Regional differences in rates and patterns of North American inland lake invasions by zebra mussels (*Dreissena polymorpha*)

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Abstract: Zebra mussels (*Dreissena polymorpha*) have spread rapidly in North America by dispersal within connected bodies of waters. This study provides the first systematic evaluation of rates of zebra mussel dispersal to inland lakes separated from source populations by functional dispersal barriers. Plankton samples were examined for this exotic species from 140 lakes during a 3-year period (1995–1997). Infestations were detected in 19% of lakes surveyed: seven of 28 Indiana lakes (25%), 15 of 49 Michigan lakes (31%), but only five of 63 Wisconsin–Illinois lakes (8%). Annual rates of infestation varied from 0 to 12%·year^{-1} among the three regions. Wisconsin–Illinois lake infestations were only detected in 1995 and 1996, whereas new Indiana and Michigan infestations were detected in all three years. Lakes with surface areas less than 100 ha had lower infestation rates than larger lakes. Incidental sightings of inland lake colonization within the study region qualitatively supported observed regional differences in rates and spatial patterns of colonization. These results demonstrate that the spread of zebra mussels into inland lakes is not occurring as rapidly as through connected waterways, and rates of inland lake colonization vary according to regional conditions and lake size.

Résumé : Les moules zébrées (*Dreissena polymorpha*) se sont rapidement répandues en Amérique du Nord en se dispersant au sein de masses d'eau interreliées. Notre étude est la première évaluation systématique des taux de dispersion de la moule zébrée dans les lacs intérieurs séparés des populations sources par des obstacles fonctionnels. Pendant une période de 3 ans (1995–1997), nous avons recherché cette espèce exotique dans des échantillons de plancton. Des infestations ont été détectées dans 19% des lacs étudiés : 7 sur 28 lacs en Indiana (25%), 15 sur 49 lacs dans le Michigan (31%), mais seulement 5 sur 63 lacs dans la région Wisconsin–Illinois (8%). Les taux annuels d'infestation variaient de 0 à 12%·an^{-1} entre les trois régions. Dans le Wisconsin–Illinois, des infestations ont été détectées seulement entre 1995 et 1996, tandis que de nouvelles infestations ont été détectées chacune des trois années dans l'Indiana et le Michigan. Les lacs à superficie de moins de 100 ha présentaient des taux d'infestation moindre que les lacs plus grands. Des observations occasionnelles de colonisation des lacs de l'intérieur dans la zone d'étude sont venues confirmer qualitativement les différences observées régionalement dans les taux et les régimes spatiaux de colonisation. Ces résultats montrent que la dispersion de la moule zébrée dans les lacs intérieurs n'est pas aussi rapide que dans le cas des masses d'eau interreliées, et que le taux de colonisation des lacs intérieurs varie selon les conditions régionales et la taille des lacs.

[Traduit par la Rédaction]

Introduction

Information on rates and patterns of invasion is essential to predict the geographic spread of exotic species (Shigesada and Kawasaki 1997). The North American zebra mussel (*Dreissena polymorpha*) invasion has been notorious (Vitousek et al. 1996), in part due to the unusually rapid range expansion of these nuisance molluscs (Neary and Leach 1992; Ludyanskiy et al. 1993; Hincks and Mackie 1997). By 1991, 3 years after their initial detection in Lake St. Clair, zebra mussels were already found throughout the Laurentian Great Lakes and connecting river systems as far away as Louisiana and Quebec. This rapid range expansion produced prominent warnings, such as that "by the year 2000, the zebra mussel can be expected to have colonized all North American rivers, lakes and reservoirs that fit its broad ecological requirements" (Ludyanskiy et al. 1993).

Lost in such predictions was the distinction between range boundaries and the internal structure of that range (Brown et al. 1996). Once the breadth of the North American range of zebra mussels was established, little attention was paid to the details of colonization inside that range boundary, especially with regard to inland lakes. The early North American distribution of zebra mussels closely matched the commercially navigable waters of the Great Lakes and Mississippi basins and included few inland lakes (Johnson and Carlton 1996). Differences in barriers to dispersal are likely to produce unequal colonization rates between connected bodies of water, such as large navigable rivers, relative to inland lakes that require overland transport for colonization (Carlton 1993; Johnson and Carlton 1996).

Downstream spread of zebra mussels occurs largely

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through the advective transport of planktonic larvae (veligers) (Stoeckel et al. 1997), although in streams less than 30 m in diameter, downstream colonization appears to be limited to distances less than 10 km (Horvath et al. 1996). This distance may define a functional dispersal barrier. Upstream spread appears to require human-mediated vectors (Carlton 1993) such as boats (Keevin et al. 1992). Thus, for transport to inland lakes without navigable or nearby (<10 km) hydrological connections to infested waters, a dispersal barrier must be crossed. Many potential overland dispersal mechanisms exist (Carlton 1993), but in general, successful overland colonization is probably more difficult due to greater stress during periods out of water (Ricciardi et al. 1995) or to low numbers of individuals transported by any given dispersal event (Johnson and Padilla 1996).

