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Patterns and pathways in the post-establishment spread of non-indigenous aquatic species: the slowing invasion of North American inland lakes by the zebra mussel

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Abstract

The zebra mussel, *Dreissena polymorpha*, has spread through eastern North American aquatic ecosystems during the past 15 years. Whereas spread among navigable waterways was rapid, the invasion of isolated watersheds has progressed more slowly and less predictably. We examined the patterns of overland spread over multiple spatial and temporal extents including individual lake districts, states, and multi-state regions in the USA and found that only a small proportion (<8%) of suitable inland lakes have been invaded, with the rate of invasion appearing to be slowing. Of the 293 lakes known to be invaded, 97% are located in states adjacent to the Laurentian Great Lakes with over half located in Michigan. Only six states have more than 10 invaded lakes and only in Michigan and Indiana have more than 10% of suitable lakes become invaded. At smaller spatial extents, invaded lakes are often clustered within a lake-rich region across southern Michigan and northern Indiana. This clustering appears primarily due to multiple overland invasions originating from the Great Lakes followed to a lesser extent by subsequent secondary overland and downstream dispersal. Downstream spread appears responsible for only one third of the inland invasions. Temporally, invasions peaked in the late 1990s, with only 13 new invasions (0.4% of suitable lakes) reported in 2003 in the four-state region surrounding Lake Michigan. Peak rates of invasion occurred 4–6 years earlier in Michigan relative to Indiana and Wisconsin, but this time lag is likely due to differences in the establishment of Great Lake source populations rather than 'stepping stone' dispersal across the landscape.

Introduction

The distribution of an invasive species is a key attribute of its potential impact (Lodge et al. 1998). Ultimately, this range is limited by the abiotic and biotic characteristics of the environment, but the location of the initial founding population, the mechanisms and pathways of dispersal, and the distribution of suitable habitats will all contribute to the determination of the evolution of an invasion. Whereas it may be possible to assess the suitability of the environment based on physical (e.g., temperature, water chemistry) or biological (e.g., productivity, the presence of predators) conditions, the relative importance of different dispersal vectors and their occurrence in space and time are often poorly known.

In this respect, lakes offer well-delineated systems with relatively clear habitat boundaries and unambiguous connectivity. Dispersal between lakes occurs either through hydrological connections or by overland 'jumps' over an inhospitable terrestrial environment. Hydrological connections are not always benign passages (e.g., turbulent motion of flowing water) nor is the terrestrial environment equally stressful to all life stages of aquatic organisms (e.g., the adult stages of aquatic insects), but in general, the terrestrial environment can represent a barrier to the dispersal of aquatic organisms between water bodies. The efficacy of this barrier to the spread of an invasive species will depend on characteristics of the species in question and the existence of anthropogenic mechanisms that can transport viable propagules overland.

The invasion of North America by the zebra mussel, *Dreissena polymorpha*, offers an exceptional opportunity to examine the post-establishment patterns of spread (Johnson and Padilla 1996). This mollusk has become a 'poster child' for aquatic invasions, and as a result of extensive scientific inquiry and public outreach, we now have particularly good knowledge of the potential distribution of this species across the aquatic landscape, its current distribution, and how this distribution has evolved over time. In terms of habitat suitability, the potential range of the zebra mussel has been estimated (largely based on calcium and pH levels) to include portions of many states and provinces (Strayer 1991; Neary and Leach 1992; Koutnik and Padilla 1994; Drake and Bossenbroek 2004). Most of the lakes, reservoirs, and rivers in the region surrounding the Great Lakes (where the zebra mussel first became established) appear particularly suitable for this species – absence from such water bodies is, therefore, most likely due to dispersal barriers.

The dispersal of the zebra mussel within and between water bodies can occur rapidly via the dissemination of planktotrophic larvae (veligers) by currents (Horvath et al. 1996) or adult stages attached to floating objects, including ships and aquatic plants (Allen and Ramcharan 2001; Horvath and Lamberti 1997). In contrast, overland dispersal is much more difficult. Natural vectors of dispersal conceivably exist (Carlton 1993) but are unlikely to be important relative to anthropogenic vectors (Johnson and Carlton 1996; Karatayev et al. 2003) of which transport by transient recreational boating (Johnson et al. 2001) is likely to be the most important in North America (e.g., Padilla et al. 1996; Schneider et al. 1998; Bossenbroek et al. 2001; but see Karatayev et al. 2003). New inland invasions can then spread naturally downstream into other lakes or river sections or eventually become sources or 'hubs' for further overland dispersal to other water bodies (MacIsaac et al. 2004). Any given inland water body can thus be invaded by one of three contrasting manners: (1) overland dispersal from a Great Lake source population, i.e., a primary overland invasion, (2) subsequent overland dispersal from a population established by a primary overland invasion, i.e., a secondary overland invasion, and (3) downstream dispersal from either of the above described overland invasions. The combination of these three processes will determine the spatio-temporal dynamics of the pattern of spread across inland waters.

The differences between dispersal within hydrologically connected waters and overland dispersal has produced contrasting patterns of spread at different spatial extents. At the continental level, zebra mussels spread rapidly, extending their range from Québec to Louisiana within 5 years of their initial detection in Lake St. Clair in 1987. In contrast, at the regional level, the initial spread to isolated inland waters has occurred much more slowly. By 1994, only a handful of inland lakes had been colonized, suggesting that a substantial time-lag exists in the process of 'filling in the gaps' of the aquatic landscape (Johnson and Carlton 1996). Differences in colonization rates between different regions (e.g., Michigan vs Wisconsin) suggested that delays in the establishment of large source populations could also greatly affect the timing of inland invasions (Kraft and Johnson 2000). The resulting expectation has been that the rate of inland invasions should begin to increase as source populations develop, both in the rapidly colonized navigable waters and in newly established inland populations that could then serve as additional sources for further invasions (Johnson and Padilla 1996; Leung et al. 2004; MacIsaac et al. 2004).

The spatial distribution of inland invasions by zebra mussels has thus not followed the simplistic predictions of reaction–diffusion models (Buchan and Padilla 1999), and the pattern of invasions corresponds more closely to that predicted by gravity models (Bossenbroek et al. 2001; Leung et al. 2004), which use a combination of the distribution of potential vectors (recreational boaters in this case), the distances between invaded and non-invaded lakes, and 'attractiveness' of different water bodies to predict invasions. Gravity models have also been shown to capture important characteristics of the recreational boater pathway (Leung et al. in press). Surveys of inland lakes have shown that rates of invasions are quite variable among different lake districts (Kraft and Johnson 2000), and the spatial pattern of inland invasions indicates that inland invasions are clustered (Kraft et al. 2002) although the precise mechanisms responsible for this pattern remain unknown.

