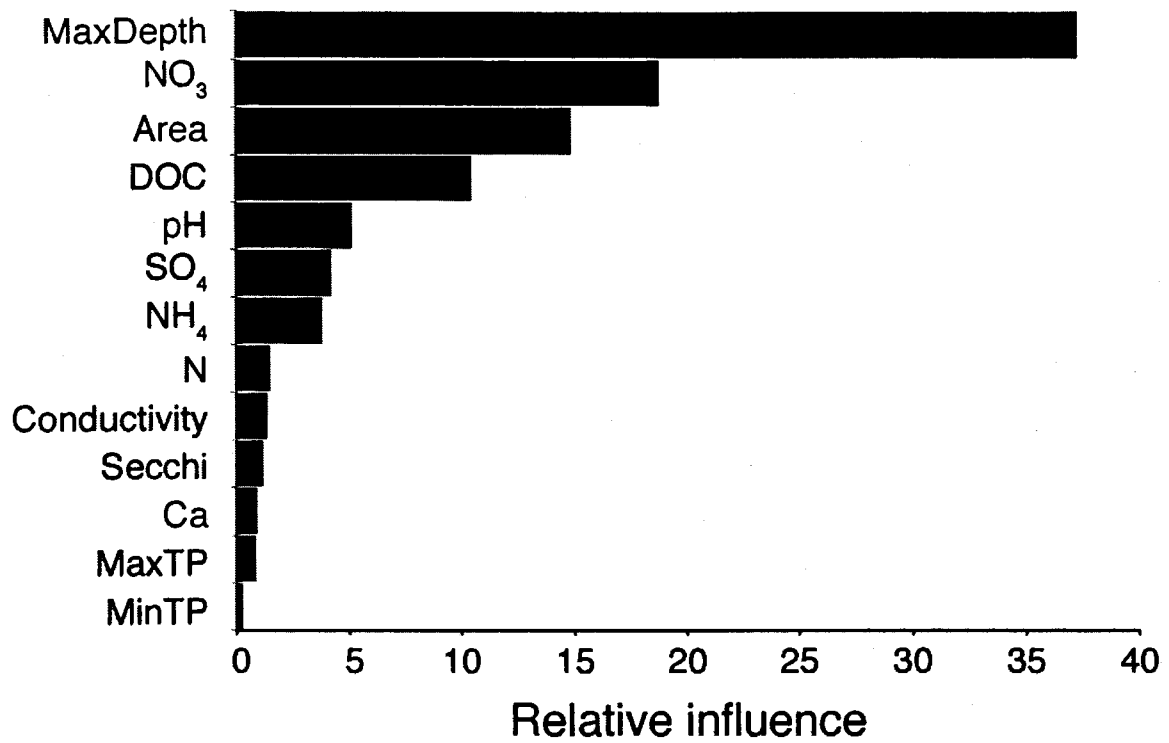
Figure 12. Influence of lake physicochemical properties related to *Bythotrephes* occurrence for lakes with high propagule pressure. Non-significant variables are not shown.

Figure 13. Marginal relationship between *Bythotrephes* occurrence and

physicochemical properties for lakes with high inbound propagule

pressure. The y-axes are scaled to log-odds of occurrence, and these

relationships are determined by integration of the regression trees.
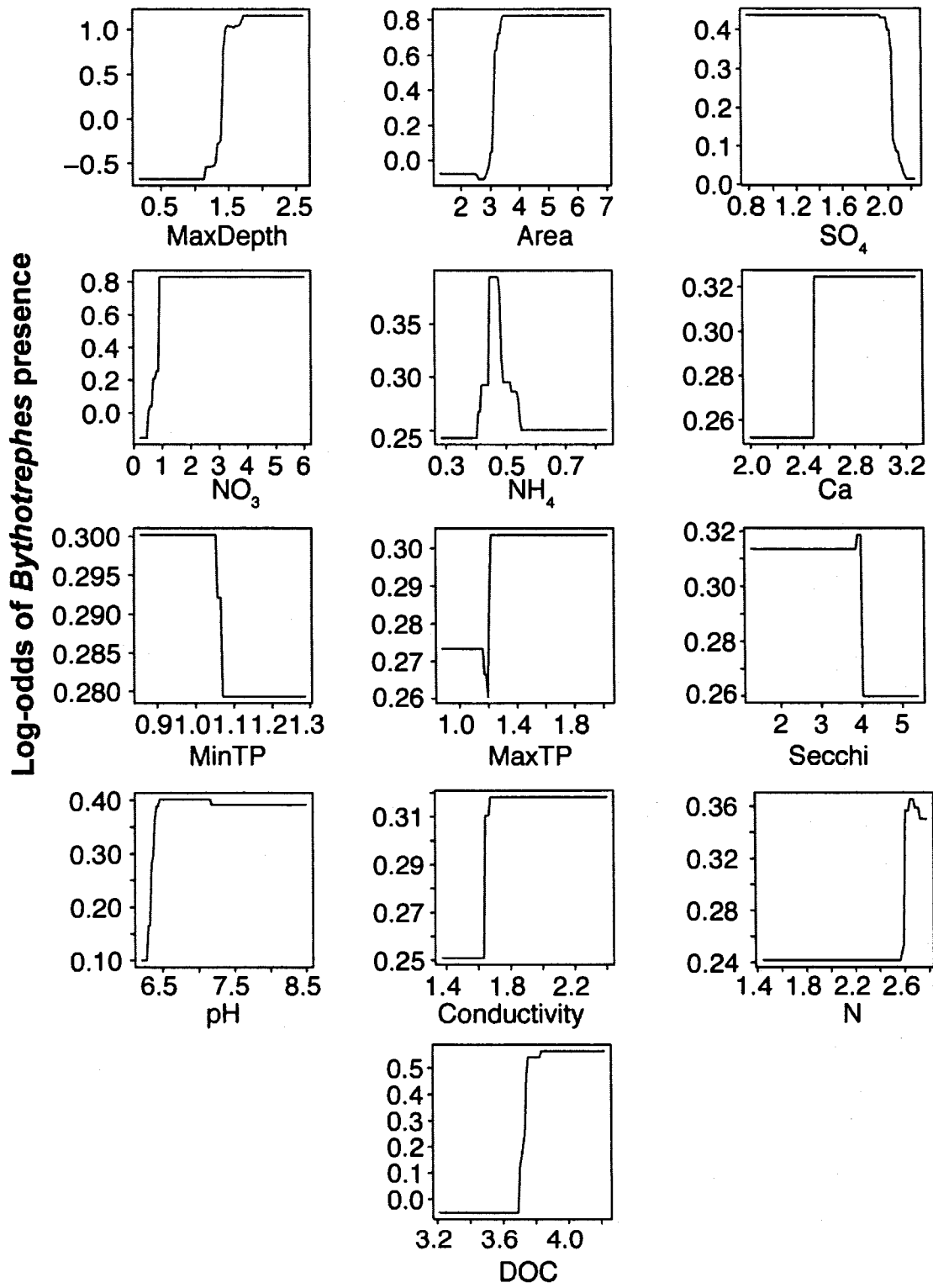
Figure 13.
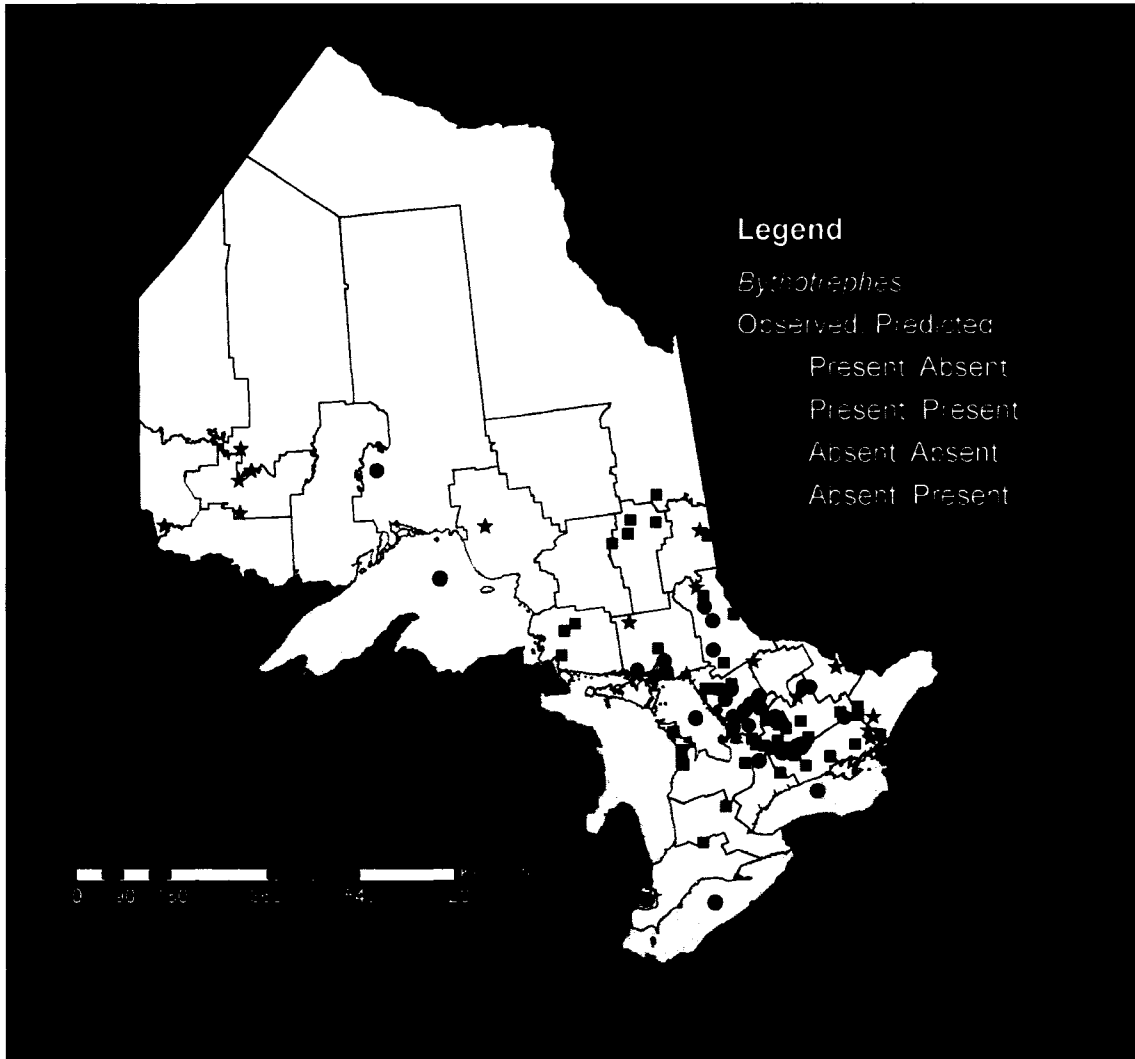
Figure 14. Classification of observed and predicted *Bythotrephes* presence and

absence in lakes with high inbound propagule pressure and suitable lake
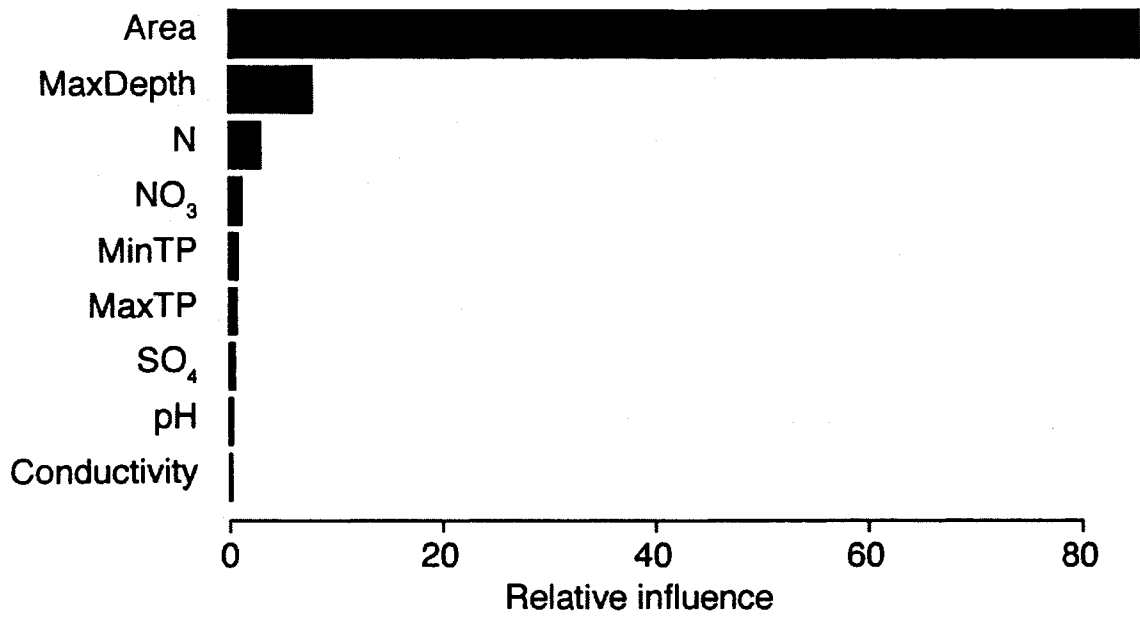
physicochemistry.

Figure 15. Influence of lake physicochemical properties on gravity inflow of *Bythotrephes.*
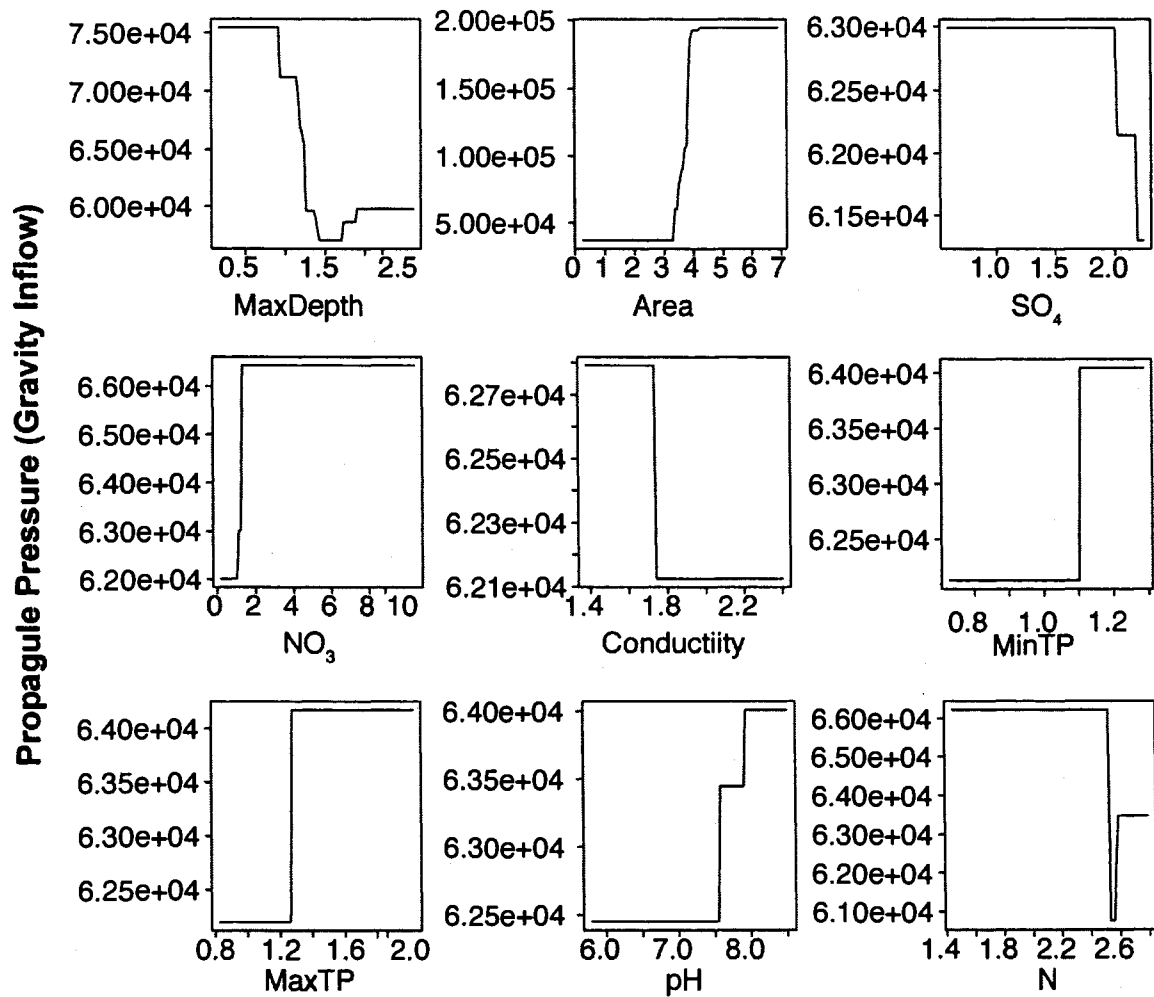
Figure 16. Marginal relationships between lake physicochemical properties and gravity inflow for *Bythotrephes*.
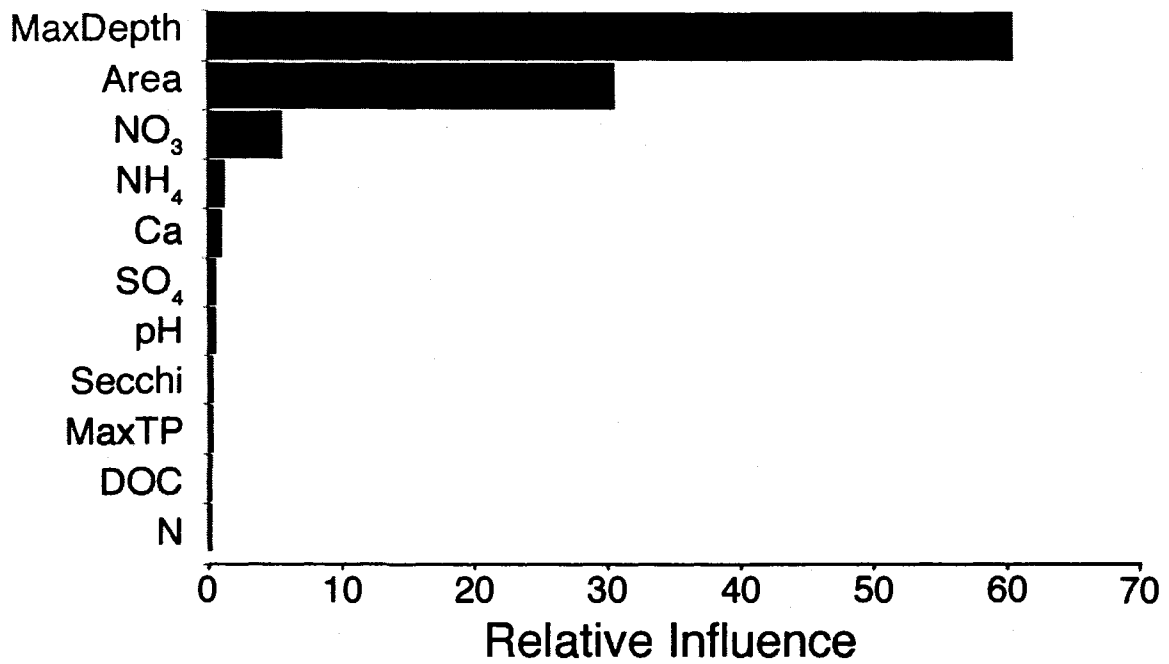
Figure 17. Influence of lake physicochemical properties related to *Dreissena* occurrence for lakes with high propagule pressure.

Figure 18. Marginal relationship between *Dreissena* occurrence and

physicochemical properties for lakes with high inbound propagule

pressure. The y-axes are scaled to log-odds of occurrence, and these

relationships are determined by integration of the regression trees.
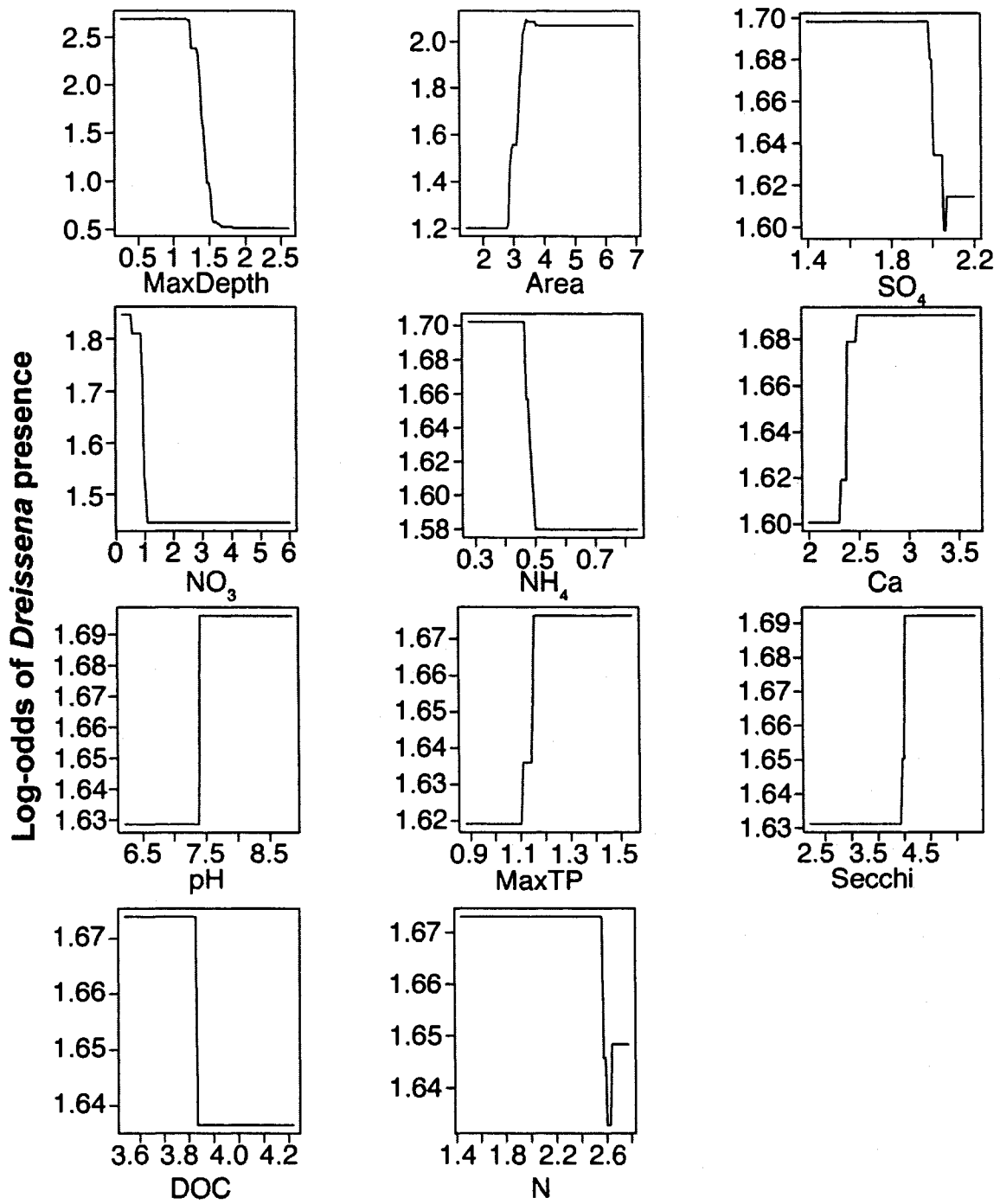
Figure 18.
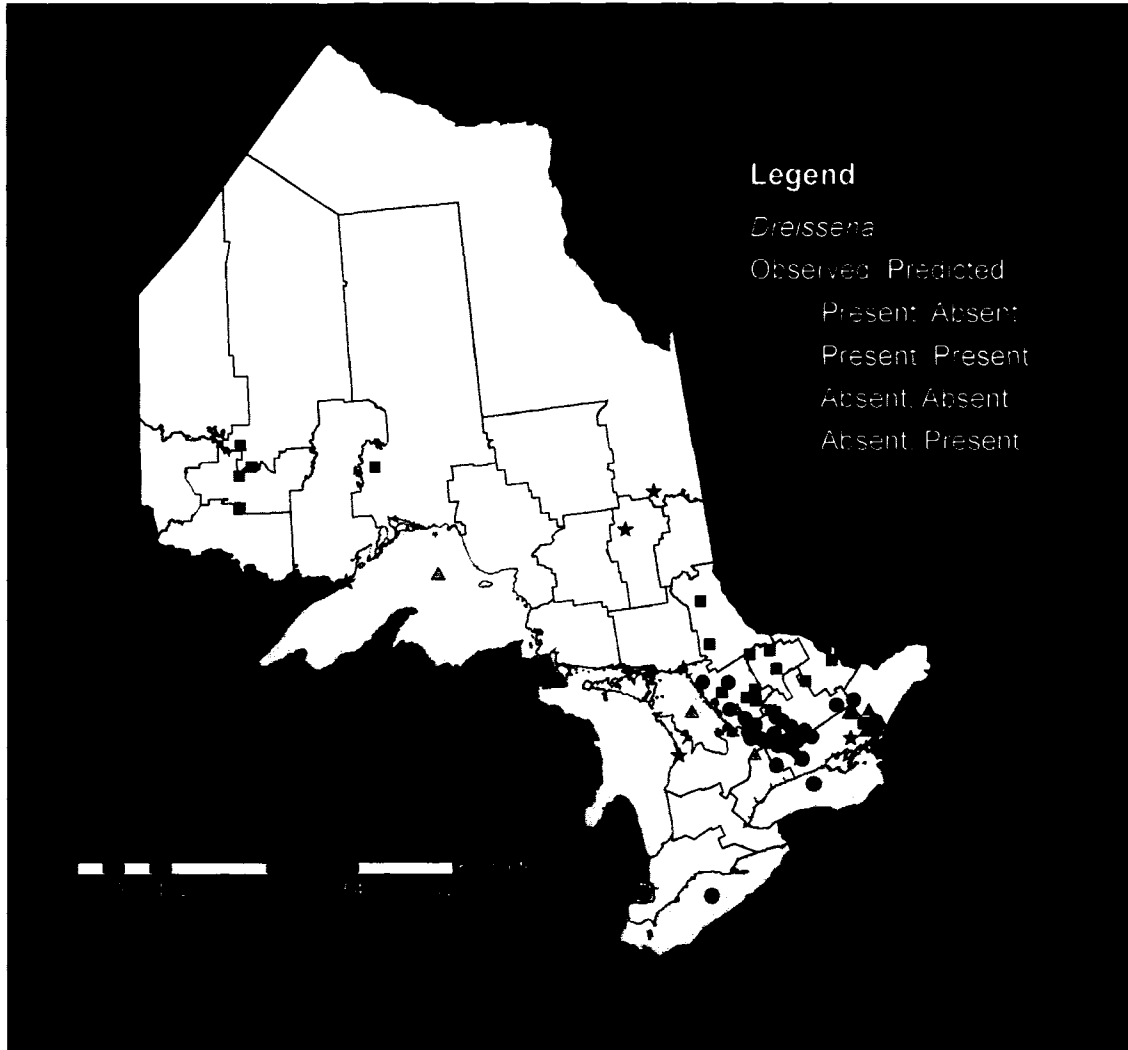
Figure 19. Classification of observed and predicted *Dreissena* presence and

absence based on lake physicochemistry for lakes with high inbound

propagule pressure.
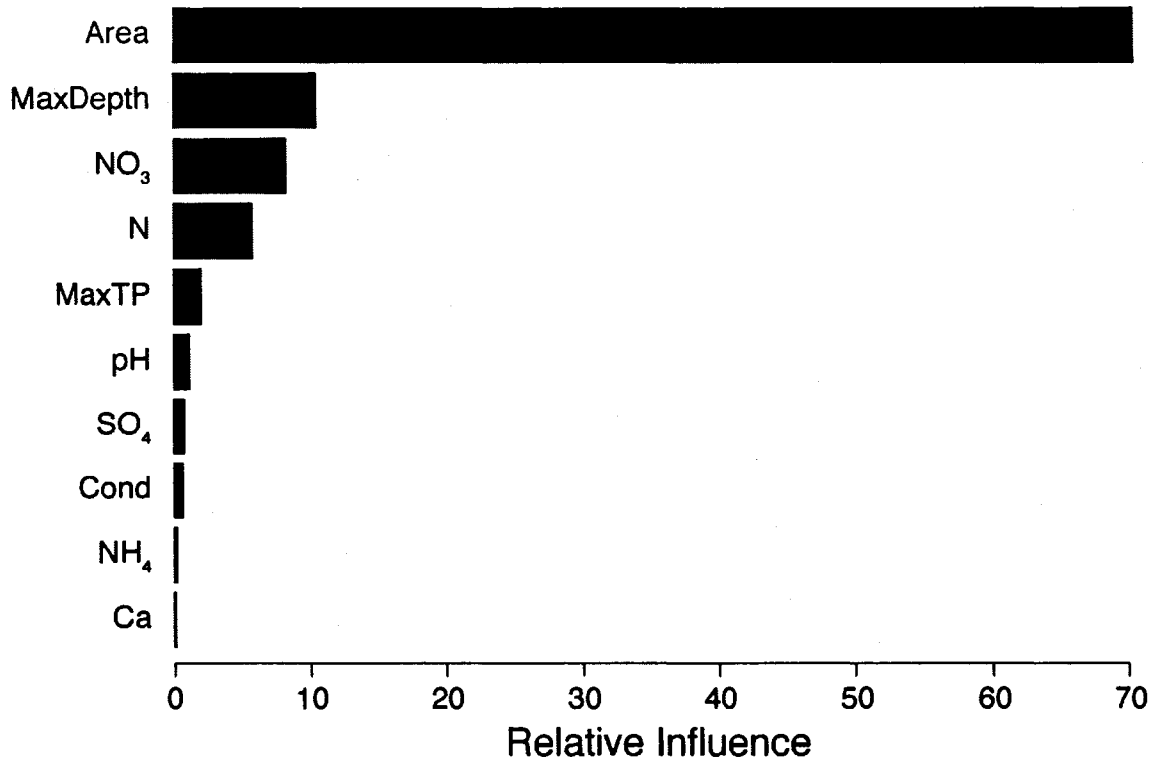
Figure 20. Influence of lake physicochemical properties on gravity inflow of

Dreissena.

Figure 21. Marginal relationships between lake physicochemical properties and

gravity inflow for *Dreissena*.

Figure 21.