Predictions of zebra mussel distributions have focused on their likely maximum range in North American waters (Strayer 1991; Neary and Leach 1992; Koutnik and Padilla 1994) based on environmental limits determined from European (Ramcharan et al. 1992*a*, 1992*b*) and North American studies (Hincks and Mackie 1997). Attempts to predict which suitable waters are likely to be first colonized are rare (Neary and Leach 1992), and no data have been published regarding the rates at which environmentally suitable North America lakes have become colonized.

In this study, we addressed two issues. First, we evaluated whether zebra mussels were colonizing North American inland lake districts as quickly as connected large lake and river systems. To do this, we examined zebra mussel colonization of inland lakes in a four-state region adjacent to the Great Lakes over a 3-year period. Second, we used our sampling results, in conjunction with verified incidental reports of inland lake colonization, to assess rates and spatial patterns of colonization over several geographical scales.

Methods

Data collection conducted in 1995, 1996, and 1997 consisted of determining the presence or absence of zebra mussels in 140 inland lakes in Illinois, Indiana, Michigan, and Wisconsin. Our sampling focused on 10 regional lake districts, which were defined as areas in which we could sample 50–100% of suitable lakes (defined below) in a 2- to 3-day sampling period. These districts included 89% of the lakes surveyed. Study lakes did not have navigable connections to other waters, and at the time of sampling, no lake was located downstream from any body of water known to be infested. During the course of the study, potential upstream source populations were found for two infested survey lakes.

Since we were specifically interested in rates and patterns of inland lake invasions, and not in environmental limitations, we only sampled lakes with water chemistry (pH > 7.3, Ca > 28 mg/L; Ramcharan et al. 1992*b*) and physical characteristics (>50 ha, >2 m mean depth, >4 m maximum depth; Strayer 1991) suitable for zebra mussel colonization. Prior to sampling, we did not know if zebra mussels were established in the study lakes. Public access was available to all study lakes, except for two Michigan lakes (Oakland district), and all lakes were located in areas with extensive recreational activity and residential development.

Relative proportions of surveyed lake sizes were similar in both Wisconsin–Illinois and Michigan–Indiana (Fig. 1). Overall, surveyed lakes included a smaller proportion of lakes between 50 and 100 ha in surface area than would be expected by randomly sampling all lakes in the study area and a larger proportion of lakes with surface areas greater than 600 ha (Fig. 1).

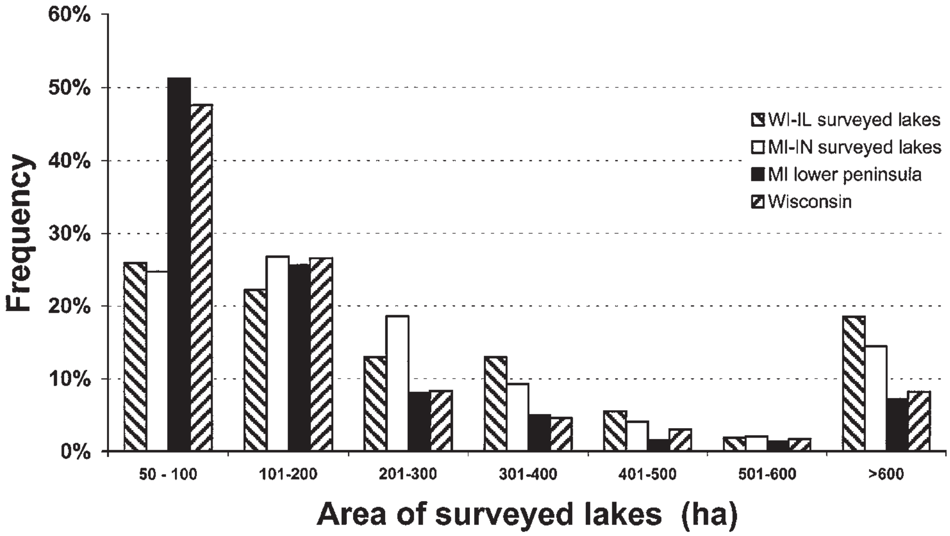
Plankton sampling provided the most efficient way to sample large numbers of lakes for zebra mussels and also offered early detection of recently colonized lakes, prior to widespread colonization of adult mussels (Kraft 1993). The field sampling program was established so that all lakes were surveyed with equal sampling effort. In a given year, we attempted to collect plankton samples from each lake on at least three dates at 3-week intervals. Most sampling was conducted from late May to mid-July, when veligers are most abundant in the plankton of small midwestern lakes (C. Kraft and L. Johnson, unpublished data), although Wisconsin and Illinois lakes were surveyed through mid-September. In rare instances, logistical difficulties (e.g., weather, equipment failure) limited sampling to two occasions during a given year. Plankton samples were collected from three sites within each lake on each sampling date. When selecting sites, we tried to include as many distinct areas of the lake as possible. For long narrow lakes, samples were collected at both ends and in the center of the lake. If a lake contained distinct basins, we tried to collect at least one sample from each basin. In lakes with one homogeneous basin, samples were collected at three locations spaced as far apart as possible.

