BACKCASTING AND FORECASTING BIOLOGICAL INVASIONS OF INLAND LAKES

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Abstract. Human introduction of nonindigenous species constitutes a serious threat to many ecosystems, particularly lakes. Recent attempts to predict invasions have focused on the supply of propagules of nonindigenous species to recipient ecosystems from source populations. Here we develop a spatially explicit ''gravity'' model to test this concept for *Bythotrephes longimanus*, a crustacean waterflea from Eurasia that is rapidly invading lakes in Ontario, Canada. The gravity model predicted spread of *Bythotrephes* based upon seven identified risk factors (e.g., use of contaminated fishing or boat anchor line) that may allow dispersal of either live individuals or their resting eggs from invaded to noninvaded lakes, as well as based on the spatial arrangement of invaded and noninvaded lakes in Ontario. Discriminant analysis of lake gravity scores successfully identified invasion status for 74% of 170 inland lakes. A retrospective analysis of 31 invaded lakes revealed that the order in which lakes were invaded was directly related to the magnitude of vector inflows from invaded sources. Analysis of the dominant vector inflow to each invaded lake revealed a ''stepping stone'' pattern in which at least five lakes were sequentially invaded from the source population in Lake Huron. One invaded lake (Muskoka) apparently served as an invasion ''hub,'' resulting in up to 18 additional direct and 17 indirect invasions. Species spread occurred via a combination of dominant, local diffusion (median distance 12.5 km) and rare, long-distance (>100 km) dispersal. Eleven of 131 lakes that were not invaded in 2000 were reported invaded in 2001. Gravity scores of these lakes were significantly higher than those of other noninvaded systems, indicating that susceptibility to invasion can be related to the magnitude of vector inflows. A GIS model based on gravity scores indicated that distribution of *Bythotrephes* is expected to expand to eastern and northwestern Ontario, although most new invasions are expected to occur in the central region of the province. Our results indicate that quantitative analysis of human dispersal vectors provides a robust starting point with which to assess vulnerability of discrete ecosystems to invasion. Management efforts focused on reducing the number and magnitude of human-mediated dispersal vectors may reduce the rate of invasion of new ecosystems.

Key words: biological invasion; Bythotrephes; *crustacean, waterflea; GIS; gravity model; Great Lakes; long-distance dispersal; nonindigenous species; spatially explicit; zooplankton.*

INTRODUCTION

Human-mediated introduction of nonindigenous species has largely supplanted natural dispersal for many taxa, and is expected to be a leading cause of biodiversity change in lakes during the 21st century (Sala et al. 2000). For example, the rate of human-mediated dispersal of nonindigenous species is up to 5×10^4 times higher than the natural dispersal rate for cladoceran zooplankton to the Laurentian Great Lakes (Hebert and Cristescu 2002). The rate of new nonindigenous species introductions to the Great Lakes and many coastal marine ecosystems has accelerated in recent years, largely as a consequence of the release by ships of ballast water contaminated with a wide diversity of taxa (e.g., Ruiz et al. 2000, Ricciardi 2001, Leppäkoski et al. 2002). Once established in the Great Lakes, non-

indigenous species may spread to adjacent inland waterways via a host of human-mediated mechanisms (e.g., Johnson et al. 2001).

Traditionally ecologists have attempted to predict establishment success and dispersal of nonindigenous species based upon life history attributes of invading species, including reproductive systems and body or offspring size (e.g., Williamson and Fitter 1996, Lonsdale 1999, Kolar and Lodge 2001, 2002, Sakai et al. 2001). Many others have sought to link invasion success to characteristics of the invaded habitats, notably the degree of human disturbance or their native species diversity (e.g., Levine and D'Antonio 1999, Lonsdale 1999, Levine 2000, Shurin 2000, Blackburn and Duncan 2001, Kolar and Lodge 2001, Lyons and Schwartz 2001, Dukes 2002, Kennedy et al. 2002). A third and often complementary approach involves an examination of the frequency and number of individuals in colonizing populations, hereafter called propagule pressure, that challenge recipient ecosystems (e.g., Williamson 1996, Grevstad 1999, Lonsdale 1999, Ruiz

et al. 2000, Forsyth and Duncan 2001, Kolar and Lodge 2001, Levine 2001). Propagule pressure has both quantitative (i.e., number of individuals moved) and qualitative (i.e., the condition, sex ratio, or size structure of individuals moved) components that may influence whether an invasion will succeed (see Carlton 1996, Ruiz et al. 2000, Wonham et al. 2001). For example, it is possible that invasions fail owing to the reduced number and poor condition of propagules upon arrival after a prolonged journey, as often occurs with species transported in ballast tanks of ships (Carlton 1996). Success may be reduced further if arriving propagules are discharged at sites that are physically or chemically mismatched to the requirements of the species (Smith et al. 1999, Havel et al. 2002).

Insight into the spatial pattern of dispersal of a nonindigenous species can be gleaned from its redistribution kernel, which describes the probability distribution that individuals will be found at specific spatial coordinates relative to the original, colonizing location (e.g., Lewis 1997). Leptokurtic redistribution kernels have a protracted tail, which allows for establishment of new colonies at great distances from the parental colony (Lewis 1997, Kraft et al. 2002). Many plant and animal species have leptokurtic redistribution kernels, which may translate in nature as stratified diffusion involving both local and jump dispersal (Hengeveld 1989, Havel et al. 2002, Kraft et al. 2002). Human vectors may disperse nonindigenous species in a manner analogous to natural, stratified diffusion, with one key difference. Natural stratified diffusion results in establishment of peripheral colonies at locations that cannot readily be predicted based on location of the parental colony (see Lewis 1997); however, it may be possible to predict relative vulnerability of both proximal and peripheral habitats to nonindigenous species invasion if humans are primary dispersal vectors and if these vectors can be quantified (Kolar and Lodge 2002, MacIsaac et al. 2002).