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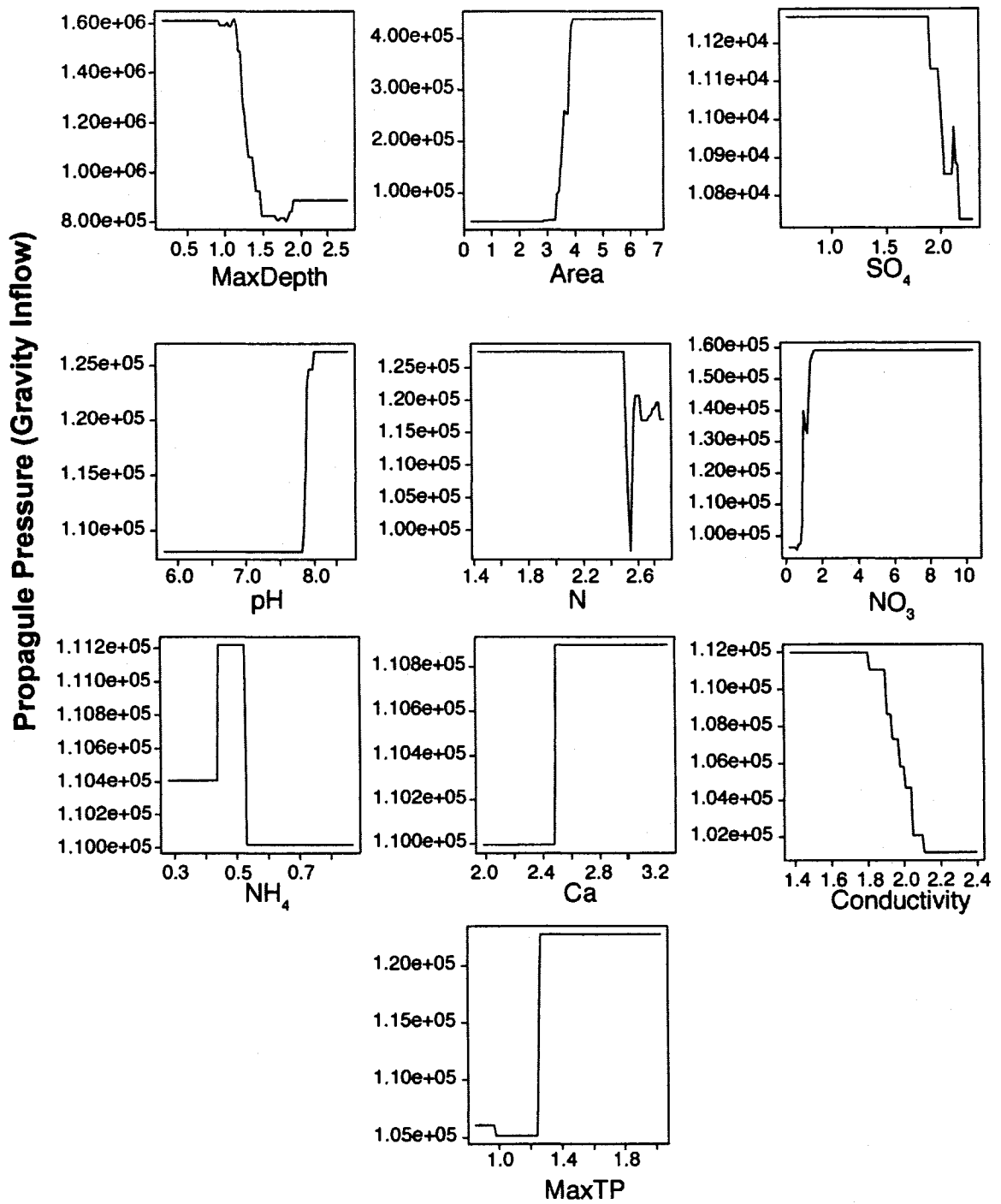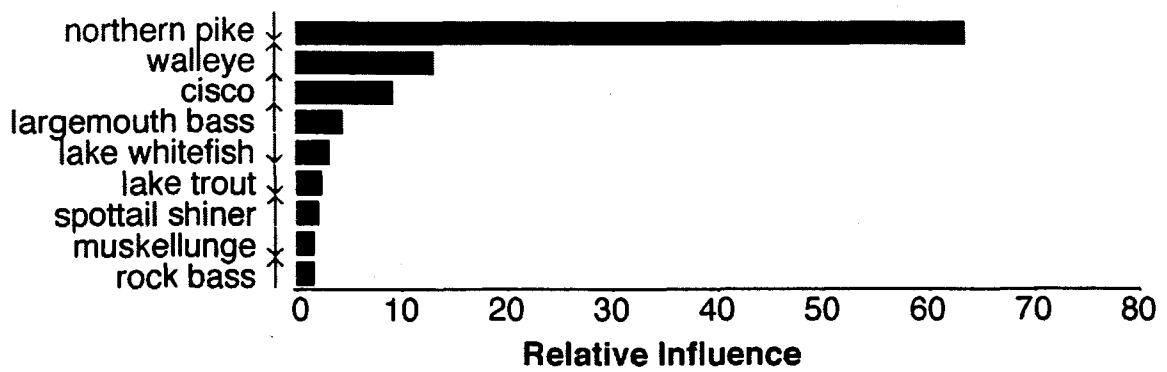
Figure 22. Influence of fish species related to *Bythotrephes* occurrence for lakes with high propagule pressure and suitable lake physicochemistry (Branch F). Upward facing arrows indicate positive relationship of each species to *Bythotrephes* occurrence and downward facing arrows indicate negative relationship.

Bythotrephes

Propagule Pressure (pp)
Observed

		0	1
Predicted	0	153	18
	1	60	42

low pp   high pp

n=171   n=102

Lake physicochemistry   Lake physicochemistry
Obs.   Obs.

		0	1
Pred.	0	128	5
	1	25	13

		0	1
Pred.	0	45	5
	1	15	37

unsuitable   suitable   unsuitable   suitable
water   water   water   water
chemistry   chemistry chemistry   chemistry
n=133   n=38   n=50   n=52

Fish   Fish   Fish   Fish
Assemblage   Assemblage   Assemblage   Assemblage
Obs.   Obs.   Obs.   Obs.

		0	1
Pred.	0	120	4
	1	8	1

		0	1
Pred.	0	23	7
	1	2	6

		0	1
Pred.	0	42	1
	1	3	4

		0	1
Pred.	0	8	3
	1	7	34

Figure 23. Hierarchical classification of lakes where *Bythotrephes* is predicted

and observed to have invaded.

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Figure 24. Classification of observed and predicted *Bythotrephes* presence and absence in lakes with high inbound propagule pressure and suitable lake physicochemistry based on fish community composition (Figure 2 Branch F).

Figure 25. Redundancy analysis biplot for the relationship between lake

characteristics and fish community composition for lakes used in the A)

Bythotrephes and B) *Dreissena* hierarchical models. The inserts in the

corner are enlargements of the main plots.

Figure 25.

Dreissena

Propagule Pressure (pp)
Observed

	0	1
Predicted 0	189	28
1	27	47

low pp   high pp

n=217   n=74

Lake physiochemistry
Obs.

	0	1
Pred. 0	169	2
1	20	26

unsuitable water chemistry n=171   suitable water chemistry n=46

Lake physiochemistry
Obs.

	0	1
Pred. 0	20	13
1	7	34

unsuitable water chemistry n=33   suitable water chemistry n=41

Fish Assemblage
Obs.

	0	1
Pred. 0	169	0
1	0	2

Fish Assemblage
Obs.

	0	1
Pred. 0	15	7
1	5	19

Fish Assemblage
Obs.

	0	1
Pred. 0	20	0
1	0	13

Fish Assemblage
Obs.

	0	1
Pred. 0	5	13
1	2	21

Figure 26. Hierarchical classification of lakes predicted to be invaded by

Dreissena. Classification based on the composition of the fish community

is shown for completeness although the model was nonsignificant in

predicting invasion status.

Hierarchical   Single model

Bythotrephes

Obs.
0 | 1

Pred.
0 | 206 | 26
1 | 7 | 34

Obs.
0 | 1

Pred.
0 | 177 | 6
1 | 36 | 54

AUC=0.82, P<0.0001   AUC=0.90, P<0.0001

Dreissena

Obs.
0 | 1

Pred.
0 | 209 | 41
1 | 7 | 34

Obs.
0 | 1

Pred.
0 | 206 | 3
1 | 10 | 72

AUC=0.78, P<0.0001   AUC=0.99, P<0.0001

Figure 27. Overall classification tables and model performance of hierarchical vs.

single modelling approaches for *Bythotrephes* and *Dreissena*.
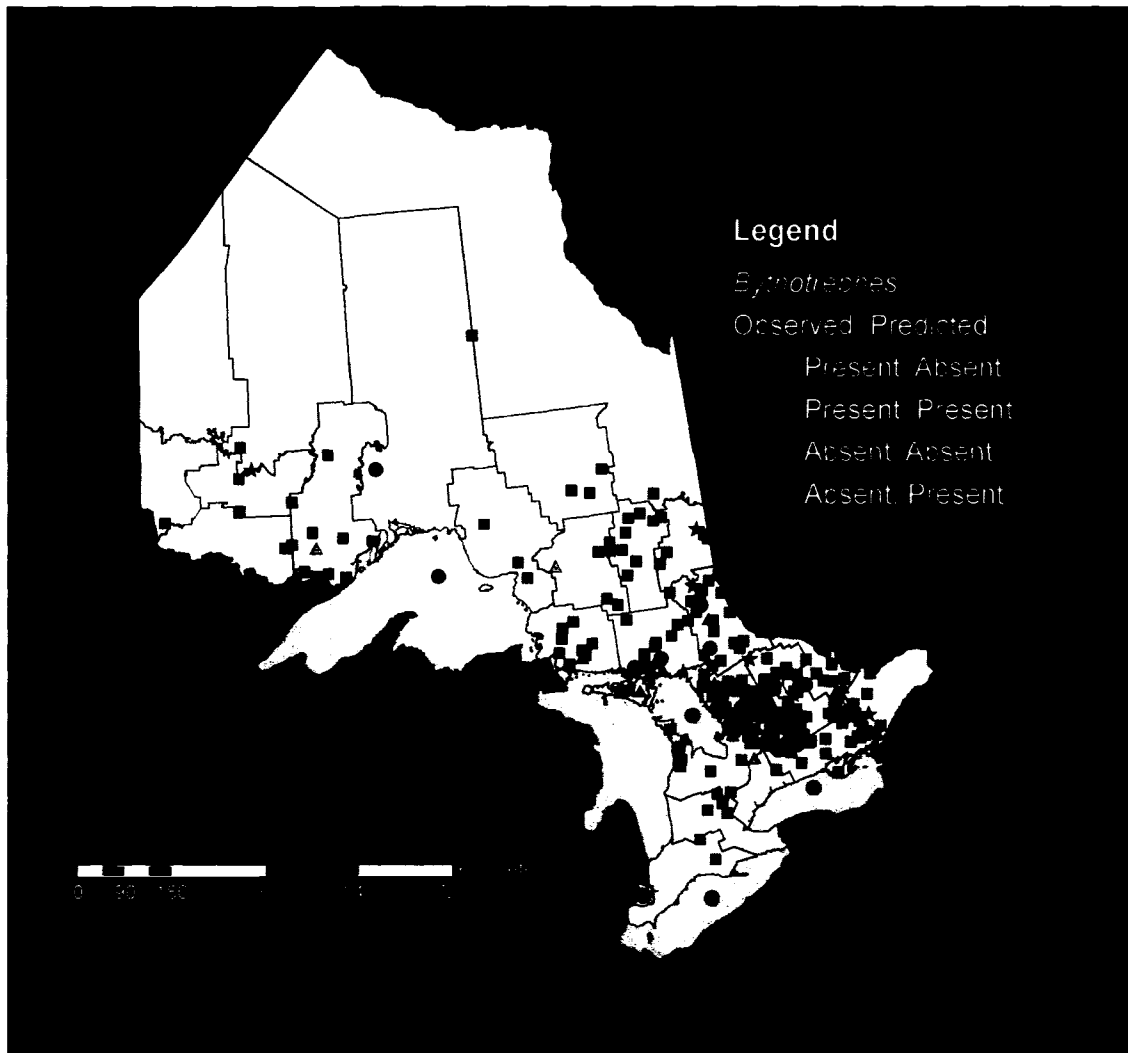
Figure 28. Spatial pattern of lakes where *Bythotrephes* is observed or predicted

to be established based on all three stages of the invasion sequence

(High propagule pressure, suitable lake physicochemistry (Branch B),

biotic integration (Branch F).
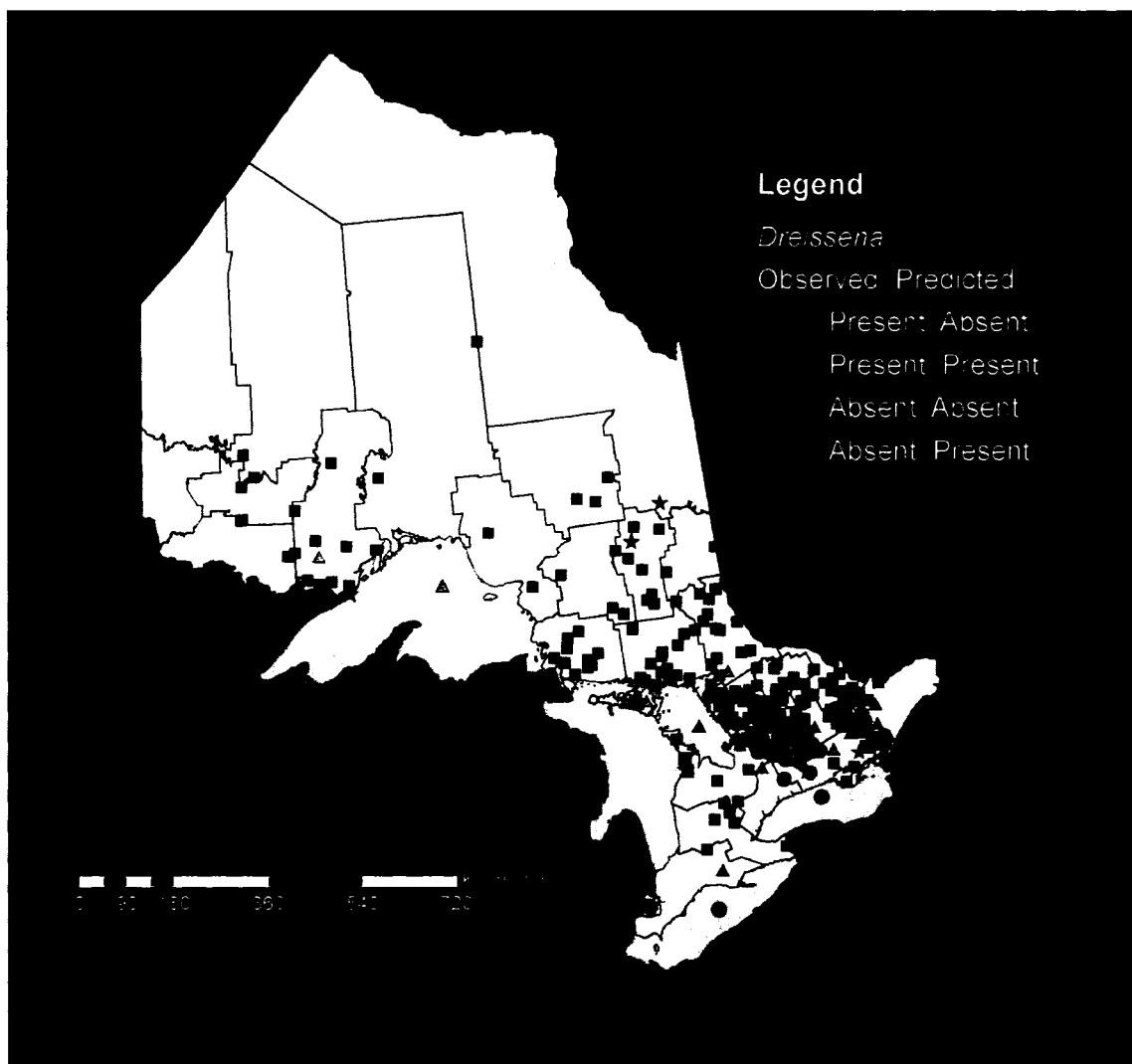
Figure 29. Spatial pattern of lakes where *Dreissena* is observed or predicted to

be established based on the first two stages of the invasion sequence

(High propagule pressure, suitable lake physicochemistry (Branch B)).
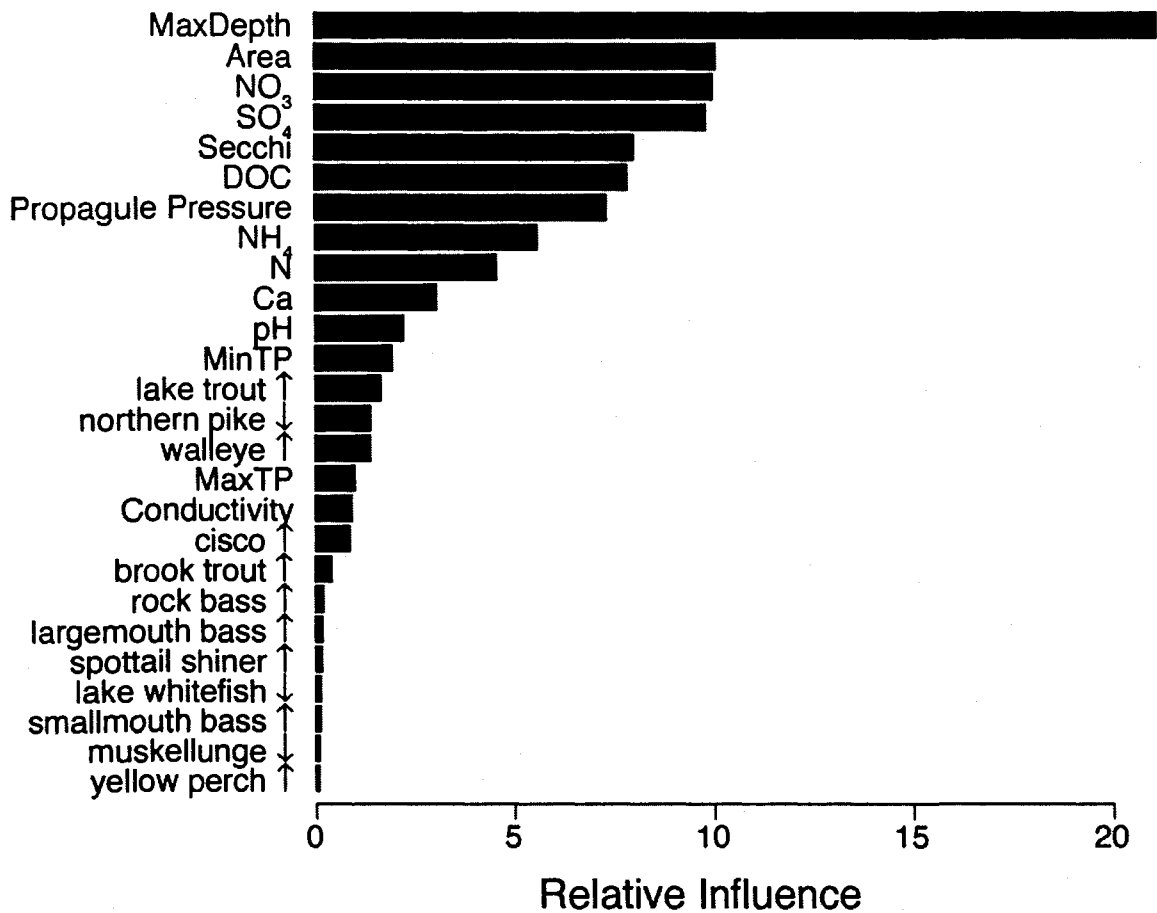
Figure 30. Influence of propagule pressure, lake physicochemical properties and

fish community composition related to *Bythotrephes* occurrence in the

boosted regression model of all parameters combined. Arrows next to fish

species indicate direction of correlation.

Figure 31. Relationships between *Bythotrephes* presence/absence and variables in the boosted regression model of all variables combined. The y-axes are scaled to log-odds of occurrence, and these relationships are determined by integration of the regression trees.

Figure 31.

Figure 32. Influence of gravity inflow, lake physicochemical properties and fish community composition related to *Dreissena* occurrence in the boosted regression model of all parameters combined. Arrows next to fish species indicate direction of correlation.

Figure 33. Relationships between *Dreissena* presence/absence and variables in

the boosted regression model of all variables combined. The y-axes are

scaled to log-odds of occurrence, and these relationships are determined

by integration of the regression trees.
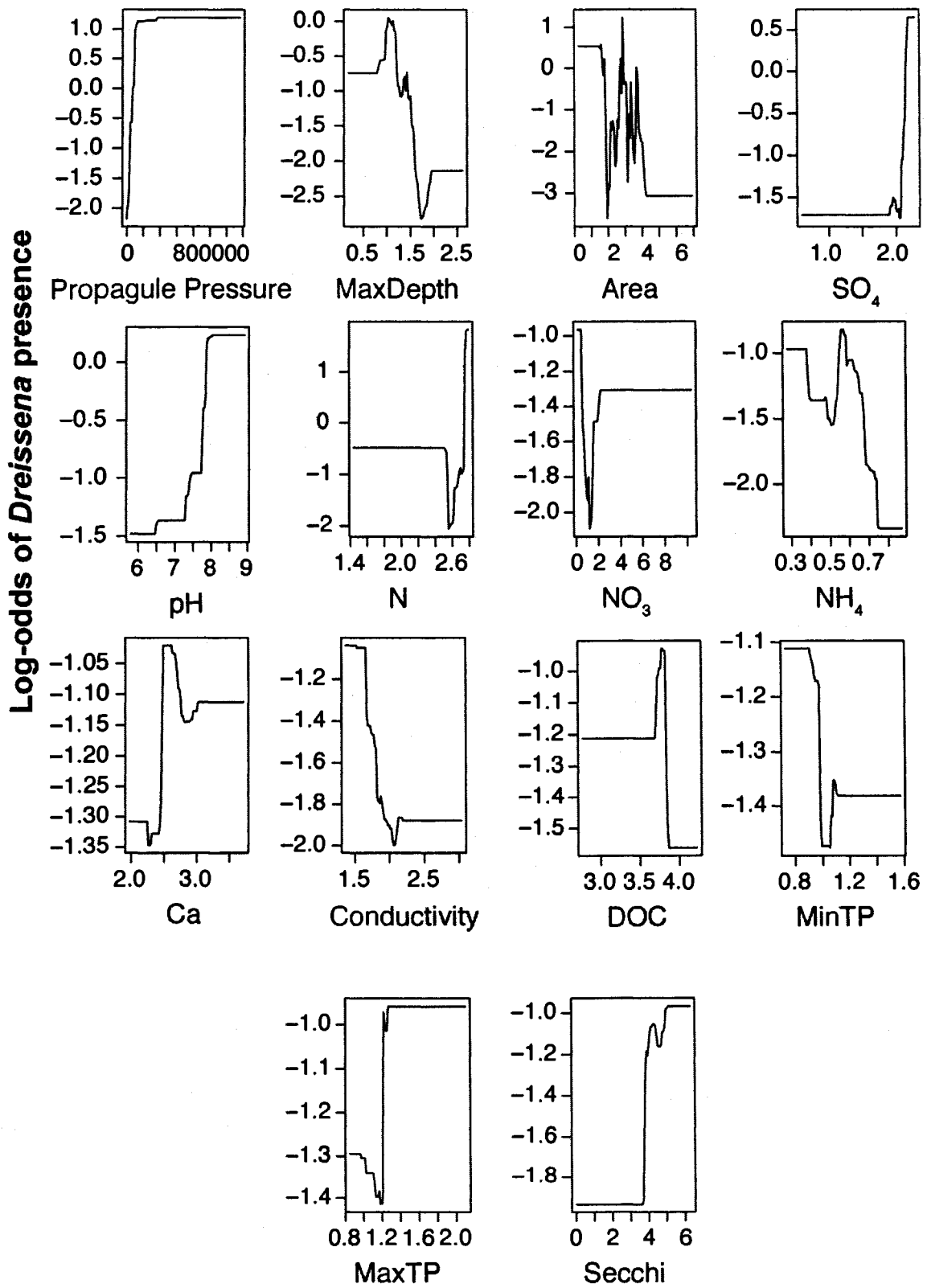
Figure 33.
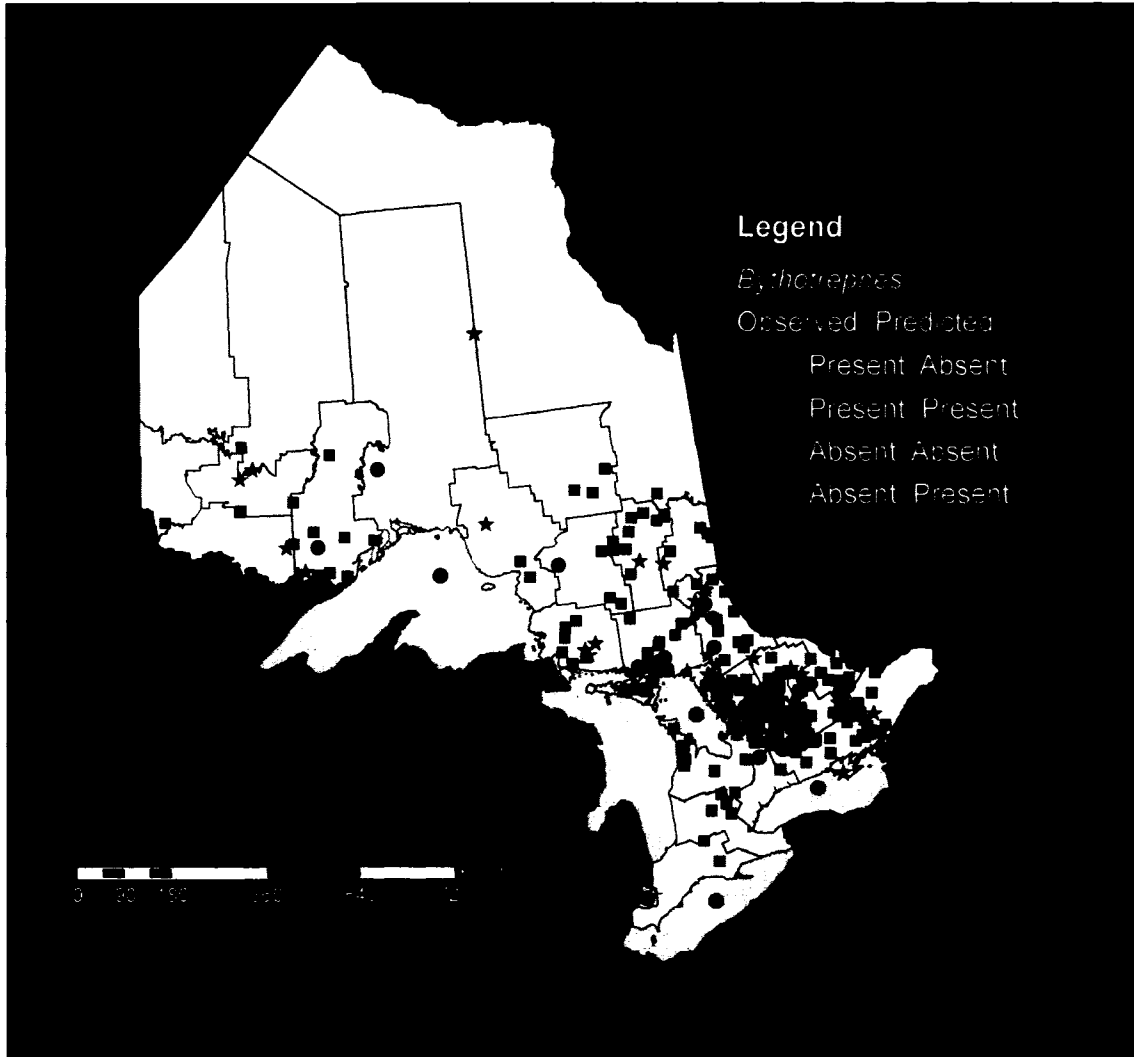
Figure 34. Spatial pattern of lakes where *Bythotrephes* is observed or predicted to occur based on the single model.
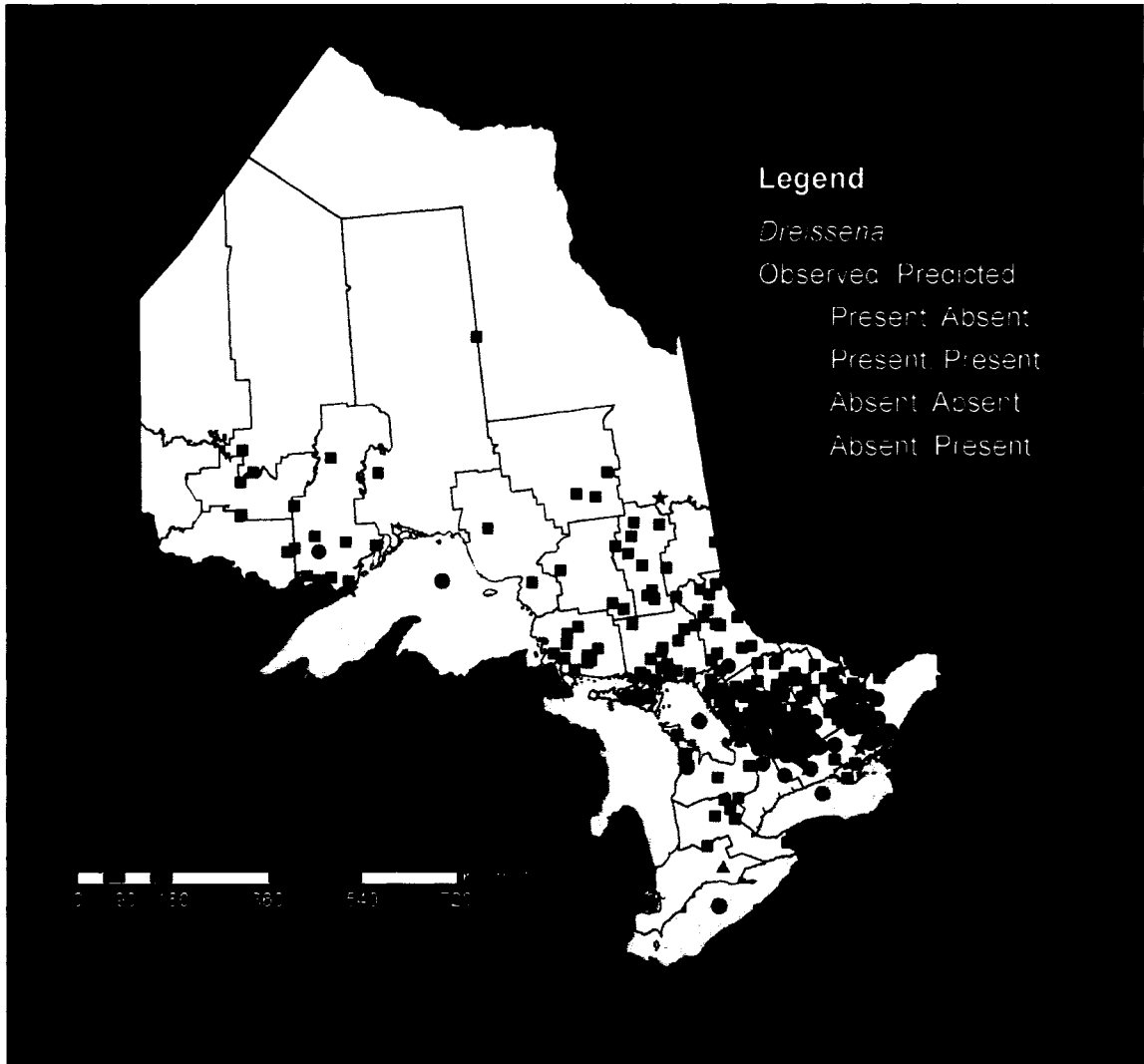
Figure 35. Spatial pattern of lakes where *Dreissena* is observed or predicted to occur based on the single model.