Plankton samples were collected with a 0.5- or 0.3-m-diameter, 64-μm-mesh plankton net with a length to mouth ratio of 5:1. Depending on water depth and net diameter, one or two vertical tows were taken from depths of 4–6 m for a total sample volume of 800 L. Samples were preserved in ethanol. Plankton nets were bathed in vinegar (minimum period of 45 min) after sampling each lake to prevent sample contamination and veliger dispersal. Prior to this study, we examined the water used to wash nets after sampling infested waters. Veligers were never found in wash water from vinegar-soaked nets but were frequently found in water from nets not exposed to vinegar (C. Kraft, unpublished data).

After field preservation, samples were examined at 40× with a stereomicroscope under cross-polarized light (Johnson 1995). During the first year, laboratory protocols were established to determine efficient methods to analyze plankton samples to detect veligers. Initially, entire samples were examined for zebra mussel veligers. We subsequently determined that as few as four veligers could be detected in a 350 mL concentrated plankton sample (the average sample volume) by examining subsamples (50 mL total) of particulate material settled at the bottom of undisturbed jars. If low numbers of veligers (<10) were found in subsamples from a lake not previously known to contain zebra mussels, we verified the detection by examining the entire sample. Our effective detection limit was 5 veligers/m^3 water sampled. This threshold would represent a total of 25 million larvae in a 100-ha lake with a 5-m average depth, which could represent the maximal reproductive output of less than 100 female mussels (Borcherding 1991).

Sampling was discontinued following confirmation that zebra mussels were established in a lake (i.e., adult mussels were observed), and additional lakes were added to the sampling program in subsequent years to maximize the number of surveyed lakes. Because the presence of veligers does not necessarily mean that a lake has become colonized by adult zebra mussels, our estimate of zebra mussel inland lake infestations could be an overestimate. However, adult mussels were usually found later, often in the same season that veligers were detected. Because detections during the first year of sampling could result from an infestation occurring in any preceding year, annual infestation rates were only calculated from lakes sampled in consecutive years (i.e., for 1996 and 1997). However, given that we could only detect the presence of zebra mussels above a certain threshold (see above), we could not conclusively determine that colonization of these lakes occurred during the preceding year.

Fig. 1. Proportion of lakes greater than 50 ha in surface area in different size categories. Surveyed lakes in Wisconsin–Illinois and Michigan–Indiana are shown as distinct categories as well as all lakes in Wisconsin and the lower peninsula of Michigan that appear on U.S. Geological Survey 1 : 24 000 topographic maps.



Both before and during the course of our study, adult zebra mussels were discovered within the study region in lakes that were not included in our planned sampling program. None of these lakes had navigable connections to Great Lakes waters. All incidental discoveries were verified by us or by state agencies and were used as auxiliary information to our sampling program to confirm regional patterns of lake infestation. These data were also used to compare the size distribution of infested lakes detected in a planned survey relative to the size distribution detected from unplanned observations.

Results

Zebra mussels were detected in 27 of the 140 lakes surveyed (19%) during this study, but the distribution of these detections was spatially variable (Fig. 2; Table 1). In general, the proportion of lakes found to be infested with zebra mussels was far greater in Michigan (15 of 49 = 31%) and Indiana (seven of 28 = 25%) than lakes surveyed in Wisconsin–Illinois (five of 63 = 8%; G test, G = 10.51, p < 0.01). Incidental discoveries of inland lake zebra mussel infestations also supported the observation that inland lake colonization was more prevalent in Michigan and Indiana by the end of 1997 than in Wisconsin and Illinois (Fig. 3).

Further variation was also apparent at the finer spatial scale of individual lake districts (Fig. 4; Table 2). In Michigan, infestations occurred in all three lake districts but at higher levels in Oakland County, north of Detroit. Similar levels were observed in Indiana with the exception of the Lagrange County district in which no infestations were detected, in spite of being located between two highly infested districts. In Wisconsin–Illinois, four of the five infestations occurred in the southeast Wisconsin district near the Wisconsin–Illinois border. Thus, 20–44% of lakes in five out of six Michigan and Indiana districts were infested, in contrast with consistently low proportions (<15%) in Wisconsin–Illinois districts.

