Journal of Applied Ecology 2005
42, 80–90

Development of inland lakes as hubs in an invasion network

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Summary

1. The ability to predict spatially explicit dispersal by non-indigenous species is a difficult but increasingly important undertaking as it allows management efforts to be focused around areas identified as susceptible to invasion. Lakes may serve as useful models for these studies because the habitats are well defined, and vectors of spread may be readily identified and quantified. In this study, we examined patterns of spread of the non-indigenous 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 non-invaded and other invaded lakes. Non-linear functions were developed to describe the cumulative number of invaded and non-invaded 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 non-invaded 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 non-invaded destinations from invaded sources follow a power function, consistent with scale-free networks. These networks indicate that small proportions 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.

Key-words: biological invasions, *Bythotrephes*, human vectors, invading species, scale-free networks

Journal of Applied Ecology (2005) **42**, 80–90
doi: 10.1111/j.1365-2664.2004.00988.x

Introduction

Humans are causing rapid homogenization of aquatic communities world-wide through extinction of endemic species and introduction of non-indigenous 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 humans 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 and its subsequent establishment depends on its ability to pass successfully through

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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.

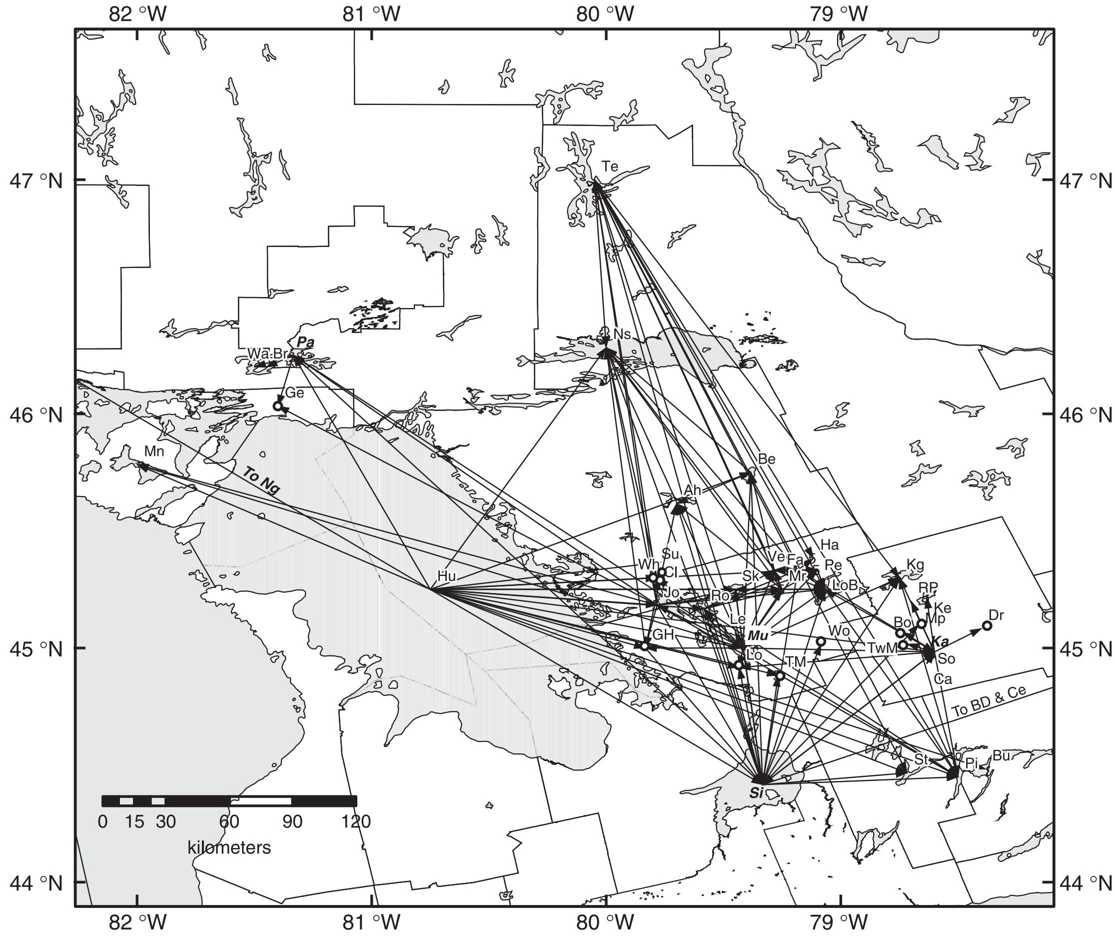
Early attempts to model the dispersal of NIS focused on simple diffusive range expansion, which assumes constant population growth and a normal distribution for propagule dispersion distance (Skellam 1951). Range expansion thus occurred as a progressive wave from the invasion source at a rate proportional 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, although the location of new satellite colonies cannot be predicted easily (Kot, Lewis & van den Driessche 1996; Lewis & Pacala 2000). Examples of aquatic species whose dispersal in the USA 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 (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 non-invaded lakes, as live NIS may be attached to trailers, boat hulls and engines, attached to macrophytes stranded on boat trailers, or contained in live well or bilge water (for a full list see Carlton 1993). 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 (Schneider, Ellis & Cummings 1998; Buchan & Padilla 1999; Bossenbroek, Kraft & Nekola 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 non-invaded 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 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 has 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 (Watts & Strogatz 1998; Albert, Jeong & Barabási 2000; 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 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, maximize economies of scale but inadvertently facilitate transport of NIS (Carlton 1996; O'Kelly 1998). For example, the comb jellyfish *Mnemiposis leidyi* was introduced into the Black Sea in the early 1980s, 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, Canada, 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