Appendix

Results of the boosted regressions for branches (A,C,D and E) in the hierarchical classification tree.

Lake morphometry and physicochemistry

<u>Bythotrephes</u>

For lakes receiving low levels of propagule pressure (Figure 2 Branch A), nitrogen concentration, maximum lake depth, lake area and minimum annual total phosphorus concentration were the four most influential variables related to *Bythotrephes* presence, accounting for 73% in error reduction (Figure A1). The likelihood of *Bythotrephes* occurrence was positively associated with all four variables and increased rapidly for lakes with a total N concentration of 400 µg L^{-1} or greater, maximum depth of 25 m, lake area of 1000 ha, and minimum annual total phosphorus concentration of 9 µg L^{-1} (Figure A2). The model at this stage of the invasion sequence predicted *Bythotrephes* establishment significantly better than random (AUC=0.88, $P<0.0001$). With a probability threshold of 0.49, this model correctly classified 88% of invaded lakes and 75% of noninvaded lakes.

<u>Dreissena</u>

The set of lakes with low inbound propagule pressure required nearly 17 times as many iterations as lakes with high propagule pressure, and thus fit the relationship between establishment success and environmental characteristics much more closely. Lake depth and area accounted for 42% of the error reduction in lakes with low propagule pressure (Figure A3). In lakes with low

propagule pressure (Figure 2, Branch A), the probability of invasion increases to a maximum at 10m depth and drops to a minimum for lakes 56m or deeper. High probabilities of Dreissena invasion were associated to lakes with area ranging from 32 to 100 ha, and then from 630 to 1585 ha. Total N and NH_4 were the most influential chemical characteristics of the lakes that received low levels of vector traffic (25% influence in error reduction). The likelihood of Dreissena presence increased for lakes with N concentration of 398 µeq L^{-1} and after reaching a minimum at NH_4 concentrations at 2.8 µeq L^{-1} or greater (Figure A4).

Fish community composition

Bythotrephes

In the sequence of models predicting Bythotrephes establishment in lakes with low levels of inbound propagule pressure, both the relative importance and direction of the relationship of fish species and establishment success differed between the sets of lakes with suitable and unsuitable physicochemistry. In lakes with low propagule pressure and unsuitable physicochemistry, lake trout, lake whitefish, smallmouth bass and brook trout were all positively related to the likelihood of Bythotrephes establishment (Figure A5 Panel A). Lake trout was the most important predictor, accounting for greater than 77% of the error reduction. This boosted regression model, however, did not predict Bythotrephes establishment significantly better than random (AUC=0.63, P=0.16) and was only able to correctly predict 20% of invaded lakes despite being able to classify 91% of lakes correctly overall (Table 4, Figure 23).

The four fish species most strongly related to *Bythotrephes* establishment in lakes with suitable characteristics were northern pike, cisco, lake whitefish and lake trout, accounting for > 81% of error reduction (Figure A5). Northern pike and lake trout were negatively related to *Bythotrephes* presence, and the other two species were positively related. This model predicted *Bythotrephes* establishment significantly better than random (AUC=0.70, P=0.02) and was only able to correctly predict less than 50% of lakes currently invaded.

The relationship between the dominant fish species and *Bythotrephes* establishment in lakes with high propagule pressure and unsuitable lake physicochemistry was similar to lakes with low inbound propagule pressure. Cisco was the strongest predictor (39% error reduction) and was positively related to *Bythotrephes* presence (Figure A5 C). Lake trout and walleye were also positively related, and northern pike was negatively correlated with *Bythotrephes*. The model for this branch of the hierarchical classification was the most significant of the fish community components (AUC=0.94, P=7.6e-4), and was able to predict the 4 out of 5 invaded lakes.

Dreissena

The direction and magnitude of the relationships between fish species and *Dreissena* establishment differed among the sets of lakes segregated by the inflow of propagule pressure and environmental characteristics. In lakes with low propagule pressure and unsuitable water chemistry, largemouth bass, mimic shiner and smallmouth bass were the most influential species in predicting establishment, accounting for approximately 80% of the variability (Figure A5

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Panel A). The largemouth bass and mimic shiner were positively related and smallmouth bass was negatively correlated with *Dreissena* establishment. This model was highly significant as the 171 lakes in this subset were all correctly classified as either present or absent (Figure 27).

Walleye, northern pike, rock bass and lake trout were the four dominant species related to *Dreissena* establishment in lakes with suitable lake physiochemistry, with walleye and northern pike positively related to *Dreissena* presence. In lakes with high levels of propagule pressure and unsuitable environmental conditions, the four most influential species – largemouth bass, black crappie, blacknose shiner and rock bass – were all positively related to *Dreissena* (Figure A6).
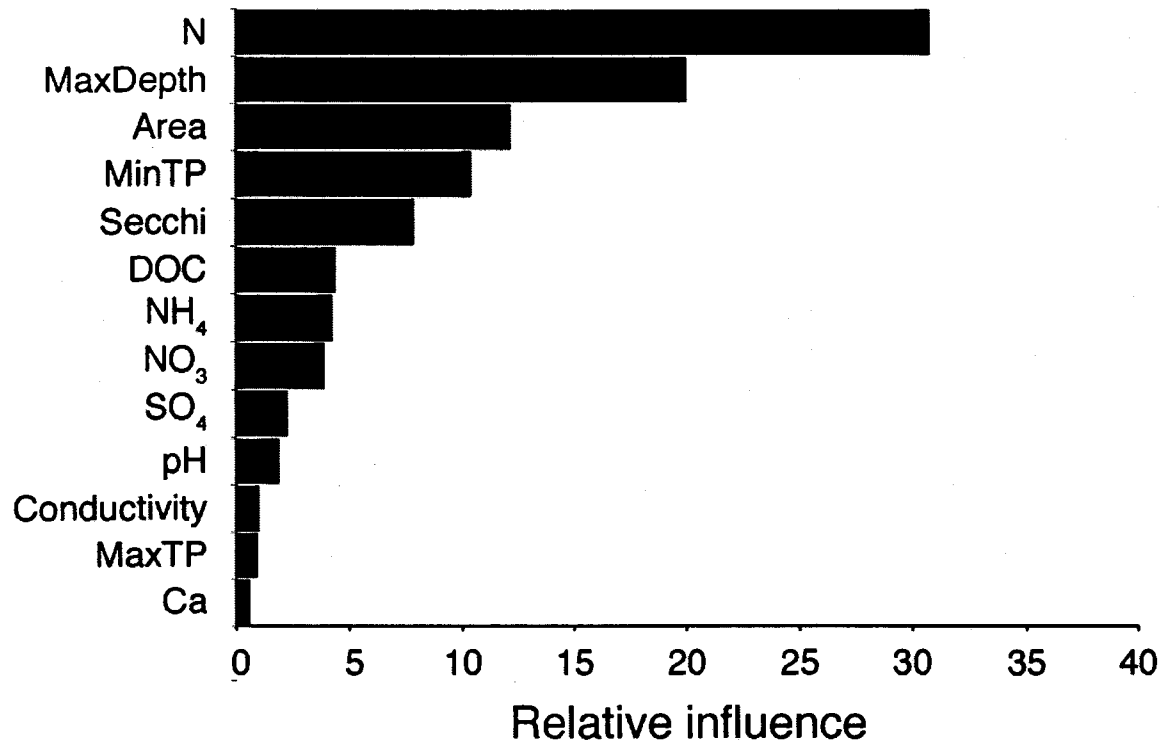
Figure A1. Influence of lake physicochemical properties related to *Bythotrephes* establishment for lakes with low propagule pressure. Non-significant variables are not shown.

Figure A2. Marginal relationships between *Bythotrephes* establishment and lake

physicochemical properties for lakes with low inbound propagule pressure.

The y-axes are scaled to log-odds of establishment, and these

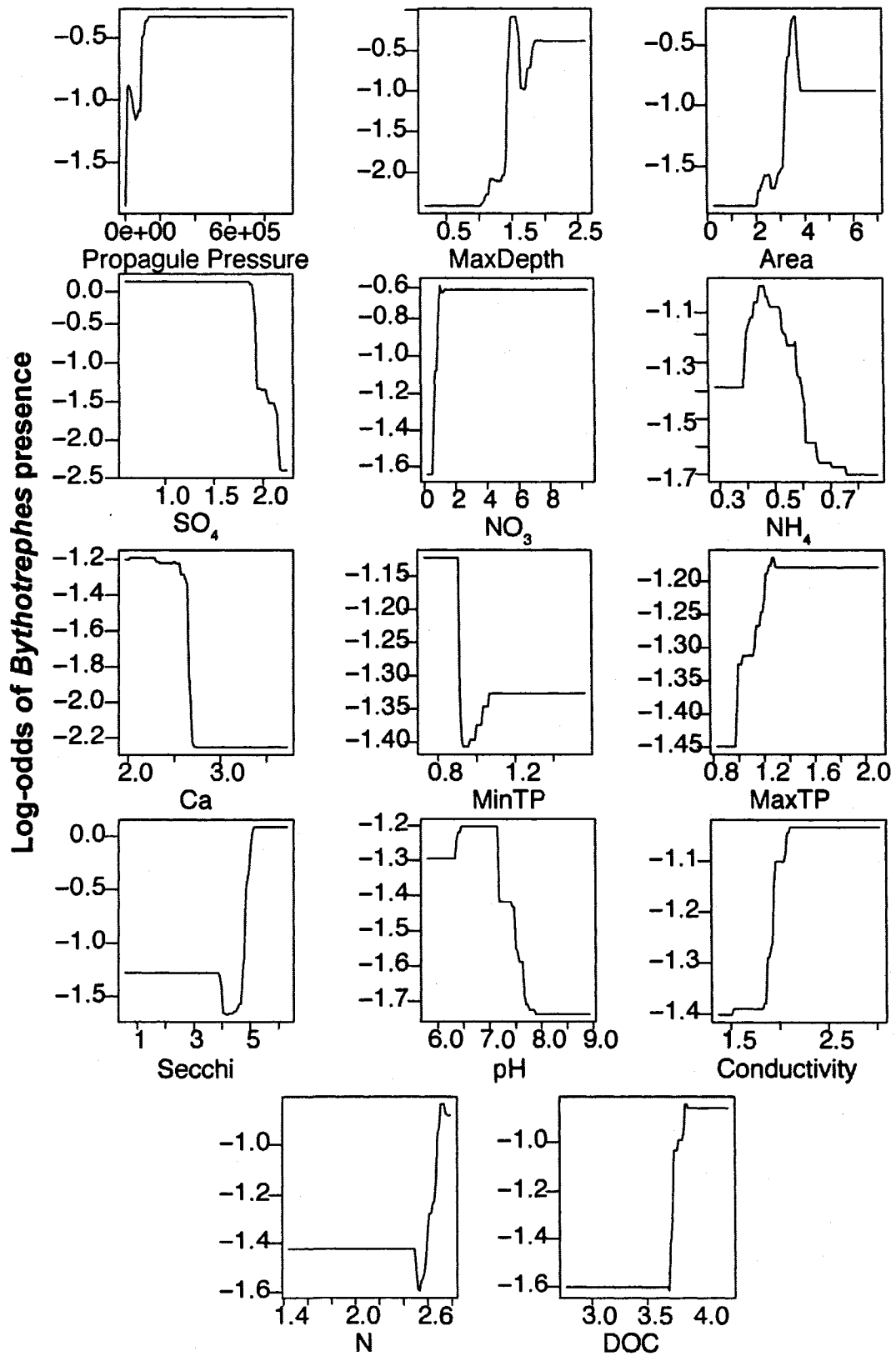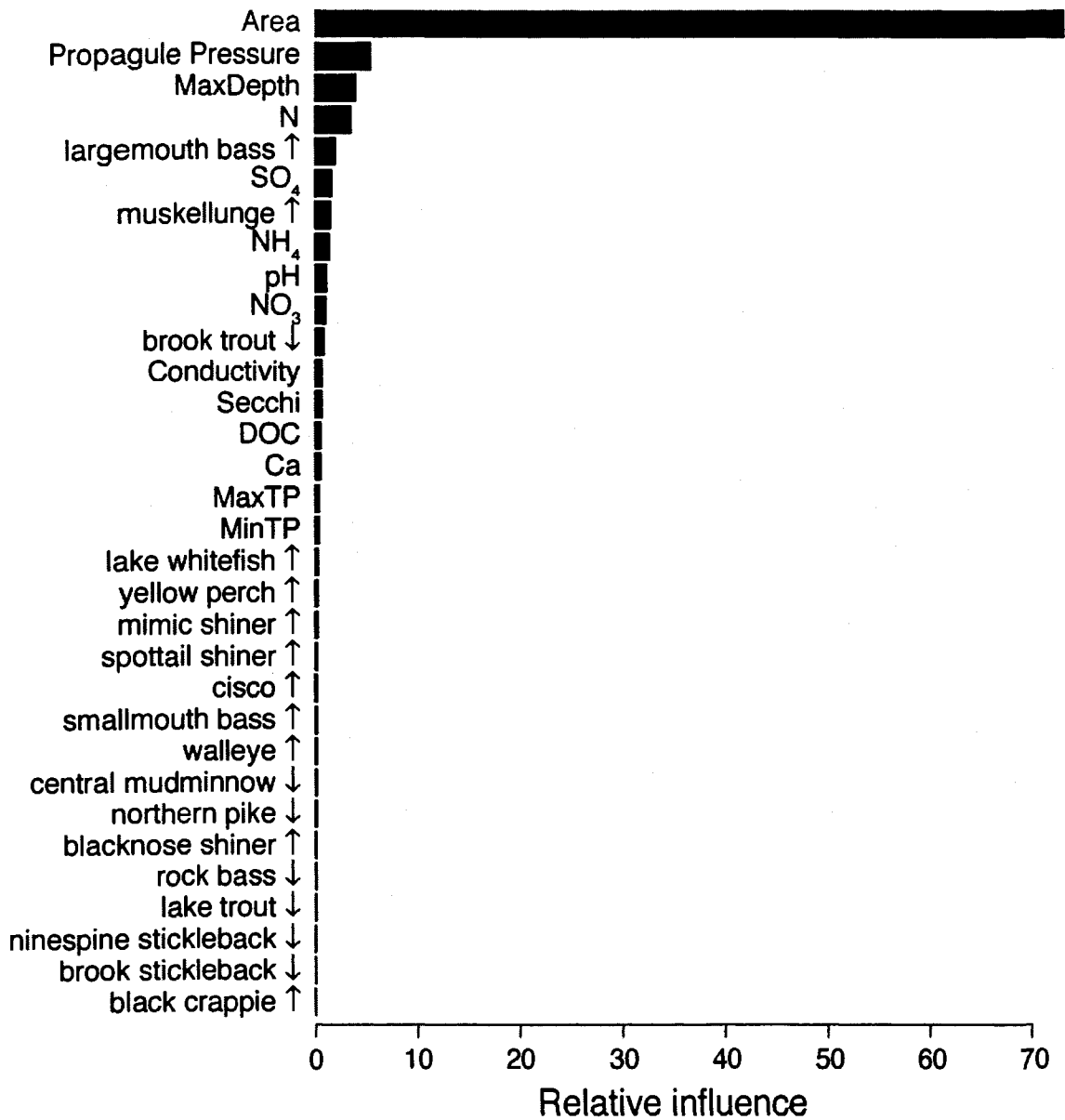relationships are determined by integration of the regression trees.
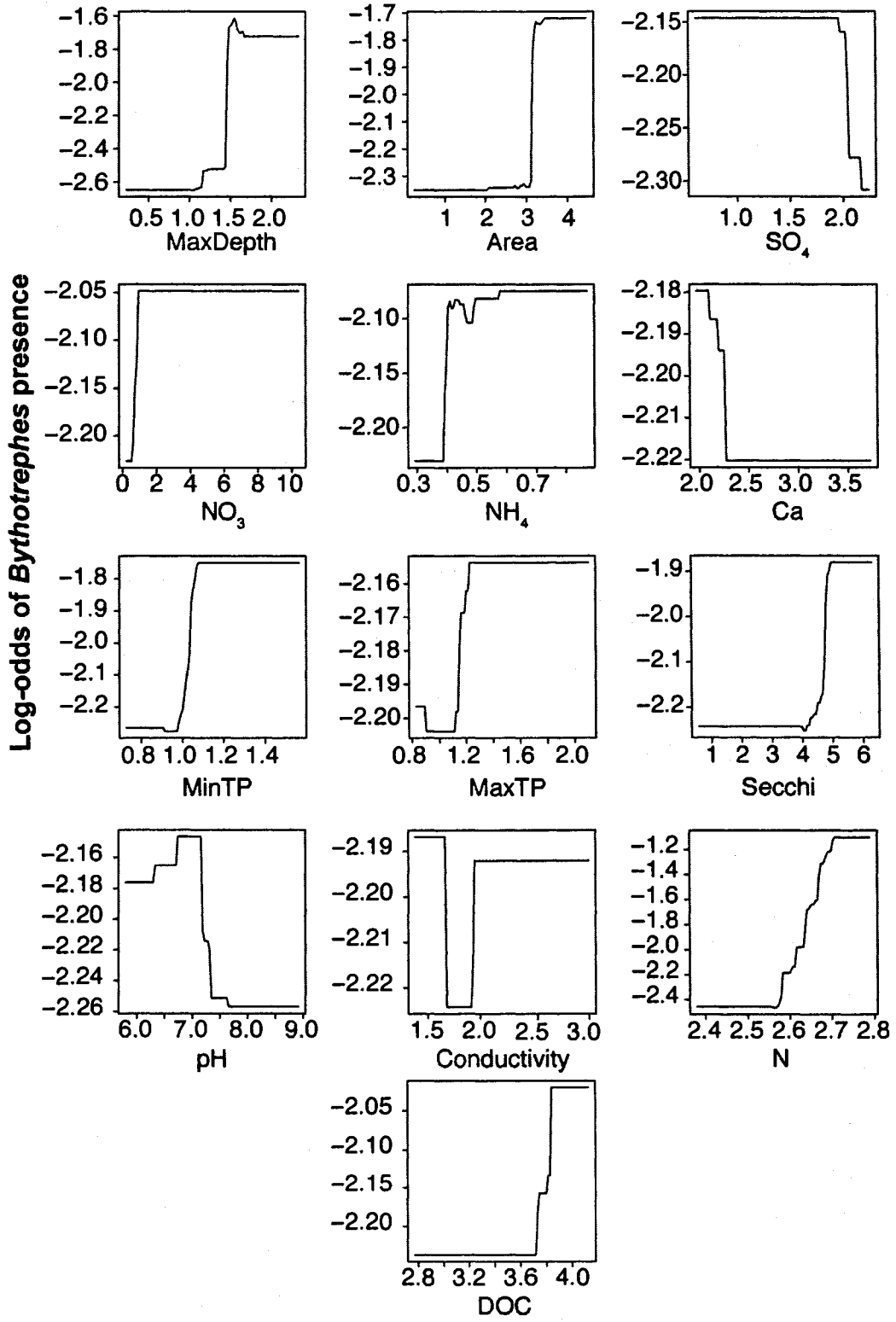
Figure A2.
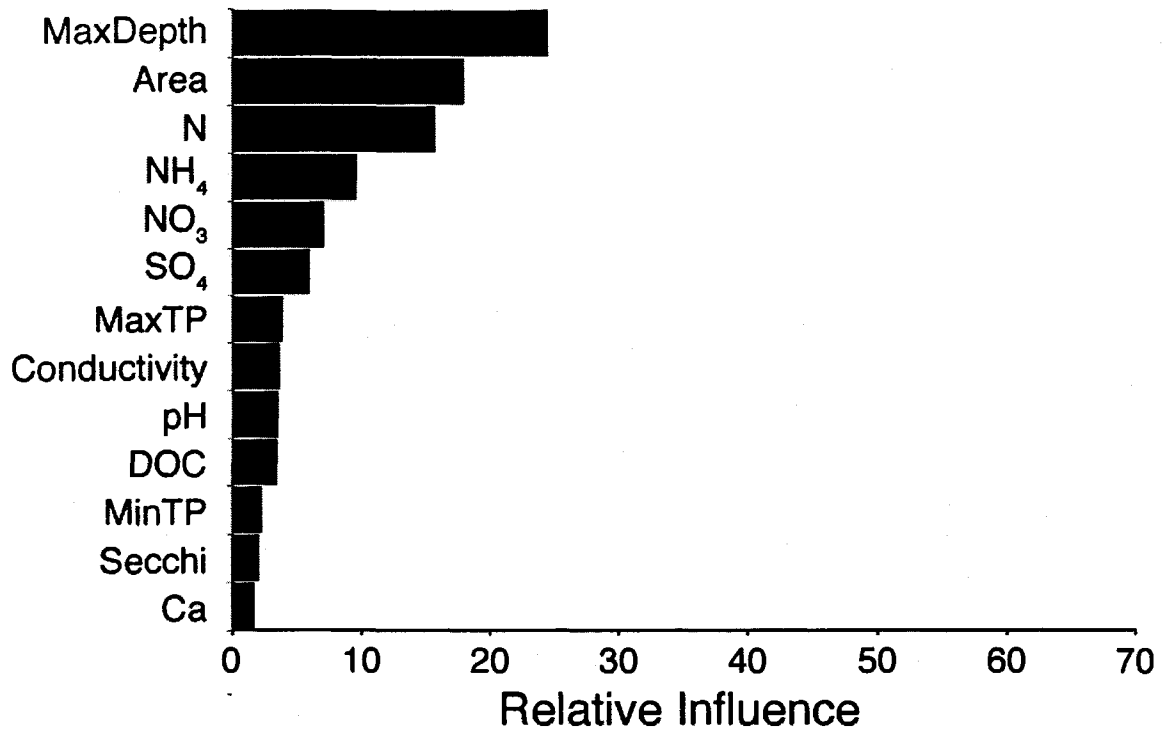
Figure A3. Influence of lake physicochemical properties related to *Bythotrephes* establishment for lakes with low propagule pressure. Non-significant variables are not shown.

Figure A4. Marginal relationship between *Dreissena* establishment and lake

physicochemical properties for lakes with low inbound propagule pressure.

Figure A4.

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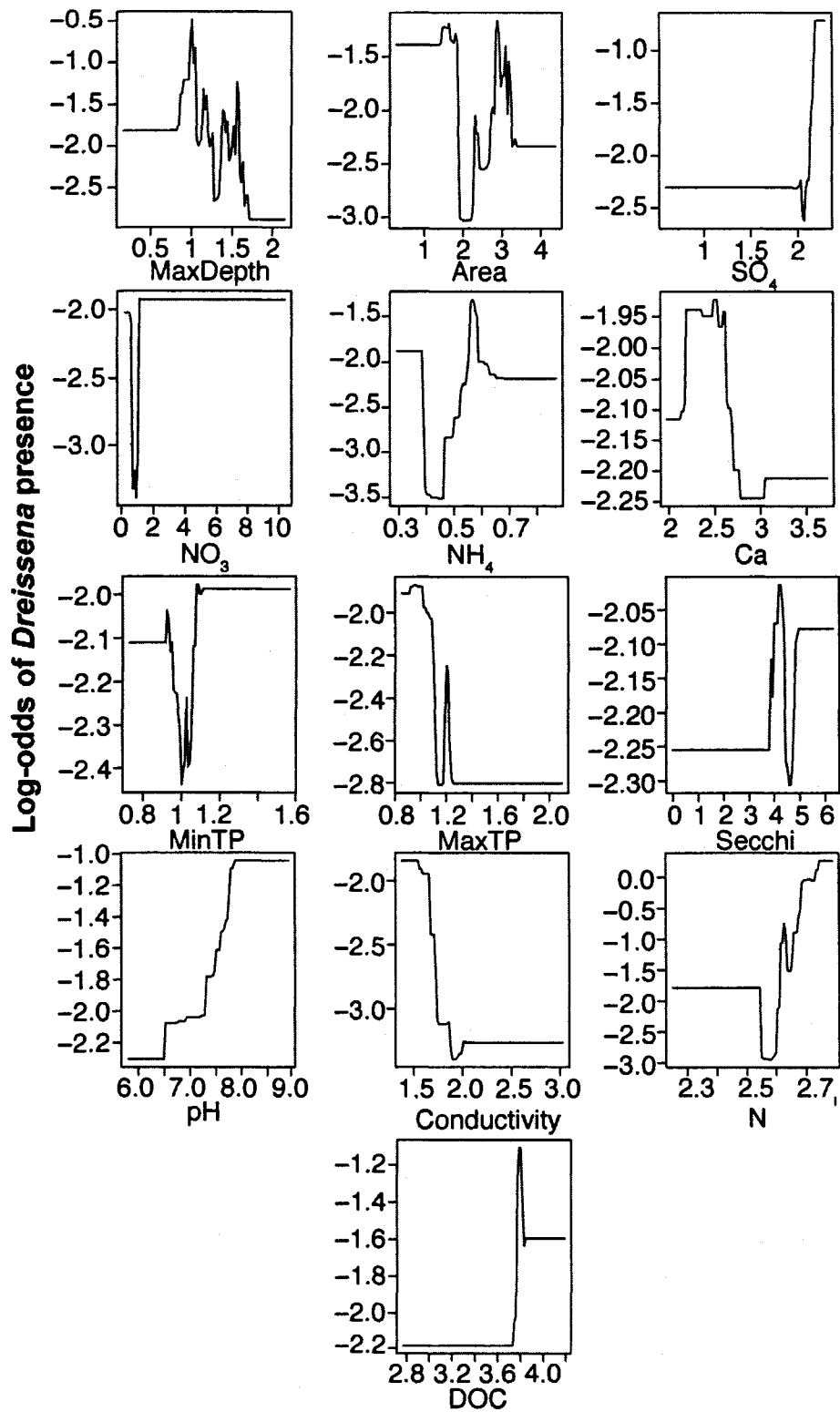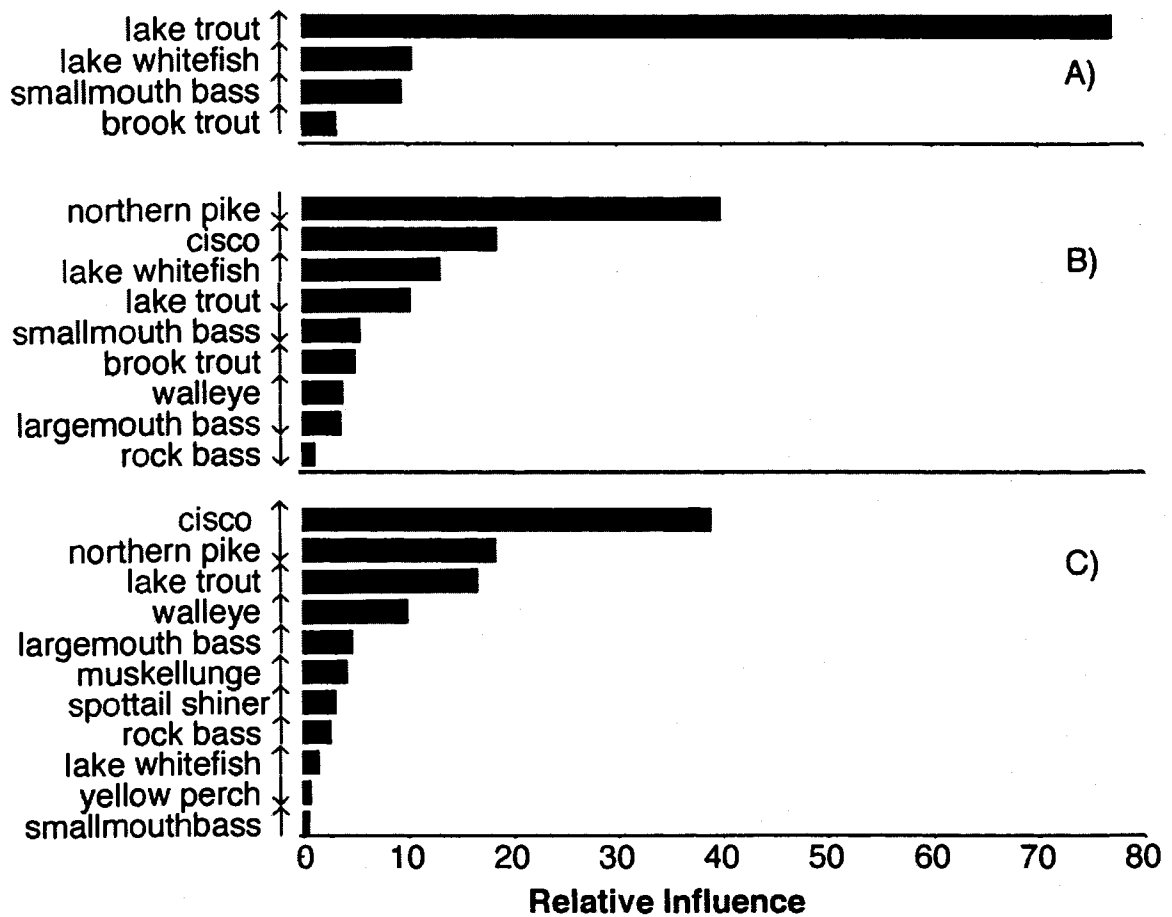
Figure A5. Influence of fish species related to *Bythotrephes* presence. Upward

facing arrows indicate positive relationship of each species to

Bythotrephes presence and downward facing arrows indicate negative

relationship. Panel A) Low propagule pressure, unsuitable lake

characteristics; Panel B) Low propagule pressure, suitable lake

characteristics; Panel C) High propagule pressure and unsuitable lake

characteristics.
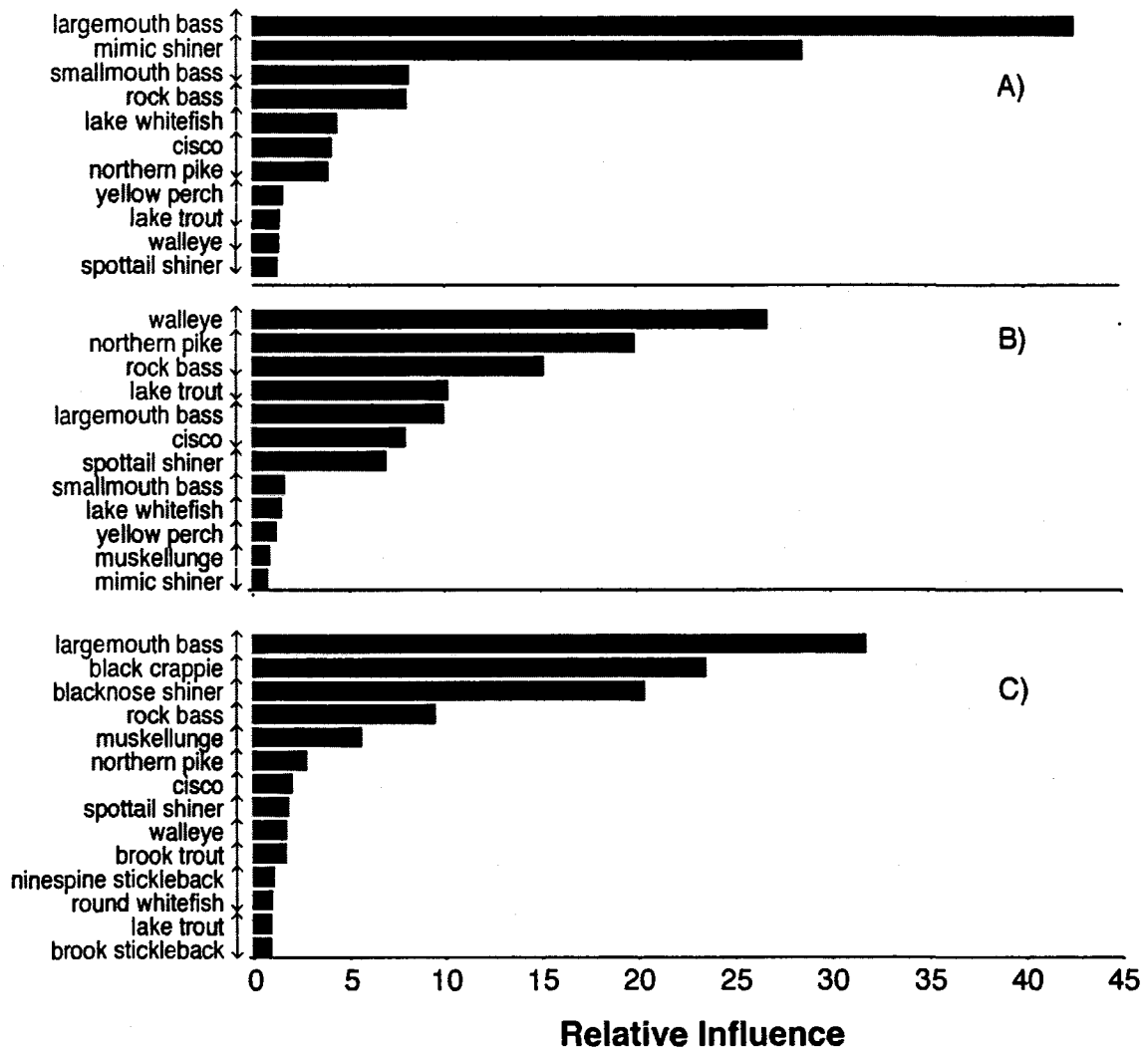
Figure A6. Influence of fish species related to *Dreissena* establishment. Upward

facing arrows indicate positive relationship of each species to *Dreissena*

establishment and downward facing arrows indicate negative relationship.