Lakes are very good systems with which to assess invasion vector models as they are distinct habitats with clearly defined borders, and because it may be relatively easy to identify and quantify invasion vectors. For example, surveys have demonstrated that boaters and anglers are major vectors responsible for dispersal of invasive macrophytes, zooplankton, and molluscs among inland lakes (Johnstone et al. 1985, Johnson and Carlton 1996, Johnson and Padilla 1996, Johnson et al. 2001, Havel et al. 2002, Kraft et al. 2002). Movement of propagules of nonindigenous species from invaded source lakes to noninvaded destination lakes can be modeled if dominant vectors can be identified. For example, Johnson and Padilla (1996) quantified interlake movement of trailered boats to predict potential patterns of zebra mussel dispersal in Michigan. These movements can be used to develop a gravity model relating the force of attraction between an origin (i.e., invaded lake) and a destination (i.e., noninvaded lake),

weighted by the distance between them, in a manner similar to how Newton's Theory of Gravity measures the attractive force between two masses.

Gravity models were first developed for use in the social sciences and economics. For example, models were used to explore rates and patterns of human migration between cities (Zipf 1946), market boundaries of competing retailers (Reilly 1931), and rates of international trade (Linneman 1966). The type of gravity model used is based on the information available. Production-constrained gravity models apply when information is available on total outflows from each origin, while attraction-constrained models utilize inflow information to each destination; production-attraction-constrained (or doubly constrained) gravity models require both inflow and outflow information for origins and destinations, respectively (Haynes and Fotheringham 1984).

A gravity model may be superior to its reaction-diffusion equivalent in forecasting spread of invading species because it allows dispersal to occur in heterogeneous environments over both short and long distances (see Buchan and Padilla 1999). Schneider et al. (1998) developed a doubly constrained gravity model to predict vulnerability of lakes in Illinois to invasion by introduced zebra mussels based upon boater activity patterns in the state. This model used information on all vector inflows and outflows for each noninvaded, invaded, or assumed to be invaded lake in the study. Bossenbroek et al. (2001) used a less spatially explicit form of gravity model to forecast spread of zebra mussels in four Great Lakes states. Their production-constrained models used the number of registered recreational boats per county as sources of vector traffic and were able to predict spread over a broader, but less geographically explicit, range than that of Schneider et al. (1998).

In this study, we assess local and long-distance dispersal of the invading zooplankter *Bythotrephes longimanus* (Leydig) to inland lakes in Ontario from the Great Lakes based upon a quantitative analysis of human-mediated vector flows between invaded source and noninvaded destination habitats as little is known about dispersal of *Bythotrephes*. Specifically, we employ a doubly constrained gravity model and discriminant analysis to determine whether invasion status of water bodies can be forecasted based upon inbound vector flows from invaded sources. Because the year of first reporting has been recorded for 31 of the invaded lakes in Ontario, we were able to develop a temporal sequence of invasion for these systems and relate patterns of spread to vector inflows from previously invaded systems. Specifically, we determine whether the sequence in which these 31 lakes were invaded is related to the total amount of vector inflow from previously invaded source lakes (i.e., backcasting model), and whether noninvaded lakes that subsequently be-
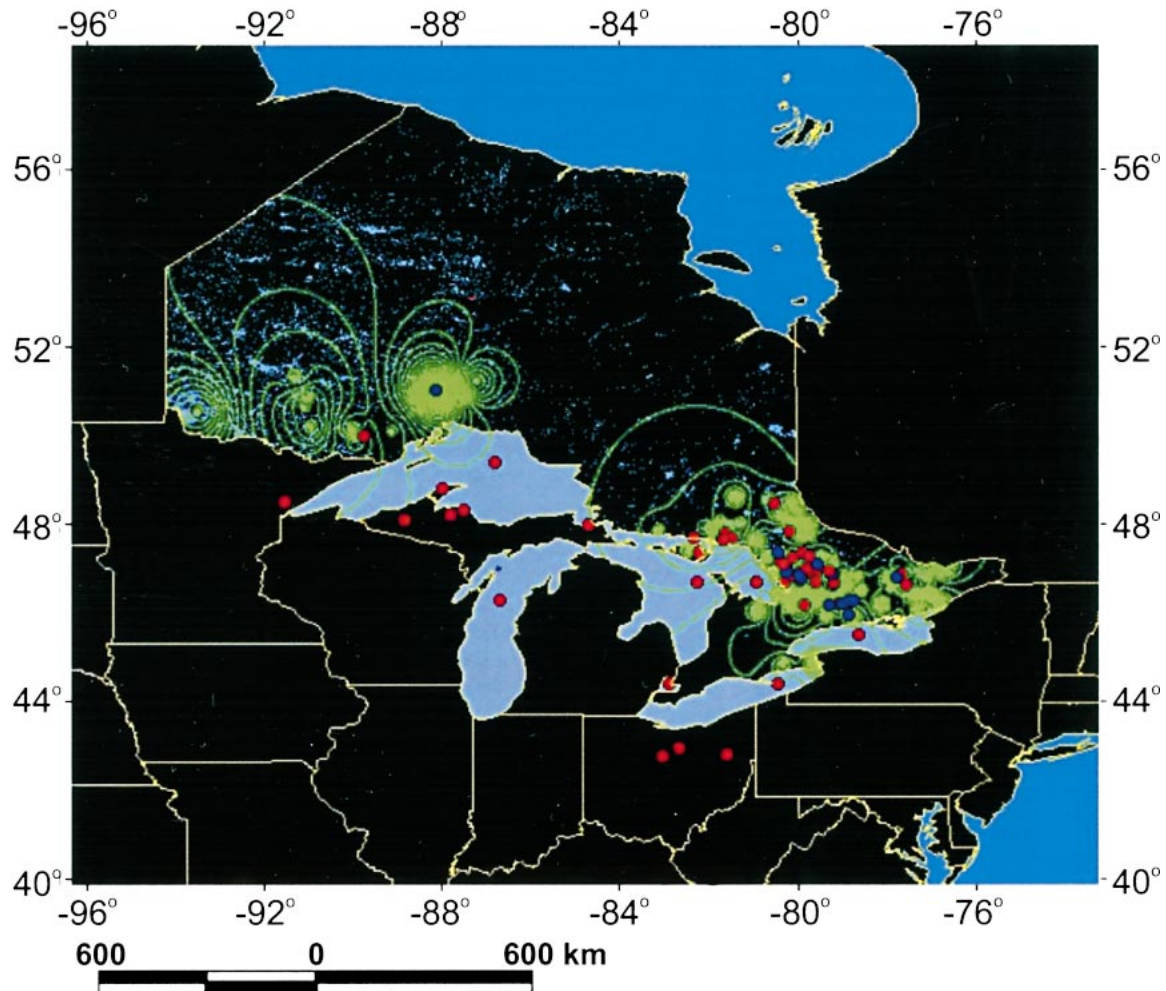
FIG. 1. Lakes in North America that have been reported invaded by *Bythotrephes* during or prior to 2000 (red dots) and during-2001 (blue dots). Invaded lakes in Ontario (pre-2001) were used to develop a vector-based gravity model based upon human activities that increase risk of spread of the species. Invasion isobars (green lines) indicate regional vulnerability to future invasion by *Bythotrephes*. Range expansion is expected primarily in the northwestern and eastern regions of the province. Lakes Nipigon (blue) and Shebandowan (red) are located north and northwest of Lake Superior, while Lake Muskoka is located in the large cluster of invaded lakes east of Georgian Bay. In addition to its occurrence in 53 lake systems in Ontario, *Bythotrephes* has been reported established in five lakes in Michigan, three in Ohio, and one in Minnesota.