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.

Fig. 1. 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.

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* 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 non-invaded destination lakes. One popular recreational lake (Muskoka) in central Ontario, Canada, has apparently caused up to 39 other inland lakes to become invaded either directly or indirectly (MacIsaac *et al*. 2004; Fig. 1). 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 non-invaded lakes occur.

In this study, we examined patterns of human vector movement to assess whether some invaded systems have the potential to develop into invasion hubs. We also examined the invasion process in terms of a growing network, and illustrated that, while the total number of connections between invaded sources and invaded and non-invaded destinations theoretically increases at a geometric rate, the realized vector traffic associated with recreational boating increases at a much-reduced rate. Finally, we provided 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, Canada, from field surveys in 1999 and 2003, which were designed to develop a production/attraction-

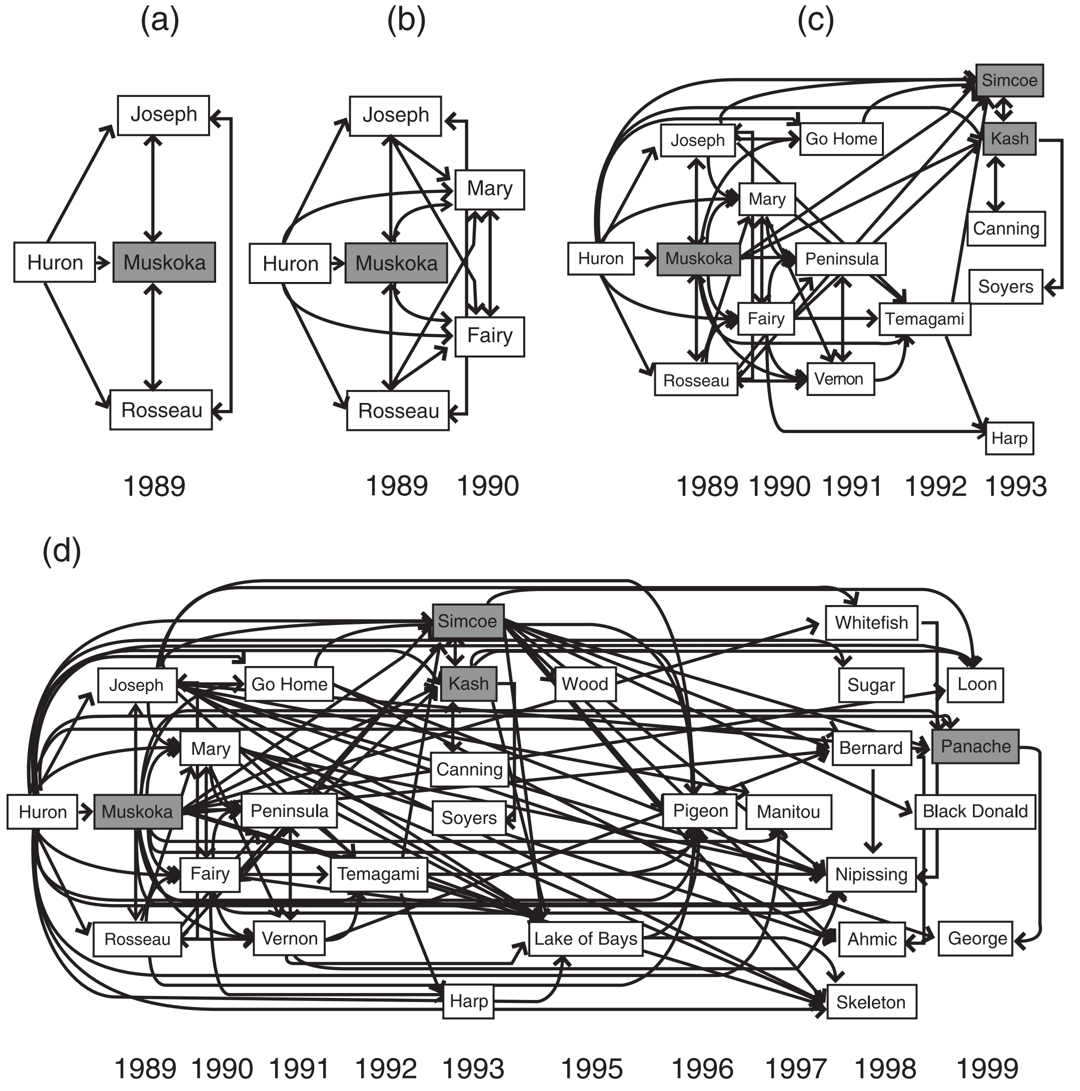


Fig. 2. Diagram of measured network traffic from previously to recently invaded lakes based on records of first reporting. Stages of the invasion network are shown for (a) 1989, (b) 1990, (c) 1993 and (d) 1999. Shaded boxes represent existing or nascent inland hubs, and Lake Kashagawigamog is abbreviated as Kash.

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 non-invaded destination habitats (MacIsaac *et al*. 2004). Surveys conducted at marinas and boat ramps were used to identify which invaded and non-invaded 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 to have been invaded by *Bythotrephes*. These five lakes (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. 2).