Panel A) Low propagule pressure, unsuitable lake characteristics; Panel

B) Low propagule pressure, suitable lake characteristics; Panel C) High

propagule pressure and unsuitable lake characteristics. The model for

lakes with high propagule pressure and suitable lake characteristics was

nonsignificant.

Chapter 4: Predictive ability of gravity models to forecast invasions

Summary

Predicting dispersal of nonindigenous species (NIS) is an essential component of risk analysis and management because preventative measures are most readily applied at this stage of the invasion sequence. Gravity models provide one of the most useful techniques available to forecast dispersal of NIS. However, to date, no study has explored differences in forecasts generated by different types of gravity models. Here, we compare the predictive ability of total-flow-constrained, production-constrained and doubly-constrained gravity models to forecast spread of the invasive invertebrate *Bythotrephes longimanus* in Ontario. Differences among the models relate to the amount of data required and constraints under which calculations of source/destination interactions are made. To assess these models, we developed a comprehensive data set describing raw propagule flow from invaded to noninvaded destinations, which was then used to develop all three types of models. The probability of a lake being invaded was derived from presence/absence data and gravity inflows via boosted regression. Production-constrained gravity models performed the best, correctly predicting 77% lakes observed as invaded, and they only had a moderate rate of false positive occurrences (18%). The doubly-constrained model correctly predicted invaded lakes well (72%), but was also the most likely to misclassify noninvaded lakes as invaded (31%). The converse was true for the total-flow-constrained model, which correctly identified only 33% of invaded lakes but only misclassified 18% of noninvaded lakes. The likelihood of invasion estimated at low introduction

effort in the doubly-constrained model was nearly twice as high than predicted by the other gravity model types, resulting in more false positives. Our results indicate that production-constrained models provide the best balance between accurately identifying invaded lakes and protecting against false positive occurrences, and should be used in forecasting dispersal of NIS.

Introduction

The global spread of nonindigenous species (NIS) has become a major environmental issue as invasions are occurring at unprecedented rates and some of these species profoundly alter recipient ecosystems (Sala et al. 2000, Davis 2003). Slowing the rate of new invasions requires development of risk assessment and management policies. The first step of risk assessment models is the determination of where NIS are expected to colonize and spread. Once accurate forecasts have been developed, risk management policies may be developed to reduce rates of spread and or establishment.

Stage-based invasion models are an important advancement to efforts to predict successful invasions because they logically examine factors affecting success at each step of the invasion process. These models begin with quantifying the introduction effort or propagule pressure (i.e. the number of introduction events, and the number and quality of individuals per event) from source populations (Richardson et al. 2000, Kolar and Lodge 2001). After arriving at a new site, propagules of introduced species must tolerate (or exploit) ambient environmental conditions at the site of release (Rouget and Richardson 2003,

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Hayes and Barry 2007; Herborg et al. 2007; Melbourne et al. 2007). Finally, the surviving propagules must integrate into the community, with possible positive, negative or neutral effects by residents (Fridley et al. 2007).

There is considerable evidence that increased propagule pressure is a key determinant of invasion success (Veltman et al. 1996, Forsyth and Duncan 2001, Lockwood et al. 2005, Von Holle and Simberloff 2005). Many of these studies derive from biological control, fisheries, bird or mammal introductions (e.g. Jeschke and Strayer 2005). However, the relationship between propagule pressure and the likelihood of a successful invasion is not always straightforward. For example, Lockwood et al. (2005) argued that the location of the introduction event and the composition of the recipient community may interact to alter the relationship between propagule pressure and invasion success.

Gravity models provide an ideal framework to model the dispersal of aquatic NIS, as they can be used to model patterns of recreationalist movement and associated propagules of NIS between discrete systems (i.e. lakes). Initially developed for use in describing immigration patterns (Zipf 1946), flows of economic goods (Linneman 1966), and optimal placement of retail services (Huff 1959), gravity models describe the flow of information between spatially-discrete origins and destinations. The flow from origin to destination is affected by the distance between them, by the amount of outflow and extrinsic 'propulsiveness' from each of the origins, and by the amount of inflow and attractiveness of different destinations. For example, a model of retail traffic from population centers to shopping centers might use variables such as population size and

retail floor space for measures of propulsiveness and attractiveness, respectively (Huff 1959).

Gravity models can be distinguished into four main classes depending on the amount of information available and the interaction flow constraints assumed between origins and destinations. Total-flow-constrained models require the least amount of data to construct, using only total flow within the system, measures of origin propulsiveness, and destination attractiveness (Haynes and Fotheringham 1984). Production-constrained models, require only moderate amounts of effort to collect data, including measures of outflow from origins and measures of destination attractiveness (e.g. lake area)(Leung et al. 2004, 2006, Bossenbroek et al. 2007). These models have been used to forecast dispersal of NIS into unknown destinations. Doubly-constrained gravity models require information about both outflows from origins (i.e. invaded lakes) and inflows to destinations (i.e. noninvaded lakes). This class of gravity model has been used to forecast spread for zebra mussels (Schneider et al. 1998) and spiny waterfleas (MacIsaac et al. 2004). Finally, attraction-constrained gravity models require information about the inflows to each destination as well as a measure of origin propulsiveness. From an invasion context, attraction-constrained models are not normally used since sources of invasion are usually known, and modelled inflow to each destination is constrained to observed inflow. That is, attraction-constrained gravity models will provide the same information as doubly-constrained models with respect to inflow to each destination.

Since reported in the Laurentian Great Lakes in the early 1980's, *Bythotrephes longimanus* (Leydig 1860*)* has spread rapidly to inland lakes throughout the province of Ontario (Johannsson et al. 1991, MacIsaac et al. 2004). In addition to advective dispersal through connected waterways, *Bythotrephes* dispersal among lakes is facilitated by human-mediated transport associated with recreational boating and fishing (Boudreau and Yan 2004, MacIsaac et al. 2004, Branstrator et al. 2006). One of the key life-history traits that may facilitate *Bythotrephes'* rapid range expansion is its production of diapausing or resting eggs. These sexually-produced, diploid eggs remain viable after passage through fish gastrointestinal tracts (Jarnagin et al. 2000), and may survive overland transport (Ketelaars and Gille 1994). Viable eggs hatch into parthenogenetic females, which may facilitate asexual population growth (Bilton et al. 2001). Females dominate populations during the spring and summer. Fishing lines drawn through the epilimnion of lakes 'snag' *Bythotrephes* by its long caudal appendage, resulting in accumulations of animals along the line. Females die shortly after emersion, but resting eggs carried by these females may remain viable. If the fishing gear is subsequently used on another lake without cleaning, dried masses of females and resting eggs may fall off the line; viable resting eggs could then hatch and cause a new invasion. *Bythotrephes* may also be introduced to new lakes in transported water, recreational or scientific gear, or in transplanted fish. *Bythotrephes* also may disperse naturally by waterfowl, although spatial patterns of invasion in Ontario are not consistent with migration as a principal dispersal mechanism (MacIsaac et al. 2004).

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In this study we compare model performance of total-flow-, production- and doubly-constrained gravity models to forecast *Bythotrephes'* invasion patterns in Ontario to illustrate how the choice of gravity model affects predicted invasion outcomes. We then make model recommendations based on the effort required to collect the prerequisite data and model performance.

Materials and Methods

We mailed 10,000 surveys were mailed in July, 2004 to owners of fishing licences registered with the Ontario Ministry of Natural Resources to assess movement patterns of recreationalists within the province. Approximately 218 surveys were sent to households in each of 46 zones based on the first two digits of their postal code, thereby minimizing bias due to differences in population density across the province.

To capture the likelihood of a recreationalist travelling a specified distance after visiting an invaded lake, a single-parameter dispersal kernel, $p = \beta \exp(-\beta x)$, was fitted to each distance traveled (x) assuming exponential decay and scaled so that $\int p(x)dx = 1$. The likelihood that a recreationalist travels a specified distance after leaving an invaded lake is assumed to be the same for each of the origin/destination lake pairs in the gravity models.

Propagule pressure

A measure of propagule flow contributed by each survey respondent was developed by combining an index of risk associated with various activities associated with recreational use of the lake. In addition, life history

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characteristics of the NIS, such as the timing of the production of resting stages and seasonal peaks in population size, were also included in the gravity model. For each survey respondent, their contribution to propagule pressure among lakes (pp) is represented by:

$$pp = \left[a * b * c * (d + e + f + g + h) \right]$$ (5)

where

a = seasonal NIS population risk due to NIS abundance in lakes; b = proportion of resting stages in NIS population during the corresponding time period; c = correction for bias in response rate; d = risk from using bait buckets; e = risk associated with transporting NIS on boat exterior and fishing/downrigger lines; f = risk due to recreational activities such as swimming or waterskiing; g = risk associated with transporting NIS via macrophytes; and h = risk associated with water-based mechanisms, such as bilge or live-well water. These components are the dominant mechanisms by which aquatic species may be transported through recreational boat use.

Propagule pressure contributed by each of these sub-vectors is further divided into the probability of that sub-vector in use, as measured by the proportion of recreationalists at risk of transporting propagules by that sub-vector, multiplied by the associated propagule load (Appendix 1).

Estimates of propagule loads

Bythotrephes' life history attributes are represented by several terms, and interact with the timing of specific activities associated with recreational use. The seasonal population risk (term a, eqn. 1) is the proportion of annual NIS

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population density in lakes during each of 3 time periods multiplied by the number of days the survey respondent's boat was used during those periods (Appendix 1). The proportion of *Bythotrephes* density was calculated using density estimates for November-March, April-May and June-October (Yan et al. (2001) (Appendix 1).

Values for *Bythotrephes'* relative abundance were derived from literature values, summed over each time period and converted into proportions of annual abundance estimates (Yan and Pawson 1998, Yan et al. 2001). The proportion of *Bythotrephes* populations that produces resting stages increases from July to a maximum in September and coincides with popular times for recreational activity (term *b*, eqn. 1, Appendix 1). Values for the proportion of resting stages in *Bythotrephes* populations were extracted from Yan et al. (2001).

Field collections for *Bythotrephes* were conducted on weekends from July 25, 2005 to August 17, 2005 to estimate relative loads for some of the sub-vectors (Appendix 1). Lake Ontario and five inland lakes were sampled with replicated vertical zooplankton net hauls (500 μm mesh size, 50 cm diameter), 10 L bait buckets, and weighted (2 oz) fishing line. When leaving each lake, all water from the transom well was filtered and contents preserved in 95% ethanol. Propagule loads for 100 L live wells were estimated assuming similar density of propagules as per bait buckets and transom wells. Propagule loads were averaged across replicates and lakes for use in models.

In addition to parameterizing propagule load based on specific mechanisms, risks associated with general recreational activities were also

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considered (eqn. 1, term *f*, Appendix 1). Propagule loads for general recreational use of lakes, such as whether the survey respondent used the lake primarily for fishing or swimming, were given lower weights than for specific mechanisms (e.g. swimming = 1 vs. bait buckets = 6).

Lake area (ha)(data provided by the Ontario Ministry of Natural Resources) was used as the external measure of attraction, with larger lakes expected to attract disproportionately more recreational traffic (Reed-Andersen et al. 2000).

Gravity model classes

The total-flow-constrained model requires the least amount of information, only requiring that the predicted total flow of the system is equal to the observed flow. The flow between origins and destinations (T_{ij}) for the total-flow-constrained model is calculated as:

$$T_{ij} = kw_j \left[\beta \exp(-\beta d_{ij}) \right] \qquad (2)$$

where w_j is the attractiveness of destination *j* as measured by the $\log_{10}(x+1)$ transformed lake area (ha), d_{ij} is the road distance (km) between origin *i* and destination *j* and *k* is a "balancing factor" to ensure that the predicted total flow (*T*) is equal to observed total flow (Haynes and Fotheringham 1984). k is calculated as:

$$k = \frac{T}{\sum_i \sum_i w_j \left[\beta \exp(-\beta d_{ij}) \right]} \qquad (3)$$

The distance decay component of eqns (2) and (3), $\beta \exp(-\beta d_{ij})$, is calculated as before. In this formulation of total-flow-constrained gravity model, the term for origin "propulsiveness" was not included (e.g. Haynes and Fotheringham 1984).

Production-constrained gravity models require information about the outflows from each source. Flows between sources and destinations are calculated as:

$$T_{ij} = A_i O_i w_j \left[\beta \exp(-\beta d_{ij}) \right] \tag{4}$$

where O_i is the propagule outflow from each origin i, w_j is the measure of attractiveness for each destination j, and A_i is a balancing factor ensuring that total predicted outflow from each source is equal to observed outflow ($\sum_j T_{ij} = O_i$) (Haynes and Fotheringham 1984).

The balancing factor, A_i is calculated by:

$$A_i = \frac{1}{\sum_j w_j \left[\beta \exp(-\beta d_{ij}) \right]} \tag{5}$$

In the doubly-constrained model, the interaction flow T_{ij} is formulated as:

$$T_{ij} = A_i O_i B_j D_j \left[\beta \exp(-\beta d_{ij}) \right] \tag{6}$$

where, D_j is the inflow to destination j, and other terms are as previously defined. The parameters A_i and B_j are "balancing factors" added to the model to ensure that the sum of the interaction flow, T_{ij}, for each origin is equal to the total outflow,

O_i, and likewise, the sum of the interaction flow for each destination is equal to the total inflow for each destination, D_j (Haynes and Fotheringham 1984).

Parameters A_i and B_j are solved iteratively as:

$$A_i = \frac{1}{\sum_j B_j D_j \left[\beta \exp(-\beta d_{ij}) \right]} \tag{7}$$

and

$$B_j = \frac{1}{\sum_i A_i O_i \left[\beta \exp(-\beta d_{ij}) \right]}, \tag{8}$$

respectively.

Inbound propagule pressure, as measured by the inflow to each destination, was determined for each class of gravity model. Since the doubly-constrained gravity model is limited to predicting inflow to destinations for which there are observations, the total-flow and production-constrained models were constrained to the same set of destinations for the purpose of comparison.

The probability of specific lakes being invaded was calculated using boosted regression trees relating inbound propagule pressure to *Bythotrephes* presence/absence (1,0). Boosted regression trees use an iterative approach and do not make any parametric assumptions about the relationships between predictor variables and species occurrence. They have been shown to be strong performers in predicting species occurrence and abundance relative to other methods (Elith et al. 2006). For each class of gravity model, the proportion of training/testing data subsets in the boosted regression was set at 70:30. To

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avoid over-fitting the models, the optimum number of iterations for each model was based on a stopping-rule at which there was zero improvement in error reduction between iterations (Breiman 1998). Estimated probabilities based on boosted regression trees were calculated using the R package gbm (Ridgeway 2007).

Lakes were classified as invaded if the estimated probabilities of invasion were greater than or equal to a threshold based on the shape of the receiver operating characteristic curve (ROC). The ROC plots the performance of the model being able to correctly predict an invasion (i.e. hit rate) versus incorrectly predicting an invasion when one has not occurred (i.e. false alarm rate) at different thresholds (Liu et al. 2005). Likewise, the 'miss rate' is defined as the proportion of invaded lakes that were misclassified as absent. The threshold was chosen based on the minimum distance from the upper left corner. Liu et al. (2005) recommended this procedure over setting a fixed threshold for the analysis. The ROC was calculated with the R package verification (NCAR - Research Application Program 2007).

The predictive power of the three classes was evaluated by assessing the area under the receiver operating characteristic curve (AUC). This test is used to evaluate whether the model can predict better than at random, independent of the threshold used. Model performance is acceptable only if the AUC is significantly greater than 0.5. In addition, contingency table analysis was used to assess differences in hit and false alarm rates among the gravity model classes.

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Results

Bythotrephes is rapidly spreading in Ontario, with 119 lakes reported

invaded as of summer 2006 (N. Yan, unpublished data). The pattern of spread is

consistent with the movement of recreationalists. Most recreationalists traveled

short distances, although long distance movement was recorded. For example,

after visiting an invaded lake, approximately 40% of recreationalists traveled 100

km or less, though 2% traveled 800 km or greater. The maximum distance

traveled was 1800 km by a single boater (Figure 1).

The fitted relationship between Bythotrephes occurrence and propagule

pressure differed greatly among the three classes of gravity models. At low levels

of propagule pressure, estimated probabilities of Bythotrephes presence

remained low for the total-flow-constrained and production-constrained models

(p(invasion)~0.2), but increased to 0.38 for the doubly-constrained model (Figure

2). Estimated probabilities of invasion reached a maximum of 0.57 for total-flow-

constrained and doubly-constrained models, and 0.62 for the production-

constrained model.

Maximal levels of estimated propagule pressure to lakes also differed

among the three classes of gravity models. Maximum inflow in the doubly-

constrained model was an order of magnitude higher than total-flow or

production-constrained models (Figure 2). Propagule pressure into the top five

lakes was 4.4 and 4.7% of total inflow for the total-flow-constrained and

production-constrained models, and 34.7% in the doubly-constrained models

(Table 1).

The membership of lakes with the highest levels of inbound propagule pressure and corresponding estimated probability of *Bythotrephes* occurrence varied by gravity model (Table 1, Figure 3). In addition, the spatial extent of estimated probabilities varied depending on the constraints on the model. Areas at risk of invasion differed strongly across models. The total-flow-constrained model identified areas north of Lake Ontario and east of Lake Huron at greatest risk (Figure 3A), while the production-constrained model identified most of south and central Ontario (Figure 3B). The doubly-constrained model identified a patchwork of vulnerable areas including southwest, central and northwest Ontario (Figure 3C).

In the total-flow-constrained model (least amount of model constraints), Lakes Muskoka and Rosseau and Lake of Bays were all major recipients of *Bythotrephes* propagules, and all are located in the same watershed, approximately 180 km north of Lake Ontario. *Bythotrephes* presence in this model was limited principally to areas north of Lake Ontario to the northern edge of Lake Huron (Figure 3A). For the production-constrained model, areas of highest probability for invasion included the above range with the addition of south-central Ontario north of Lake Erie (Figure 3B). In the doubly-constrained model, areas corresponding to high likelihood of *Bythotrephes* presence were more dispersed across the province (Figure 3C). Vulnerability 'hotspots' included a set of lakes northwest and northeast of Lake Superior. Only Lakes Ontario and Simcoe were among the top five in all three model types (Table 1).

All three gravity model types were able to predict the likelihood of *Bythotrephes* occurrence better than at random (AUC, all P< 0.0001), though important differences were noted among the models (Table 2). The thresholds derived from the ROC used to classify invasion status were similar to the prevalence of lakes invaded by *Bythotrephes* (22%) (Table 2). In terms of the ability to accurately predict invaded lakes (hit rate), the production-constrained model was most successful (77%), followed by the doubly-constrained model (72%) and the total-flow-constrained model (63%). However, the total-flow-constrained model was the least susceptible to misclassifying a lake as invaded when it was not (false alarm rate = 18%), followed by the production-constrained and doubly-constrained models (27% and 31%, respectively).

Discussion

Estimating the dispersal of a NIS is the significant first step in risk management because preventative measures are most readily applied at the introduction stage of the invasion sequence (Lodge et al. 2006). Heretofore, ecologists have used a variety of gravity models without consideration of the importance of method used, with selection usually based upon the nature of available data. In this study, we compared the predictive ability of 3 types of gravity models to forecast invasions of by the spiny waterflea, *Bythotrephes*. Simulation results indicate that ecologists should be cognizant that the method used may have strong consequences on forecasted patterns of spread.

Evaluation of the total-flow-, production- and doubly-constrained gravity models revealed differences in each model's ability to successfully detect invasions (hit rate), as well as their respective likelihoods to overpredict invasions (false alarms or false positives). The production-constrained model was best able to detect invasions (high hit rate), and it had a low miss rate (i.e. false negative or incorrectly predicting invaded lakes as noninvaded). One detracting aspect of the production-constrained model was its moderately susceptibility to false positives. Depending on the NIS, the "cost" of not detecting an invasion (miss) is likely greater than the cost of a false alarm, thus the production-constrained model would offer the most protective management option. It is also noteworthy that some false alarms may, over the long term, correctly predict invasions even if they are incorrect in the short-term. For example, invasions are time-sensitive, thus lakes identified as vulnerable may already be invaded (though at non-perceptible population levels), or they may be the most susceptible to invasion in the future. Thus, if longer time scales are considered, many of the lakes incorrectly predicted to be invaded by current biological surveys may eventually become invaded and properly classified.

The production-constrained model is also recommended on the basis of the largest AUC test statistic (Table 2). Fortunately, the ability to successfully detect invasions was not dependent on the amount of data required to populate the model. Both the doubly-constrained and total-flow-constrained models, which require complete and minimal information about propagule flow throughout the system of connected lakes, respectively, had lower hit rates. Production-

constrained gravity models provide balance between predictive ability and the amount of information required to populate the model, thus offering important advantages over doubly-constrained models (e.g. Schneider et al. 1998, MacIsaac et al. 2004). For example, the data required to produce a production-constrained model is often readily available from government agencies, thereby reducing both cost and time in development of new models. Conversely, doubly-constrained models require the largest amount of data collection effort, and forecast invasions are limited to the sets of lakes for which there are observations. Production-constrained gravity models, in contrast, require minimal amounts of information such as lake size and the number of registered boaters leaving specific counties (Bossenbroek et al. 2001, Bossenbroek et al. 2007). Total-flow-constrained models require the total number of registered boaters plus measures of attractiveness and propulsiveness, though the model produced here was the least useful of those tested.

Our results on estimates of propagule outflow from invaded sources differ slightly from those in MacIsaac et al. (2004). In our production-constrained and doubly-constrained models, the largest sources of propagule flow to currently noninvaded lakes came from Lake Ontario, followed by Lakes Simcoe, Huron, Buckhorn and Pigeon. The latter two lakes are part of the Trent-Severn waterway and are located north of Lake Ontario. MacIsaac et al. (2004) identified Lakes Simcoe, Kashagawigamog and Huron as primary sources of propagules to noninvaded lakes. Differences in the two studies may be the result of the number of invaded and noninvaded lakes used in the constructed models. In the latter

study, 35 lakes including the Great Lakes served as sources for vector traffic to 131 noninvaded lakes, whereas interaction flow was modeled for 60 invaded to 231 noninvaded lakes in this study.

Gravity models are more applicable to modeling the spread of aquatic NIS than other methods, such as reaction-diffusion models, because lakes are discrete patches within a heterogeneous (terrestrial) landscape. In addition, gravity models are better suited for describing the vector movement of propagules assuming that recreational movement is the dominant mechanism (Johnson et al. 2001, MacIsaac et al. 2004). Reaction-diffusion or integro-difference models assume a continuous landscape and are better suited for modeling spread in aerial, terrestrial, or marine environments (e.g. Greene and Johnson 1989, Veit and Lewis 1996, Cowen et al. 2000). Earlier attempts to forecast aquatic NIS spread *via* reaction-diffusion models tended to either overestimate or underestimate rates of spread. For example, Buchan and Padilla (1999) incorporated a dispersal kernel fitted to boater movements into a reaction-diffusion model, but found that the reaction-diffusion model overpredicted the rate of spread of zebra mussels among inland lakes. Their model was developed, however, early during the invasion sequence, thus many lakes that were overpredicted may now be invaded, as described above.

In describing the likelihood that recreationalists will move a specified distance from their origin (i.e. dispersal or redistribution kernel), previous studies using gravity models have typically used straight-line distances from origins to destinations based on survey data (Bossenbroek et al. 2001, Leung et al. 2006).

Forecasts of NIS spread based on the dispersal kernels using straight-line distances may underestimate the extent of spread relative to dispersal kernels using road-distances. Road distances are often substantially longer than straight-line distances, which would reduce connectivity between the systems. There has been no formal assessment, however, of the effect of using straight-line versus road-distance on forecast range expansion. This could be further complicated by the quality of the road (e.g. interstate vs. stare highway), which could influence the likelihood of recreationalists using that particular artery.

Gravity models are well-suited to model spread of disease, providing that knowledge of vectors responsible and areas currently infected areas are known. For example, gravity models seem to provide a suitable mechanism for forecasting spread of the pathogen causing Sudden Oak Death (*Phytophthora ramorum*), which was first reported in central California in 1995 (Garbelotto et al. 2001). In this case, a gravity model could be constructed using information on the commercial movement of hosts susceptible to disease (e.g. oaks, rhododendrons), the locations of infested nurseries, and measures of attraction to other (uninfested) locales.

Gravity models provide a flexible modeling framework and can be used in conjunction with other models in multistage invasion models. For example, models of propagule pressure can be combined with models on habitat suitability and biotic integration into the recipient assemblage. Herborg et al. (2007) used the volume of ballast water transported in transoceanic vessels as a proxy of propagule pressure, in combination with environmental niche models (Genetic

Algorithm for Rule-set Prediction) to assess habitat suitability for the Chinese mitten crab *Eriocheir sinensis* in North America. Rouget and Richardson (2003) provided semi-mechanistic models for the percentage cover and species occurrences for three nonindigenous plant species in South Africa. Their multistage model indicated that propagule pressure – as measured by the distance from invasion foci -- and environmental variables were able to account for 70% of successful invasions.

The next stage in the development of gravity models for use in risk assessment requires the inclusion of NIS population dynamics such as growth rate and mortality. This would enable gravity models to serve as a bridge from describing dispersal of individual propagules to that describing population spread of NIS at a landscape level. For example, models describing population growth can be coupled with gravity models describing immigration and emigration among systems, in a manner analogous to metapopulation models. Currently, gravity models are used primarily to describe relative vector traffic to different lakes, usually in terms of boater numbers (Schneider et al. 1998, Bossenbroek et al. 2001, Johnson et al. 2006, Leung et al. 2006, Bossenbroek et al. 2007). This study is one of the first attempts to provide a more quantitative approach to modeling propagule pressure with gravity models by attempting to quantify the number of propagules that can be transported via specific mechanisms associated with boating and recreational travel.

In conclusion, our empirical data set provided an opportunity to evaluate the relative sensitivity of different gravity models to forecasting invasions. Our

study provides guidance for choosing the best model to describe propagule pressure and the amount of effort required to collect data in the planning stage of an experiment. Our analyses indicate that production-constrained gravity models provide a high hit:miss ratio, with only a moderate false alarm rate. Because data required to formulate production-constrained gravity models is often readily accessible, we recommend this procedure over other possibilities for future studies.

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Tables

Table 1. Top five lakes with highest levels of inbound propagule pressure with percentage of total inbound propagule pressure for each class of gravity model. Lakes in boldface are noninvaded and are at risk of invasion.