came invaded had higher inbound vector flows than other noninvaded lakes (i.e., forecasting model).

METHODS

Bythotrephes longimanus

Bythotrephes is a cyclic, parthenogenetic waterflea native to the Palearctic region (Therriault et al. 2002). It was first reported in North America in Lake Ontario during 1982, and established populations likely as a consequence of ballast water discharge by a ship whose origin was the eastern Baltic Sea region (Therriault et al. 2002). The species subsequently colonized each of the other Great Lakes, as well as inland lakes and reservoirs in Michigan, Minnesota, and Ohio (MacIsaac et al. 2000). Initial invasions in Ontario were limited to the region adjacent to Georgian Bay, Lake Huron;

however, by summer 2001 *Bythotrephes* was established in at least 53 inland lakes and lake systems throughout the province (Fig. 1) and its rate of new invasions was increasing rapidly (Fig. 2). *Bythotrephes* is an efficient predator that may cause extirpation of small zooplankton species (Yan et al. 2002), thus managerial attempts to limit its ecological impact will require information regarding its current and predicted distributions.

We modeled the cumulative number of invaded inland lakes in Ontario using assembled reports of first occurrences obtained from the Ontario Federation of Anglers and Hunters, the Federation of Ontario Cottagers' Associations, Dr. Norman Yan (*unpublished data*), and by field assessments made with vertical hauls of a 253-μm plankton net during summer months (R.
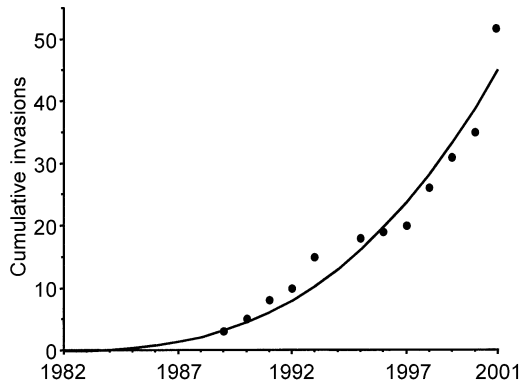
FIG. 2. Cumulative number (CN) of *Bythotrephes* invasions of inland lakes reported in Ontario since 1982 (year 1): CN = 0.007 × year$^{2.895}$, r^2 = 0.94, N = 13.

Colautti, *unpublished data*). We assessed the rate of reported invasions through time using nonlinear regression (Systat 8.0; Systat Software, Richmond, California, USA), with the initial report of *Bythotrephes* in Lake Ontario taken as year one (1982). Because zooplankton including *Bythotrephes* also may be spread by natural mechanisms, notably by diving waterfowl (see review, Green et al. 2002), we conducted an indirect test of this alternative dispersal model. The proximity to the nearest major road for invaded and adjacent noninvaded lakes from the same watershed was explored using a *t* test, with the expectation that if waterfowl were a major vector of *Bythotrephes* dispersal, there should be no relationship between proximity to roads and invasion status of lakes.

Doubly constrained gravity model

We constructed a doubly constrained gravity model to analyze invasion patterns for *Bythotrephes* in inland lakes in Ontario. The gravity model forecasts spatial interaction patterns based on human-associated vector activities that increase risk of *Bythotrephes* dispersal to 142 noninvaded inland lakes from 31 invaded ones and the Great Lakes. The gravity model was developed based upon surveys of 824 boaters, anglers, and other recreationalists during July and August 2000 at marinas and public boat launches located on lakes throughout Ontario that have been invaded by *Bythotrephes*. Survey respondents were asked to identify all source and destination lakes visited that year and whether they had engaged in behaviors that may have inadvertently dispersed *Bythotrephes* by any recognized mechanism(s) including use of contaminated fishing or anchor lines, discharge of contaminated live well or bilge water from recreational boats, release of live minnow bait or bait bucket water, or by contaminated airplane pontoons, SCUBA diving, or waterskiing gear. *Bythotrephes* is commonly reported fouled on trawled fishing line by sport anglers in the Great Lakes basin (H. MacIsaac, *personal observations*). Clumps of animals fouled on

fishing line pose an invasion risk to other lakes because they may include encysted resting eggs produced as early as mid summer (Yan and Pawson 1998) that remain viable long after the females carrying them have died.