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 and Table 1). Separate saturation functions were developed for outbound vector traffic to invaded and to non-invaded 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) (equation 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 was:

$$y = \frac{\alpha\beta x^{\gamma}}{1 + \beta x^{\gamma}} \qquad \text{eqn 1}$$

Table 1. Fitted asymptotic functions for the cumulative number of invaded or non-invaded 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	$y = \dfrac{37{\cdot}00 \times 0{\cdot}06x^{0{\cdot}75}}{1 + 0{\cdot}06x^{0{\cdot}75}}$	0·999	101
	Non-invaded	$y = \dfrac{60{\cdot}79 \times 0{\cdot}01x^{0{\cdot}79}}{1 + 0{\cdot}01x^{0{\cdot}79}}$	0·997	101
Panache	Invaded	$y = \dfrac{201{\cdot}65 \times 0{\cdot}01x^{0{\cdot}88}}{1 + 0{\cdot}01x^{0{\cdot}88}}$	0·996	19
	Non-invaded	$y = \dfrac{90{\cdot}78 \times 0{\cdot}02x^{0{\cdot}94}}{1 + 0{\cdot}02x^{0{\cdot}94}}$	0·998	19
Muskoka	Invaded	$y = \dfrac{44{\cdot}77 \times 0{\cdot}06x^{0{\cdot}68}}{1 + 0{\cdot}06x^{0{\cdot}68}}$	0·999	110
	Non-invaded	$y = \dfrac{36{\cdot}98 \times 0{\cdot}004x^{1{\cdot}05}}{1 + 0{\cdot}004x^{1{\cdot}05}}$	0·994	110
Kashagawigamog	Invaded	$y = \dfrac{36{\cdot}37 \times 0{\cdot}05x^{0{\cdot}82}}{1 + 0{\cdot}05x^{0{\cdot}82}}$	0·999	44
	Non-invaded	$y = \dfrac{80{\cdot}60 \times 0{\cdot}01x^{0{\cdot}93}}{1 + 0{\cdot}01x^{0{\cdot}93}}$	0·996	44
Lake Huron	Invaded	$y = \dfrac{39{\cdot}11 \times 0{\cdot}07x^{0{\cdot}67}}{1 + 0{\cdot}07x^{0{\cdot}67}}$	0·998	93
	Non-invaded	$y = \dfrac{103{\cdot}68 \times 0{\cdot}01x^{0{\cdot}82}}{1 + 0{\cdot}01x^{0{\cdot}82}}$	0·998	93