Total-flow-constrained	Production-constrained	Doubly-constrained
Lake Muskoka (0.92%)	Lake Ontario (1.00%)	Lake Ontario (8.07%)
Lake Ontario (0.91%)	**Lake Scugog** (0.95%)	**Rice Lake** (6.98%)
Lake of Bays (0.87%)	Lake Simcoe (0.92%)	Lake Simcoe (6.72%)
Lake Simcoe (0.87%)	**Rice Lake** (0.92%)	Lake Huron (6.51%)
Lake Rosseau (0.83%)	Sturgeon Lake (0.88%)	**Lake Chemong** (6.37%)

Table 2. Contingency table analysis, AUC and probability thresholds used

for classifying invasion status for three gravity models.

Gravity model	Observed-predicted invasion status (Present=1, Absent=0)				AUC	P(AUC)	Threshold from ROC
	0,0	0,1	1,0	1,1			
Total-flow-constrained	174	39	22	38	0.79	< 0.0001	0.270
Production-constrained	156	57	14	46	0.80	< 0.0001	0.240
Doubly-constrained	146	67	17	43	0.74	< 0.0001	0.255
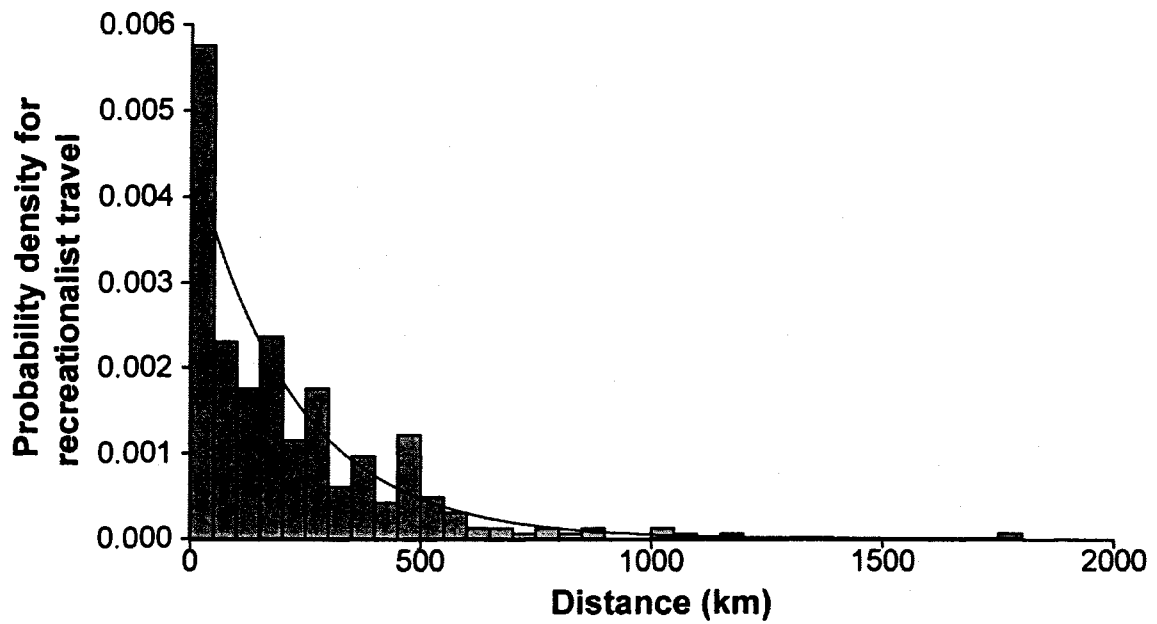
Figure 1. Dispersal kernel for recreationalist travel after visiting a lake invaded by

Bythotrephes. The equation for the fitted line is

$p(x) = 0.005 \exp(-0.005x)$, n=332.
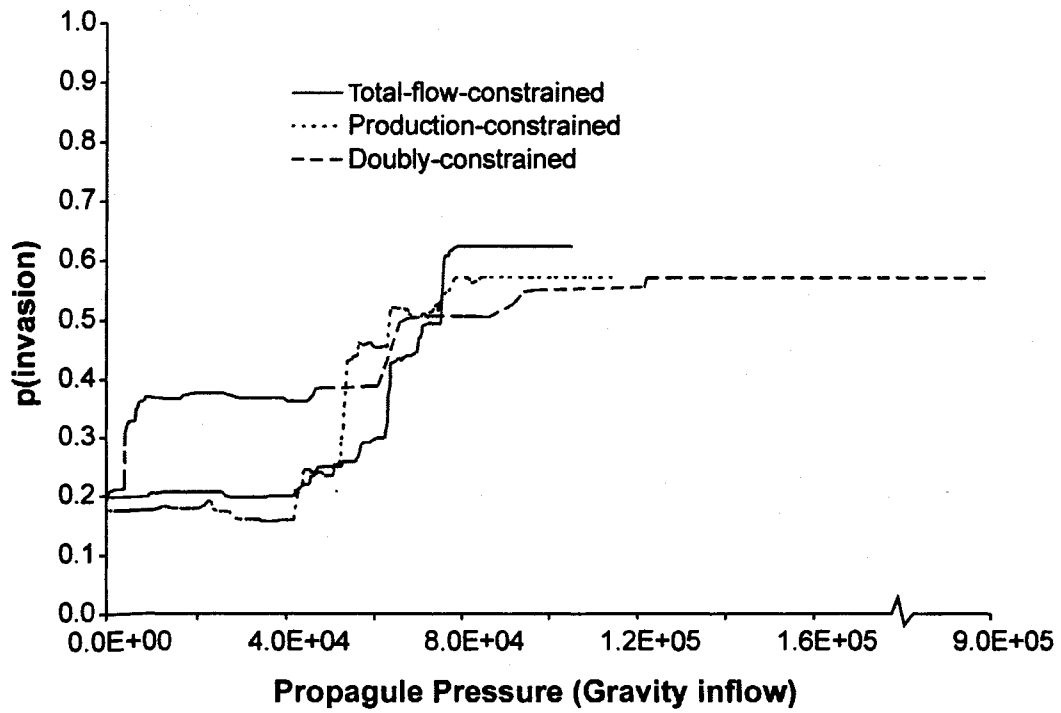
Figure 2. Estimated probabilities of *Bythotrephes* occurrence from boosted

regression trees of gravity inflow to invaded and noninvaded lakes.
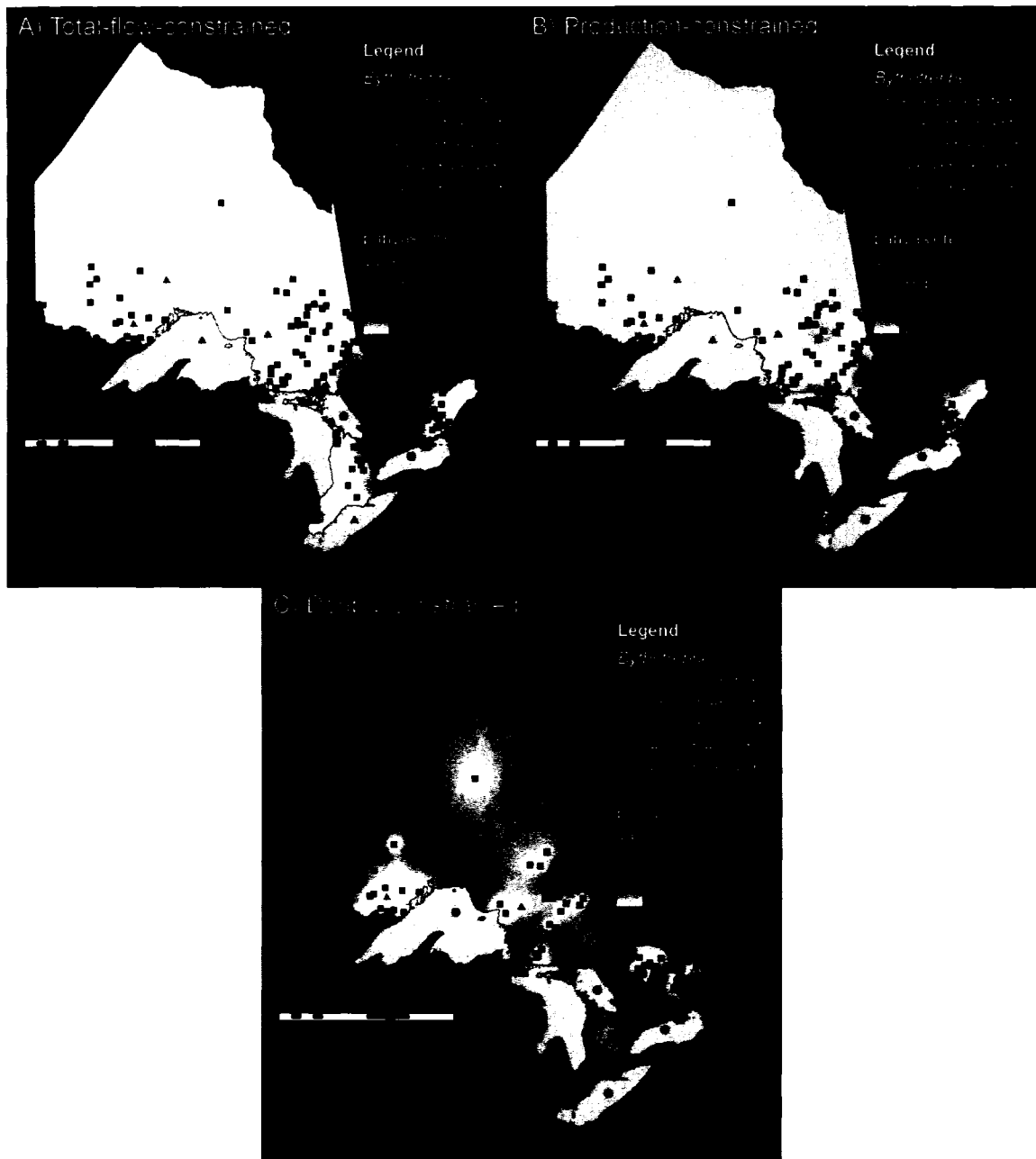
Figure 3. Estimated probabilities of *Bythotrephes* occurrence and classified

invasion status for A) Total-flow-constrained, B) Production-constrained,

and C) Doubly-constrained gravity models. Probabilities of occurrence

were interpolated using Inverse Distance Weighting for display purposes

only.

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Chapter 4 Appendix. Proportion of recreationalists transporting *Bythotrephes*

propagules with associated propagule loads for each mechanism.

Propagule loads are scaled on an index from 0-5 individuals unless

indicated.

Risk factor	Proportion of recreationalists	Propagule Load
Date risk[1]		0.001*# days in Nov-Mar
		+ 0.14*# days in Apr-May
		+ 0.86*# days in Jun-Oct
Proportion of resting stages in population[1]		Jan 1-Jul 3: 0
		Jul 4-9: 0.05
		Jul 10-16: 0.03
		Jul 17-24: 0.49
		Jul 25-31: 0.72
		Aug 1-6: 0.44
		Aug 7-14: 0.40
		Aug 15-21:0.67
		Aug 22-Sep 30: 0.71
		Sep 31-Dec 30: 0
Bait buckets	0.389	6^3
Anchor	0.704	1
Downrigger	0.220	10^3

Fishing line	0.797	10^3
Recreational activities		
Boating	0.714	1
Fishing	0.881	1
Swimming	0.624	0
SCUBA	0.066	1
Water skiing	0.325	1
Macrophytes	0.016	1
Water-based		
Live well	0.005	60^3
Engine cooling	0.184	1
Bilge water	0.139	1
Transom well	0.087	1^2

[1] Estimated from data extracted from Yan et al. (2001)

[2] Measured from field surveys

[3] Estimated based on average *Bythotrephes* abundance of 6.9 ind. m^{-3} from field surveys and relative volume of each mechanism.

Chapter 5: Influences of life history variation on dispersal of aquatic nonindigenous species

Summary

Across taxonomic groups, successful colonization by nonindigenous species (NIS) in novel habitats is influenced by an array of factors including the number, size and quality of propagules introduced (i.e. propagule pressure) and by tolerance of ambient environmental conditions. Within taxonomic groups, differences in life-history attributes may interact with specific transport mechanisms, resulting in major differences in patterns of dispersal. In this study, I used production-constrained gravity models to assess the importance of propagule pressure on the comparative dispersal of two groups of related NIS – the cladocerans *Bythotrephes longimanus* and *Cercopagis pengoi* and bivalves *Dreissena polymorpha* and *D. rostriformis bugensis*. These models provide a composite measure of propagule flow by incorporating relevant life-history attributes of these species with the movement of recreationalists who disperse the species to lakes in Ontario. *Bythotrephes* and *D. polymorpha* successfully invaded inland lakes within seven years of their initial reporting, whereas *Cercopagis* and *D. r. bugensis* did not. *Bythotrephes'* spread across the landscape occurred more rapidly than that for *D. polymorpha*, and it had the highest propagule inflow to lakes of the species tested. The two species that have not spread had the lowest propagule inflow to lakes in both year 1 and year 7 following their initial reports in the Great Lakes. Thus, the rapid spread of *Bythotrephes* and *D. polymorpha,* and the lack of spread of

Cercopagis and *D. r. bugensis,* are consistent with each species' relative propagule

pressure to inland lakes. The low of propagule pressure of *Cercopagis* may result from

low production of resting stages, whereas that of *D. r. bugensis* may be related to a

higher mortality when transported from lakes and lower abundance in the littoral zone.

Comparative differences in patterns of spread of these four invaders illustrate that life-

history differences among species have important consequences on the mechanisms

and rates of dispersal.

Introduction

Ecologists have attempted to identify determinants of invasion success by

nonindigenous species (NIS) for almost fifty years. This search has been

complicated by recognition that successful invasions involve a complex series of

interactions between species-specific characteristics of the NIS and those of the

recipient environment and its ecological community. Interactions are structured

such that propagules of the NIS must pass through a sequence of 'filters', in

which only a subset survive (Richardson et al. 2000, Kolar and Lodge 2001).

Recent work has established that different factors may influence success at

different stages of the invasion process (Kolar and Lodge 2002).

Characteristics common to many successful invasions across taxonomic

groups include propagule pressure of NIS, and histories of successful invasions

and of climatic matching between native and introduced ranges of the NIS

(Hayes and Barry 2007). In many instances, characteristics of successful NIS are

often specific to stages of the invasion pathway (Kolar and Lodge 2002, Lloret et

al. 2005). For example, successful NIS of plants often produce many seeds of low mass that are easily dispersed by wind (Greene and Johnson 1993). As well, some successful NIS may be characterized by broad environmental tolerance, or high genetic variability or phenotypic plasticity (Morton 1996; Richards et al. 2006; Hayes and Barry 2007). Most of the traits of successful NIS relate to their ability to integrate into the recipient community and are associated with population growth, such as high reproductive rate, rapid sexual maturity, or asexual or vegetative reproduction (Heger and Trepl 2003). Caution is required, however, with these sweeping assessments, as many have never been subjected to experimental validation or statistical analysis (Lodge 1993). A central problem exists with establishing appropriate control groups against which the features of successful NIS are compared. Plant ecologists, in particular, have resorted to phylogenetically controlled contrasts when assessing the importance of life history attributes to invasion success (Crawley et al. 1996, Gordon 1998).

Invasions of the spiny waterflea (*Bythotrephes longimanus*), fishhook waterflea (*Cercopagis pengoi*), zebra mussel (*Dreissena polymorpha*) and quagga mussel (*D. rostriformis bugensis*) provide an opportunity to compare dispersal and invasion success for two groups of taxonomically related species. The spiny waterflea is a predatory cladoceran that was reported in Lake Ontario in 1982 (Bur et al. 1986), which has since spread to the other Great Lakes and to 119 inland lakes (Ontario Federation of Anglers and Hunters, unpublished data). The fishhook waterflea is a more recent invader, first observed in Lake Ontario in

1998 (MacIsaac et al. 1999), which has since spread only to Lake Erie, Lake Michigan and adjacent Lake Muskegon, and to seven finger lakes in New York State adjacent to Lake Ontario; this species has not been reported in inland lakes in Ontario. Both waterflea species possess a caudal appendage (i.e. spine) that deters predation by juvenile planktivorous fish, thus allowing both species to survive and compete with small fish for zooplankton prey. Both spiny and fishhook waterfleas produce resistant diapausing (resting) eggs that remain viable even after the parent has died. Accumulation of a 'resting' egg bank serves to replenish populations after adverse weather conditions kill off planktonic individuals. These propagules may be dispersed overland to novel systems, thereby facilitating spread of the species. Overland transport occurs mainly *via* water-based mechanisms associated with recreational boat use and angling (MacIsaac et al. 2004). Specifically, caudal appendages of both species may become snagged on fishing lines trawled through surface waters of lakes (Jacobs and MacIsaac 2007). While the adults die almost immediately upon emersion, viable resting eggs may be transported to other systems and 'seed' invasions unless the fishing gear is cleaned beforehand.

Invasion success by the zebra and quagga mussels has been linked to high fecundity, production of planktonic larvae, and byssal-pelagic drifting by juveniles in river systems (Griffiths et al. 1991). Zebra mussels were first detected in Lake Erie in 1988 (Hebert et al. 1989). The species is of the most successful invaders globally, having spread widely throughout temperate, eastern North America, including to at least 128 lakes in Ontario (Ontario

Federation of Anglers and Hunters, unpublished data). Quagga mussels were first recorded in Lake Erie in 1989 (Mills et al. 1993), and have since spread to Lakes Ontario, Michigan and Huron. However, this species has not yet exhibited regional spread in the Great Lakes region, although a dramatic invasion was reported in January 2007 in Lake Mead, Nevada. The closest population occurs some 2500 km away in Lake Michigan, thus highlighting the importance of long-distance transport. Since its report in Lake Mead, the species has been found downstream in Lake Havasu, California, as well as in reservoirs adjacent to San Diego. Zebra and quagga mussels may be spread by more than 20 different natural and human-mediated vectors (Carlton 1993). Mussel veliger larvae may be transported overland in all forms of water carried by boats (Johnson et al. 2001). Adults disperse overland fouled to boats or on aquatic vegetation stranded on boats trailered out of the invaded lake.

In this study, I model comparative patterns of spread to inland Ontario lakes for two waterflea and two mussel species using information on propagule pressure, and life-history variation and its attendant influence on dispersal mechanisms. More specifically, I address how differences in the patterns and rates of spread due to species-specific characteristics may explain the failure of some NIS to transition from the Laurentian Great Lakes to Ontario inland lakes.

Materials and methods

To correct for biases when comparing patterns and rates of spread among the species due to different lengths of time between the years of first record and

our survey, models of propagule pressure and invasion status were based on the number of years since the first reported invasion. That is, the range of one species may be larger relative to another simply due to a longer period of time since its first recorded invasion rather than a higher rate of spread from year-to-year. For *Bythotrephes, Cercopagis, D. polymorpha* and *D. rostriformis bugensis* (hereafter *D. rostriformis*), Year 1 corresponds to 1982 (Bur et al. 1986), 1998 (MacIsaac et al. 1999), 1988 (Hebert et al. 1989) and 1989 (Mills et al. 1993), respectively, as the first recorded years of invasion in the Laurentian Great Lakes.

Gravity models of propagule pressure

Propagule pressure to inland lakes was modelled using production-constrained gravity models. Gravity models allow for the calculation of flow from spatially discrete origins to destinations and are well-suited for modeling dispersal of aquatic NIS (Schneider et al. 1998). To collect data on recreationalist movement among Ontario lakes, 10,000 surveys were mailed to owners of fishing licences registered with the Ontario Ministry of Natural Resources in July 2004. The surveys were sent to households according to a spatially stratified procedure to 46 zones within Ontario as identified by the first two digits of their postal code. This method minimizes bias due to differences in population density across the province.

Recreationalist movement from invaded lakes was described by a single-parameter dispersal kernel, $p = \beta \exp(-\beta x)$, and was fitted to each distance

traveled (x) assuming exponential decay and scaled such that $\int p(x)dx = 1$. The probability that a recreationalist is willing to travel a specified distance after leaving an invaded lake is assumed to be the same for each of the origin/destination lake pairs in the gravity models.

A measure of propagule flow contributed by each survey respondent was developed by combining an index of risk associated with various mechanisms associated with recreational use of the boat. In addition, life history characteristics of the NIS such as the timing of the production of resting stages and seasonal peaks in population size were also included in the gravity model. For each survey respondent, the contribution to propagule flow among lakes (pp) is represented by:

$$pp = \left[a * b * c * \left(d + e + f + g + h + i \right) \right] \tag{1}$$

where

a = seasonal NIS population risk due to NIS abundance in lakes; b = proportion of resting stages in NIS population during the corresponding time period; c = correction for bias in response rate; d = risk from using bait buckets; e = risk associated with transporting NIS on boat exterior and fishing/downrigger lines; f = risk due to recreational activities; g = risk of transporting viable propagules after leaving lake; h = risk associated with transporting NIS via macrophytes; and i = risk associated with water-based mechanisms such as bilge water. These components are the dominant mechanisms by which these aquatic NIS may be transported through recreational boat use. Propagule pressure contributed by each of these subvectors is further divided into the probability of that subvector in

use, as measured by the proportion of recreationalists at risk of transporting propagules by that subvector, multiplied by the associated propagule load (Appendix 1).

Estimates of propagule loads

Life history attributes of *Bythotrephes, Cercopagis, D. polymorpha* and *D. bugensis* are represented in the model by several terms, and interact with the timing and specific activities associated with recreational use. The seasonal population risk (term a, eqn. 1) is the proportion of NIS population in lakes during three time periods multiplied by the number of days the survey respondent's boat was used in those periods (Appendix 1). Values for NIS relative abundance were derived from the literature, summed over each time period and converted into proportions of annual abundance estimates (Dermott et al. 1993, Fraleigh et al. 1993, Mills et al. 1993, Nalepa et al. 1995, Yan and Pawson 1998, Makarewicz et al. 2001, Yan et al. 2001).

The production of resting eggs is an important life-history attribute that may facilitate *Bythotrephes* and *Cercopagis'* invasion success (Ketelaars and Gille 1994). The proportion of populations that produces resting stages increases from July to a maximum in September and coincides with popular times for recreational activity (term *b*, eqn. 1, Appendix 1). Values for the proportion of resting stages in *Bythotrephes* and *Cercopagis* populations were extracted from Yan et al. (2001) and Makarewicz et al. (2001). Since *Dreissena* does not produce resting stages, this term remained constant in the model.

Survival of propagules once a boat is trailered out of the water was also incorporated into the model. Resting stages for *Bythotrephes* and *Cercopagis* are assumed to be resistant to desiccation and so survival in the boat or on fishing gear is invariant over short periods of time (Appendix 1). Survival of *Dreissena* propagules, in particular the adult stages, decreases rapidly once they are aerially exposed. The relationship between propagule survival and the time since the boat was removed from the invaded lakes was derived from Ricciardi (1995) for both dreissenid species, and scaled to a maximum of 5.

Field collections for *Bythotrephes* were conducted on weekends from July 25, 2005 to August 17, 2005 to estimate relative loads for some of the subvectors (Appendix 1). Lake Ontario and five inland lakes were sampled with replicated vertical zooplankton net hauls (500 μm mesh, 43.7 cm diameter), 10 L bait buckets, and weighted (2 oz.) fishing line. When leaving each lake, water from the transom well was filtered and contents preserved in ethanol. Propagule loads for 100 L live wells were estimated assuming similar density of propagules as per bait buckets and the transom wells. Propagule loads were averaged across replicates and lakes for use in the models. Estimates for *Dreissena* propagule loads were extracted from Johnson et al. (2001).

In addition to estimating propagule load based on specific mechanisms, risks associated with general recreational activities were also considered (eqn. 1, term *f*, Appendix 1). Propagule loads for general recreational use of lakes, such as whether the survey respondent used the lake primarily for fishing or swimming, were given lower weights than for specific mechanisms.

Correction for spatial bias in survey return rate

The gravity models were corrected for bias in the survey return rate from each of the postal zone strata (eqn. 1 term *c*). For each survey respondent, the corresponding gravity flow was multiplied by a correction factor of the total number of surveys divided by the number returned from that postal zone. Thus, trips made by survey respondents were given a greater weight if the number of surveys returned from that area was low. This correction in spatial bias ensures that differences in propagule pressure to different areas in the province are a result of differences in the attractiveness of those lakes versus artificial differences in the survey response rate.

Propagule flow between origins and destinations

The flow of propagules between each origin and destination was calculated as the sum of the trips made by the survey respondents (*pp*). Flows between sources (*i*) and destinations (*j*) are calculated as:

$$T_{ij} = A_i O_i w_j \left[\beta \exp(-\beta d_{ij}) \right] \qquad (2)$$

where O_i is the propagule outflow from each origin *i*, w_j is the measure of attractiveness for each destination *j*, and A_i is a balancing factor ensuring that total predicted outflow from each source is equal to observed outflow ($\sum_j T_{ij} = O_i$).

The balancing factor, A_i is calculated by:

$$A_i = \frac{1}{\sum_j w_j \left[\beta \exp(-\beta d_{ij}) \right]} \qquad (3)$$

Log$_{10}$-transformed Lake area (in ha)(data provided by the Ontario Ministry of Natural Resources) was used as the external measure of attraction (w_j).

Statistical comparison of patterns of spread

To account for differences in patterns of spread among the four species due to different lengths of time between the years of first record and the survey, propagule inflow to lakes ($T_j = \sum_i T_{ij}$) was backcast to years 1 through 7 of first record. That is, only lakes invaded within the first 7-year interval were considered as sources for outflow in the gravity models (O_i). Seven years was chosen as the interval since it is the maximum amount of time elapsed from the establishment of the most recent genus, *Cercopagis*, in 1998 to the 2004 survey.

Propagule inflow to 3215 lakes with a surface area greater than 25ha and within 5 km of a major road in Ontario was calculated for each of the species and for two time periods, years 1 and 7. Differences in patterns of inflow to each lake among species and time periods was tested by a 2-factor repeated-measures ANOVA, with species and time period as repeating factors.

Rates of spread

Annual rates of spread of *Bythotrephes* and *D. polymorpha* were calculated in ArcGIS (version 9.1, ESRI) by finding the minimum convex polygon formed by the centroids of each of the lakes including the Great Lakes. Rates of spread were standardized to year 1 of each species' invasion (i.e. Year 1 corresponds to 1982 and 1988 for *Bythotrephes* and *D. polymorpha*,

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respectively). Calculated rates of spread for *Cercopagis* and *D. rostriformis* were not possible due to their limited dispersal and the requirement of 3 points to form a polygon. The choice of nonlinear model fit to the data was based on minimum Akaike Information Criterion (Akaike 1983).

Relationship between propagule pressure and invasion success

The relationship between propagule pressure and invasion status for *Bythotrephes* and *D. polymorpha* was modeled using boosted regression trees with gravity inflow scores to lakes as the independent variable and species presence/absence as the response variable (1/0). This modeling approach is recommended over other methods since it is able to take into account nonlinear relationships that are often present in ecological data (Elith et al. 2006). Although model training in boosted regression includes cross-validation as part of the fitting process (Ridgeway 2002), the data set of *Bythotrephes* and *D. polymorpha* indices of propagule pressure and lake invasion status were split prior to the analysis into two time periods. For *Bythotrephes*, the training portion of presence data set consisted of lakes invaded from 1982 to 1995 (years 1-14). Propagule pressure to inland lakes was backcast based on total inflow from lakes invaded up to 1994. That is, the invasion status of lakes in a given year depends on the propagule pressure from previously invaded lakes only. Lakes invaded from 1996 to 1999 (years 15-18) were used in the testing subset along with propagule pressure backcast to 1998. Analysis of propagule pressure was truncated at 1998 for *Bythotrephes* (Year 17) to compare with estimated Year 17 propagule

pressure for *D. polymorpha* (2004). 2004 was the final year for which data was available to calculate propagule pressure. Remaining lakes (noninvaded) were randomly assigned to the training/testing subsets in a 70:30 ratio. The same procedure was repeated for *D. polymorpha*, with lakes invaded between 1988-2001 and 2002-2005 for training/testing subsets. Boosted regression trees were modeled and evaluated with the R package gbm (Ridgeway 2007).

Lakes were classified as invaded if the estimated probability from the boosted regression models was greater than or equal to a threshold based on the shape of the receiver operator characteristic curve (ROC). The ROC plots the performance of the model being able to correctly predict an invasion (hit rate) versus incorrectly predicting an invasion when one had not occurred (false alarm rate) at different thresholds (Liu et al. 2005). The threshold was chosen based on the minimum distance from the upper left corner (i.e. departure from 100% model accuracy), with values often comparable to the prevalence of invaded lakes. The ROC was calculated with the R package verification (NCAR - Research Application Program 2007). Model performance was evaluated based on the area under the receiver operator characteristic curve (AUC). This criterion is used to test whether the model can predict better than at random, independent of the threshold used. Model performance is acceptable only if the AUC is significantly greater than 0.5 (random).

In the relationship between observed and classified invasion status, the 'hit rate' is the proportion of lakes correctly classified as invaded, and the 'false alarm rate' is the proportion of noninvaded lakes incorrectly classified as invaded.

Results

Bythotrephes and D. polymorpha have much broader distributions in Ontario, and elsewhere, than Cercopagis or D. rostriformis. These differences in distributions were reflected in broad differences in gravity score values and propagule pressure to Ontario lakes. The levels and pattern of propagule pressure differed significantly among the four species (Table 1). In year 1, propagule pressure was much higher for Bythotrephes than for D. polymorpha, both of which were much higher than Cercopagis and D. rostriformis (Figure 1). There was no difference in ranked gravity inflow between Cercopagis and D. rostriformis (Tukey HSD, p = 0.79). Gravity inflows also differed significantly between species in year 7, with inflow for D. polymorpha increasing the most, but still lower than that of Bythotrephes (Figure 1). D. rostriformis and Cercopagis had the lowest gravity scores in year 7, both of which were only marginally higher than in year 1. No consistent difference was observed in propagule pressure for the waterfleas versus those of the molluscs.

Patterns of propagule pressure differ greatly between Bythotrephes and Cercopagis in years 1 and 7 based on first recorded invasion. In the first year, propagule pressure for both Bythotrephes and Cercopagis originated only from Lake Ontario; even here, propagule pressure for Bythotrephes was twice that of Cercopagis (Figure 2 A, C). By year 7, Lakes St. Clair, Huron, Erie and Superior were all invaded and contributed 7, 34, 15 and 2% of the total propagule outflow, respectively (backcast to 1988; Figure 2 B). For Cercopagis, distribution was

limited to Lakes Ontario and Erie by year 7, and consequently, highest levels of gravity inflow were restricted to the southwestern corner of Ontario (Figure 2 D). Lakes Ontario and Erie contributed 54% and 46%, respectively, of total outflow during this period.