Detections of new infestations were variable from year to year, and the Wisconsin–Illinois results again contrasted sharply with those from Michigan and Indiana. After the first year of the study (1995) during which four Wisconsin infestations were discovered, no additional infestations were found in the initial set of survey lakes during the second and third years of sampling (Table 1; one additional infestation was found in an Illinois lake added to the sampling program in 1996). Overall, using only lakes surveyed in consecutive years (Table 1), the annual infestation rate was 4.6% (3.0% (2/67) for 1995–1996 and 5.6% (6/108) for 1996–1997). Among these same lakes, annual infestation rates were consistent in Indiana (11–12%) while more variable in Michigan (5–12%). The annual infestation rate for Wisconsin study lakes was 0% during both periods.

Infested lakes were more likely to have surface areas between 100 and 500 ha, and lakes smaller than 100 ha and greater than 500 ha were less likely to be infested (Fig. 5A). By contrast, 25% of the incidental sightings came from lakes greater than 500 ha in surface area (Fig. 5B).

Discussion

The impact of any invasive species will depend on its geographic range, and other studies have predicted the ultimate range of zebra mussels at continental (Strayer 1991) and regional scales (e.g., Neary and Leach 1992; Koutnik and Padilla 1994). Unfortunately, simple range boundaries can be misleading, since most maps of geographic ranges ignore the area inside the range boundary (Brown et al. 1996). For invasive species, "jump" or long-distance dispersal often produces patchy patterns of colonization (Shigesada and Kawasaki 1997). Our results show that the colonization of inland lakes by zebra mussels is patchy at regional and district-level spatial scales, and inland lakes are becoming colonized more slowly than the initial range expansion through North American navigable waterways. This slower rate of spread is undoubtedly due to functional dispersal barriers that reduce dispersal to and within watersheds. A majority of the infestations detected either incidentally (73%) or as a part of our survey (93%) occurred in lakes without navigable connec-

Fig. 2. Lakes surveyed as part of this study in the lower peninsula of Michigan, Wisconsin, northern Indiana, and northern Illinois. Lakes infested with zebra mussels are shown with solid circles, and lakes that were uninfested as of 1997 are shown with open circles.

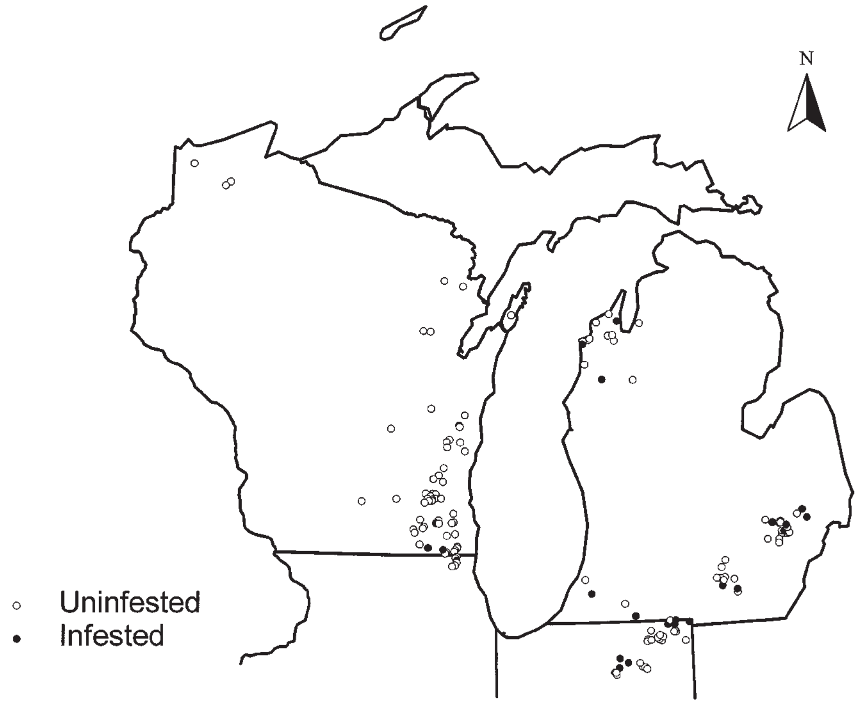


Table 1. Percentage of sampled lakes with zebra mussel infestations in three regions: lower peninsula of Michigan (MI), northern Indiana (IN), and Wisconsin – northern Illinois (WI–IL).