where y is the mean cumulative number of visited invaded or non-invaded destination lakes, x is the number of surveys sampled, and α, β and γ are estimated parameters.

To predict the number of invaded and non-invaded destinations that boaters may visit during a single season (24 May to 2 September), 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 differed, 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 ($k_{\mathrm{inv},t}$) for a given year, t, to newly invaded lakes ($n_{t,o}$) from previously invaded lakes (m) described by:

$$k_{\mathrm{inv},t} = \sum_{o=1}^{p} n_{t,o}m \qquad \text{eqn 2a}$$

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

As lakes become invaded, the number of non-invaded 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 non-invaded lakes from previously invaded lakes ($k_{\mathrm{non},t}$) for each year is:

$$k_{\mathrm{non},t} = \left(l - \sum_{o=1}^{p} n_{t,o} - m\right)m \qquad \text{eqn 2b}$$

where $n_{t,o}$ and m are newly and previously invaded lakes, and l 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 non-invaded lakes and to provide a means of comparing a theoretical network of invaded and non-invaded 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 non-invaded 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 non-invaded destinations in each of 1999 and 2003, and constructed frequency distributions. We fitted

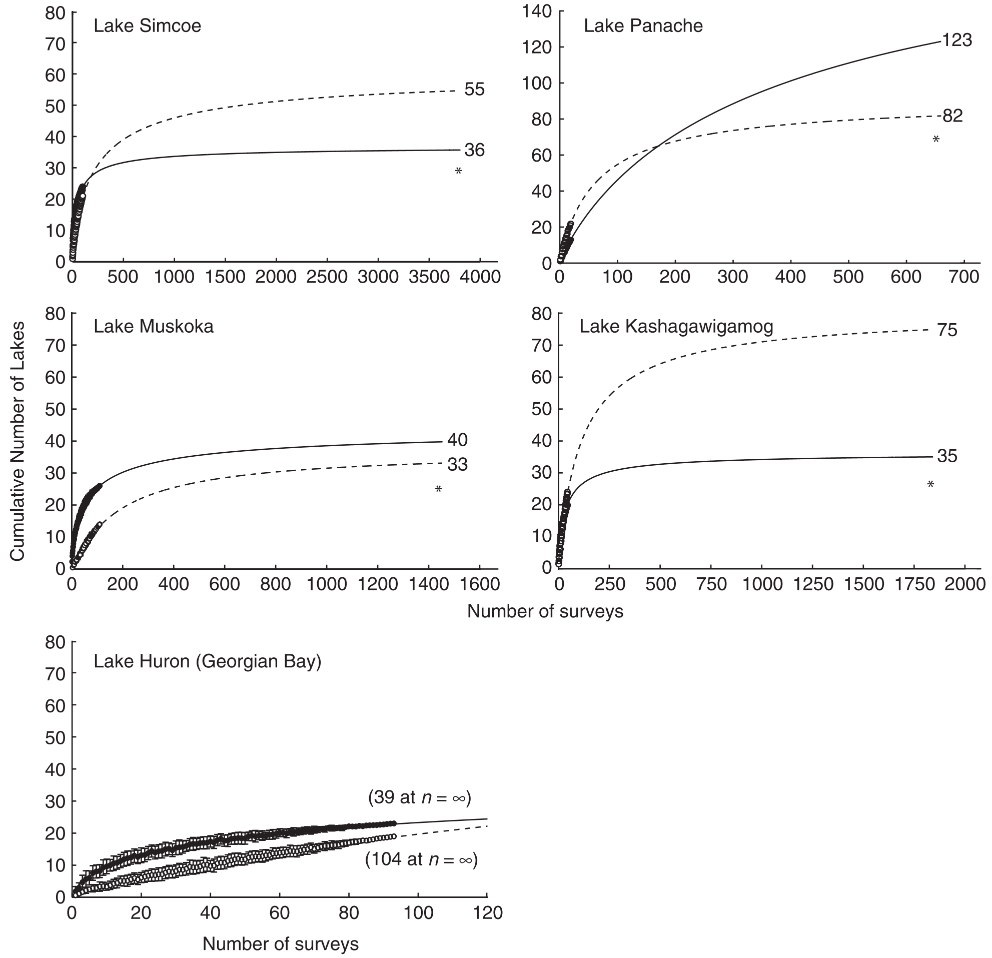


Fig. 3. Cumulative number of different invaded (solid circles) and non-invaded (open circles) lakes visited by boaters departing from five invaded lakes in central Ontario. Values presented are mean ± SE; standard errors of estimates smaller than symbol sizes are not shown. Monte Carlo simulations were 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.