Gravity inflow to inland lakes for both *D. polymorpha* and *D. rostriformis* was limited to the southwestern corner of Ontario, as Lake Erie was the primary source in year 1. Gravity flow was only slightly higher for *D. polymorpha* than *D. rostriformis* in year 1 (Figure 2 E, G). By year 7, the spatial extent of high levels of propagule pressure for *D. polymorpha* greatly exceeded that of *D. rostriformis* (Figure 2 F, H). Four dominant sources of *D. polymorpha* propagules, Lakes Huron, Simcoe, Ontario and Rice Lake, contributed to 21, 18, 14 and 16% of the total outflow, respectively. *For D. rostriformis*, Lakes Ontario and Erie contributed 72% and 28%, respectively, of propagule outflow in year 7.

Range expansion for Bythotrephes and D. polymorpha

The rate of range expansion in Ontario differed between *Bythotrephes* and *D. polymorpha* and was largely influenced by *Bythotrephes* invasion into Lake Superior. *Bythotrephes* expanded its range at a near linear rate, whereas that for *D. polymorpha* asymptoted near year 11 (Figure 3). New *Bythotrephes* invasions are still occurring outside of its existing spatial range, including Lake-of-the-Woods in Northwestern Ontario in 2007, whereas most new *D. polymorpha* invasions are occurring within its current range, infilling the species' distribution in central Ontario.

Propagule pressure and invasion status

The overall relationship between gravity inflow and NIS presence in lakes differed between *Bythotrephes* and *D. polymorpha* based on boosted regression models. The likelihood of occurrence was much higher for *Bythotrephes* than for *D. polymorpha* at low levels of inbound propagule pressure (Figure 4). However, the likelihood of a lake being invaded increased more rapidly for *D. polymorpha* at higher levels of propagule pressure, and, in fact, exceeded the likelihood for *Bythotrephes* at very high levels of propagule pressure (Figure 4).

The boosted regression models performed very well for both species (AUC, $p < 0.0001$ for all models)(Table 2). The *Bythotrephes* model, formed on the training set from year 1982 to 1994, was able to correctly classify 88% of lakes invaded between 1982 and 1995, based on a threshold of 0.006. That is, lakes with an estimated probability of occurrence of 0.006 or greater were classified as invaded. When applied to the testing data set, the boosted regression model also correctly classified invasion status for 9 out of 10 lakes invaded between 1996 and 1999 (Table 2). The training model for *D. polymorpha* predicted 95% of the lakes invaded between 1988 and 2001 (training data set), and 93% of lakes invaded between 2002 and 2005.

Lakes where *Bythotrephes* was correctly predicted to occur based on the boosted regression model applied to pooled training and testing data sets (i.e. invaded from 1982-1999 inclusive) are located north of Lake Ontario and southeast of Georgian Bay (Lake Huron) (Figure 5A). Lakes that were misclassified included Lake Superior and Lake Shebandowan, a large lake

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located northwest of Lake Superior. Lakes invaded between 1988 and 2005 for which *D. polymorpha* occurrences were classified correctly included clusters north of Lake Ontario and northwest of the St. Lawrence River (Figure 5 B). Lakes Superior and Shebandowan were predicted to lack *D. polymorpha*, despite reports of larval zebra mussels in those lakes (Griffiths et al. 1991), as well as a cluster of lakes northwest of the St. Lawrence River.

Discussion

The ability to forecast dispersal is essential to development of effective risk assessment models and management policies for NIS, as preventative measures are often more cost-efficient that post-invasion control or eradication (Leung et al. 2002, Lodge et al. 2006). In this study, I developed the first set of refined dispersal models that utilized information on species' life-histories and associated differences in importance of dispersal mechanisms to characterize spread of four aquatic NIS.

Propagule pressure, climate/habitat matching between the source and recipient regions, and history of invasion success are the only consistent attributes associated with invasion success across a wide range of taxa (Hayes and Barry 2007). Studies have revealed the importance of the number of propagules per introduction event for freshwater fish (Marchetti et al. 2004), birds (Cassey et al. 2005), insects (Memmott et al. 2005) and beetles (Grevstad 1999). Introduction of large numbers of individuals serves as a buffer against mortality caused by stochastic events during a founding event (Lockwood et al. 2005).

Invasion success has also been associated with the number of introduction events for mammals (Forsyth et al. 2004). A combination of the number of propagules per event and number of transportation events may assist establishment success of birds (e.g. Veltman et al. 1996).

Many of the life-history traits associated with propagule pressure enhance NIS dispersal by interfacing with specific transport mechanisms. Some of the traits that facilitate dispersal in plants include low seed mass (Greene and Johnson 1993) and the high nutritional value of fruit and nuts, which assist in attracting consumers/dispersers (see Howe and Smallwood 1982). Some life-history traits may inadvertently enhance human-mediated dispersal, including vegetative propagation and production of diapausing eggs. For example, vegetative fragments of Eurasian watermilfoil (*Myriophyllum spicatum* L.) initiate colonies in new lakes following drift from colonized upstream locations (Madsen 1998), as well as by overland transport via fouled boat trailers (Newroth 1993).

For the cladocerans in this study, differences exist between the two species in the timing of seasonal peaks in population abundance and the proportion of the population with resistant resting stages coinciding with peak recreational activity. Although *Cercopagis* has greater absolute abundance than *Bythotrephes*, which is reflected in the propagule loads for specific mechanisms (Appendix 1), 99% of *Cercopagis* abundance occurs from June through October, whereas *Bythotrephes* populations increase earlier in the season (14% of population density occurring in April and May) (Appendix 1). In this study, 98% of those surveyed boated or fished in July and August, and therefore I expected

higher numbers of *Cercopagis* propagules based on relative abundance. Timing

of the proportion of resistant resting stages also differs between species and may

interface with human activity patterns to determine the extent of human-mediated

dispersal. Peak abundance of *Cercopagis* females with resting stages did not

occur until mid-August in Lake Ontario (Makarewicz et al. 2001), and has been

observed as late as Sept. 25th in the Baltic Sea (Gorokhova et al. 2000).

Seasonal recreational boating activity is declining at this time, thereby reducing

the likelihood of human-mediated species dispersal.

Life-history characteristics of *D. polymorpha* and *D. rostriformis* that may

result in dissimilar patterns of propagule pressure include differential mortality as

adults when trailered from a lake. Mortality of *D. rostriformis* adults due to aerial

exposure is higher than for *D. polymorpha* over comparable time periods

(Ricciardi et al. 1995). Estimates of veliger mortality during overland transport

are not available, although it is expected to be high (A. Ricciardi, pers. comm.).

Differences in the relative abundance of the two species also may be a key factor

in explaining their differential rates of spread. In the early 1990's, *D. rostriformis*

constituted a small fraction (2-7%) of dreissenid abundance in Lake Erie,

especially in the littoral zone where entrainment by boats and boat trailers is

most likely (Mills et al. 1993). By 1995, *D. rostriformis* became the dominant

dreissenid species in eastern Lake Erie and Lake Ontario, particularly in the

hypolimnion, where it accounted for between 64-98% of individuals at depth >

65m (Mills et al. 1999). At shallower depths (< 15 m), *D. rostriformis* comprised

less than 3% of dreissenid densities during the same time period. Thus,

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opportunities for human-mediated dispersal may have been far higher for *D. polymorpha* than for *D. rostriformis* during the first 18 years in the Great Lakes owing to differing depth distributions. If this is correct, *D. rostriformis* should spread much more quickly now, considering that it is now commonly encountered in shallow areas of the Great Lakes.

Many of the life-history characteristics associated with invasion success relate to the establishment of a self-sustaining population, providing the propagules are able to tolerate environmental conditions upon arrival and are able to integrate into the recipient community. Characteristics oft-cited for a number of taxonomic groups usually include the ability to colonize a wide variety of habitats (Morton 1996), minimal juvenile period (Rejmánek and Richardson 1996) and asexual or parthenogenetic reproduction (Lodge 1993), among others. For example, Thuiller et al. (2006) examined interactions between life-history attributes of nonindigenous plant species, environmental characteristics and human usage in a joint multivariate analysis. Human use (e.g. silviculture vs. ornamental import), life forms (e.g. tree vs. shrub) and seed size were the main correlates with NIS presence/absence.

Although this study focused on life-histories and propagule pressure, environmental tolerances may account for different patterns of invasion among the four species. Differences in thermal requirements for reproductive development and spawning, upper thermal tolerance, tolerance of hypoxia, and calcium requirements for shell production may be important considerations in the relative spread of *D. polymorpha* and *D. rostriformis*. Evidence of gonadal

development was reported for temperatures as low as 4.8°C for *D. rostriformis* in Lake Erie (Roe and MacIsaac 1997), though a minimum temperature of 12°C is reported for reproduction of *D. polymorpha* (Borcherding 1995). The relationship between temperature and reproduction is not straightforward, as hypolimnetic temperatures in Lake Ontario usually do not exceed 5°C (Mills et al. 1993). Adaptation of *D. polymorpha* and *D. rostriformis* to littoral and profundal habitat, respectively is another important consideration. In littoral habitat, *D. polymorpha* are able to tolerate temperatures up to 30°C for short periods of time, whereas the upper limit for D. rostriformis is 25°C (Spidle et al. 1995). Quagga mussels, on the other hand, demonstrate higher tolerances of hypoxic conditions more prevalent in hypolimnetic habitat. Lower respiration rates in the quagga mussel may confer a competitive advantage only if hypoxic conditions limit zebra mussel colonization (Stoeckmann 2003).

Low calcium concentration is a limiting factor in shell development of bivalves, but evidence for differential calcium requirements between the two species is limited. For example, *D. rostriformis* was relatively more abundant in the Manych River (Russia) where calcium concentrations were higher than in the Don River (Zhulidov et al. 2004). Lower threshold concentations for *D. polymorpha range* from 15 mg L^{-1} (Mellina and Rasmussen 1994) to 28.3 mg L^{-1} (Ramcharan et al. 1992). For most of the inland lakes in northern Ontario, calcium concentration ranges from 0.5 - 5 mg L^{-1} (data provided by Bill Keller, Ontario Ministry of the Environment), thus establishment is unlikely in these systems even if propagule pressure is high.

Differences in the upper thermal tolerance between *Bythotrephes* and *Cercopagis* may confer a reproductive advantage on the latter, although this would only apply to relatively shallow lakes. Evidence suggests *Bythotrephes'* metabolic limit occurs at ~26°C (Garton et al. 1990), whereas populations of *Cercopagis* have been noted between 24 - 30°C (MacIsaac et al. 1999). Higher temperatures allow for shorter embryonic development times (Lehman and Branstrator 1995), and thus population growth for *Cercopagis* is expected to be higher. As well, tolerance of high temperatures in the epilimnion may provide a thermal refuge for *Cercopagis* from planktivorous fish restricted to cooler waters such as lake herring (Coulas et al. 1998). Despite this, *Cercopagis* has exhibited little propensity to spread in North America (beyond the Finger Lakes, NY), whereas *Bythotrephes* has a very broad and ever-expanding occurrence in Ontario and, to a lesser extent, US states adjacent to the Great Lakes.

In summary, the four aquatic AIS profiled here differ dramatically in observed rate of spread and geographic range in Ontario. Range is positively associated with propagule pressure, as the two widespread species - *Bythotrephes* and *D. polymorpha* – have propagule loads that far exceed those of the species that have failed to spread (*Cercopagis* and *D. rostriformis*). No broad taxonomic differences existed with respect to patterns of spread. This study highlights that differences in life-history attributes influence the importance of different human-mediated dispersal vectors, which, in turn, affect rate of spread even for closely related species.

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Table 1. ANOVA summary of differences in propagule pressure for all 3215 lakes and all four species. The model tests for differences in propagule pressure among species for the two time periods, year 1 and year 7.

Effect	d.f.	MS	F	p
Year	1	1.70E+09	2226.77	< 0.0001
Error for Year	3214	7.65E+05		
Species	3	5.56E+08	1989.48	< 0.0001
Error for Species	9642	2.79E+05		
Species*Year	3	4.00E+08	1789.12	< 0.0001
Error for Species*Year	9642	2.23E+05		

Table 2. Classification of observed and predicted invasion status of lakes for *Bythotrephes* and *D. polymorpha* based upon gravity scores. Predictive ability of the boosted regression models was assessed by statistical significance of the area (AUC) under the receiver operating characteristic curve (ROC). Thresholds at which the probability of species' occurrence is classified as present were derived from the ROCs.

Species	Data subset	Observed-predicted invasion status (Present=1, Absent=0)				AUC	P(AUC)	Threshold from ROC	Hit rate	False alarm rate
		0,0	0,1	1,0	1,1					
Bythotrephes	Training	2374	286	3	21	0.94	< 0.0001	6.00E-03	0.88	0.11
	Testing	960	164	1	9	0.93	< 0.0001	3.00E-03	0.90	0.15
D. polymorpha	Training	2067	530	4	72	0.94	< 0.0001	1.20E-02	0.95	0.20
	Testing	866	247	2	26	0.92	< 0.0001	5.00E-03	0.93	0.22

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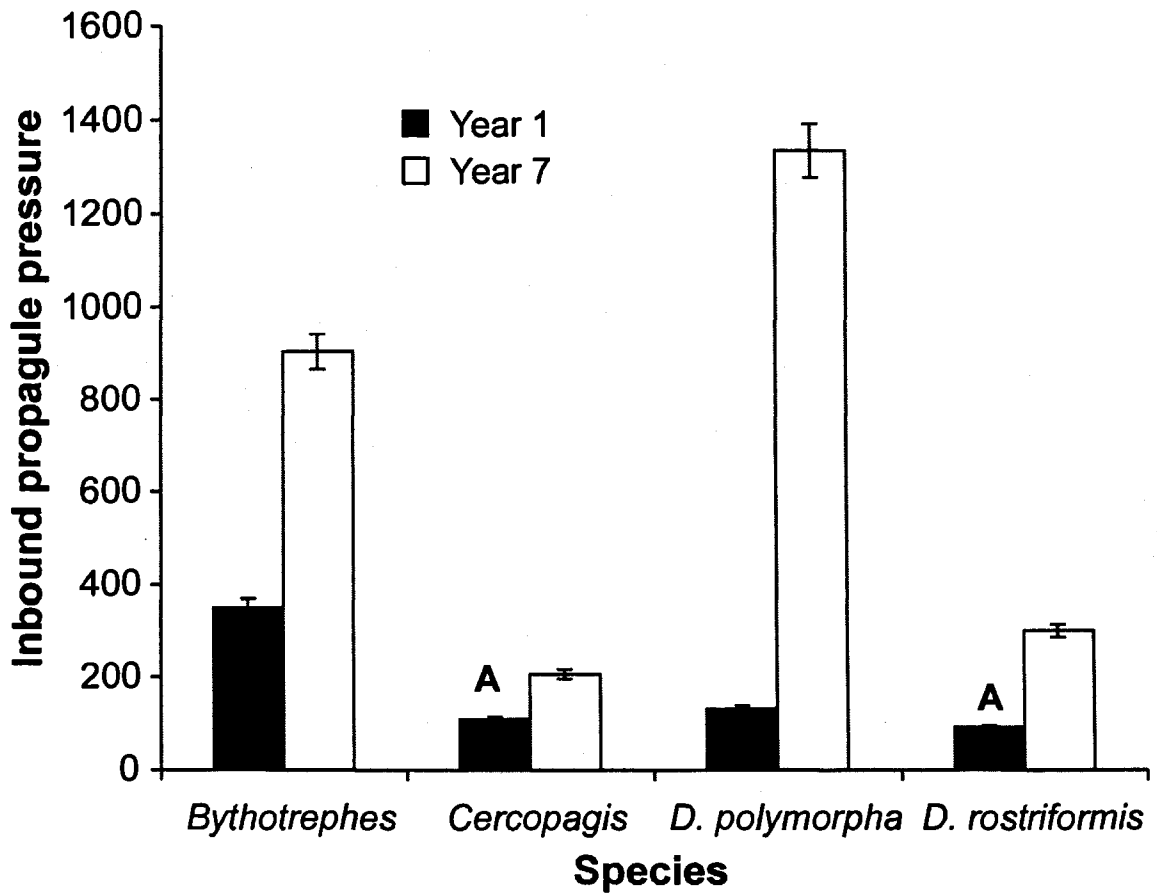
Figure 1. Mean (+/- 95% CI) of propagule inflow for species by year interaction from the repeated-measures ANOVA. Significant differences in gravity inflow occur between each combination of species by year except between *Cercopagis* and *D. r. bugensis* in year 1.
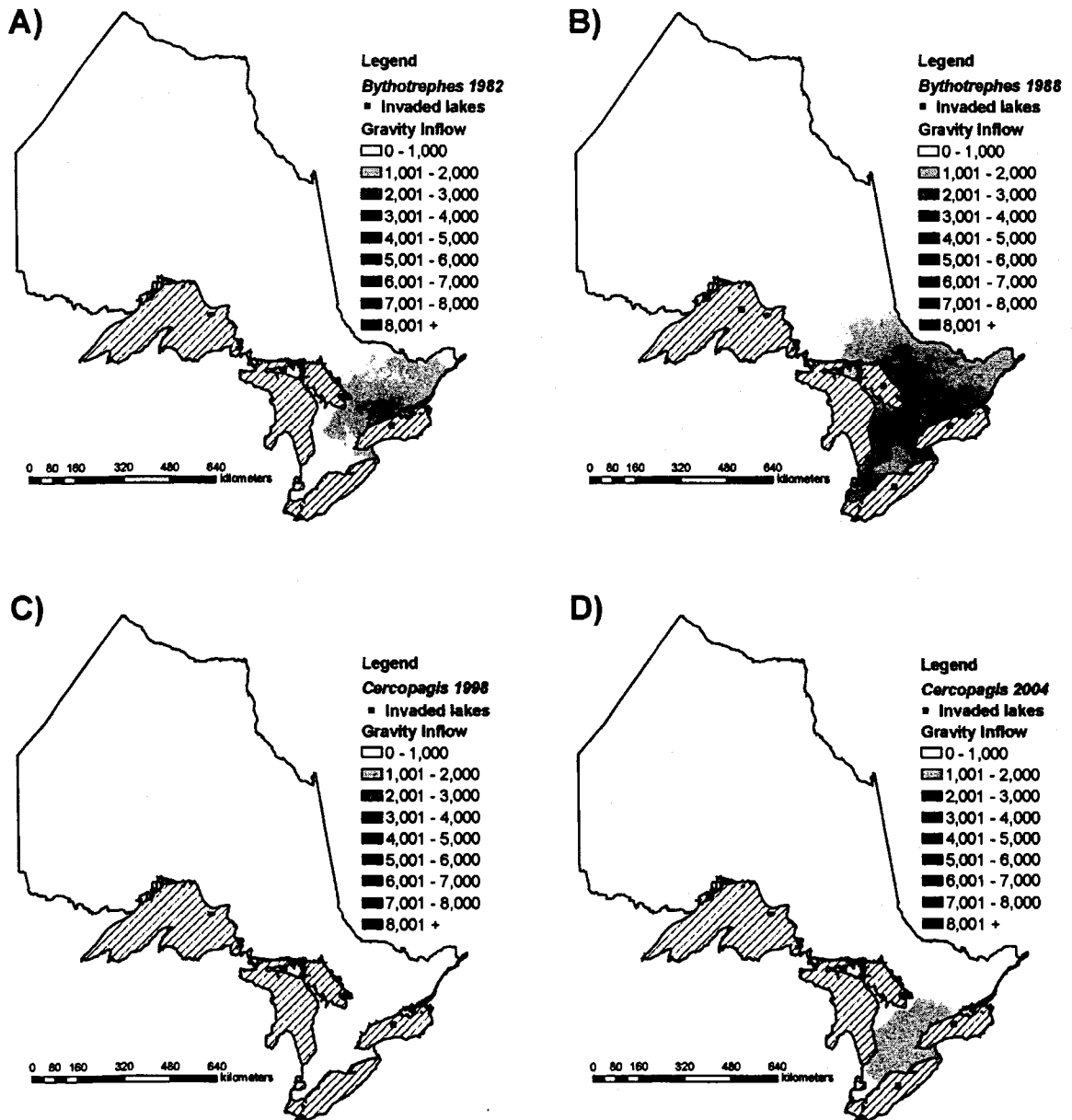
Figure 2. Maps of gravity inflow to Ontario lakes for *Bythotrephes* (Panel A,B),

Cercopagis (C,D), *D. polymorpha* (E,F) and *D. rostriformis* (G,H) in years

1 and 7 of their respective invasion sequences.

E)

Legend
D. polymorpha 1988
■ Invaded lakes
Gravity Inflow
☐ 0 - 1,000
▦ 1,001 - 2,000
■ 2,001 - 3,000
■ 3,001 - 4,000
■ 4,001 - 5,000
■ 5,001 - 6,000
■ 6,001 - 7,000
■ 7,001 - 8,000
■ 8,001 +

0   80 160   320   480   640
kilometers

F)

Legend
D. polymorpha 1994
■ Invaded lakes
Gravity Inflow
☐ 0 - 1,000
▦ 1,001 - 2,000
■ 2,001 - 3,000
■ 3,001 - 4,000
■ 4,001 - 5,000
■ 5,001 - 6,000
■ 6,001 - 7,000
■ 7,001 - 8,000
■ 8,001 +

0   80 160   320   480   640
kilometers

G)

Legend
D. rostriformis 1989
■ Invaded lakes
Gravity Inflow
☐ 0 - 1,000
▦ 1,001 - 2,000
■ 2,001 - 3,000
■ 3,001 - 4,000
■ 4,001 - 5,000
■ 5,001 - 6,000
■ 6,001 - 7,000
■ 7,001 - 8,000
■ 8,001 +

0   80 160   320   480   640
kilometers

H)

Legend
D. rostriformis 1995
■ Invaded lakes
Gravity Inflow
☐ 0 - 1,000
▦ 1,001 - 2,000
■ 2,001 - 3,000
■ 3,001 - 4,000
■ 4,001 - 5,000
■ 5,001 - 6,000
■ 6,001 - 7,000
■ 7,001 - 8,000
■ 8,001 +

0   80 160   320   480   640
kilometers

Figure 2 E-H.

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Figure 3. Rates of spread (km^2 yr^{-1}) for *Bythotrephes* and *D. polymorpha* in

Ontario based upon year of first reported invasion in the Great Lakes.

Year 1 corresponds to 1982 for *Bythotrephes*, and 1988 for *D.*

polymorpha. Equations for fitted curves are $y=-258x^2+24322x$ and $y=-382x^2+16077x$ for *Bythotrephes* and *D. polymorpha*, respectively.
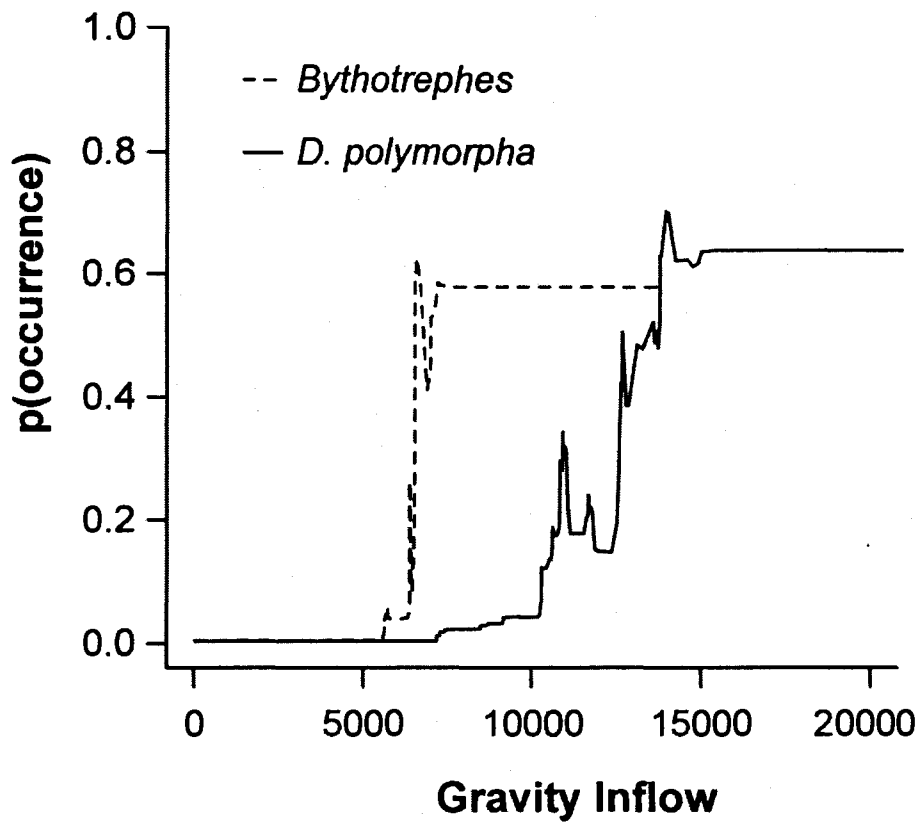
Figure 4. Plot of probability of occurrence and gravity inflow for *Bythotrephes* (A)

and *D. polymorpha* (B) based on the boosted regressions.

Figure 5. Estimated probability of occurrence based upon boosted regression of gravity scores and classification of invaded lakes for *Bythotrephes* and *D. polymorpha*.
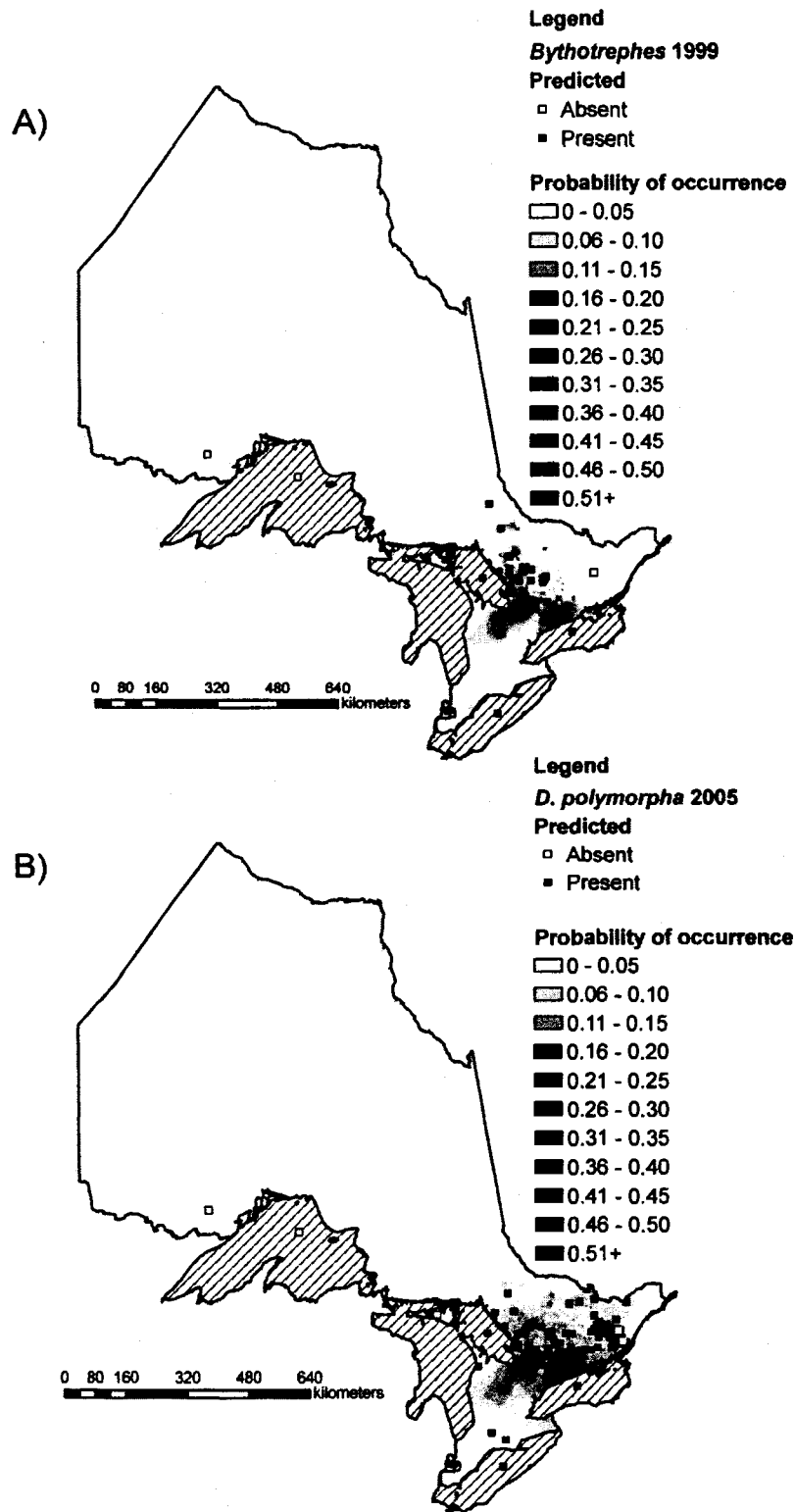
Figure 5.

Chapter 5 Appendix. Proportion of recreationalists at risk of transporting *Bythotrephes*, *Cercopagis*, *D. polymorpha* and *D. rostriformis* propagules with associated propagule loads for each mechanism. Propagule loads are on an index from 0-5 individuals unless indicated.

Risk factor	Proportion of recreationalists	*Bythotrephes longimanus*	*Cercopagis pengoi*	*D. polymorpha*	*D. rostriformis*
Date risk[1,2]		0.001*# days in Nov-Mar + 0.14*# days in Apr-May + 0.86*# days in Jun-Oct[1]	0.01*# days in Nov-Mar + 0*# days in Apr-May + 0.99*# days in Jun-Oct[7]	0.37*# days in Nov-Mar + 0.04*# days in Apr-May+ 0.59*# days in Jun-Oct)[2]	0.29*# days in Nov-Mar + 0.05*# days in Apr-May+ 0.66*# days in Jun-Oct)[9]

Proportion of

resting stages

in population[1]

Jan 1-Jul 3: 0	Jan 1-Jul 3: 0.001	1
Jul 4-9: 0.05	Jul 4-9: 0.007	
Jul 10-16: 0.03	Jul 10-16: 0	
Jul 17-24: 0.49	Jul 17-24: 0	
Jul 25-31: 0.72	Jul 25-31: 0.014	
Aug 1-6: 0.44	Aug 1-6: 0.087	
Aug 7-14: 0.40	Aug 7-14: 0.055	
Aug 15-21:0.67	Aug 15-21:0.111	
Aug 22-Sep 30:	Aug 22-Sep 30:	
0.71	0.0263	
Sep 31-Dec 30: 0	Sep 31-Dec 30: 0	1

Bait buckets	0.389	6[3]	240[8]	31[5]	13[9]
Anchor	0.704	1	1	2	2
Downrigger	0.220	10[4]	400[8]	1	1
Fishing line	0.797	10[4]	400[8]	1	1

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Recreational activities					
Boating	0.714	1	1	2	2
Fishing	0.881	1	1	2	2
Swimming	0.624	0	0	0	0
SCUBA	0.066	1	1	1	1
Water skiing	0.325	1	1	1	1
Propagule viability after leaving lake		5	5	$v_{load} = \begin{cases} 4, \#days \leq 1 \\ 0.5, 1 < \#days \leq 4 \\ 0, \#days > 4 \end{cases}$ [6]	$v_{load} = \begin{cases} 2.7, \#days \leq 1 \\ 0.2, 1 < \#days \leq 4 \\ 0, \#days > 4 \end{cases}$ [6]
Macrophytes	0.016	1	1	2^5	$1^{5,9}$
Water-based					
Live well	0.005	60^4	2408^8	1230^5	$529^{5,9}$
Engine cooling	0.184	1	1	16^5	$7^{5,9}$

Bilge water	0.139	1	12^5	$5^{5,9}$
Transom well	0.087	1^3	40^8	12^5	$5^{5,9}$

[1] Estimated from data extracted from Yan et al. (2001).