Beyond the theoretical interest in invasion dynamics, such information is necessary for the proper management of invasions, for both predicting the imminent invasion of specific bodies of water (e.g., those downstream from or in the vicinity of primary overland invasions) and targeting prevention efforts. For example, if inland invasions are mostly the result of primary overland invasions, prevention efforts should focus on vectors originating from Great Lake access sites. In contrast, if primary overland invasions give rise to a number of secondary overland invasions in nearby, but hydrologically isolated, water bodies, then preventive measures should immediately focus on managing anthropogenic vectors originating from the site of any primary overland invasion.

Here we examine the current and past distribution of zebra mussels, primarily in the four-state region surrounding Lake Michigan. Although the initial establishment of zebra mussels occurred in Lake St. Clair and western Lake Erie at the eastern boundary of this region, our choice is based on a variety of reasons: geologically, this is a lake-rich region; historically, this region was the focus of a previous study on the distribution of zebra mussels (Kraft and Johnson 2000); and politically, US agencies have supported consistent data collection and development of a national database for documenting the distribution of aquatic nuisance species. Using data from multiple sources, we analyze the spatial and temporal patterns of zebra mussel spread into inland lakes over multiple extents to identify changes in invasion rates and the importance of different dispersal processes in creating observed patterns of distribution.

Materials and methods

Information on the temporal and spatial distribution of the zebra mussel from 1991 to 2003 was gathered from a variety of sources. For smaller spatial extents, we used a combination of data obtained from both surveys of targeted lakes and incidental sightings. The most rigorous data were obtained in 1995–1997 when lakes were specifically sampled in four states for the presence of zebra mussels (Kraft and Johnson 2000). The surveys consisted of periodic sampling of inland lakes two to four times during summer. Initial efforts began in 1993 but were limited to approximately 30 lakes in Michigan (L. Johnson, unpubl. data). A larger effort was initiated in 1995 when the program was expanded to include lakes in other states and focused on 10 lake districts approximately 400–700 km^2 in area distributed across the lower peninsula of Michigan, northern Indiana and Illinois, and Wisconsin. In general, the lakes were ≥2 m in depth and ≥40 ha in surface area, and most had some form of public access. Details of the sampling protocols are described elsewhere (Kraft and Johnson 2000), but in brief, vertical plankton tows were collected on at least two sampling dates during the summer after spawning (i.e., late May) and examined for the presence of veligers (Johnson 1995). Other state or county-coordinated sampling or monitoring programs (e.g., Michigan College Sea Grant Program) provided additional data. Information on incidental sightings was obtained from the United States Geological Survey Aquatic Nuisance Species (USGS-ANS) database (http://nas.er.usgs.gov/), which catalogs new sightings of zebra mussels provided by government agencies, university researchers, state and county agencies, and other sources. Whereas one might expect incidental sightings to have a higher threshold of detection relative to directed surveys, we generally found that public reports of invasions often occurred in the same year or the year after our detections, and thus we assume here that both survey detections and incidental sightings provided similar data. For simplicity, we used the year of detection as the year of invasion although the detection of an invasion most certainly occurs one to several years after the actual dispersal to a lake. Hydrological connections between lakes were determined by using information found in the USGS Hydrography Data Set (http://nhd.usgs.gov), and we designated any invasion that was downstream from a known population of zebra mussels as a downstream invasion although it could theoretically have resulted from an overland invasion (Shurin and Havel 2002).

Using these data, our analysis was conducted at three different spatial extents: nation, state, and district. At the largest extent, we combined data from states for which more than 10 invaded lakes had been reported by 2003 to assess national trends. In assessing the percentage of inland lakes and reservoirs invaded, we excluded all lakes that (1) were <25 ha because zebra mussels are not usually found in smaller lakes, (2) were predicted to be environmentally unsuitable (Drake and Bossenbroek 2004) and thus unlikely to support populations, or (3) had navigable connections to the Great Lakes or connecting waterways such as the Erie Canal (e.g., drowned river mouths of the Great Lakes states).

At an intermediate spatial extent, we examined increases in both the absolute number of invaded lakes and the invasion rate (i.e., the proportion of suitable lakes invaded) over time in individual states and in two multi-state regions (Michigan–Northern Indiana and Wisconsin–Northern Illinois). Although partially based on political boundaries, this latter division reflects a natural difference in the proximity of source populations. The Michigan–Northern Indiana region is surrounded by the Great Lakes on three sides, including Lake St. Clair and the western basin of Lake Erie, where the initial establishment of large zebra mussel populations occurred. In contrast, the Wisconsin–Northern Illinois region is only bordered by Lake Michigan, which did not have large populations of zebra mussels until several years after the initial invasion of the lower Great Lakes.

At the smallest spatial extent, we also estimated annual invasion rates of 10 multi-county lake districts in Indiana, Illinois, Michigan and Wisconsin previously sampled by Kraft and Johnson (2000) and compared the 1995–1997 period to the past 6 years (1998–2003). As no surveys of these lakes have been conducted since 1997, the average annual rate of invasion for the 1998–2003 period was estimated from incidental sightings of zebra mussels in lakes known not to be invaded in 1997, the end of the previous study. We also used survey and incidental sightings within these districts to calculate annual rates of invasion for each year from 1996 to 2003 (again limiting the analysis to the set of lakes known not to be invaded from the sampling in 1995) to compare with state-wide patterns (see above).

At the smallest spatial extent, we also used both incidental and survey data to reconstruct the temporal and spatial pattern of invasion within a given district during the initial stages of invasion (i.e., up until 1997, the last year of extensive surveys). Of the 10 districts previously surveyed, only four had a sufficient number of invasions to assess the relative importance of different processes of invasion. These districts were all located within a band of lakes that stretches from southeastern Michigan through northern Indiana (Figure 1) and are referred to by the principal county of each lake district: Oakland Co., Michigan (83°22′ W, 42°41′ N), Jackson Co., Michigan (84°24′ W, 42°15′ N), Steuben Co., Indiana (84°59′ W, 41°39′ N), and Kosciusko Co., Indiana (84°51′ W, 41°15′ N), in order from east to west. Oakland Co. is located within 40 km of Lake St. Clair, where zebra mussels were first discovered in the late 1980s (Hebert et al. 1989). The other lake districts are located at progressively greater distances from Lake St. Clair and Lake Erie, another large primary source of zebra mussels (Griffiths et al. 1991). Although the Kosciusko district is farthest from these Great Lake source populations (190 and 260 km, respectively), it is the closest district to southern