two-parameter power ($y = b_0x^{b1}$) and exponential [$y = b_0\exp(b_1x)$] curves to the frequency distributions of links using least-square methods. Analyses utilized the median number of connections for each connection category (Fig. 4). 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 revealed 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 non-invaded lakes (excepting the Great Lakes). Secondly, the total amount of traffic leaving this source was high, as we estimated 1452 individuals trailered boats from the lake each year. While this lake was critical in the initial dispersal of *Bythotrephes* among inland lakes (Fig. 2), 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 non-invaded destinations, respectively, from Lake Muskoka.

Two other lakes, Simcoe and Kashagawigamog, exhibited the opposite pattern of outbound vector flow. For example, the ratio of non-invaded to invaded destination visitations was 1·53 and 2·14 for the former lakes, while that of Lake Muskoka was only 0·83 (Fig. 3). Moreover, the total number of non-invaded 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 non-invaded 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

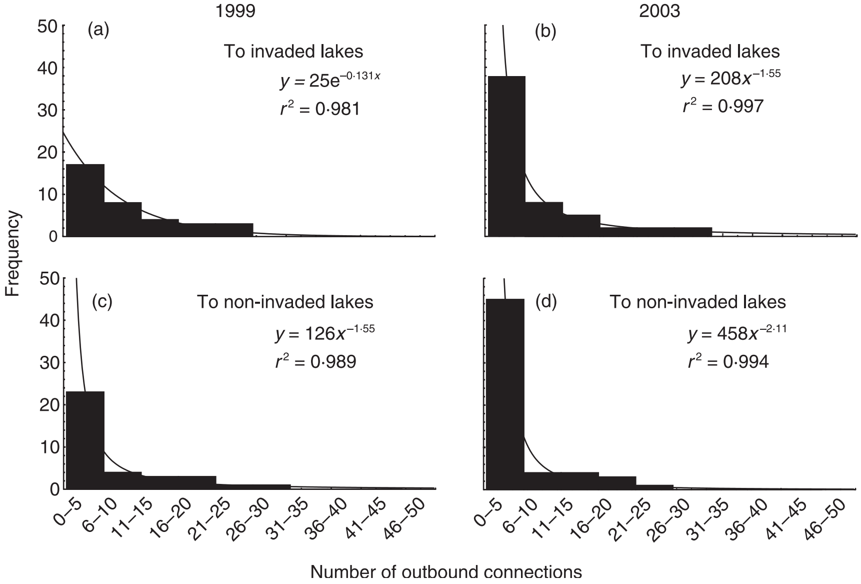


Fig. 4. Frequency histograms of the number of functional links from invaded sources to (a, b) invaded and (c, d) non-invaded destinations in 1999 and 2003. Lakes that had a high number (e.g. 26–30) of connections to non-invaded destinations in 1999 served as nascent hubs and probably influenced the rate of spread for *Bythotrephes*. Best-fit exponential (a) and power function (b–d) curves were fitted using link frequencies and the median of each connection category.