[2] Estimated from data extracted from Dermott et al. (1993), Fraleigh et al. (1993), Nalepa et al. (1995).

[3] Measured from field surveys

[4] Estimated based on average *Bythotrephes* abundance of 6.9 ind. m^{-3} from field surveys and relative volume of each mechanism.

[5] Estimated adult or veliger abundance from Johnson et al. (2001)

[6] Estimated from data extracted from Ricciardi (1995).

[7] From Makarewicz et al. (2001)

[8] Estimated from relative abundance of *Bythotrephes* (6.9 ind. m^{-3}) and *Cercopagis* (281 ind. m^{-3}) from Makarewicz et al. (2001).

[9] Data based on Johnson et al. (2001) and relative abundance from Mills et al. (1993).

Chapter 6: Development of inland lakes as hubs in an invasion network

Summary

1. The ability to predict spatially-explicit dispersal by nonindigenous species is a difficult but increasingly important undertaking as it allows us to focus management efforts around areas identified as susceptible to invasion. Lakes may serve as useful models for these studies since the habitats are well defined, and vectors of spread may be readily identified and quantified. In this study, we examine patterns of spread of the nonindigenous spiny waterflea *Bythotrephes longimanus* to inland lakes in Ontario, Canada to identify lakes for which management efforts to reduce traffic would be most effective.

2. We surveyed people using lakes for recreational purposes to quantify movements of trailered boats and other risky activities to model relative vector traffic from invaded lakes to noninvaded lakes and to other invaded lakes. Nonlinear functions were developed to describe the cumulative number of invaded and noninvaded destination lakes visited by people leaving five important lakes already invaded by the spiny waterflea (Huron, Simcoe, Muskoka, Panache and Kashagawigamog). The relative difference in these functions was used to identify which lakes will develop into future invasion hubs and will therefore be most important to future dispersal of the species.

3. In the recent past, Lake Muskoka has been an important hub from which the spiny waterflea has invaded other lakes. It is unlikely to continue to be a source for waterflea invasion as most outbound traffic is to previously invaded

lakes. Conversely, most outbound traffic from Lakes Kashagawigamog and Simcoe is to noninvaded lakes, and therefore, these lakes are likely to develop into hubs in the future.

4. *Synthesis and applications.* These data on zooplankton in lake systems and associated mechanisms of transport indicate patterns not only of intrinsic value to lake management, but also of potential importance in understanding invasions more generally. Frequency distributions of the number of outbound connections to both invaded and noninvaded destinations from invaded sources follow a power function, consistent with scale-free networks. These networks indicate that a small proportion of sources function as hubs. Management efforts targeted to remove developing hubs from the invasion network, rather than equal effort applied to outbound vector traffic from all sources, may reduce the predicted rate of new invasions.

Introduction

People are causing rapid homogenization of aquatic communities world-wide through extinction of endemic species and introduction of nonindigenous species (NIS) (Hall & Mills 2000; Rahel 2002). The rate of introduction of NIS in coastal habitats and in the Laurentian Great Lakes has been increasing at an exponential rate for the past 200 years, reflecting intensive utilization of these habitats by people for transportation, recreation and food resources (Ruiz *et al.* 2000; Ricciardi 2001). Once successfully established in the Great Lakes, some NIS begin to colonize inland systems. The introduction of a NIS to a new habitat

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and its subsequent establishment depends on its ability to successfully pass through sequential 'filters' in the invasion sequence, beginning with introduction effort (Richardson *et al.* 2000; Kolar & Lodge 2001; Colautti & MacIsaac 2004). Introduction effort is composed of the number of introduction events, and the number of individuals introduced during each event.

Early attempts to model the dispersal of NIS focused on simple diffusive range expansion, which assumes constant population growth and a normal distribution for propagule dispersion distance (Skellam 1951). Range expansion thus occurred as a progressive wave from the invasion source at a rate proportional to the species' intrinsic rate of growth and its coefficient of diffusion. Invasions of lakes by NIS cannot be modelled by simple diffusion, however, because their discontinuous nature violates the assumption of spread in a homogeneous landscape. Despite this limitation, lakes may nevertheless provide excellent model systems with which to develop and test invasion concepts, including patterns and mechanisms of dispersal, as they consist of well-delineated patches of suitable habitat in an unsuitable, terrestrial matrix. Dispersal of some aquatic species appears consistent with stratified diffusion, in which the redistribution kernel is leptokurtic (Kot, Lewis & van den Driessche 1996). Here range expansion occurs by a combination of local and long distance dispersal (Hengeveld 1989). A thicker tail in the redistribution kernel increases the range of colonization, though the location of new satellite colonies cannot be predicted easily (Kot *et al.* 1996; Lewis & Pacala 2000). Examples of aquatic species whose dispersal in the United States is seemingly consistent with

stratified diffusion include the zebra mussel *Dreissena polymorpha* and waterflea *Daphnia lumholtzi* (Bossenbroek, Kraft & Nekola 2001; Havel, Shurin & Jones 2002; Kraft *et al.* 2002).

Human-mediated dispersal to inland lakes and reservoirs has been demonstrated for NIS of zooplankton, molluscs, macrophytes and fishes (e.g. Johnstone, Coffey & Howard-Williams 1985; Schneider, Ellis & Cummings 1998; Dzialowski, O'Brien & Swaffar 2000; Havel & Stelzleni-Schwent 2000; Johnson, Ricciardi & Carlton 2001; Rahel 2002). Pleasure boaters represent a potentially strong dispersal vector if vessels are moved from invaded to noninvaded lakes, as live NIS may be attached to trailers, boat hulls or engines, attached to macrophytes stranded on boat trailers, or contained in live well or bilge water (see Carlton 1993 for a full list). Dispersal rate and area of colonization can be determined empirically using the distance boaters travel after visiting an invaded lake or by the distance-decay relationship used to weigh the interaction strength between two masses in gravity models (e.g. Schneider *et al.* 1998; Buchan & Padilla 1999; Bossenbroek *et al.* 2001). The combination of emersion tolerance by some NIS life stages and dispersal events associated with recreational boating can increase the effective dispersal rate and range of NIS, and allow identification of specific lakes vulnerable to invasion. Groups of invaded and noninvaded lakes may, therefore, form a network linked by the movement of boaters and NIS propagules.

Networks are characteristic of many aspects of modern life, ranging from the structure of the brain to social relationships and electric power grids (Watts

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2003). Despite their ubiquity, common aspects of network structure and properties remained poorly understood until quite recently. Networks consist of linked nodes, with the structure of the former affected by the degree of connectedness of the latter. A number of studies have revealed that many networks are not randomly assembled, but rather contain a large number of nodes with only one or a few connections, and a small number that have a large number of connections. Networks conforming to this structure are termed scale-free, because the distribution of nodes classified by the number of connections follows a power law (Barabási & Bonabeau 2003). Highly connected nodes, or hubs, in such a network can potentially have an unlimited number of links (Barabási & Bonabeau 2003), although this possibility seems remote in the context of ecosystems linked through invasion by NIS. The development of scale-free networks requires both growth through addition of nodes to the network, and preferential attachment of new links to existing nodes in proportion to the number of links already connected to that node (i.e. 'the rich-get-richer'; Barabási & Bonabeau 2003). Examples of scale-free networks include the Internet, neural networks and research collaborations (Albert, Jeong & Barabási 2000; Watts & Strogatz 1998; Barabási & Bonabeau 2003).

Biological invasions of lakes may be considered as a developing network in that lakes form discrete nodes connected to one another by natural or, more commonly, human dispersal vectors; additional nodes are created as more lakes become invaded. It may be possible to develop insights into patterns of dispersal of NIS from the topology of invasion networks. These models require information

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on the interaction strength among nodes based on the relative amount of vector traffic, and whether the nodes act as hubs (i.e. have high connectivity) or are relatively unimportant (i.e. have few connections). In marine systems, a transport network exists in which cargo ships travelling to major ports-of-call, which act as hubs, maximizes economies of scale but inadvertently facilitates transport of NIS (Carlton 1996; O'Kelly 1998). For example, the comb jellyfish *Mnemiposis leidyi* was introduced into the Black Sea in the early 1980's, and subsequently dispersed to the Azov, Marmara, Mediterranean and Caspian Seas, most probably as a consequence of ballast water discharge from a cargo ship (Ivanov *et al.* 2000).

The spiny waterflea *Bythotrephes longimanus* (Leydig) was discovered in Lake Ontario in 1982, and has since dispersed to the other Great Lakes and to adjacent inland lakes (Bur, Klarer & Krieger 1986; MacIsaac *et al.* 2004). A key life-history characteristic of the spiny waterflea that facilitates its dispersal to new lakes is its ability to produce resting eggs that remain viable long after the parent has died. Resting eggs are highly resistant to adverse environmental conditions, including desiccation and passage through fish digestive tracts. *Bythotrephes* adults with resting eggs may become fouled on fishing gear or other submerged materials in invaded lakes, and subsequently detach and hatch in novel lakes if the same contaminated equipment is used (MacIsaac *et al.* 2004). Some lakes invaded by *Bythotrephes* may serve as invasion hubs if departing boaters and anglers travel to large numbers of noninvaded destination lakes. One popular recreational lake (Muskoka) in central Ontario has apparently caused up to 39

other inland lake to become invaded either directly or indirectly (MacIsaac *et al.* 2004; Fig. 2). Patterns of dispersal strongly support the concept that Lake Muskoka has served as an invasion hub. Other well-connected lakes could develop into invasion hubs, particularly in other parts of the province where thousands of noninvaded lakes occur.

In this paper, we examine patterns of human vector movement to assess whether some invaded systems have the potential to develop into invasion hubs. We also examine the invasion process in terms of a growing network, and illustrate that while the total number of connections between invaded sources, and invaded and noninvaded destinations theoretically increases at a geometric rate, the realized vector traffic associated with recreational boating increases at a much-reduced rate. Finally, we provide evidence that lakes invaded by *Bythotrephes* form a scale-free network in which vector traffic to other lakes is non-random.

Methods

Identification of nascent hubs

We obtained data on recreational boater movement in Ontario from field surveys in 1999 and 2003, which were designed to develop a production/attraction-constrained gravity model of *Bythotrephes* dispersal (MacIsaac *et al.* 2004). Gravity models can be used to predict dispersal from invaded source habitats based upon their interaction strength with noninvaded destination habitats (see MacIsaac *et al.* 2004). Surveys conducted at marinas

and boat ramps were used to identify which invaded and noninvaded destinations were frequented by boaters, anglers and other recreational users departing from invaded lakes. For this study, we chose a subset of that data, consisting of five lakes reported invaded by *Bythotrephes*. These five lakes (i.e. Huron, Simcoe, Muskoka, Kashagawigamog and Panache) collectively had the highest quantified amount of outbound vector traffic and were reported to have been invaded in different years (Fig. 1).

To determine the degree of redundancy in outbound vector traffic associated with different boaters, we conducted a Monte Carlo simulation of the cumulative number of different lakes visited as a function of the number of surveys sampled. We randomly selected samples of incremental size, without replacement, from $i = 1$ to n, where n is the total number of surveys conducted for that source lake. This procedure was repeated for 100 bootstrap iterations, with the average and standard error of the cumulative number of destinations calculated (Fig. 3). Separate saturation functions were developed for outbound vector traffic to invaded and to noninvaded lakes. Saturation functions were fitted as asymptotic (i.e. hyperbolic) curves to the averages of the iterations, using Statistica (v. 5.5, Statsoft Inc., Tulsa, OK, USA) (Eqn. 1). Models were built used least-squares loss functions and Hooke-Jeeves/Quasi-Newton root solving methods (Hooke & Jeeves 1961). Asymptotic functions were selected after preliminary inspection of the data. The non-linear model utilized to describe the number of independent lakes visited is:

$$y = \frac{\alpha \beta x^{\gamma}}{1 + \beta x^{\gamma}} \tag{1}$$

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where y is the mean cumulative number of visited invaded or noninvaded

destination lakes, x is the number of surveys sampled, and α, β and γ are

estimated parameters.

To predict the number of invaded and noninvaded destinations that

boaters may visit during a single season (May 24 to September 2), we obtained

estimates of lake use by contacting marinas, cottage associations and

government agencies. We then extrapolated the saturation function curves to

the expected number of people using the lake for recreational purposes. We

repeated this procedure for each of the five major source lakes in the study to

determine whether risk profiles of the source lakes differ, indicating differing

propensities of becoming future invasion hubs.

Network of invaded lakes

As lakes become invaded, the number of actual and theoretically possible

connections changes. We assessed these changes by tabulating the number of

actual connections to newly invaded lakes for each year, and by calculating the

theoretical number of connections ($k_{inv,t}$) to newly invaded lakes ($n_{t,o}$) from

previously invaded lakes *(m)* described by:

$$k_{inv,t} = \sum_{o=1}^{p} n_{t,o} m \qquad (2a)$$

where p is the number of newly invaded lakes for a particular year.

As lakes become invaded, the number of noninvaded destinations is

decreased by the same number that invaded lakes increase (i.e. there exists a

finite number of lakes in the network). The theoretical number of vector inflows

to noninvaded lakes from previously invaded lakes ($k_{non,t}$) for a particular year is:

$$k_{non,t} = (I - \sum_{o=1}^{p} n_{t,o} - m)m \tag{2b}$$

where $n_{t,o}$ and m are newly and previously invaded lakes, and I is the total

number of lakes identified in surveys of people using the lake for recreational

purposes. Total lake number is based on survey data to set a boundary on the

network of potential noninvaded lakes and to provide a means of comparing a

theoretical network of invaded and noninvaded lakes to the actual network of

boater traffic. The actual number of connections from previously invaded lakes

to other lakes considered only the presence/absence of flows between lake

couples, and was not weighted by the intensity of flow.

We tracked annual development of both invaded to invaded, and invaded

to noninvaded networks by calculating the ratio of cumulative actual to theoretical

number of connections, or clustering coefficient (Watts 2003). Clustering

coefficients near 1 indicate that theoretical connections are realized by actual

boater traffic, and that the network consists of a few, large clusters, whereas

small coefficients indicate many smaller, more diffuse clusters.

To assess properties of the network, we tallied the number of connections

from invaded lakes to invaded and noninvaded destinations in each of 1999 and

2003, and constructed frequency distributions. We fitted 2-parameter power

($y = b_0 x^{b_1}$) and exponential ($y = b_0 \exp(b_1 x)$) curves to the frequency distributions

of links using least-square methods. Analyses utilized the median number of

connections for each connection category (Fig. 5). Networks that develop without preferential attachment of links are characterized by an exponential rather than power distribution and are not scale-free (Barabási & Bonabeau 2003).

Results

Boater traffic patterns

Differences in the slope and asymptote of the curves fit to the potential number of destination lakes visited by recreational boaters reveals the development of some source lakes as existing or potential invasion hubs (Fig. 3). Lake Muskoka was the first inland lake reported invaded, in 1989. It quickly developed into a regional hub for two reasons. First, all of its outbound traffic was to noninvaded lakes (excepting the Great Lakes). Secondly, the total amount of traffic leaving this source was high, as we estimate 1452 individuals trailered boats from the lake each year. While this lake was critical in the initial dispersal of *Bythotrephes* among inland lakes (Fig. 1), it appears unlikely that Lake Muskoka will continue to serve as an invasion hub because more vector outflow is directed to lakes already invaded than to those that have not been invaded (Fig. 3). Boaters are predicted to visit 40 invaded and 33 noninvaded destinations, respectively, from Lake Muskoka.

Two other lakes—Simcoe and Kashagawigamog—exhibit the opposite pattern of outbound vector flow. For example, the ratio of noninvaded to invaded destination visitations was 1.53 and 2.14 for the former lakes, while that of Lake

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Muskoka was only 0.83 (Fig. 3). Moreover, the total number of noninvaded lakes

visited from these sources (55 and 75, respectively) was much higher than that

from Lake Muskoka (Fig. 3). When combined with the total number of visits to

noninvaded lakes from surveys and seasonal estimates of the number of

recreationalists departing Lakes Simcoe (3774) and Kashagawigamog (1840),

these systems are expected to develop as invasion hubs. Available evidence is

consistent with this forecast. For example, eight lakes were reported to have

been invaded in Ontario during 2003, of which five were included in our original

survey, all with 'noninvaded' status. For three of those lakes, Lake Simcoe was

the single largest source of inbound boater traffic to one of these lakes (Maple),

whereas Lake Kashagawigamog was the dominant vector source for the other

two (Boshkung and Drag).

Boater traffic from Lake Huron followed a similar trend to that from Lake

Muskoka at low survey numbers, as a disproportionate amount of outflow is to

other invaded lakes (Fig. 3). However, the actual number of boaters utilizing this

lake is enormous (but unmeasured), and at high (e.g. 2000) seasonal usage, the

asymptotic number of noninvaded lakes visited (104) greatly exceeds that to

invaded lakes (39).

Boaters from Lake Panache were initially more likely to visit noninvaded

than invaded lakes. However, at a moderate number of boaters (~ 200), the

curves extrapolating boater behaviour intersect, and traffic to other invaded lakes

was more common. We project that ~660 boats are trailered out of this lake

seasonally, suggesting that most outbound vector traffic is destined to other

invaded lakes. This finding may not be robust, however, owing to the low sample size of boaters in our survey (n = 19) used to construct the curve, as well as to the poor asymptotic fit to the available data (Fig. 3). Nevertheless, Lake Panache was identified in our surveys as the source of two of the eight newly invaded lakes (Walker and Bear).

Network complexity, growth and development

Most of the early invasions by *Bythotrephes* occurred in central Ontario following initial invasions of Lakes Muskoka, Joseph and Rosseau (Fig. 1A). By summer 2003, at least 57 inland lakes and lake systems were invaded (Fig. 2). The sequence in which the lakes appear in the network is directly related to the amount of inbound vector flow from invaded sources, indicating a priority effect based on the intensity of connectance (MacIsaac *et al.* 2004). Thus, we propose that actual or nascent hubs in the network were invaded in the following sequence: Lake Huron (1986), Lake Muskoka (1989), Lakes Simcoe and Kashagawigamog (1993), and Lake Panache (1999) (Fig. 1D). Each of these lakes has large amounts of outflow traffic to other lakes.

Once a lake has become invaded, it can theoretically serve as a source to all the other noninvaded lakes in the system. The actual number of total connections from invaded sources to noninvaded destinations increased in a stepped fashion (Fig. 4A). Initially, 39 inland lakes were connected via vector flow from Lake Huron. This number increased sharply in 1989 with invasion of Lakes Muskoka, Joseph and Rosseau, and again in 1992 when Lake Temagami

was invaded. The latter lake lies at the northernmost boundary of *Bythotrephes'* distribution in Ontario and has outflows to some lakes not associated with the previous three. Total number of connections to noninvaded lakes increased again in 1993 when Lakes Simcoe and Kashagawigamog were invaded. Finally, all noninvaded lakes in the network were connected to at least one invaded lake by 1999 when Lake Panache was reported to have been invaded (Fig. 4A).

The relationship between the actual and theoretical number of connections from invaded lakes differed temporally for newly invaded and noninvaded destinations (Fig. 4B). The theoretical rate of growth in any given year is geometric for traffic among invaded lakes, and for traffic from invaded lakes to noninvaded lakes. The latter rate of growth is, however, much steeper. The clustering coefficient to invaded lakes was always higher for invaded than for noninvaded systems (Fig. 4B), indicating that invaded lakes form a tighter network among themselves than with noninvaded lakes. In addition, the clustering coefficient declined over time for both networks, as lakes with fewer contacts to other invaded or noninvaded systems became invaded (Fig. 4B). Clustering coefficients declined because the theoretical number of connections grew at a faster rate than did actual traffic.

A scale-free invasion network

With one exception (Fig. 5A), the network of actual connections from invaded lakes to other lakes followed a scale-free topology (Fig. 5B,C,D). Most invaded lakes (49-79%) have few (≤ 5) connections to other lakes, while a few

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had many connections (> 20) (Fig. 5). An exponential curve provided a slightly better fit to the distribution of links from invaded to invaded lakes in 1999 (r^2 = 0.981) than did a power curve (r^2 = 0.952) (Fig. 5A). However, the distribution of links for traffic to noninvaded lakes in 1999 was better described by a power law function (r^2 = 0.989) than by an exponential one (r^2 = 0.968), indicating a scale-free topology. Similarly, in 2003, the distribution of links was best described by a power law function for traffic to both invaded (r^2 = 0.996) and noninvaded (r^2 =0.994) lakes, indicating that the few invaded lakes with large numbers of contacts with noninvaded systems may develop as future hubs (Fig. 5D). Slopes of fitted power curves increased in steepness from 1999 to 2003, supporting the view that newly invaded lakes had fewer connections to other lakes during the latter period.

Discussion

Accurate prediction of potential range expansion is a key component of attempts to limit ecological and economic harm wrought by NIS, as it is often easier and less costly to prevent new invasions than to mitigate impacts once species have become established (Kolar & Lodge 2002; Leung *et al.* 2002). In this paper, we examined the development of lakes as invasion hubs based upon analyses of human vector behaviour, in particular the volume of vector flow from invaded sources as well as the ratio of that volume that is directed to noninvaded versus invaded destinations. Our analysis indicates that human vector activities

result in the creation of clusters of invaded lakes centred on existing or nascent hubs.

Ecologists have implicitly recognized the existence of hubs and their importance in facilitating invasion of novel habitats (e.g. Carlton 1996; Leppäkoski *et al.* 2002), though clear examples of functioning hubs are rare. Simberloff & Boecklen (1991) demonstrated that invasion of nonindigenous birds to Oahu and Kauai often resulted in introduction to other Hawaiian islands shortly thereafter. However, many of the clearest examples of functioning hubs derive from studies of coastal marine ecosystems. For example, Leppäkoski *et al.* (2002) reported a large number of successfully established NIS in the Baltic Sea, and noted that some of these species later colonized the Great Lakes and other ecosystems through secondary invasions. Likewise, Ruiz *et al.* (2000) observed that colonization by NIS of coastal habitats utilized by transoceanic vessels may result in 'stepping-stone' invasion sequences. Perhaps the best example of an invasion hub is provided by the zebra mussel *Dreissena polymorpha* in the Great Lakes. Since the species was first reported in Lake St. Clair in 1988 (Hebert, Muncaster & Mackie 1989), it has dispersed to a tremendous number of ecosystems throughout eastern North America that are linked directly or indirectly to the Great Lakes (e.g. Kraft & Johnson 2000; Bossenbroek *et al.* 2001; Johnson *et al.* 2001).

Lake Muskoka was the first inland lake invaded by *Bythotrephes*, owing to its dominant vector inflow from Lake Huron (Fig. 1). Lake Muskoka is a very popular recreational lake and has very strong links to other lakes in the region via

departing boaters and anglers. Indeed, in the initial years of network formation, up until 1991 inclusive, the matrix of links among invaded lakes was symmetrical, with all systems having vector outflows to the others (Fig. 4). Thereafter, the clustering coefficient for the invaded lakes network declined quickly as new systems with few links were added to the network (Fig. 4). The degree of clustering among invaded lakes continued to decline through 2003, although it remained consistently higher than that between invaded and noninvaded lakes. The clustering coefficient for invaded to noninvaded lakes peaked during 1989, reflecting the establishment of *Bythotrephes* in Lake Muskoka. Clustering of invaded to noninvaded lakes was otherwise consistently low, typically < 20% of the number of possible connections (Fig. 4B).

While Lake Muskoka has served as an invasion hub, and was apparently responsible for 39 direct and indirect invasions of other lakes as of 2003, it is less likely than either Lake Simcoe or Lake Kashagawigamog to function as a hub in the future. More of the projected outflow of recreational traffic from Lake Muskoka is to lakes that are invaded as opposed to noninvaded (Fig. 3). Conversely, outflows from Lakes Simcoe and Kashagawigamog are directed principally to noninvaded lakes. These lakes also have a higher ratio of outbound flow directed toward noninvaded lakes than does Lake Muskoka. Consequently, it seems likely that these lakes will serve as future hubs.

Two other lakes also merit consideration as possible future hubs. Lake Panache and Lake Nipigon are located in northern Ontario, distal to the current cluster of invaded lakes centred on Lake Muskoka. Vector outflow from Lake

Nipigon has yet to be quantified, though both it and Lake Panache support large recreational fisheries and are located in lake districts with few reported invasions by *Bythotrephes*. Moody & Mack's (1988) theoretical model suggested that the overall rate of spread of NIS may be reduced if 30% of satellite colonies are eliminated. Long-term control of satellite colonies of the invasive wood weed *Mimosa pigra* prevented the development of large stands in Australia's Kakadu National Park (Cook, Setterfield & Maddison 1996). Likewise, eradication programmes appear to have eliminated populations of black-striped mussels *Mytilopsis sallei* from northern Australian coastal waters, and of the green alga *Caulerpa taxifolia* in southern California before either could function as a hub for regional range expansion (Ferguson 2000, Jousson *et al.* 2000). In this study, nascent hubs must be considered as 'supercritical' (Moody & Mack 1988), as these lakes are already invaded and have high apparent connectance to noninvaded systems.

The role of humans as dispersal vectors has been examined for several NIS and can be used to predict patterns and rates of spread. For example, recreational boating has been implicated in the transportation of aquatic macrophytes and molluscs (Johnstone *et al.* 1985; Padilla, Chotkowski & Buchan 1996; Bossenbroek *et al.* 2001; Johnson *et al.* 2001). Backcast and forecast gravity models of *Bythotrephes* movement among Ontario lakes based on recreational boating were able to predict not only which lakes were likely to be invaded, but also the order in which they were invaded (MacIsaac *et al.* 2004). In any given year, lakes that became invaded received significantly more traffic

from invaded sources than lakes that remained noninvaded. Alternative vectors

for *Bythotrephes* transport include the passive dispersal through connected

waterways, and transportation via waterfowl and through ingestion of resting

eggs by fish, although the latter two are inconsistent with existing patterns of

species dispersal and seem unlikely to be major vectors.

For application to terrestrial systems, vector analysis requires discrete

habitat patches. Thus, the analysis may be limited to metapopulations of

nonindigenous species or to situations where the vector distance involved in

human-mediated transport is greater than that possible by passive dispersal. For

example, the dispersal of the Argentine ant (*Linepithema humile*) and

nonindigenous plants has been accelerated due to human-mediated

introductions at several locations (Mack & Lonsdale 2001; Suarez, Holway &

Case 2001).

Scale-free Networks

The scale-free topology of the invasion networks and the presence of a

mature and two nascent hubs have implications for the management of

Bythotrephes dispersal. The topology of the scale-free network stems from

growth and preferential attachment to earlier hubs (i.e. "rich-get-richer", Barabási

& Bonabeau 2003). From this premise, Lake Muskoka, established as the

earliest invasion hub, should have had the highest number of connections to

other lakes. However, surveys indicated that boaters leaving Lake Muskoka

travelled to only 0.36 other lakes per capita, whereas those departing from Lakes

Simcoe and Kashagawigamog visited 0.45 and 1.0 lakes per capita, respectively

(Fig. 3). These lakes may have greater connectance to other lakes than does

Lake Muskoka because their average distance from other invaded and

noninvaded study lakes (85 and 48 km, respectively) is lower than that (102 km)

from Lake Muskoka. Lakes located near the hubs are likely to be invaded first,

as recreationalists usually travel shorter distances after visiting invaded lakes

(e.g. Schneider *et al.* 1998; Bossenbroek *et al.* 2001; MacIsaac *et al.* 2004).

The slopes of the power curves fitted to the distribution of links ranged from

-1.6 to -2.1 (Fig. 5), and are slightly lower than those reported for the scale-free

networks of internet (-2.45, Albert *et al.* 1999) and metabolic reactions (-2.2,

Jeong *et al.* 2000). The increase in slope steepness in the network of

connections to noninvaded lakes in 2003 relative to 1999 (Fig. 5) reflects the

growth of the network, encompassing more invaded lakes with fewer outbound

connections to other systems. This temporal change contrasts with theoretical

expectations for scale-free networks, in which the power-law distribution of links

is independent of time (Barabási & Albert 1999). This difference in slopes may

be an artifact of the relatively low number of studied lakes comprising the

network, as theoretical models usually contain several orders of magnitude more

connections (Barabási & Albert 1999).

The scale-free topology of the invasion network increases its resistance to

random perturbations, as nodes with few connections have the same probability

of removal as major hubs. However, scale-free networks such as protein

interactions (Jeong *et al.* 2001), the internet (Albert *et al.* 2000), and some food

webs (Dunne *et al.* 2002), are highly susceptible to attacks directed against the nodes with highest connectance. After 18% of the most connected hubs were removed, the scale-free network proposed by Albert *et al.* (2000) collapsed into a series of smaller, independent clusters. One consequence of this disruption is the requirement of additional connections to propagate a signal across the network. For management purposes, if vector outflow from established or developing hubs were reduced, it might be possible to retard the rate at which *Bythotrephes* disperses to new lakes. This feat might be accomplished through fewer outbound trips from these lakes (an unlikely event), or by reducing the number and/or viability of propagules exported per transport event (e.g. by cleaning of fishing gear and/or boats).

Currently, analysis of the dominant vector flow indicates that the longest path (i.e. stepping-stone) across which the *Bythotrephes* invasion signal could propagate in Ontario is from Lake Huron → Muskoka → Simcoe → Kashagawigamog → Soyers and Canning (MacIsaac *et al.* 2004). However, for some invasion networks with scale-free topologies, a reduction in invasion risk depends upon the nature of the transport mechanism(s). Although the network of major shipping ports and cargo ship traffic follows a scale-free topology, Drake & Lodge (2004) found that overall invasion rate to the world's coastal marine ecosystems could be reduced more effectively by a small per capita decline in invasion risk for all ships than by 'knocking-out' key invasion hubs. This possibility must be weighed against the cost and opportunity to implement either strategy.