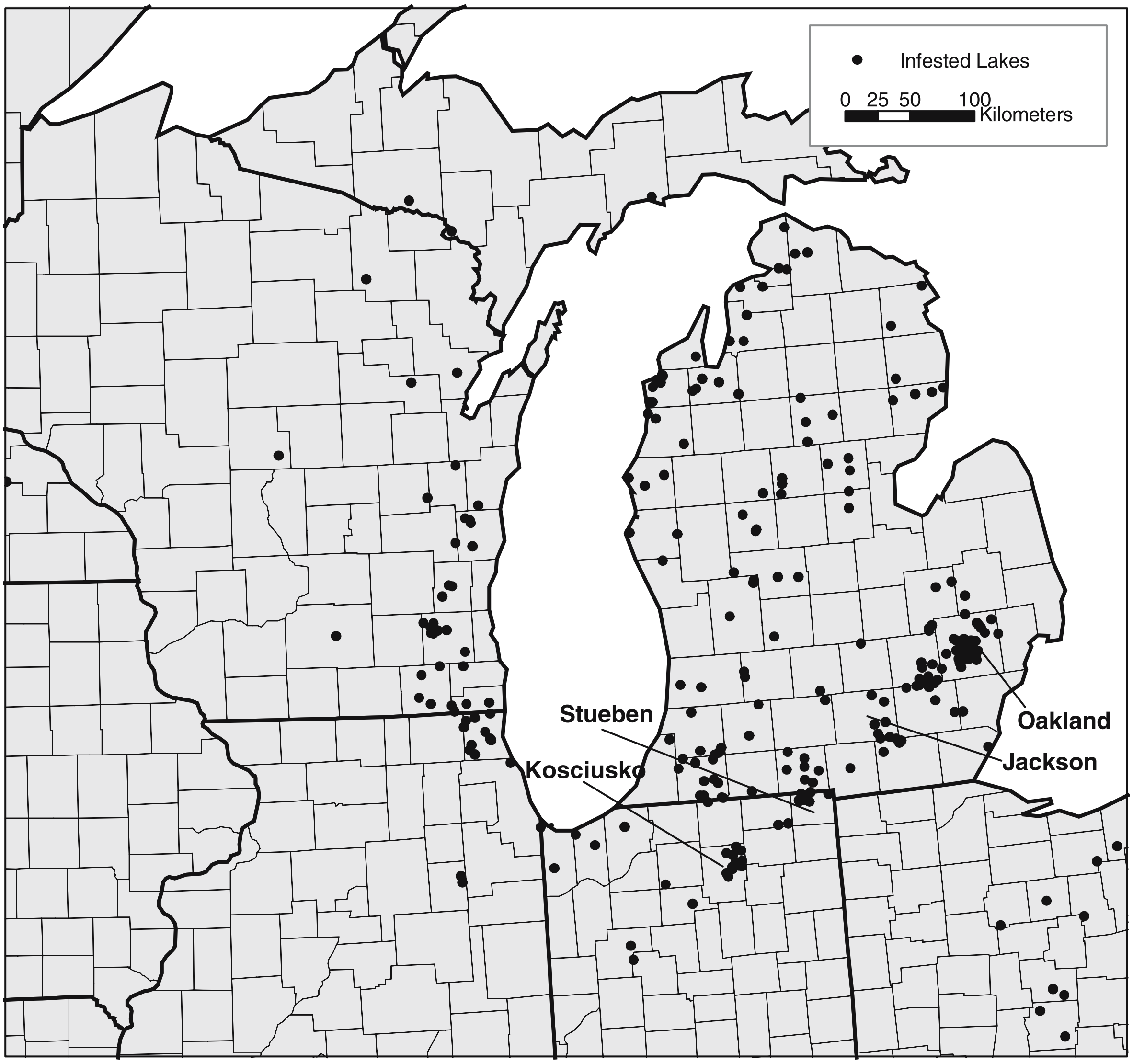

Figure 1. Distribution of invaded inland lakes in the states surrounding the western Great Lakes as of 2003. Counties are indicated for the lake districts in which initial invasion patterns were documented.

Lake Michigan (90 km). Within each district, there was a bias towards larger lakes, both in the selection of survey lakes and the reporting of incidental sightings (Kraft and Johnson 2000). Smaller lakes were, however, represented within each district. Unless otherwise indicated, distances between hydrologically connected lakes are reported as the length of the stream, river, or canal; for hydrologically isolated lakes, distances are reported as the shortest straight-line distance from shore-to-shore. Survival of mussels during overland transport decreases with time (Ricciardi et al. 1995). The difference in time required to travel between lakes separated by 10s vs 100s of kilometers is, however, probably unimportant relative to the time that boats are usually stored out of water between uses (Johnson et al. 2001). Thus, we assume that the distance between lakes over regional spatial extents acts primarily on the probability of boat movement between them and not on survival during transit.

Results

In only six states were more than 10 inland invasions observed, and these states accounted for 97% of the 293 lakes reported to be invaded in the USA (Table 1). For the four states surrounding Lake Michigan, < 8% of suitable lakes greater than 25 ha had been invaded by 2003. The invasion rate of suitable lakes varied between 3 and 12% among the states, with the lowest percentage in Illinois and the highest in Michigan (Table 1). Overall, the four states appear to fall into two groups: Michigan–Northern Indiana (11%) and Wisconsin–Northern Illinois (3%). The other two states had either an intermediate level (Ohio–5.9%) or lower level of invasion (New York–2.2%).

Although the number of invaded lakes has increased over time, the rate of invasions has decreased. At the district level, annual invasion rates have decreased over the past 6 years in Michigan (17% decrease, average of 3 districts) and Indiana (49% decrease, average of 3 districts) relative to the 1995–1997 period (Figure 2). This trend was not, however, consistent across the lake districts in Michigan where the annual invasion rate increased slightly (9%) in the Oakland district compared to an average decrease of 29% for the other two districts. In contrast to the state-wide trends in Michigan and Indiana, the annual invasion rate in Wisconsin–Illinois increased by 350% between the two periods at a rate of 0.074 year^{-1} (average of 4 districts) – a level equivalent to that in Indiana in 1995–1997 but only half that at any time in Michigan (Figure 2).