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 'non-invaded' 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 was to other invaded lakes (Fig. 3). However, the actual number of boaters utilizing this lake was enormous (but unmeasured), and at high (e.g. 2000) seasonal usage the asymptotic number of non-invaded lakes visited (104) greatly exceeded that to invaded lakes (39).

Boaters from Lake Panache were initially more likely to visit non-invaded than invaded lakes. However, at a moderate number of boaters (*c.* 200), the curves extrapolating boater behaviour intersect, and traffic to other invaded lakes was more common. We project that *c.* 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, because of 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. 2a). By summer 2003, at least 57 inland lakes and lake systems were invaded (Fig. 1). The sequence in which the lakes appeared in the network was 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. 2d). 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 non-invaded lakes in the system. The actual number of total connections from invaded sources to non-invaded destinations increased in a stepped fashion (Fig. 5a). 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. The total number of connections to non-invaded lakes increased again in 1993 when Lakes Simcoe and Kashagawigamog were invaded. Finally, all non-invaded lakes in the network were connected to at least one invaded lake by 1999, when Lake Panache was reported to have been invaded (Fig. 5a).

The relationship between the actual and theoretical number of connections from invaded lakes differed temporally for newly invaded and non-invaded destinations (Fig. 5b). The theoretical rate of growth in any given year was geometric for traffic among invaded lakes, and for traffic from invaded lakes to non-invaded

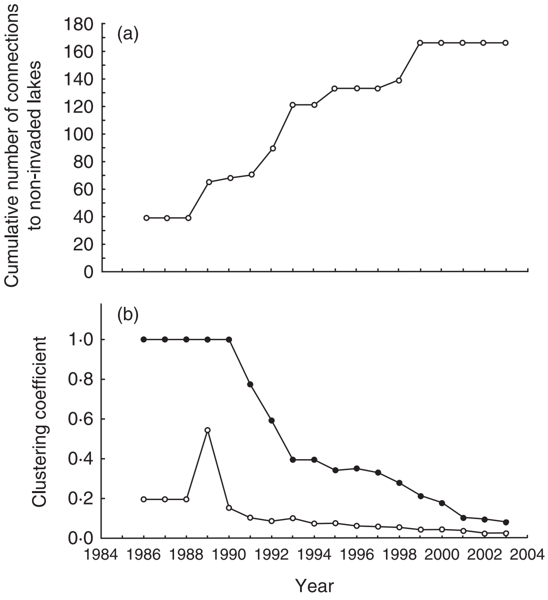


Fig. 5. (a) Cumulative number of connections from invaded to non-invaded lakes. (b) Network clustering coefficient, reflecting the ratio of the cumulative, actual to theoretical number of connections from invaded sources to other invaded (solid circles) and non-invaded (open circles) destination lakes. High clustering coefficients reflect tight linkage between invaded and other lakes. Values decline through time as more isolated lakes, with fewer links to other systems, become invaded.

lakes. The latter rate of growth was, however, much steeper. The clustering coefficient to invaded lakes was always higher for invaded than for non-invaded systems (Fig. 5b), indicating that invaded lakes form a tighter network among themselves than with non-invaded lakes. In addition, the clustering coefficient declined over time for both networks, as lakes with fewer contacts with other invaded and non-invaded systems became invaded (Fig. 5b). Clustering coefficients declined because the theoretical number of connections grew at a faster rate than the actual traffic.