The gravity model generates highly resolved, spatially explicit predictions of species dispersal patterns, but requires detailed information on all outflows and inflows between sources and destinations. Vector flow from an invaded to a noninvaded lake, P_{ij}, was quantified as

$$P_{ij} = \sum_1^g \sum_1^n (r_n + w_n)tp \qquad (1)$$

where *g* is number of individuals moving from lake *i* to lake *j*, *n* is the number of mechanisms (e.g., fouled fishing lines), *r* is ranked risk for each invasion mechanism (i.e., likelihood that the mechanism transferred any individuals), *w* is ranked vector load for each mechanism (the number of individuals dispersed), *t* is ranked time of fishing or boating activity, and *p* is ranked proximity to a major road. Ranked values were based on survey results, with values ranging from 1 (least important) to 5 (most important) and the combined risk of spread and vector load varied by dispersal mechanism (Table 1). The ranked time of activity corresponded with *Bythotrephes* abundance: boating or fishing during July and August received ranks of 5, while activity during the winter months received ranks of 1, for example. A matrix was constructed for all P_{ij} values from all invaded origins (rows) and all noninvaded destinations (columns). P_{ij} values were summed for each column (D_j) and each row (O_i) to estimate risk of dispersal due to flow to noninvaded lake *j* and risk of dispersal due to flow from invaded origin *i*. These values were used to determine T_{ij}, the interaction between any pair (*i* and *j*) of lakes:

$$T_{ij} = \frac{A_iB_jO_iD_j}{d_{ij}^\beta} \qquad (2)$$

where A_i and B_j are balancing factors, d_{ij} is straight line distance between lakes *i* and *j*, and β is an empirically determined distance adjustment function relating attractiveness to distance between lakes (see Schneider

TABLE 1. Dispersal mechanisms for overland transport of *Bythotrephes*, with ranks of the risk of transport and corresponding load. Low values indicate low probability of transport and low vector load of *Bythotrephes*.

Mechanism	Risk of dispersal	Vector load
Live well water	1	1
Bait buckets	2	1
Bilge water	3	3
Fishing line/nets	5	5
Anchor line	4	3
Float plane pontoons	1	2
Tubing/water skiing/SCUBA	2	2

et al. 1998). A_i and B_j were solved iteratively based on survey results and ensure that the total inflow to a lake is balanced with the outflow. β was conservatively estimated from the antilog of the slope describing the distance-decay pattern of trailered boats (i.e., frequency of movement vs. log [distance moved]); β thus corresponded with the square root of distance (0.5). The gravity score for an individual destination lake was computed by summing T_{ij} values for all source lakes with which it had vector activity. Total outflow from an invaded lake was calculated by summing T_{ij} values to all noninvaded destinations with which it had vector contact. Two separate standardizations were conducted to prevent bias originating from unequal response rates for different source lakes. First, to correct for differing numbers of surveys for each destination, T_{ij} values were adjusted as

$$T_{ij} = \frac{A_i B_j O_i D_j (d_{ij}^{\beta})^{-1}}{\sum\limits_j D_j}\%. \tag{3}$$

A second calibration corrected for unequal numbers of surveys from each invaded origin lake by replacing the denominator in Eq. 3 with $\Sigma_i\, O_i$. We developed a discriminant function using Systat 8.0 to test predicted calibrated gravity scores for all inland lakes against the year 2000 invasion status of *Bythotrephes*. Differences in gravity scores of invaded and noninvaded lakes in the survey were analyzed using a *t* test. All gravity scores were $\ln(x + 1)$ transformed prior to analysis to stabilize variance.

We tested two dispersal models using the gravity values calculated for invaded and noninvaded lakes. First, we tested the ability of the gravity model to backcast the sequence in which lakes were invaded. To do this, for each of the 31 lakes that were invaded by the year 2000, and beginning with the year of the first reported invasion of an inland lake (1989), we calculated gravity scores for each of the lakes invaded in that year as well as for those that were not yet invaded. Only vector inflow information from lakes that were previously invaded was used to calculate gravity scores for both the newly invaded and not yet invaded lakes. This process was repeated for each year. Gravity scores for each lake changed each year as more vectors were sequentially added from lakes invaded the previous year. We tested whether invaded and not yet invaded lakes differed with respect to inbound vector flows using two-way ANOVA with interaction, with year of invasion and invasion status as factors. In order to ensure independence of temporal data, gravity scores of invaded lakes were used only in the year in which the lake was invaded. Thereafter, vector flows from a previously invaded lake were used to compute gravity scores of all remaining not yet invaded lakes, but the gravity score of the lake was not used in the ANOVA model for that year.

We developed a forecasting model to determine whether vector inflows from invaded sources differed for noninvaded lakes that were subsequently invaded or which remained noninvaded. For example, eleven noninvaded lakes from the year 2000 survey were reported invaded during 2001. We used a Kolmogorov-Smirnov test to compare the distribution of gravity scores for these lakes to that for 131 other lakes that remained noninvaded through 2001.

A Geographic Information Systems (GIS) model was developed, using ArcView GIS 3.2 (ESRI, Redlands, California, USA), to depict a possible future dispersal pattern of *Bythotrephes* in Ontario based upon gravity scores, lake positional information, visitation frequency from possible invasion sources, and mean distance boats were trailered to noninvaded lakes. Data overlay and manipulation was performed using a geographic projection. The GIS model used inverse distance weighting interpolated over an area and was based on gravity scores.

RESULTS

Survey data revealed that 81% of respondents were male, and 60% of individuals were between 32 and 64 years old. Sixty-two percent of individuals fished on an invaded lake. Respondents were more likely to clean their boat hull or anchor line (57%) than fishing lines potentially fouled with *Bythotrephes* (20%). Two hundred and fifty three respondents (31%) reported visiting a noninvaded lake after boating or fishing on an invaded lake.

