

LANDSCAPE PATTERNS OF AN AQUATIC INVADER: ASSESSING DISPERSAL EXTENT FROM SPATIAL DISTRIBUTIONS

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Abstract. Assessing the spatial distribution of organisms across landscapes is a key step toward determining processes that produce observed patterns. The spatial distribution of an invasive aquatic mollusk, the zebra mussel (*Dreissena polymorpha*), was examined in two lake-rich areas (Belarus and midwestern United States) with contrasting invasion histories. Spatial distribution patterns of invaded lakes were determined using Ripley's *K*. Aggregation of invaded lakes was found at similar spatial extents (<50 km) in both regions; segregation was found at spatial extents >120 km in Belarus. The observed spatial extent of aggregation likely reflected the scale of secondary geographic spread, whereas the scale of long-distance dispersal events was reflected by the spatial extent of segregation. Isolated Belarus lakes were less likely to be invaded than those connected by waterways. Although one-dimensional aggregation of invaded lakes along connected Belarus waterways was not observed, nearest neighbor analysis indicated that zebra mussel dispersal occurred at distances <15 km within these waterways. Based on observed spatial pattern, we concluded that zebra mussels have not yet saturated European and North American lake landscapes, including many suitable lakes. Similar distribution patterns of invaded lakes in Belarus and North America suggest that similar processes have influenced zebra mussel spread in both landscapes.

Key words: Belarus; colonization; dispersal; *Dreissena polymorpha*; invasion; invasive species; lakes invaded; landscape ecology; Ripley's *K*; spatial pattern and distribution; upper Midwest (USA); zebra mussel dispersal.

INTRODUCTION

Plant ecologists have a long tradition of using pattern analysis to infer processes determining spatial patterns (Watt 1947, Greig-Smith 1964, Pielou 1969). Although spatial pattern analysis techniques also have the potential to explain patterns of species invasion in heterogeneous landscapes, these techniques have not been applied to invasive species problems. In this paper, we evaluate spatial pattern in the distribution of an invasive organism, the zebra mussel, (*Dreissena polymorpha* Pallas) whose underlying pattern of suitable habitats exhibits a nonrandom distribution. By detecting and describing spatial distribution patterns, we provide a better understanding of processes responsible for dispersal of this nuisance invader, information that can be used to more effectively target dispersal prevention efforts.

Humans have accelerated the incidence of biological invasions across natural biogeographical barriers, thereby producing major ecological disturbances (Elton

1958, Vitousek et al. 1996). These invasions begin with the initial establishment of a founding population, followed by local population growth, and subsequent dispersal to other suitable habitats. The overall impact of an invader depends, in part, on the expansion of its geographic range (Elton 1958, Lodge et al. 1998), which is influenced by both an organism's dispersal ability and the connectivity or isolation of suitable habitats.

Most early analyses of invasions assumed that the spread of invaders could be characterized with reaction-diffusion models, in which the invasion proceeds across a landscape as a radiating front (Hengeveld 1994, Shigesada and Kawasaki 1997). Such diffusion-based modeling efforts generally followed the example of Skellam (1951), using macroscale data, thereby considering the landscape as homogeneous. However, more recent studies have recognized the influence of environmental heterogeneity and long-distance dispersal events in producing patchy distributions and uneven range expansions by invasive organisms (Moody and Mack 1988, Andow et al. 1990, Higgins and Richardson 1996, Buchan and Padilla 1999).

The assumptions of habitat homogeneity and radi-

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ating range expansions are particularly unsuitable for freshwater lake organisms, for which colonizable habitats occur as discrete entities within an uncolonizable terrestrial landscape. In landscapes with many lakes, the geographic range expansion of aquatic invaders depends on a combination of two contrasting modes of dispersal: overland dispersal across hostile terrestrial habitats, and dispersal through connecting waterway corridors (e.g., streams, rivers, canals) (Johnson and Padilla 1996). By examining patterns of geographic spread through time, one should be able to discern the rate of geographic spread and the relative importance of contrasting dispersal mechanisms for an invasive organism, as well as predict the spatial extent of future invasions.

Data sets suitable for evaluating spatial or temporal patterns of aquatic invasions are rare compared to terrestrial invasions (Cohen and Carlton 1998). The spread of zebra mussels in Europe and North America provides a unique opportunity to address these questions. Zebra mussels are brackish to freshwater epibenthic bivalves. Adult mussels are relatively sessile and can survive out-of-water for several days (Ricciardi et al. 1995). They have a planktonic feeding larval stage that attaches to benthic substrates within two months after spawning, and can move between lakes by human-mediated or passive transport through streams, rivers, and canals. Numerous vectors have the potential for dispersing zebra mussels overland (Carlton 1993), and human activities are the dominant overland dispersal vector (Johnson and Carlton 1996, Buchan and Padilla 1999).

Because of their potential economic and ecological impacts (Karatayev et al. 1997, Strayer et al. 1999), the distribution of zebra mussels has been closely monitored in one lake-rich area in Europe (the Belarussian Lake District; Karatayev and Burlakova 1995; A. Y. Karatayev, *unpublished data*) and another in North America (the midwestern region of the United States; Kraft and Johnson 2000). Lakes within these two regions are similar in morphology, chemistry, and background geology, yet differ substantially in the history and likely vectors for invasion by zebra mussels. In Belarus, zebra mussels first colonized rivers in the early 19th century during an intense period of canal construction and increased commercial shipping (Kinzelbach 1992, Starobogatov and Andreeva 1994). In contrast, zebra mussels were first reported from North America in 1989 (Hebert et al. 1989), after which they spread rapidly through the Great Lakes and connecting navigable river systems. Zebra mussel invasion of inland lakes has occurred more slowly than the spread through connected waterways (Kraft and Johnson 2000). In the United States, transient recreational boaters are the most likely vector for zebra mussel dispersal (Padilla et al. 1996, Buchan and Padilla 1999), whereas in Belarus, commercial fishing activity appears to play that role (A. Y. Karatayev, *unpublished data*).