A SCALE-FREE INVASION NETWORK

With one exception (Fig. 4a), the network of actual connections from invaded lakes to other lakes followed a scale-free topology (Fig. 4b–d). Most invaded lakes (49–79%) had few (≤ 5) connections with other lakes, while a few had many connections (> 20) (Fig. 4). An exponential curve provided a slightly better fit to the distribution of links from invaded to invaded lakes in 1999 ($r^2 = 0{\cdot}981$) than a power curve ($r^2 = 0{\cdot}952$) (Fig. 4a). However, the distribution of links for traffic to non-invaded lakes in 1999 was better described by a power law function ($r^2 = 0{\cdot}989$) than by an exponential one ($r^2 = 0{\cdot}968$), 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 ($r^2 = 0{\cdot}996$) and non-invaded ($r^2 = 0{\cdot}994$) lakes, indicating that the few invaded lakes with large numbers of contacts with non-invaded systems may develop as future hubs (Fig. 4d). Slopes of fitted power curves increased in steepness from 1999 to 2003, supporting the view that newly invaded lakes had fewer connections with 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 study, 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 non-invaded vs. 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), although clear examples of functioning hubs are rare. Simberloff & Boecklen (1991) demonstrated that invasion of non-indigenous 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 (Kraft & Johnson 2000; Bossenbroek, Kraft & Nekola 2001; Johnson, Ricciardi & Carlton 2001).

Lake Muskoka was the first inland lake invaded by *Bythotrephes*, owing to its dominant vector inflow from Lake Huron (Fig. 2). Lake Muskoka is a very popular recreational lake and has very strong links with other lakes in the region via departing boaters and anglers. Indeed, in the initial years of network formation, up to and including 1991, the matrix of links among invaded lakes was symmetrical, with all systems having vector outflows to the others (Fig. 5). Thereafter, the clustering coefficient for the invaded lakes network declined quickly as new systems with few links were added to the network (Fig. 5). The degree of clustering among invaded lakes continued to decline through 2003, although it remained consistently higher than that between invaded and non-invaded lakes. The clustering coefficient for invaded to non-invaded lakes peaked during 1989, reflecting the establishment of *Bythotrephes* in Lake Muskoka. Clustering of invaded to non-invaded lakes was otherwise consistently low, typically < 20% of the number of possible connections (Fig. 5b).

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 non-invaded (Fig. 3). Conversely, outflows from Lakes Simcoe and Kashagawigamog are directed principally to non-invaded lakes. These lakes also have a higher ratio of outbound flow directed towards non-invaded lakes than 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, although 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 non-invaded 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, Coffey & Howard-Williams 1985; Padilla, Chotkowski & Buchan 1996; Bossenbroek, Kraft & Nekola 2001; Johnson, Ricciardi & Carlton 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 would be invaded (MacIsaac *et al.* 2004). In any given year, lakes that became invaded received significantly more traffic from invaded sources than lakes that remained non-invaded. Alternative vectors for *Bythotrephes* transport include 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 NIS 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 non-indigenous 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. the '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 Lake Muskoka because their average distance from other invaded and non-invaded 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 (Schneider, Ellis & Cummings 1998; Bossenbroek, Kraft & Nekola 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. 4), and are slightly lower than those reported for the scale-free networks of the Internet (–2·45; Albert, Jeong & Barabási 1999) and metabolic reactions (–2·2; Jeong *et al.* 2000). The increase in slope steepness in the network of connections to non-invaded lakes in 2003 relative to 1999 (Fig. 4) 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 artefact 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, Jeong & Barabási 2000), and some food webs (Dunne, Williams & Martinez 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, Jeong & Barabási (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 is 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 to Muskoka to Simcoe to Kashagawigamog to 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 the 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 non-invaded 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 non-invaded 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.

Acknowledgements

We thank Dr Norman Yan for *Bythotrephes* distribution data and Gerry Moraal for Lake Kashagawigamog creel data. This study was supported by NSF grant DEB02-13698 (to D. M. Lodge), an NSERC Collaborative Research Opportunity grant (to M. A. Lewis and H. J. MacIsaac), and an Invasive Species Research Chair from DFO Canada (to H. J. MacIsaac). J. R. Muirhead gratefully acknowledges receipt of the Paul W. Rodgers scholarship from the International Association for Great Lakes Research.

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Received 24 February 2004; final copy received 13 October 2004