At a finer temporal extent, a more striking pattern is evident in the very high annual invasion rates observed from 1999 to 2001 followed by very low rates in 2002 and 2003 (Figure 3). Thus the statewide invasion rates (based on surveyed lake districts only) generally peaked approximately 10 years after the initial establishment of zebra mussels in the Great Lakes. The pattern for all districts combined largely resembles that for Michigan where the majority of invasions occurred. The peaks for both Wisconsin–Illinois and Indiana are not as pronounced as Michigan and lag by just a year, with inexplicable variations in annual rates in the years preceding the peaks (e.g., 2000 in Wisconsin–Illinois; Figure 3).

These trends were consistent with those developed from the USGS-ANS database, i.e., all reports of zebra mussels within different states. Again, peaks in the number of new invasions occurred from 1998 to 2001 with very low rates in 2002 and 2003 (Figure 4a) – indeed, only 13 invasions (0.4% of suitable lakes) were reported from the four states in 2003. In Michigan there appeared to be two peaks in invasions, one in 1993–1995 and a larger one in 1998. A weak peak in Indiana coincided with the 1998 peak in Michigan whereas a clear peak occurred in Wisconsin in 2001. Examination of invasion rates (i.e., proportion of suitable lakes invaded) over time shows both the more rapid colonization of lakes in Michigan and Indiana and the slowing of the invasions in all states, except Illinois (Figure 4b). In spite of the similarity of the temporal trends between the district-based

Table 1. Status of the zebra mussel invasion of states with more than 10 invaded lakes.

State	Lakes	Suitable	Invaded	% Invaded	% National	% Downstream
Michigan	1770	1476	176	11.9	58.3	32.7
Indiana	346	346	32	9.2	10.6	31.3
Wisconsin	1950	1047	34	3.2	11.3	26.5
Illinois	461	461	15	3.3	5.0	13.3
New York	1189	637	14	2.2	4.6	–
Ohio	322	320	19	5.9	6.3	–

'Lakes' includes all lakes and reservoirs greater than 25 ha in size; 'Suitable' includes only lakes with a high probability of supporting zebra mussels based on a genetic algorithm for rule-set production (Drake and Bossenbroek 2004); 'Invaded' is the number of lakes in each state with a reported zebra mussel population, '% National' is the percentage of all reported invasions in the USA occurring in each state; '% Downstream' is the percentage of reported invasions in each state that are downstream from a reported invasion.

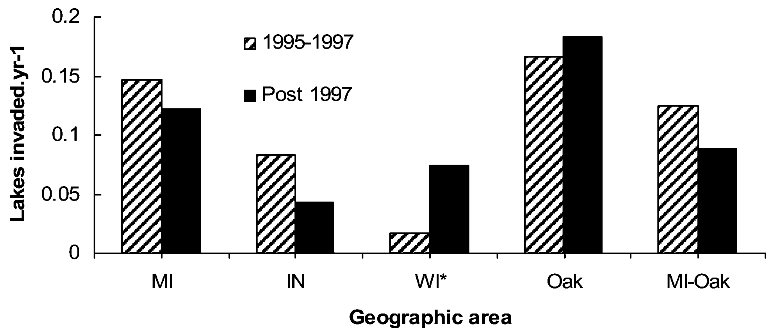

Figure 2. Comparison of annual rates of invasion of surveyed lakes districts located in three states (MI = Michigan; IN = Indiana; and WI = Wisconsin). Data for Michigan are also shown for just the Oakland district (Oak), the most invaded district in the state, and the rest of the state of Michigan (MI-Oak). 1995–1997 data are taken from Kraft and Johnson (2000), except for Wisconsin (*) where the rate is estimated from the 1993–1997 period due to a lack of invasions during the survey period (an estimated invasion rates of 0.0). This modification permitted the inclusion of the five invasions known in Wisconsin at the beginning of the survey and provides a maximal estimate of invasion rates as it assumes that these lakes would have been include in the set of 63 lakes selected for the surveys.

and the state-based estimates of invasion rates (e.g., $R^2 = 0.55$ for Michigan), the absolute estimates of invasion rates differed by an order of magnitude (e.g., ranges of 0.004–0.025 vs 0.045–0.26 for state-based and district-based estimates, respectively).

The portion of invaded lakes in each state that could be ascribed to downstream dispersal from upstream sources varied from 15 to 33%

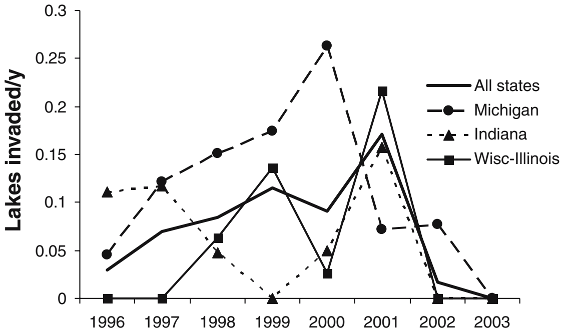

Figure 3. Annual rates of invasion (proportion of suitable lakes invaded per year) estimated from surveyed lake districts from 1996 to 2003. Detections in 1996 and 1997 were from lake surveys in which zebra mussels were not detected in surveys of preceding year (Kraft and Johnson 2000) whereas detections from 1998 to 2003 in surveyed lakes were based on incidental reports and assume that the likelihood of detection was similar to survey efforts. 'All states' represents the pooled results from all 10 lake districts surveyed in the four-state region.

(Table 1). Once again, Michigan had the largest percentage, but only slightly greater than in Indiana (31%). The proportion of invaded lakes that were connected to an upstream source initially ranged from 20 to 50%, then dropped below 20% after 1999 in Michigan and after 2000 for other states (Figure 5).

At the smallest spatial extent, divergent patterns of invasion were observed among the four districts examined. At one extreme were the Jackson and Steuben districts in which several hydrologically isolated lakes were invaded in a short period of time. In the Jackson district, zebra mussels were found in the five largest lakes over a 3-year period (Vineyard 1993; Clark 1994; Wamplers 1994; Devils 1994; Sand 1995). In 1997 one additional population of zebra mussels (Columbia Lake, another large hydrologically isolated lake) was detected among the eight lakes surveyed in that district during a 3-year period. A similar pattern of invasion occurred in the Steuben district. Zebra mussels were first detected in 1995 (James), followed by three other lakes in 1996 (Gage, Clear, and George), only one of which was hydrologically connected to James Lake.