Region	Year detected	Year first sampled 1995	1996	1997	Row total
MI	1995	15% (4/26)	—	—	15% (4/26)
MI	1996	5% (1/22)*	14% (2/14)	—	8% (3/36)
MI	1997	19% (4/21)*	0% (0/12)*	44% (4/9)	19% (8/42)
MI	All years	35% (9/26)	14% (2/14)	44% (4/9)	31% (15/49)
IN	1995	25% (3/12)	—	—	25% (3/12)
IN	1996	11% (1/9)*	10% (1/10)	—	11% (2/19)
IN	1997	13% (1/8)*	11% (1/9)*	0% (0/6)	9% (2/23)
IN	All years	42% (5/12)	20% (2/10)	0% (0/6)	25% (7/28)
WI–IL	1995	10% (4/40)	—	—	10% (4/40)
WI–IL	1996	0% (0/36)*	4% (1/23)	—	2% (1/59)
WI–IL	1997	0% (0/36)*	0% (0/22)*	—	0% (0/58)
WI–IL	All years	10% (4/40)	4% (1/23)	—	8% (5/63)

Note: Data are cross-tabulated by the year in which infestations were detected and by the year in which lakes were first sampled. Values in parentheses represent the number of infested lakes per number of lakes sampled. Asterisks indicate values used to estimate annual rates of infestations.

tions to infested downstream waters or upstream source populations (C. Kraft and L. Johnson, unpublished data). We believe that these slow rates of spread are largely due to limitations in overland dispersal and that concerns over the rapid overland dispersal of zebra mussels (e.g., Griffiths et al. 1991; Ricciardi et al. 1995), although legitimate, may be overly fatalistic.

We have clearly documented that the inland spread of zebra mussels has been less extensive for Wisconsin–Illinois lakes than for either Michigan or northern Indiana lakes. Assuming other factors being equal, this pattern might be initially attributed to the way in which nearby source populations developed in the Great Lakes. Zebra mussels were first discovered in Lake St. Clair and western Lake Erie (1988), subsequently became established in eastern and southern Lake Michigan (1990), and finally colonized western Lake Michigan in 1991 (Griffiths et al. 1991; Kraft 1993; Cope et al. 1997). Consequently, nearby source populations for potential infestations of southeastern Michigan lakes developed 2–3 years earlier than for Wisconsin lake districts. Indiana districts were in an intermediate position: farther from Lake St. Clair and western Lake Erie shorelines but a similar distance from southeastern Lake Michigan. Additionally, Lake Wawasee, Indiana's largest inland lake, became infested relatively early (1991) and therefore could have served as a local source.

Fig. 3. Inland lakes (in the lower peninsula of Michigan, Wisconsin, northern Indiana, and northern Illinois) that had confirmed zebra mussel infestations through 1997. Detections shown include those resulting from this study (solid circles) as well as confirmed infestations from unplanned observations (open circles) made both during the course of this study (1995–1997) and prior to 1995.

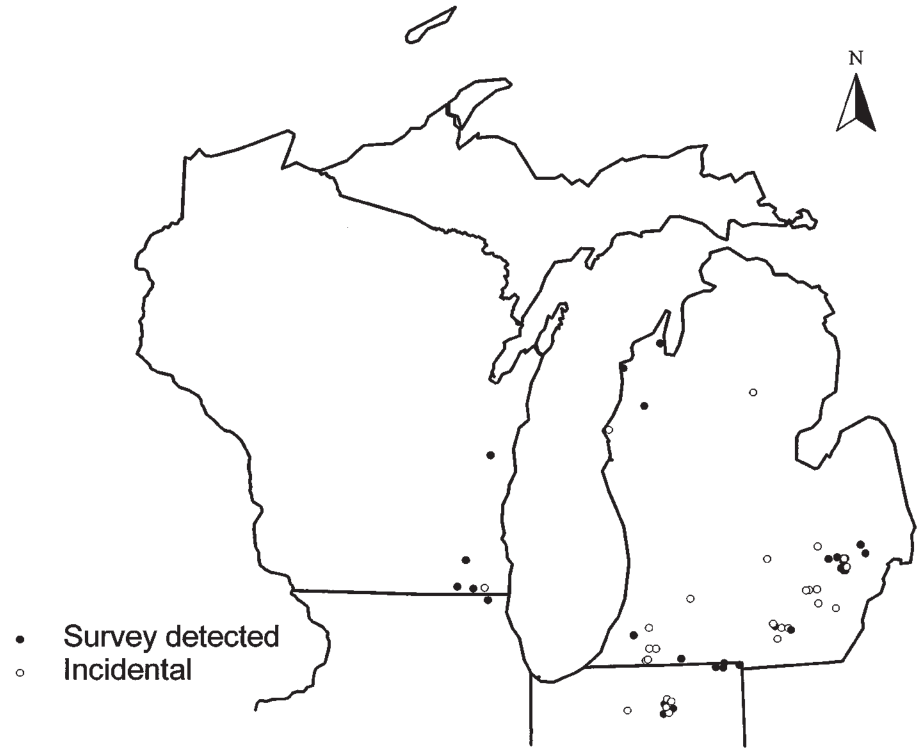


Fig. 4. Regional differences in relative rates of lake infestation by zebra mussels. The relative size of pie charts is proportional to the number of lakes surveyed within a region on which the pie chart is centered. The proportion of infested lakes is shown in black, and proportion of lakes remaining uninfested as of 1997 is shown in grey.