The overall rate of *Bythotrephes* invasion in Ontario has increased very rapidly over the past 13 years (Fig. 2). Most invasions have occurred in a central zone just north of Georgian Bay, the putative source of the initial inland invasions, although invaded lakes now occur from eastern to northwestern regions of the province (Fig. 1). The dispersal pattern of *Bythotrephes* corresponds with stratified diffusion, as median distance between an invaded lake and its putative source (i.e., dominant vector) was only 12.5 km, although two distant lakes (107 km and 200 km) also were invaded. These findings are broadly consistent with the distribution of trailered boat distances from invaded source lakes in Ontario (Fig. 3).

It is very unlikely that waterfowl were major vectors responsible for dispersal of *Bythotrephes* in Ontario. Invaded lakes were significantly closer to roads than adjacent noninvaded ones ($t = 3.96$, $P < 0.001$), a pattern unexpected if waterfowl were major vectors. Moreover, most invasions have occurred immediately north of the Great Lakes. Seasonal phenology of *Bythotrephes* populations, which typically do not populate lakes until mid June and do not achieve population maxima until July or August, is temporally mismatched with the vernal, northern migrations of waterfowl.
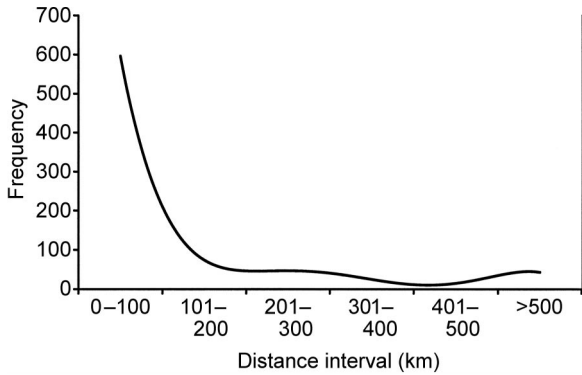
FIG. 3. Frequency distribution of distances over which boats were trailered in Ontario, based upon surveys conducted at lakes invaded by *Bythotrephes*.

Absent other identified dispersal vectors, we constructed a human-vector model based on movements of boaters, anglers, and other recreationalists to inland lakes. The source of initial inland lake invasions was Georgian Bay (Lake Huron), although total vector outflow from this lake to other lakes that later became invaded was lower than that from Lake Muskoka and Lake Simcoe (Fig. 4). Lakes Kashagawigamog and Joseph were also important vector sources to other lakes that subsequently became invaded (Fig. 4). Dominant vector flow patterns from invaded to noninvaded lakes were slightly different. Lakes Simcoe, Kashagawigamog, and Georgian Bay are the primary source of propagules to inland lakes that have not been invaded, followed by Panache and Black Donald lakes.

The expansion of the number of invaded lakes over time, and the attendant increase in outbound vector flows to noninvaded lakes, are responsible in part for the increasing rate of reported new introductions (Fig. 2). Analysis of dominant vector flows indicates a "stepping stone" invasion pattern, with up to four lakes invaded in succession from the original source (i.e., Lake Huron → Muskoka → Simcoe → Kashagawigamog → Soyers and Canning; Fig. 4). This chain could be longer if invasions were occurring by some of the many subdominant vector flows. Lake Muskoka is an extremely popular tourist lake near Georgian Bay in central Ontario that appears to have played a particularly important role in the initial spread of *Bythotrephes*. For example, based on patterns of dominant vector flow into noninvaded lakes, Lake Muskoka has apparently served as the source of up to 18 direct and 17 indirect (i.e., secondary) invasions (Fig. 4). However, once these lakes were invaded, Lake Muskoka became a much less important threat of invasion to additional lakes, owing to relatively low outbound flows to remaining noninvaded lakes. Conversely, Lake Simcoe has been an important source of past invasions and remains a threat to numerous other lakes owing to its diversified outbound vector flow patterns.
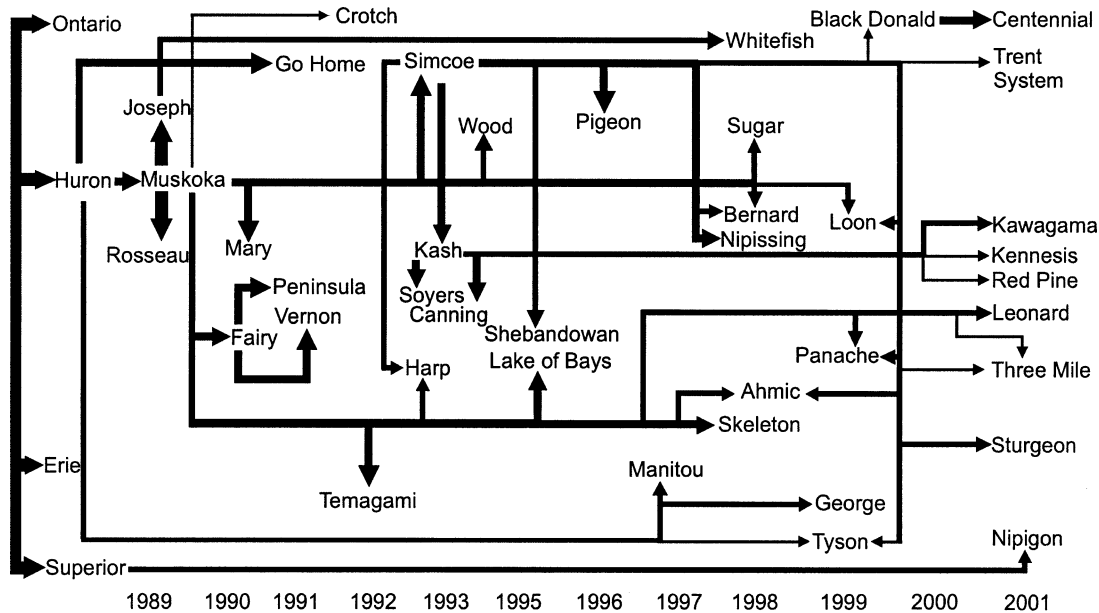