Contrasting patterns were observed in the other two districts. In the Kosciusko district (Figure 6), the first North American inland lake population of zebra mussels was discovered in Lake Wawasee in 1991. The invasion spread

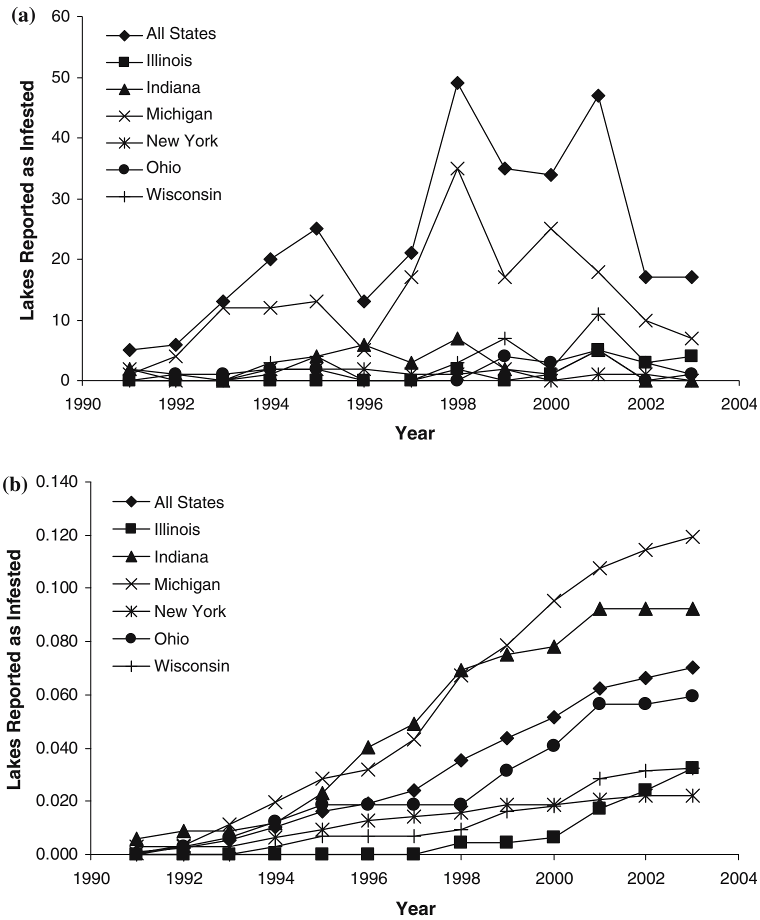

Figure 4. (a) Annual numbers of invasions in the six states known to have 10 or more invasions of inland waters and for the entire USA ('All states'); (b) Cumulative rates over time for individual states and all states combined. Rates are calculated on the number of invasions reported to the United States Geological Survey-Aquatic Nuisance Species database for each year divided by the number of suitable lakes (Drake and Bossenbroek, submitted).

quickly downstream to a nearby lake (Syracuse 1992), but other invasions were not detected until 3–6 years later (Tippecanoe 1994; Kuhn 1995; Dewart 1995; Papakeekie 1996; Chapman 1997; Webster 1997; Waubee 1997 and Winona 1997). All these lakes were either hydrologically isolated or upstream from Wawasee, although two (Waubee and Tippecanoe) were likely colonized by downstream dispersal from other lakes (the 1994 discovery in Tippecanoe was a single mussel that probably dispersed from a large zebra mussel population in Kuhn Lake that was first detected in 1995).

Within the Oakland district, downstream dispersal and other hydrological connections also made a larger contribution to the pattern of invasion, accounting for a third of the invasions (Figure 7). Veligers were found in 1993 in two lakes, Walled and Cass, but the latter invasion likely resulted from downstream dispersal from a large zebra mussel population found latter that year in Loon Lake, a much smaller lake located 11 km directly upstream on the Clinton River. The river facilitated additional spread during the next several years, downstream (Sylvan-Otter 1994), upstream (Silver 1994; Schoolhouse 1996) and to lakes that used water pumped from the river to maintain water levels (Orchard 1994 and Watkins 1995). The unexpected invasion of lakes upstream from Loon Lake was undoubtedly

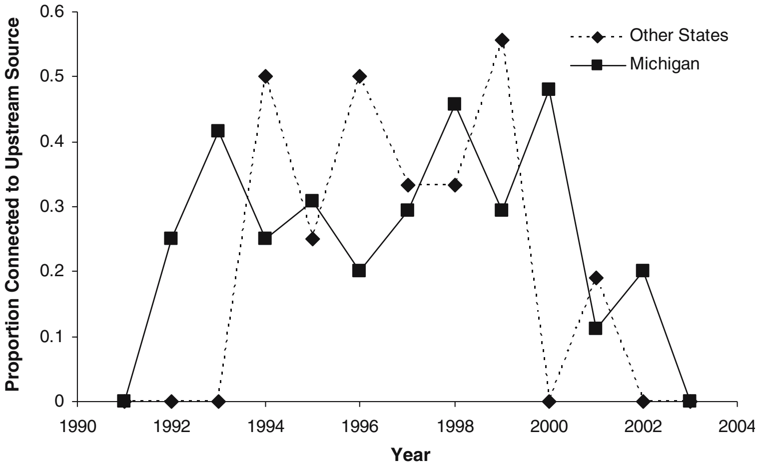

Figure 5. Annual estimates from 1991 to 2003 of the proportion of invaded lakes that were hydrologically connected to an upstream source population of zebra mussels. Given its advance state of invasion, Michigan is presented separately from all other states.

facilitated by navigable connections (Schoolhouse) or occasional wind-induced reversals of flow through short culverts (Silver). During 1994–1997, there were nine other invasions of hydrologically isolated lakes (Elizabeth 1994; Kent 1994; Stony Creek Impoundment 1995; Lakeville 1995; Watkins 1995; Pine 1997; Union 1997; Maceday 1997; White Lake 1997; Figure 7).

Discussion

The spread of an invasive species begins from the point of initial establishment and then increases in spatial extent according to the underlying distribution of suitable habitats and the action of various dispersal mechanisms. The importance of the distribution of source populations in this process is apparent at several spatial extents. At the continental level, almost all overland invasions of zebra mussels have occurred in states adjacent to the Great Lakes, and at the regional extent, invasion rates were highest for Michigan, Indiana, and Ohio, the three states closest to Lake St. Clair and Lake Erie where zebra mussels first became abundant. Numerically, most invasions have occurred in Michigan due to its abundance of lakes and high rates of invasion, but even within Michigan, invasions at the district extent have occurred predominately near Lake St. Clair. Whereas this pattern is partially due to the high density of lakes in this region, the close proximity of a large, established zebra mussel population is undoubtedly a major factor, especially considering the high level of transient boating in the area (Johnson and Padilla 1996; Johnson et al. 2001).