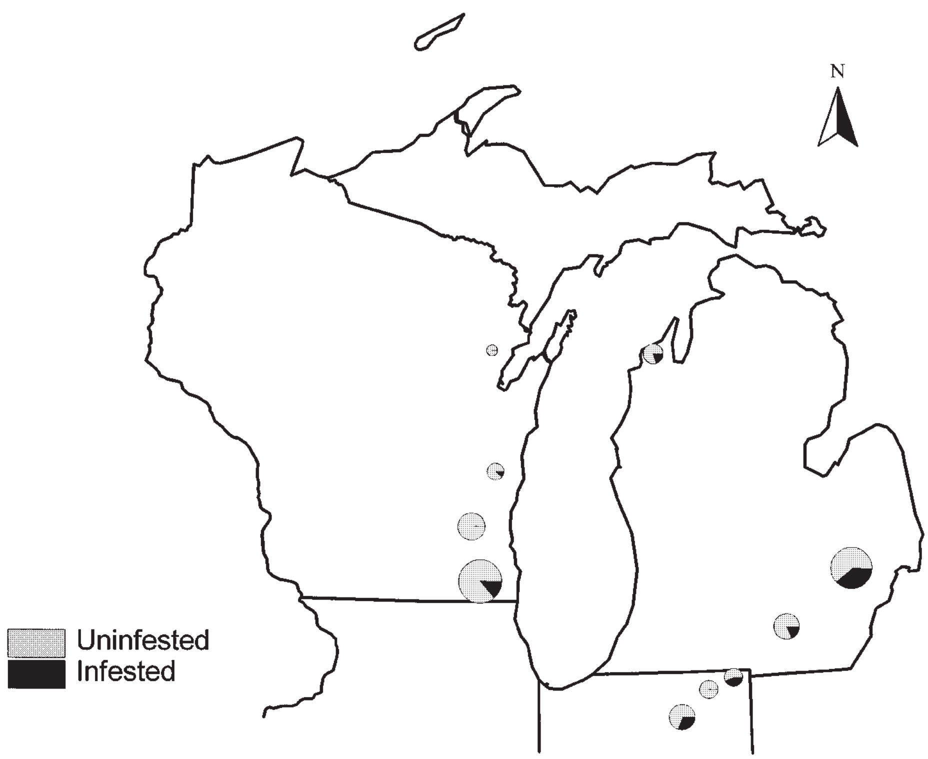


Table 2. Number of survey lakes in which zebra mussels were found according to survey districts. Not all lakes surveyed were included in these districts. Also shown is the number of lakes in each region from which zebra mussels were reported based on incidental discoveries reported through unplanned observations (1991–1997).

District	State	No Mussels (surveyed)	Mussels (surveyed)	Mussels (incidental)
Steuben	Indiana	5	4	0
Lagrange	Indiana	9	0	0
Kosciusko	Indiana	7	3	4
Oakland	Michigan	13	8	6
Jackson	Michigan	8	2	4
Leelanau	Michigan	8	2	0
Northeast	Wisconsin	5	0	0
Sheboygan	Wisconsin	7	1	0
Western Milwaukee	Wisconsin	15	0	0
Southeast	Wisconsin–Illinois	24	4	1

Although plausible, this scenario does not explain observed colonization patterns because it is inconsistent with the timing of the infestations observed within each region. Given the east–west time lag in the establishment of Great Lakes source populations, if the rates and patterns of dispersal were similar in all regions, we would have predicted fewer Wisconsin–Illinois inland lake infestations in 1995 than in subsequent years. Instead, four Wisconsin–Illinois infestations were found in 1995, one in 1996, and none in 1997.

Several alternative hypotheses may explain the observed differences between Michigan–Indiana and Wisconsin–Illinois. First, inland lakes might be less suitable for zebra mussels in Wisconsin–Illinois. Second, dispersal vectors might be less common or have different behaviors in Wisconsin–Illinois. Third, dispersal vectors might be less efficient at transporting zebra mussels in Wisconsin–Illinois.

Lake characteristics in the study region are similar and not restrictive for zebra mussel colonization. Summer total phosphorus levels in lakes within the study region exceed 15 g/L (Omernik et al. 1988), and total alkalinity exceeds 2000 μequiv./L (Omernik and Powers 1983; Omernik et al. 1988). Lakes surveyed as part of this study were located in regions with carbonate bedrock, which is a good predictor of lake types suitable for zebra mussel colonization (Neary and Leach 1992; Koutnik and Padilla 1994). Relative proportions of surveyed lake sizes were similar in both study regions.