In summary, we have demonstrated that analyses of vector outflows from invaded source lakes may allow identification of lakes that currently or potentially function as invasion hubs, permitting the dispersal of the waterflea *Bythotrephes*. A network of vector flow exists linking invaded lakes together, whereas a much weaker network links invaded and currently noninvaded lakes. The degree of connectance of lakes in both networks has decreased considerably over time, as lakes newly added to the network are likely to have few outbound connections. Outbound vector traffic from hubs with large flows to noninvaded destinations should be targeted for management efforts to restrict the transportation of propagules across the network and to reduce the rate at which NIS disperse to novel sites.

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Tables

Table 1. Fitted asymptotic functions for the cumulative number of invaded or noninvaded destination lakes receiving trailered boats from five source lakes (see Fig. 3). The proportion of variance explained by the model (r^2) and total number of surveys collected from the source lake (N) are provided.

Lake	Destination status	Equation	r^2	N
Simcoe	Invaded	$y = \dfrac{37.00 \cdot 0.06x^{0.75}}{1+0.06x^{75}}$	0.999	101
	Noninvaded	$y = \dfrac{60.79 \cdot 0.01x^{0.79}}{1+0.01x^{0.79}}$	0.997	101
Panache	Invaded	$y = \dfrac{201.65 \cdot 0.01x^{0.88}}{1+0.01x^{0.88}}$	0.996	19
	Noninvaded	$y = \dfrac{90.78 \cdot 0.02x^{0.94}}{1+0.02x^{0.94}}$	0.998	19
Muskoka	Invaded	$y = \dfrac{44.77 \cdot 0.06x^{0.68}}{1+0.06x^{0.68}}$	0.999	110
	Noninvaded	$y = \dfrac{36.98 \cdot 0.004x^{1.05}}{1+0.004x^{1.05}}$	0.994	110
Kashagawigamog	Invaded	$y = \dfrac{36.37 \cdot 0.05x^{0.82}}{1+0.05x^{0.82}}$	0.999	44
	Noninvaded	$y = \dfrac{80.60 \cdot 0.01x^{0.93}}{1+0.01x^{0.93}}$	0.996	44
Lake Huron	Invaded	$y = \dfrac{39.11 \cdot 0.07x^{0.67}}{1+0.07x^{0.67}}$	0.998	93
	Noninvaded	$y = \dfrac{103.68 \cdot 0.01x^{0.82}}{1+0.01x^{0.82}}$	0.998	93

Figure 1. Diagram of measured network traffic from previously to recently

invaded lakes based on records of first reporting. Stages of the invasion

network are shown for 1989 (A), 1990 (B), 1993 (C) and 1999 (D).

Shaded boxes represent existing or nascent inland hubs, and Lake
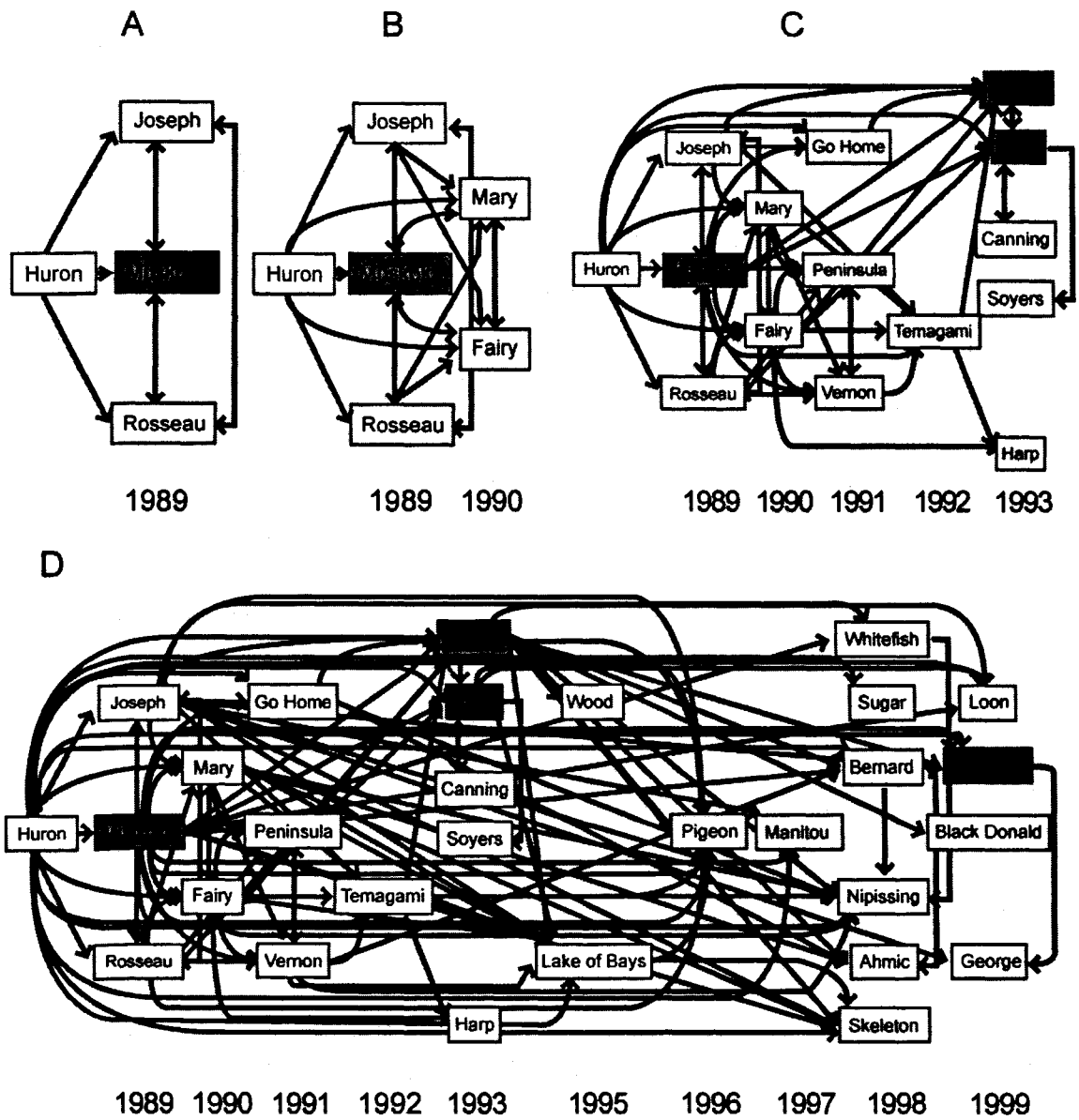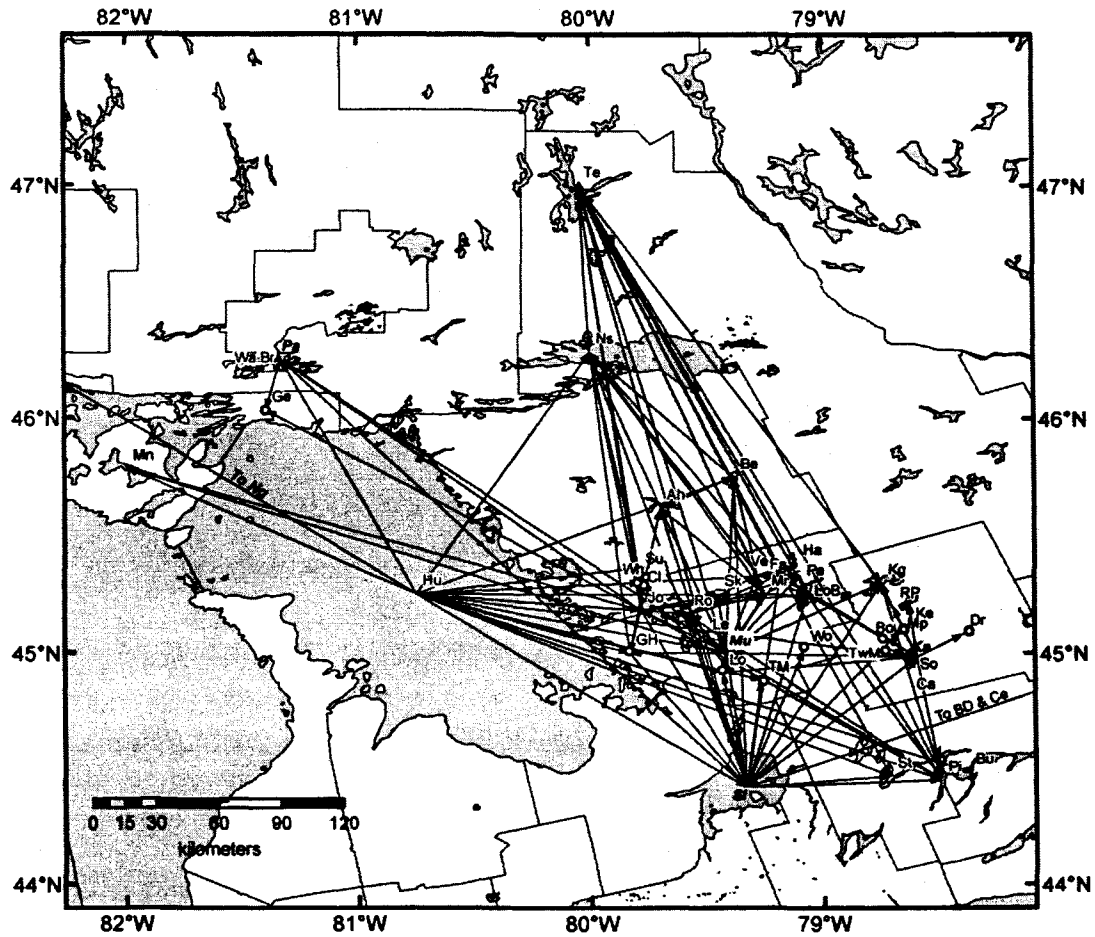
Kashagawigamog is abbreviated as Kash.

Figures

Figure 1.

Key: Ah - Ahmic, Br - Bear, Be - Bernard, BD - Black Donald, Bo - Boshkung, Bu - Buckhorn, Ca - Canning, Ce - Centennial, Cl - Clear, Dr - Drag, Fa - Fairy, Ge - George, GH - Go Home, Ha - Harp, Hu - Huron, Jo - Joseph, *Ka - Kashagawigamog*, Kg - Kawagama, Ke - Kennisis, LoB- Lake of Bays, Le - Leonard, Lo - Loon, Mn - Manitou, Mp - Maple, Mr - Mary, *Mu - Muskoka*, *Ng - Nipigon*, Ns - Nipissing, *Pa - Panache*, Pe - Peninsula, Pi - Pigeon, RP - Red Pine, Ro - Rosseau, *Si - Simcoe*, Sk - Skeleton, So - Soyers, St - Sturgeon, Su - Sugar, Te - Temagami, TM - Three Mile, TwM - Twelve Mile, Ve - Vernon, Wa - Walker, Wh - Whitefish, Wo – Wood.

Figure 2. Current map of network traffic from previously to recently invaded lakes.

Italicized lake names represent existing or nascent inland hubs. Lakes

Nipigon, Black Donald and Centennial are not shown at this scale.

Figure 3. Cumulative number of different invaded (solid circle) and noninvaded

(open circle) lakes visited by boaters departing from five invaded lakes in

central Ontario. Values presented are mean +/- SE; standard errors of

estimates smaller than symbol sizes are not shown. Monte Carlo

simulations were conducted to determine the expected number of

visitations to these lakes, as a function of the number of surveys

considered. Results were bootstrapped 100 times. The expected number

of lakes visited was estimated based upon creel surveys of lake users

(asterisks), except for Lake Huron, which assumed an infinite number of

boaters. Equations for fitted curves are provided in Table 1.
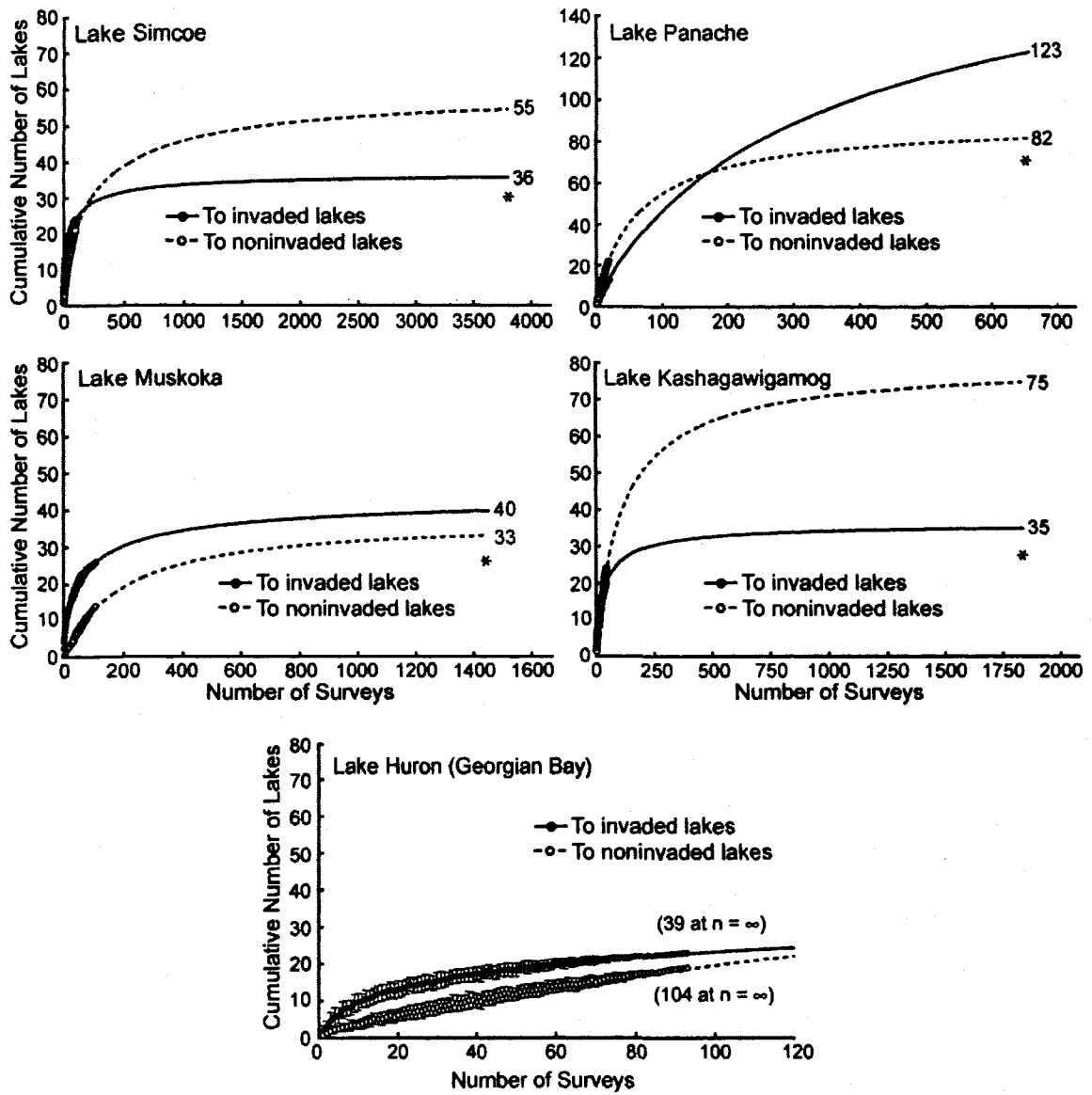
Figure 3.

Figure 4 (A). Cumulative number of connections from invaded to noninvaded

lakes. (B). Network clustering coefficient, reflecting the ratio of the

cumulative, actual to theoretical number of connections from invaded

sources to other invaded (solid symbol) or to noninvaded (open symbol)

destination lakes. High clustering coefficients reflect tight linkage between

invaded and other lakes. Values decline through time as more isolated

lakes, with few links to other systems, become invaded.
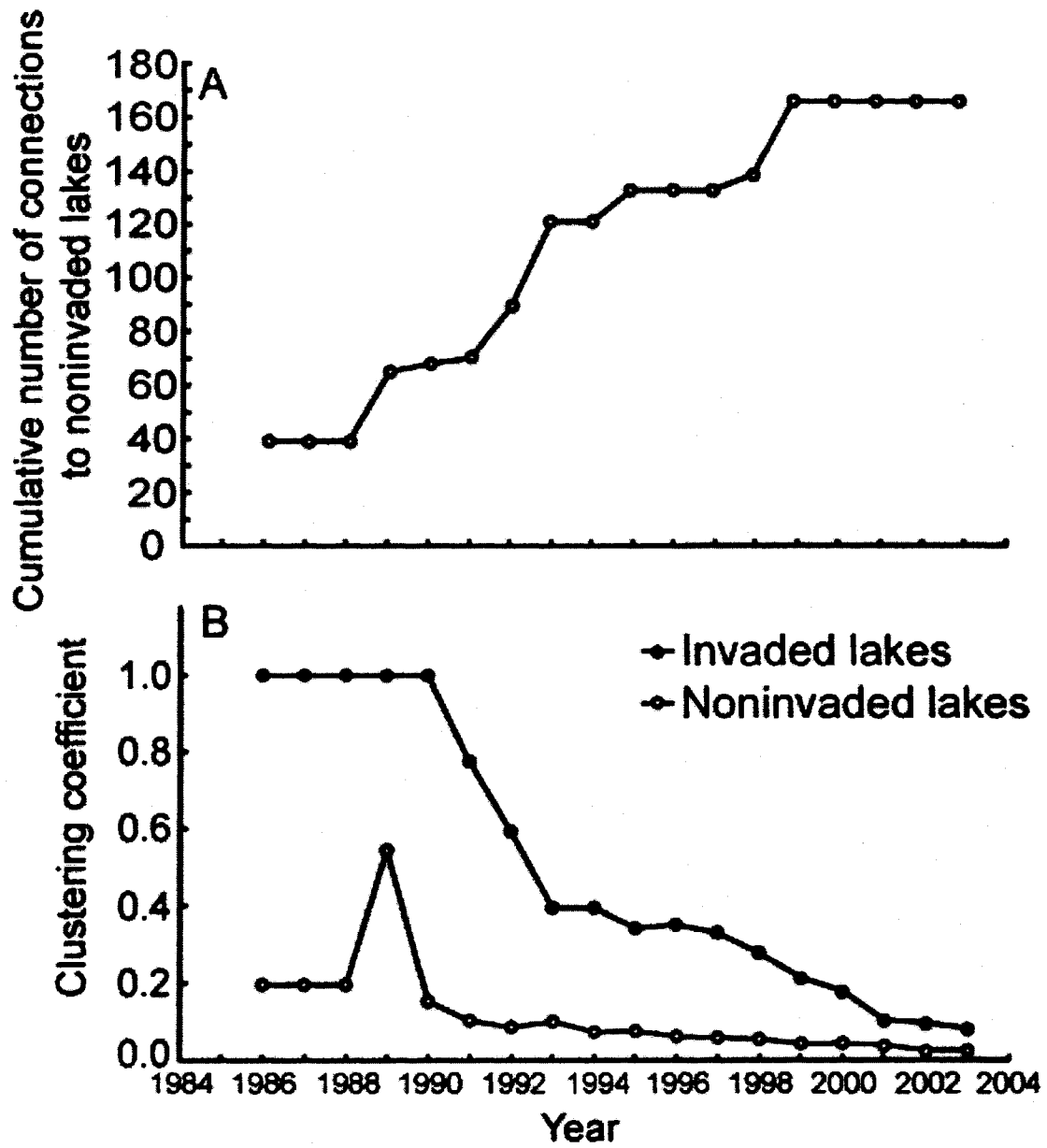
Figure 4.

Figure 5. Frequency histograms of the number of functional links from invaded

sources to invaded (top panels) or noninvaded (bottom panels)

destinations in 1999 and 2003. Lakes that had a high number (e.g. 26-30)

of connections to noninvaded destinations in 1999 served as nascent

hubs and probably influenced the rate of spread for *Bythotrephes*. Best-fit

exponential (4A) and power function (4B,C,D) curves were fitted using link

frequencies and the median of each connection category.

1999

2003

A — To invaded lakes
$y = 25e^{-0.131x}$
$r^2 = 0.981$

B — To invaded lakes
$y = 208x^{-1.55}$
$r^2 = 0.997$

C — To noninvaded lakes
$y = 126x^{-1.55}$
$r^2 = 0.989$

D — To noninvaded lakes
$y = 458x^{-2.11}$
$r^2 = 0.994$

Number of outbound connections
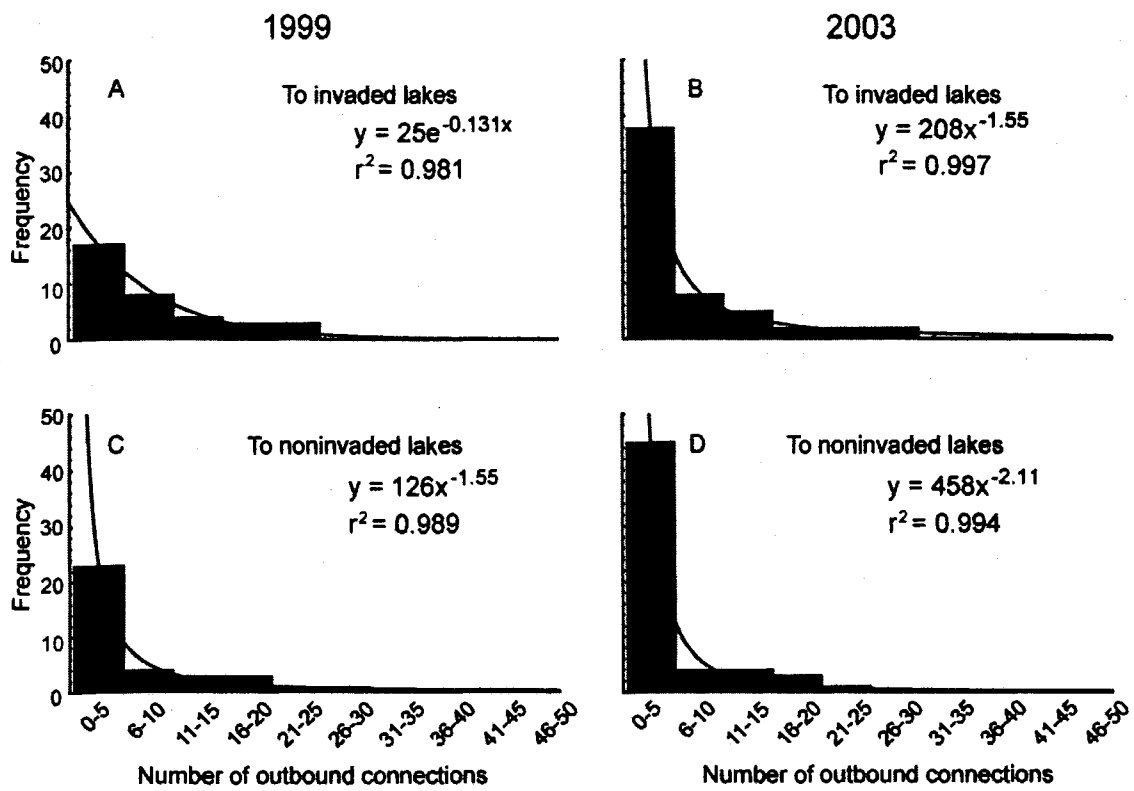
Number of outbound connections

Figure 5.

General Discussion and Conclusion

A common theme underlying this dissertation is that understanding the dispersal of nonindigenous species and related pattern and intensity of propagule pressure is the first, and perhaps most important, step in forecasting invasions. As such, models forecasting invasions should focus on the initial stage of the invasion sequence when dispersal is occurring. Although NIS spread can be forecast with some success simply based on the pattern of past invasions, specific knowledge of the mechanisms involved allow for more refined predictions of where the species may spread.

A pattern of spread common to many terrestrial and aquatic NIS is 'stratified diffusion' (Hengeveld 1989), in which multiple dispersal mechanisms operate simultaneously on different spatial scales. In 'stratified diffusion', the invasion wavefront initially spreads via local diffusion from a founding population. As time progresses, the invasion spreads via a series of long-distance dispersal events that form isolated colonies, followed by local infilling of sites closer to the sources (Moody and Mack 1988, Shigesada et al. 1995). Evidence of this pattern of spread has been reported for several groups of nonindigenous taxa including thistles (*Carduus acanthoides*) (Jongejans et al. 2007), gypsy moths (*Lymantria dispar*) (Johnson et al. 2006a), and cereal leaf beetles (*Oulema melanopus*) (Andow et al. 1990).

The spatial and temporal scale of stratified diffusion depends on the scale at which the dispersal mechanisms operate. For example, most of the invasions of the invasive thistle (*Carduus acanthoides*) occurred as a consequence of

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infilling from neighbouring plots, although in some instances, long-distance

dispersal via wind is likely to have carried seeds no more than 50 m per dispersal

event (Jongejans et al. 2007). In contrast, long-distance dispersal of medflies

(*Ceratitis capitata*) occurs to a maximum of 9.5 km based on adult flight potential

(Meats and Smallridge 2007) and to scales of 1000s of km for human-mediated

dispersal of the quagga mussel, *Dreissena rostriformis bugensis*. In the latter

case, quagga mussels were reported in Lake Mead, Nevada and Lake Havasu,

California in January 2007, approximately 2500 km away from the westernmost

known potential source, Lake Michigan (unpub. data).

The same pattern of spread is apparent for the NIS in this dissertation.

The spread of the emerald ash borer occurs via local diffusion based on flight

potential of adult beetles, in conjunction with human-mediated transport of the

beetle in infested firewood or ash products. In this case, local diffusion cannot

account for many of the new invasions distal to previously invaded areas, though

long-distance forecasts based on firewood transportation and human population

density met with mixed results (Chapter 2). Likewise, dispersal of aquatic NIS

such as spiny waterfleas and zebra mussels occurs across the landscape via a

combination of local dispersal through connected waterways (i.e. advection) in

conjunction with long-distance, human-mediated transport (MacIsaac et al. 2004,

Johnson et al. 2006b, Bossenbroek et al. 2007). In particular, many of the lakes

invaded by spiny waterfleas become locations for 'founding populations' in

stratified diffusion. Some of these lakes then serve as hubs for propagule outflow

to isolated colonies (i.e. remote lakes) with which they have outbound boater or

angler connections (Chapter 6). For both species, the measure of propagule pressure based on human-mediated transport was strongly related to the invasion status of Ontario lakes (Chapters 3 and 5). In general, the likelihood of NIS occurrence increased as a function of propagule pressure, but the functional form of this relationship was dependent on the type of gravity model used to quantify propagule pressure. For doubly-constrained gravity models, the likelihood of occurrence increased much faster at low levels of propagule pressure than for either production- or total-flow-constrained models (Chapter 4). In general, production-constrained gravity models performed better than doubly-constrained models, despite requiring less information (Chapter 4).

Although not specifically tested here, connected waterways are likely an important dispersal mechanism for aquatic NIS dispersal in Ontario. For other NIS such as the waterflea *Daphnia lumholtzi*, for example, advective flow in waterways is responsible for invasions of significantly more downstream lakes than those where *D. lumholtzi* is not located upstream (Shurin and Havel 2002).

In addition to transporting propagules of NIS over distances far greater than possible under their own power, human-mediated transport occurs at much faster rates, thus increasing the survival of propagules and essentially allowing the NIS to bypass the first filter of the invasion sequence (e.g. Hebert and Cristescu 2002). For invasions of spiny and fishhook waterfleas, and zebra and quagga mussels, many of the recreationalists used their boats within a few days of leaving an invaded lake and trailered up to 1800 km in a single trip (Chapter 3-5). Some life-history characteristics of the NIS may be well suited for interaction

with human-mediated transport to facilitate survival of the propagules. Production of resting or diapausing stages of the waterfleas, and the ability of mussel adults to survive brief aerial exposure reduce mortality during overland transport of propagules (Chapters 3-6). For beetles like the emerald ash borer, mortality of the eggs and larvae in the transported ash products is likely very low as larvae are adapted for overwintering under the bark of ash trees.

Through the identification of mechanisms, pathways and spatially-explicit invasion 'hotspots' (Chapters 2-5), management efforts become more feasible and cost effective (Leung et al. 2002). For example, by distinguishing high-risk destinations from those of lower risk, forecasts can guide prevention or rapid response efforts at sites of highest risk of invasion, while not wasting money protection of low risk sites. Alternatively, management efforts may be focused on sources with high propagule outflow, thereby reducing overall rate of propagule dispersal and NIS spread (Chapter 6). Although human-mediated transport is responsible for long-distance dispersal of many NIS, it is also at this stage where management can be most effective by controlling the vectors themselves. Quarantines combined with legislation prohibiting the transport of products were effective only when sites invaded by the emerald ash borer were detected early (Chapter 2). For aquatic NIS like spiny and fishhook waterfleas and zebra mussels, education efforts promoting awareness of the NIS in specific lakes, such as those provided by local agencies is one course of action. In Ontario, the Ontario Ministry of Natural Resources and Ontario Federation of Anglers and Hunters jointly operate an Invasive Species Hotline devoted to education and

outreach. As the invasion grows, management strategies may change from 'eradication' to 'slow-the-spread' to 'do-nothing' as effectiveness decreases (Sharov et al. 2002, Sharov 2004).

Models based upon propagule pressure are only the first of three steps utilized in this dissertation to forecast spread of NIS. In chapter 3, I combined gravity models, environmental quality data (i.e. water chemistry and lake morphometry), and ecological information (i.e. fish community composition) to develop staged hierarchical models of spread for the spiny waterflea and zebra mussel. Only lakes with high propagule pressure were considered in the second stage (environment), and only those lakes with suitable environmental quality were considered in the ecological model (fish community). I compared performance of these models against otherwise similar models in which propagule pressure, environmental quality, and ecological conditions were considered simultaneously. Surprisingly, the latter models were better able to correctly identify invaded lakes, though they also tended to have higher false positive rates. Hierarchical models had lower 'hit' rates and lower false positive rates. Despite the intellectual appeal of the latter models, they generally do not perform as well as 'all-in-one' models.

In this dissertation, I have demonstrated how models forecasting NIS spread by incorporating various components of the multistage invasion sequence as well as multiple dispersal mechanisms are successful in predicting invasions. For future studies, life-history characteristics of NIS that are commonly linked with invasiveness should be examined in the context of the invasion sequence.

Specifically, these traits should be incorporated into measures of propagule

pressure associated with specific dispersal mechanisms.

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