Indiana also has a relatively large proportion of invaded lakes, but the remoteness of Indiana lakes with respect to Great Lake source populations suggests that multiple overland invasions from the Great Lakes (as observed in Jackson and Oakland districts) are unlikely to be responsible for this high level of invasion. Instead, secondary dispersal from a rare long-distance primary dispersal event (i.e., the 1991 invasion of Lake Wawasee) appears responsible for the large number of lake invasions in the Kosciusko district, which contains almost a third of all Indiana invasions. The low percentage of invaded lakes in Ohio, a state with a long coast along Lake Erie, is less consistent with the idea that proximity to source populations increases the probability of invasions. However, the low density of lakes in Ohio may have reduced the probability of spread by decreasing vector activity.

The clustered distribution of invaded lakes (Kraft et al. 2002) appears to have multiple causes. In two of the four cases examined here

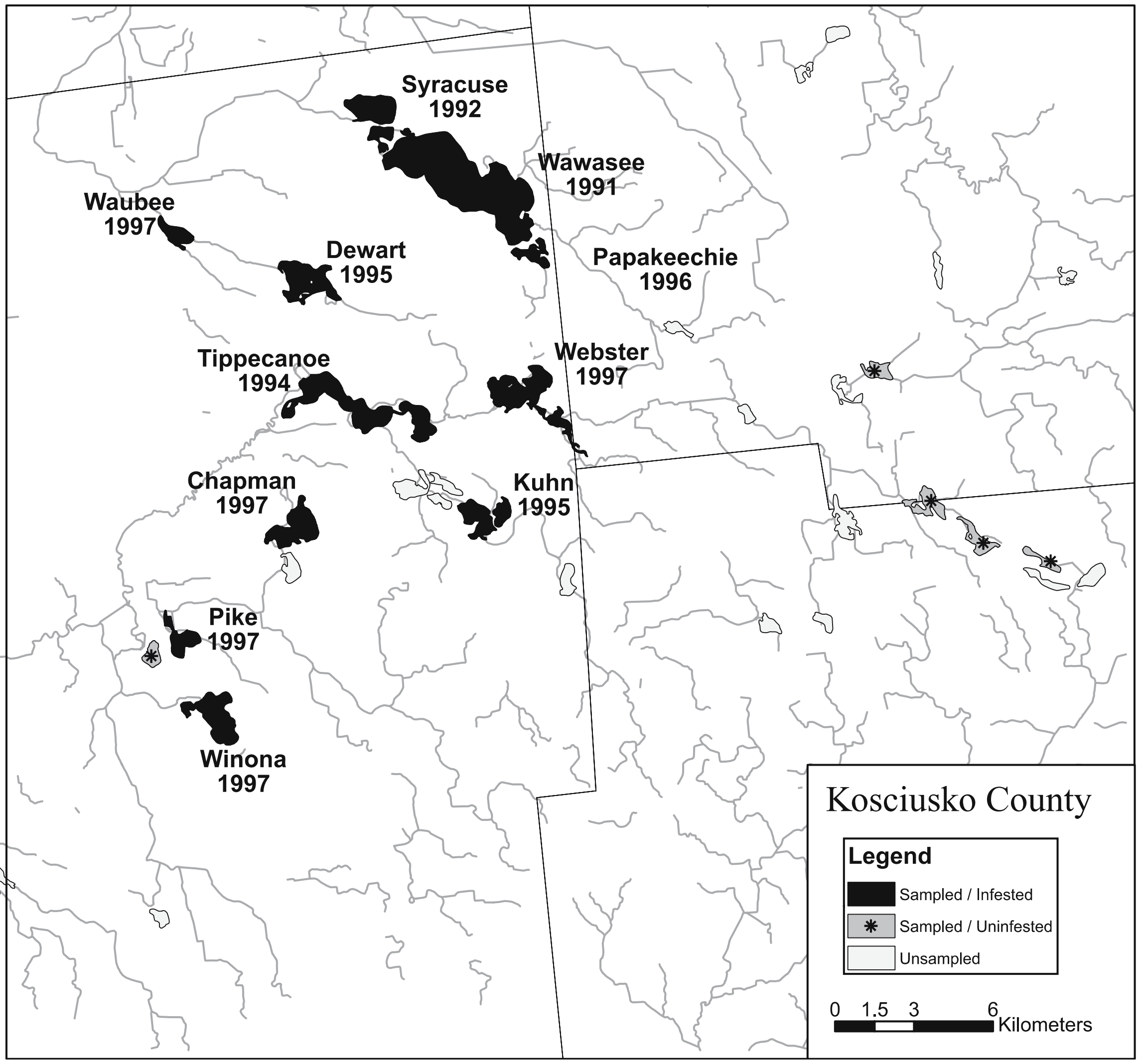

Figure 6. Map of the Kosciusko district showing the names and detection dates of lakes with known populations of zebra mussels at the end of 1997. Others lakes in the district, including those surveyed for zebra mussels, are also shown.

(Jackson and Steuben districts), the almost simultaneous occurrence of most of the invasions and the general lack of hydrological connections between these lakes strongly suggest that overland dispersal from the Great Lakes (minimum distances of 75 and 130 km for Jackson and Steuben districts, respectively) was the principal process of invasion, i.e., multiple independent overland invasions from Great Lake sources created these clusters of invaded lakes. Although less clear, invasions in Oakland County probably also resulted from multiple primary overland invasions, but the close proximity to Great Lake sources (i.e., Lake St. Clair – 40 km away), and the high levels of boat traffic among these inland lakes (Johnson and Padilla 1996) makes it particularly difficult to distinguish between primary and secondary overland invasions in this district. This clustering of multiple primary overland invasions indicates that certain districts may be particularly attractive to boaters using Great Lakes waters and thus represent pathways for such invasions. In the case of the Oakland district, this interpretation is not surprising given its