Transient recreational boating is considered to be the primary mechanism for overland zebra mussel dispersal (Johnson and Carlton 1996; Schneider et al. 1998), and recreational boats are used sequentially between Great Lakes waters and inland waters (Padilla et al. 1996; Buchan and Padilla 1999). Although precise measures of boat use for each region are lacking, the number of recreational boats registered in the study region suggests that boat use cannot explain large differences in rates and patterns of colonization. In 1997, 760 000 boats were registered in Michigan, 490 000 in Wisconsin, 207 000 in northern Illinois, and 70 000 in northern Indiana (Bossenbroek 1999).

Differences may also exist in the efficiency by which mussels are transported upon recreational boats. One possible difference is the degree to which zebra mussels are transported on macrophytes entangled on boats leaving infested waters (Johnson and Carlton 1996). We have observed evidence of this type of dispersal at Great Lakes boat ramps in southeastern Michigan but never at ramps along Wisconsin's Lake Michigan shoreline (Johnson and Carlton 1996; C. Kraft and L. Johnson, unpublished data). Thus we speculate that zebra mussels might have been transported on entangled macrophytes in higher numbers or at greater frequency from source populations in Lake St. Clair and western Lake Erie than from source populations in western Lake Michigan.

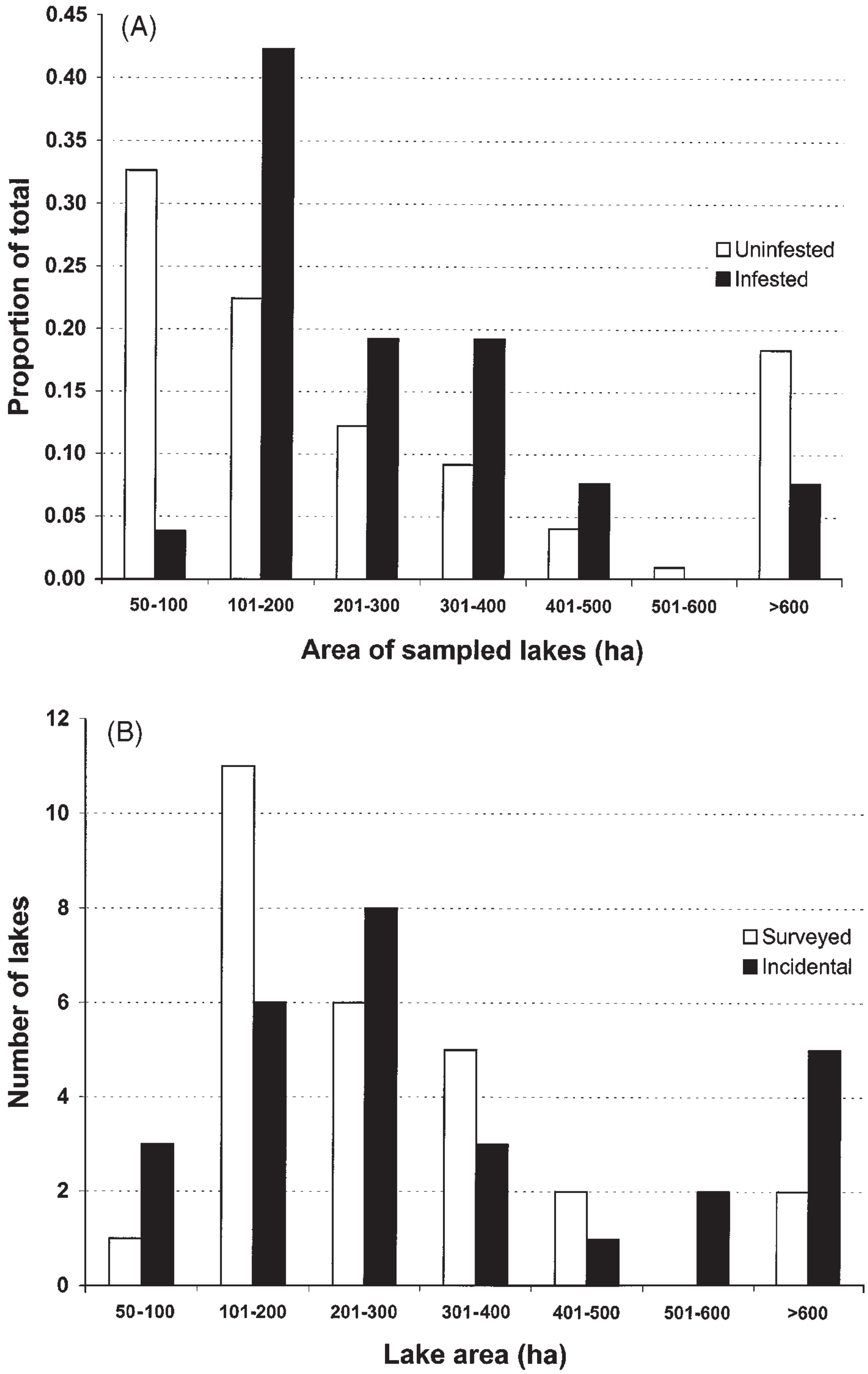
However, even without knowing the precise mechanisms involved, we believe that observed regional differences were due to differences in rates of dispersal, not to differences in habitat features. A simulation model of zebra mussel dispersal in this region has shown that infested lake distributions within our study area can be predicted without invoking differences in lake habitat suitability (Bossenbroek 1999).