FIG. 4. Putative sequence of invasion of inland lakes in Ontario by *Bythotrephes longimanus* between 1989 (left side) and 2001 (right side) from the Great Lakes. The model is based upon the dominant vector flow into a noninvaded lake from an invaded source. The magnitude of an invasion vector is directly related to arrow thickness. Two inflows are shown for lakes in which the dominant and secondary inflows differed by ≤1%. Lake Muskoka has apparently served as an invasion "hub" responsible for up to 18 direct and 17 indirect invasions of other lakes in a sequence extending at least four lakes from Lake Huron. Lakes Simcoe and Kashagawigamog (Kash) have highest vector outflows from invaded inland lakes to others that are noninvaded (not shown), and thus may be particularly important sources of future invasions. No vector flow information was available for three and four lakes invaded during 2000 and 2001, respectively.
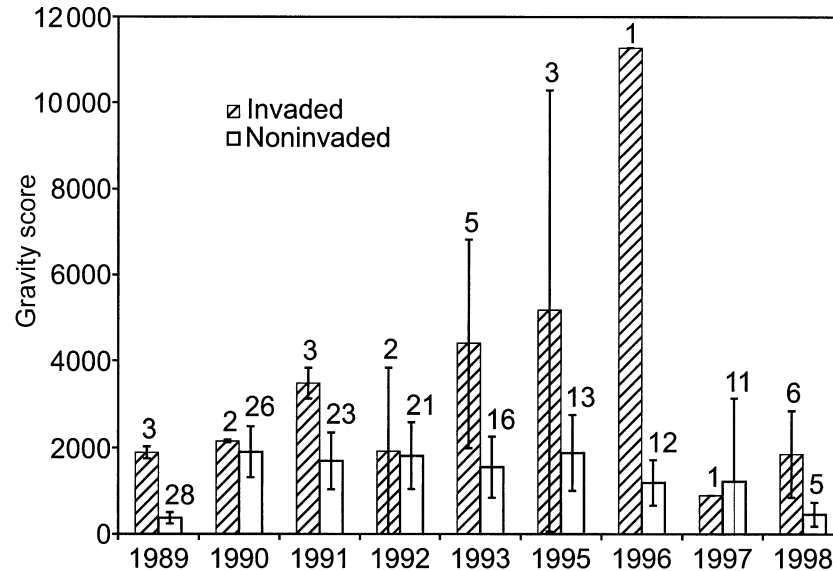
FIG. 5. Backcasting analysis of invaded lakes to determine whether systems invaded in a particular year (hatched bars) had higher vector inflows than lakes that were invaded in subsequent years (open bars). Values shown are mean gravity scores ($\pm$ 1 SE), with number of lakes in each category shown above the bars. Gravity scores are the sum of T_{ij} values for all source lakes with which the destination lake had vector activity (see Eq. 2). Initially, only vector inflows from the Great Lakes were responsible for gravity scores, although the number of inflows typically grew as more lakes became invaded. Crotch Lake was invaded in 1992 despite very low vector inflows, whereas Pigeon Lake was invaded in 1996, three years after its dominant inflow source (Lake Simcoe) was reported invaded. Lakes invaded in 1997 and 1998 had low gravity scores owing to little contact with the Great Lakes or with invaded inland "hubs."

A discriminant function based on gravity scores successfully predicted *Bythotrephes* invasion status for 65% of invaded lakes and 76% of noninvaded lakes based on year 2000 occurrence data (74% overall, Wilks' lambda = 0.86, F = 27.5, P < 0.0001). Invasion status was directly related to vector strength, as invaded lakes had significantly higher gravity scores than noninvaded ones (t = 4.4, df = 34, P < 0.0001). The discriminant function misclassified 11 of 31 invaded lakes, while 33 of 139 noninvaded lakes were predicted to be invaded.

To determine whether the sequence in which lakes were invaded was related to the intensity of vector inflows, we recalculated gravity scores for each year new invasions were reported between 1989 and 1999 (Fig. 5). This backcasting analysis considered inflows only from lakes that were invaded previously. Gravity scores of lakes invaded in any particular year were significantly greater than those of lakes invaded at a later time, indicating that the magnitude of vector inflows and proximity to invaded sources determined the order in which lakes became invaded (Fig. 5; ANOVA, F = 10.7, df = 1, 163, P = 0.0016). Lake gravity scores were affected by neither year of invasion (F = 1.78, df = 8, 163, P = 0.0835) nor interaction between invasion year and invasion status (F = 1.32, df = 8, 163, P = 0.2350). Crotch Lake was invaded in 1992, despite having the lowest gravity score of any invaded lake (Fig. 5). Overall, however, gravity scores were consistent indicators of time to invasion. For example,

gravity scores of the first three inland lakes (Muskoka, Joseph, Rosseau) to be invaded were the highest of any in the study and 20 times greater than those for the five lakes invaded during 1999. Invasion of some lakes was delayed until other lakes, with which they had high vector inflows, themselves became invaded. For example, Pigeon Lake had the twelfth highest gravity score (105), but it was not invaded until 1996, three years after the invasion of Lake Simcoe, its dominant source of vector inflow (Figs. 4 and 5).