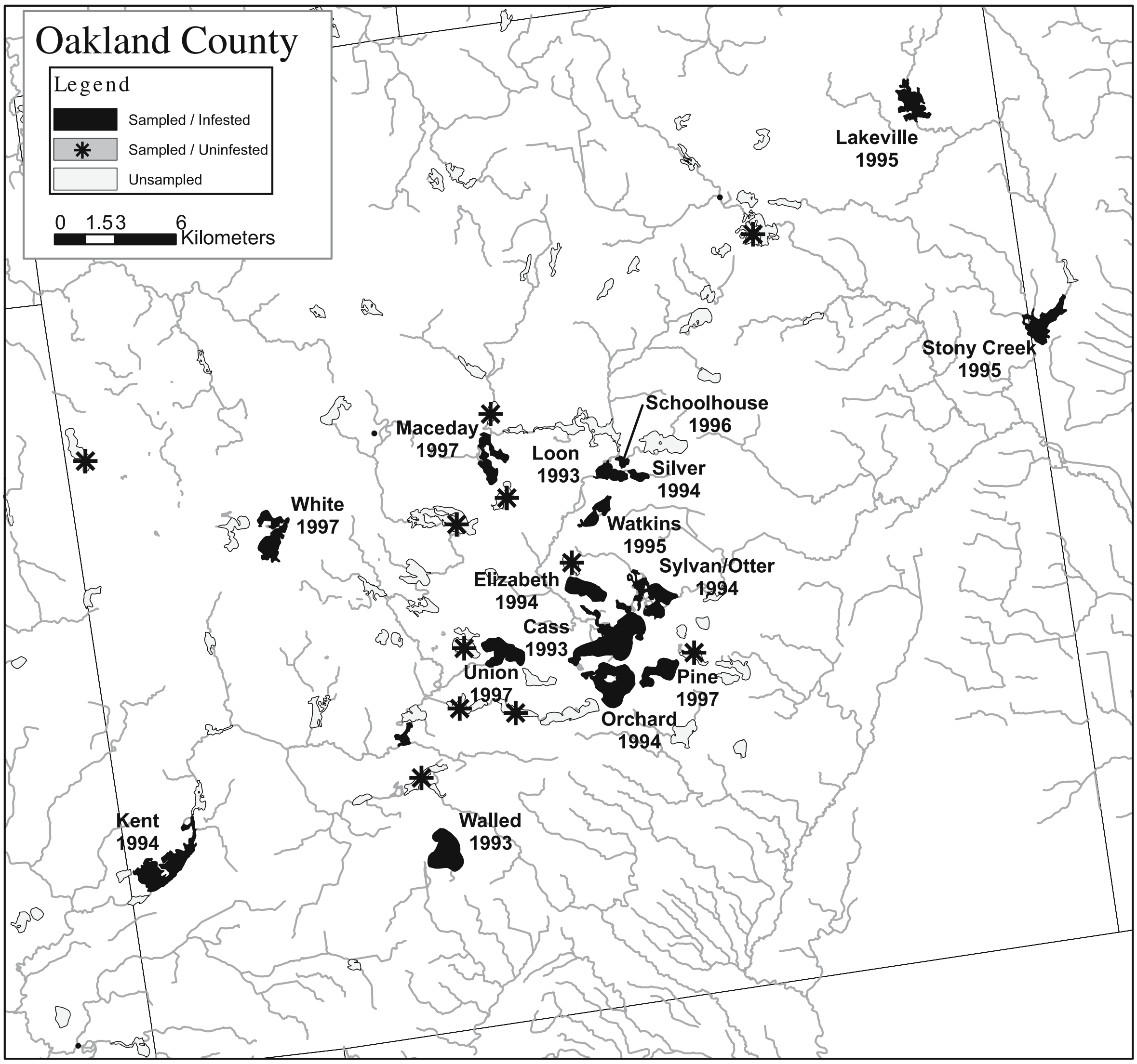

Figure 7. Map of the Oakland district showing the names and detection dates of lakes with known populations of zebra mussels at the end of 1997. Others lakes in the district, including those surveyed for zebra mussels, are also shown.

proximity to Lake St. Clair and the large number of boats registered in the area (this district is primarily a suburban area of Detroit). The apparent attractiveness of the other two lake districts is less intuitive (rural areas 1–2 h drive from Great Lake sources) and reinforces the utility of gravity models (e.g., Bossenbroek et al. 2001; Leung et al. 2004), which can integrate the distribution of boaters, negative effects of distance, and the positive effects of certain lake features (e.g., surface area).

The invasion pattern of the Kosciusko district suggests that secondary overland dispersal can also contribute substantially to the invasion process, especially when the initial overland invasion is far from source populations. Invasions of nearby but hydrologically isolated lakes occurred 4–7 years after the initial invasion of Lake Wawasee which gives an estimate of the time-lag involved in this type of sequential invasions. These lakes ranged from 0.2 to 20 km (mean = 9 km) from Lake Wawasee, suggesting the spatial extent of secondary overland dispersal as well. This scenario of a regionally popular lake becoming the initial hub for subsequent local invasions (see also MacIsaac et al. 2004) is not, however, universally applicable, as in several other districts, smaller, more obscure lakes were the first to be colonized (e.g., Eagle Lake (Cass County, MI) and Loon Lake (Oakland County, MI), both smaller lakes with limited public access). Such observations remind us that other mechanisms besides transient recreational boating may be operating, e.g., the transfer of boats with new lakeshore property owners (Johnson et al. 2001), which may make important contributions to the overall pattern, especially if they are responsible for long-distance jumps into non-invaded regions.

Direct downstream dispersal can both increase the invasion rate and contribute to the clustering of invaded lakes. The contribution of downstream dispersal to any particular system of lakes will, of course, depend on the relative frequency of overland invasions, their precise locations, and their hydrological connectivity with other lakes (Shurin and Havel 2002). For example, in a series of lakes connected by a river, the contribution of downstream dispersal would be minimal if the initial invasion occurred in the lake farthest downstream. In general, however, the proportion of lakes invaded by downstream dispersal should increase over time as veligers or adults are transported to water bodies located downstream from invaded waters. Surprisingly, after an initial increase, the proportion of invasions attributed to downstream dispersal did not increase over time in Midwestern states, and even after 12 years, the overall contribution of downstream dispersal was less than half that of overland dispersal for the four-state region. The proportion of invaded lakes attributed to downstream dispersal has actually dropped in recent years, further supporting the idea that overland dispersal events still dominate the invasion process. Although the mechanisms underlying downstream dispersal are well documented (Horvath and Lamberti 1997), it can be difficult to distinguish downstream spread from overland dispersal (Shurin and Havel 2002). Thus, we may have even overestimated the frequency of downstream invasions.

Temporally, the annual invasion rate within a given area should initially be low as the source population grows, followed by a high rate of invasion as primary overland invasions increase along with associated secondary overland dispersal or downstream spread. The invasion rate should then slow down as the system becomes 'saturated', i.e., the pool of non-invaded lakes becomes fewer in number as well as possibly less 'attractive' vis-à-vis environmental suitability, vector activity, or hydrological connections. The temporal patterns of invasions at the national level and for the three states with the largest number of invasions (MI, IN, and WI) follow this general bell-shaped pattern through time. However, the decline in invasion rates has occurred at a surprisingly low level of infestation (i.e., near 10% of lakes invaded), suggesting that the decline has not occurred due to a lack of environmentally suitable lakes. Instead, lakes appear to differ substantially in their probability of being invaded, some with high connectivity (from either high vector activity or short hydrological connections) and others with low connectivity. If this is the case, the invasion process should then consist of a rapid colonization of high invasion probability lakes followed by a more protracted period of occasional invasions of low invasion probability lakes. Indeed, this pattern is precisely what appears to have occurred in Belarussian lakes over the past 200 years where a large fraction of the inland lakes have not yet been invaded (Kraft et al. 2002; Karatayev et al. 2003).