We do not have data to examine the characteristics of infested lakes, except that we observed that lakes larger than 100 ha were more likely to become infested. This is consistent with studies in Europe (Karataev and Burlakova 1995) and surveys of European data (Strayer 1991; Ramcharan et al. 1992*b*). Because the majority of lakes in Wisconsin and the lower peninsula of Michigan are smaller than 100 ha, overall lake infestation rates would be substantially lower than reported in this study, since we disproportionately sampled larger lakes. We believe that our observation of low infestation rates for large lakes (>600 ha) was an artifact of the distribution of large lakes within our lake districts, since 16 of 18 large lakes (>600 ha) sampled were located in districts that had low overall rates of infestation. Moreover, at the start of our study, many of the larger lakes in our lake districts were already infested and thus were not included in our survey.

The public is highly aware of zebra mussels, and people have been encouraged to report new sightings. Although data from such reports can be useful for general comparisons, they provide insufficient precision to examine rates and patterns of geographic spread. Unplanned sampling efforts cannot be standardized in either space or time and therefore may be biased. This problem is reflected in our observation that incidental discoveries of infestations occurred more frequently from lakes greater than 600 ha in surface area, where more people are likely to be looking for mussels. In addition, the absence of zebra mussels is not reported in such databases, and thus, neither rates nor proportions of infestations can be calculated. We established a systematic monitoring program with consistent sampling protocols to avoid such problems.

The recognition that many aquatic habitats across North America are ecologically suitable for zebra mussels, and the fact that this invader spread rapidly over a broad geographic range, has promoted the unfounded assumption among journalists, educators, the public, and even scientists that the invasion of all suitable habitats by zebra mussels is a "fait accompli." Indeed, journalists have so frequently reported the zebra mussel's rapid spread throughout North America

Fig. 5. (A) Proportion of surveyed inland lakes that were infested (solid bars) and uninfested (open bars) by zebra mussels as of 1997 according to lake surface area and (B) number of infested lakes discovered through surveys conducted as part of this study (surveyed 1995–1997, open bars) and incidental discoveries reported through unplanned observations (1991–1997, solid bars) according to lake surface area. All incidental discoveries were verified (see text).



that it has become a metaphor for rapidly occurring events ("the data communications industry is growing faster than zebra mussels in a drainpipe..." (*Fortune*, March 7, 1995) "...brew pubs that have been spreading like zebra mussels across the country" (*Ithaca Journal*, December 5, 1998)). Yet zebra mussel dispersal involves two distinct methods that have produced vastly different rates of spread. Whereas the commercially navigable and connected inland waters of North America were quickly colonized by zebra mussels, our results demonstrate that dispersal to inland lakes has been taking place more slowly. When evaluating rates of zebra mussel dispersal, it will be critical to distinguish between dispersal occurring within connected and nonconnected waterways. Other scientists have implicitly made this distinction by only describing the rapid spread of zebra mussels through river systems (e.g., Mellina and Rasmussen 1994; Hincks and Mackie 1997) without referring to the subject of dispersal rates to inland lakes.

This distinction is particularly important for education and outreach efforts that have been initiated with the premise that zebra mussels are spreading rapidly throughout North America. The slower spread into inland lakes will provide more opportunities to mount an effective effort to diminish the overland spread of zebra mussels to inland lakes but will also require a long-term, sustained commitment focused on preventing dispersal to susceptible lakes.

Our results have documented the early stages of the colonization of inland North American lakes by zebra mussels and suggest that new inland lake infestations will continue for decades. Our data on rates and patterns of this invasion have already been used to forecast future inland lake distribution patterns (Bossenbroek 1999; J. Bossenbroek, Colorado State University, Fort Collins, Co., unpublished data). Since data sets suitable for evaluating spatial or temporal patterns of aquatic invasions are rare (Cohen and Carlton 1998), additional studies detailing spatial and temporal patterns of aquatic invasions will provide an improved predictive capability regarding the spread of aquatic invasive species.

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