Future dispersal of *Bythotrephes* can be forecasted based on its distribution during 2000 and the vector matrix extant at that time (Fig. 6). For example, 11 lakes classified as noninvaded during 2000 were confirmed invaded during 2001. The distribution of gravity scores for these lakes differed significantly from that of lakes that remained noninvaded during 2001 (Kolmogorov-Smirnov test, P = 0.0211; Fig. 6), reflecting greater vector inflow to newly invaded systems. One of these invaded systems, Lake Nipigon, is located directly north of, and was likely invaded from, Lake Superior (Figs. 1 and 4). A GIS representation of current and projected spread of *Bythotrephes* in Ontario, based on vector flow patterns in 2000, revealed that Lake Nipigon was among the most vulnerable systems to invasion (Fig. 1). The overall distribution of *Bythotrephes* is expected to expand further into northwestern Ontario, possibly including Lake of the Woods on the Minnesota and Manitoba border, as well as further in eastern Ontario (Fig. 1). However, most new invasions
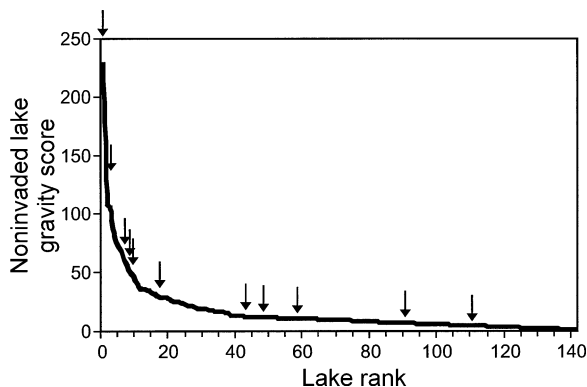
FIG. 6. Gravity scores of noninvaded lakes based upon year 2000 presence/absence data. Lakes confirmed as invaded during 2001 are indicated by arrows. Gravity scores of newly invaded lakes differ significantly from (i.e., are higher than) those of lakes that remained noninvaded during 2001, indicating that the magnitude of vector inflows corresponds with lake vulnerability to invasion.

are anticipated to occur in central Ontario in close proximity to lakes that have already been invaded (Fig. 1).

DISCUSSION

Forecasting vulnerability of ecosystems to species invasion is a very high priority for ecologists and ecosystem managers worldwide (e.g., Hayes 2002, Kolar and Lodge 2002). In this study we developed a spatially explicit gravity model to forecast occurrence of waterflea invasions based upon human vector activity from, and proximity to, invaded source lakes. The model successfully backcasted the invasion sequence of inland lakes based upon relative strength of inbound vectors (Fig. 5), and forecasted new invasions of noninvaded lakes (Fig. 6). These findings are consistent with the quantitative component of the propagule pressure concept, whereby invasion success is related to the frequency and intensity with which ecosystems are challenged by nonindigenous species (Williamson 1996, Lonsdale 1999, Ruiz et al. 2000, Kolar and Lodge 2001).

Sexual and asexual reproductive modes of *Bythotrephes* result in production of encysted resting eggs or clonal offspring, respectively. If, as we expect, transfer of resting eggs is the primary means by which humans disperse *Bythotrephes*, then propagule condition may be a relatively unimportant component of propagule pressure. Confamilial *Cercopagis pengoi* (Ostroumov) waterfleas likely invaded a series of lakes in the Finger Lakes (New York, USA) region by a similar human-vectored mechanism (Cristescu et al. 2001). Although northbound migrating waterfowl have been attributed with introductions of zooplankton in the northern hemisphere (e.g., Green et al. 2002), they appear incapable of dispersing *Bythotrephes* in the manner reported here owing to a temporal mismatch between when the migrations occur and when zooplankton are available to

be transported in lakes. Also, the paucity of invasions in lakes south of the Great Lakes (Fig. 1) suggests that autumnal, southern migrations of waterfowl have not dispersed sufficient numbers of *Bythotrephes* as to facilitate new invasions there. If migrating waterfowl were significant vectors, more invasions should have been reported in lakes south than north of the Great Lakes since *Bythotrephes* would be more abundant in waters later in the year and the likelihood of endozoochorous or epizoochorous transport also would be greater, all other factors being equal. Waterfowl could be responsible for local dispersal of *Bythotrephes*, although the pattern of spread would likely be omnidirectional as opposed to unidirectional if caused by migrating individuals.

Most respondents (62.5%) in our study traveled to lakes <15 km from their principal-use lake, although a small percentage (5.4%) of individuals trailered boats >500 km (Fig. 3). The greatest distance between an invaded source lake and a destination lake invaded from it was 200 km (i.e., from Lake Muskoka to Lake Temagami in the north-central region of the province). This source–recipient pattern, whereby most invasions occur over short distances but some occur over much greater ones, is consistent with stratified diffusion (Fig. 7; Hengeveld 1989, Lewis 1997, Shigesada and Ka-
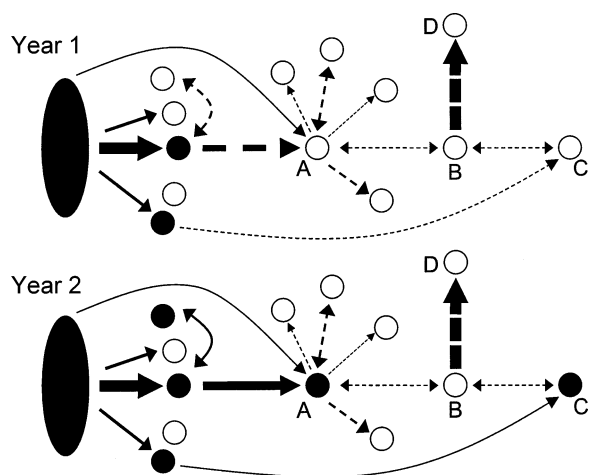

FIG. 7. Conceptual landscape model for invasion of inland lakes (circles) from a Great Lakes source (ellipse). The magnitude of vector flows is indicated by arrow thickness; solid lines denote functional vectors from lakes that are invaded, while dashed lines indicate contact between systems that are not yet (or have just become) invaded. Invaded and noninvaded lakes are shown as solid and open circles, respectively. The overall pattern is suggestive of stratified diffusion, with dominant local dispersal and few long-distance (to lake C) invasion events. All invasions result from vector inflows from invaded sources, although not all vector inflows result in successful invasions. Some lakes (A) will serve as invasion "hubs" (e.g., Lake Muskoka). Delayed invasion of some lakes (D; Pigeon and Centennial lakes) occurs despite strong contact with other lakes (B; Simcoe, Black Donald) because the inbound vector is not functional until the source itself becomes invaded.

wasaki 1997). Analyses of overland boat movement patterns also indicate that dispersal of zebra mussels, *Daphnia* waterfleas, and macrophytes is expected to occur locally or regionally, with a much lower probability of long-distance transfer (Buchan and Padilla 1999, Bossenbroek et al. 2001, Havel et al. 2002, Kraft et al. 2002). Human-mediated stratified diffusion has also been reported with other nuisance nonindigenous species, notably the Argentine ant *Linepithema humile* (Mayr) (Suarez et al. 2001).