A time lag in the peak invasion rates should be expected for regions further from the original source population, in this case, first in Michigan, next in Indiana, and most recently in Wisconsin. Whereas this pattern might seem evident in the data, such an interpretation appears to be incorrect. The delay in invasions in Indiana appears largely dependent on the time-lag of secondary invasions originating from Lake Wawasee, which accounted for over half of the invasions in the 1995–1997 period. Secondary invasions may have similarly accounted for the second and larger peak of invasions in Michigan that occurred 4–6 years after the initial peak, which is consistent with gravity model analyses that show a shift in the source of invasions from Great Lakes to inland lakes in Michigan (Leung et al. 2004). Indeed their model estimated that by 2001 a third of the propagule pressure in Michigan came from invaded inland lakes. In contrast, the approximately 6-year delay in invasions in Wisconsin was undoubtedly due in large part to delays in the development of a large population of zebra mussels in Lake Michigan, the most likely source of propagules for Wisconsin. Thus, the time lags observed among these regions are almost certainly not due to any type of 'stepping stone' process as observed in other invasions (MacIsaac 2004), but rather to the unique features of the spread of zebra mussels in the Great Lakes, the primary source of inland lake invasions in the Midwest. Invasion hubs that increase the invasion rate of local lakes can occur (i.e., Lake Wawasee in the Kosciusko district), but it does not appear that they act as jumping-off points for major extensions in the distribution of the zebra mussel, at least within the Midwest region.

Perhaps the most striking temporal pattern is the general decline in the number of new invasions in recent years. Indeed, there was a near absence of invasions in the four-state region in 2003 with just 13 new invasions reported. This unexpected observation is not simply due to a lack of uncolonized lakes in the region. Only 7.5% of the lakes in the four-state region have been invaded, and over 3000 suitable lakes >25 ha in surface area remain uncolonized. The 2003 results thus represent an annual rate of invasion of just 0.004 lakes year^{-1}, barely one third of previous peaks in annual invasion rates. Several non-mutually exclusive explanations could account for this trend. This decline could be due to a decreased interest in reporting new populations (i.e., an underreporting of new invasions by the public), but this is unlikely to be the entire explanation given that interest in exotic species has grown at all levels and state and federal programs are still actively soliciting and recording information on the distribution of invasive species. Indeed, the intensive education efforts aimed at informing the public how to slow the spread of aquatic invasive species may have contributed to these declining invasion rates, offering an additional explanation for the decline.

The more likely explanation, however, is that the rates of invasion are truly declining due to the rapid spread into lakes that are most susceptible to invasion followed by slower spread into less susceptible lakes. As described above, this process can explain the decline in invasion rates at smaller spatial extents (i.e., within a district), but it can apply equally well at larger spatial extents in that different regions may vary in ways similar to those described above for different lakes, i.e., environmental conditions, vector activity, or connectivity. For example, transport of zebra mussels on macrophytes entangled on transient recreational boats, frequently observed in Michigan (Johnson et al. 2001), may be much less common in Wisconsin where macrophytes are not abundant along the Lake Michigan shoreline (C. Kraft, pers. obs.). Thus, the greater invasion rates in Michigan may simply reflect the near ideal conditions for inland invasions found there (i.e., an enormous source population nearly surrounding the state, a high density of lakes suitable for zebra mussels, and a high level of vector activity involving 1 million registered boats). The slowing overall rate of invasion may then be due to the fact that remaining non-invaded regions are less conducive to the spread of this species. Indeed, in spite of the increasing propagule pressure arising from the combination of Great Lakes and recently invaded inland waters (Leung et al. 2004), the period of relatively rapid invasion of inland waters may largely have ended as other regions not adjacent to the Great Lakes may be too far from these vast source populations to have high levels of primary overland invasions. Future patterns of invasions are thus more likely to follow that seen in the Kosciusko Co. district – rare long-distance invasions followed by limited secondary spread.

The slow spread of the zebra mussel across this landscape contrasts with that of two other recent freshwater invaders, the cladocerans *Daphnia lumholtzi* and *Bythotrephes longimanus* (the spiny water flea). *D. lumholtzi* increased its distribution from 6 to 34% of sampled lakes over a 6-year period (Havel et al. 2002). Whereas this rate of spread is comparable to those measured within some of the lake districts we examined, these latter estimates are based on the targeted selection of districts containing large lakes and high densities of lakes, two factors that are likely to increase the probability of invasions (Kraft and Johnson 2000). In contrast, estimates of invasion rates based on reports from all suitable lakes were an order of magnitude lower. Thus, the invasion rates of *D. lumholtzi* are probably truly much greater due to a combination of anthropogenic dispersal (Havel and Stelzleni-Schwent 2001) and natural dispersal, especially wind or waterfowl dispersal of dormant eggs, but possibly also including downstream dispersal (Shurin and Havel 2002). For *B. longimanus*, the number of invaded lakes in Ontario (Canada) has increased exponentially over the past 20 years (MacIsaac et al. 2004) although the absolute number of invaded lakes (53) remains rather low.

The low proportion of lakes invaded by zebra mussels and the apparent slowing of the rate of invasions stand in stark contrast to the initial and general perception that the zebra mussel would rapidly colonize all suitable habitats (Ludyanskiy et al. 1993), a view that implicitly assumes adequate dispersal mechanisms are operating over all spatial extents. Whereas this outcome has largely been true for the natural dispersal within watersheds (O'Neil and Dextrase 1994), the overland dispersal has proceeded relatively slowly (Johnson and Carlton 1996; Kraft and Johnson 2000), and our results suggest that this inherently slow invasion is itself decelerating. This conclusion is not intended to be reassuring and should be instead taken as a cautionary update requiring periodic reevaluation. Given that the currently invaded lakes are among the largest and most heavily used, a low proportion of invaded lakes does not necessarily reflect a low overall impact. The zebra mussel invasion of inland lakes has not ended and will continue to produce ecological and economic impacts, but our analysis does show that biological invasions of aquatic systems can occur at a rate that would allow preventative measures to be successful.

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