Gravity model

The discriminant function misclassified 11 of the invaded lakes as noninvaded, and 33 of the noninvaded ones as invaded. Invaded lakes may have been misclassified because our gravity model, which included only seven human vector mechanisms, may have been incomplete, or because the existing mechanisms were not correctly estimated. Lakes may have been misclassified as invaded owing to a type II error, which could result if populations were present below a detectable threshold (Shigesada and Kawasaki 1997) despite receiving high amounts of vector traffic. Low population density could, in turn, be caused by a host of mechanisms including absence of preferred prey (Yan and Pawson 1998), suppression by fish predators (e.g., Yan et al. 2001), or because the population was only recently established. Also, it is possible that some invasion vectors were overestimated based on our surveys. Finally, some of these lakes may not yet have been invaded owing to the stochastic nature of the invasion process. As evidence, five of the lakes that were reported invaded in Ontario during 2001 were among the 33 noninvaded lakes incorrectly designated by the discriminant function.

Analysis of invasion vectors

Given the apparently local nature of *Bythotrephes* dispersal, it is not surprising that the overall pattern is suggestive of a "stepping stone" invasion sequence (Figs. 4, 7). For example, the close proximity of lakes in central Ontario, coupled with high vector flows within this lake matrix, has resulted in a sequential pattern of invasion involving at least three lakes. Vector analysis reveals that this analogy cannot be extended in all directions, however, as outbound vectors typically demonstrated geographical asymmetry. For example, while Lake Temagami is the most northern lake in central Ontario that has been invaded to date, its vector outflows were primarily to the south and southeast, thus further northern dispersal from this lake appears unlikely (Fig. 1).

Analysis of invasion vectors must incorporate information regarding the sequence with which lakes become invaded. As an example, Lake Simcoe had very strong vector flows to Pigeon Lake (lakes B and D in Fig. 7), but the vector was not functional until the former lake was invaded. Likewise, strong vector inflow to Centennial Lake was not realized until after Black Donald Lake was invaded in 1999. Even though some lakes that were invaded relatively recently have high vector inflows (e.g., Pigeon, Nipissing, Centennial), the overall pattern is suggestive of early invasion of lakes with high connectivity to invaded systems followed by invasion of lakes with progressively weaker inflows (Fig. 4).

Verification of invasion vectors is needed because subdominant flows exist for many invaded lakes. For example, there were seven additional flows from other lakes into Pigeon Lake in addition to the dominant flow from Lake Simcoe. Collectively these flows were 50% greater than that from Lake Simcoe, although the largest subdominant flow was only 57% as large as that from the dominant source. We are currently exploring relationships between genetic (i.e., microsatellite) architecture of inland populations and their putative source populations. Previous works with invasive waterfleas (*Cercopagis pengoi*) and Chinese mitten crabs (*Eriocheir sinensis* Milne Edwards) have demonstrated the utility of genetic probes in ascertaining the origin of invasive nonindigenous species populations (e.g., Cristescu et al. 2001, Hanfling et al. 2002).

Vector analysis permits development of forecasts regarding vulnerability of specific local and distant ecosystems to invasion, an unlikely possibility with either reaction-diffusion or natural, stratified diffusion models. For example, vector flows indicate that additional invasions are anticipated in central Ontario and range expansion is expected in eastern and northwestern regions of the province (Fig. 1). Of particular concern is the 2001 invasion of Lake Nipigon (Fig. 1). This lake was likely invaded from Lake Superior, although other possible sources include Lakes Simcoe and Panache to the southeast and Shebandowan to the southwest (Figs. 1, 4). Lake Nipigon supports a large tourist-based, recreational fishery and, while its outflows have not been quantified, will almost certainly serve as an invasion hub, much the way Lakes Muskoka and Simcoe have in central Ontario (Figs. 4, 7). Surprisingly, with the possible exception of Lake Nipigon, most invasions of inland lakes resulted from either direct or indirect vector flows from Lake Huron. While recreationalists moved from the other Great Lakes to inland systems, our study indicates that these vectors were relatively minor in comparison to those originating from Lake Huron.

The importance of different inland lakes as invasion sources changed through time as noninvaded lakes became invaded. For example, Lake Muskoka had the highest vector outflows to lakes that later became invaded, although total outflows to currently noninvaded lakes are highest for Lakes Simcoe and Kashagawigamog. Consequently, the latter two systems may serve as future invasion hubs. Interestingly, vectors from these lakes to other inland lakes were typically stronger than the vector between Lake Huron and Lake Muskoka

that apparently began the invasion sequence of inland lakes. Our study also indicates that lakes with proximity to major roads are vulnerable to inadvertent introduction of *Bythotrephes* by humans owing to enhanced access opportunities. Because *Bythotrephes* has adverse impacts on native zooplankton diversity (Yan et al. 2002) and causes nuisance fouling of anglers' fishing lines, reducing its spread is a desirable objective. Management intervention to slow the dispersal of *Bythotrephes* to new lakes must be targeted to achieve maximal cost efficiency. We propose that this can be achieved through a public education campaign jointly targeting the export of live individuals or resting stages from lakes with the greatest outbound vector flows (e.g., Simcoe, Kashagawigamog, Georgian Bay) and those most likely to serve as invasion hubs (e.g., Simcoe, Nipigon).

In summary, our study illustrates that spatially explicit analysis of dispersal vectors holds considerable promise for identifying lake susceptibility to invasion by the waterflea *Bythotrephes*. *Bythotrephes* has apparently invaded lakes through a combination of diffusion and long-distance dispersal. Attempts to reduce the rate of spread will require concerted efforts to identify and eliminate vectors responsible for transfer of propagules from important major source lakes that are frequented by humans. More generally, our study illustrates the value of vector-based analyses to assess ecosystem vulnerability to invasion by nonindigenous species.

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