We used spatial pattern analysis to evaluate dispersal processes related to the formation of zebra mussel distribution patterns in Europe and North America. Specifically, we addressed three major questions concerning patterns of inland lake colonization by zebra mussels. First, given that invasive species may initially colonize many loci within a landscape, we asked whether determining the spatial aggregation and segregation of such loci could provide a measure of effective dispersal distances for an invader, and we compared these measures in two contrasting landscapes. Second, by studying spatial occurrence patterns in landscapes with different colonization histories, we evaluated the extent to which loci coalesced through time, thereby indicating whether an invader had colonized all suitable habitats. Third, we assessed the functional connectivity of invaded lakes by examining one-dimensional spatial occurrence patterns within a waterway network. To address the first two questions, we applied a second-order spatial point pattern analysis technique (Ripley 1977), in conjunction with Monte Carlo simulations, to distinguish the spatial scales of aggregation and segregation of invaded lakes in Belarus and the United States apart from underlying lake distribution patterns. To address the third question, we used an analogous one-dimensional Ripley's K analysis to evaluate distribution patterns of connected, invaded Belarus lakes, and examined nearest neighbor distances of invaded lakes along connected Belarus waterways.

METHODS

The Belarus data set was based on a survey of 522 lakes ≥ 5 ha in surface area conducted in northern Belarus from 1971 to 1986 (Karatayev and Burlakova 1995; A. Y. Karatayev, *unpublished data*). Lake water chemistry data were collected during the survey, and 390 lakes were considered suitable for zebra mussel colonization based on minimum requirements of pH > 7.3 and calcium concentrations > 24 mg/L (Ramcharan et al. 1992). The presence or absence of zebra mussels was determined from benthic samples systematically collected across each lake and plankton samples examined for zebra mussel larvae. Zebra mussels were found in 93 lakes (Fig. 1). The hydrology of these Belarussian lakes, including all connecting rivers, streams, and canals, was digitized from regional maps available at a scale of 1:200 000. The resulting ArcInfo coverage included 522 lakes and 1528 connecting arcs. Nodes were placed at all lake inlets and outlets for calculating distances along the waterway network. Lakes without connecting inlets or outlets were considered isolated.

For the U.S. analysis, we included all lakes with surface areas ≥ 25 ha within a 439 081-km² region excluding the Laurentian Great Lakes (Fig. 2). This region included 3600 lakes in Michigan (1600), Wisconsin (1722), Illinois (55), Indiana (215), and Ohio (8). The minimum size of 25 ha was chosen to reduce the

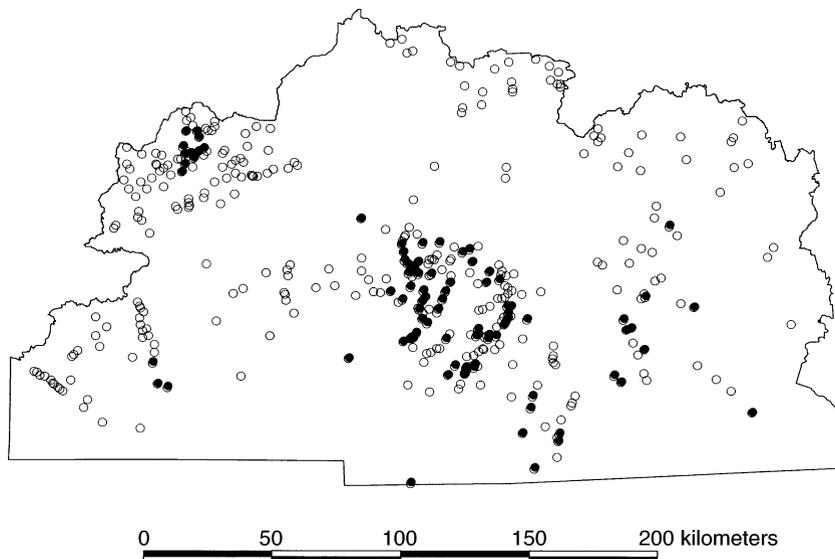


FIG. 1. Distribution of lakes invaded by zebra mussels in northern Belarus (Karatayev and Burlakova 1995). Black circles represent invaded lakes. Open circles represent lakes with suitable pH and Ca, not invaded by zebra mussels.

number of lakes in Wisconsin and Michigan, which have more than 25 000 lakes >5 ha (the minimum lake size included in the Belarus data set). This cutoff is biologically reasonable: the smallest known invaded North American lake is 15 ha (Kraft and Johnson 2000), and European lakes <40 ha are rarely invaded (Strayer 1991, Ramcharan et al. 1992). Water chemistry data for these lakes were obtained from the EPA STORET data bank (U.S. Environmental Protection Agency, Office of Water 1999). Based on these data and criteria

provided by Ramcharan et al. (1992), 1756 lakes were considered suitable for zebra mussel colonization (Bos-senbroek et al. 2001).

The presence of zebra mussels in inland lakes within this U.S. region was reported by Kraft and Johnson (2000), based on data collected prior to December 1997. For surveyed lakes, the presence or absence of zebra mussels was assessed by systematic plankton sampling for zebra mussel larvae. A total of 60 lakes were known to be colonized by zebra mussels as of

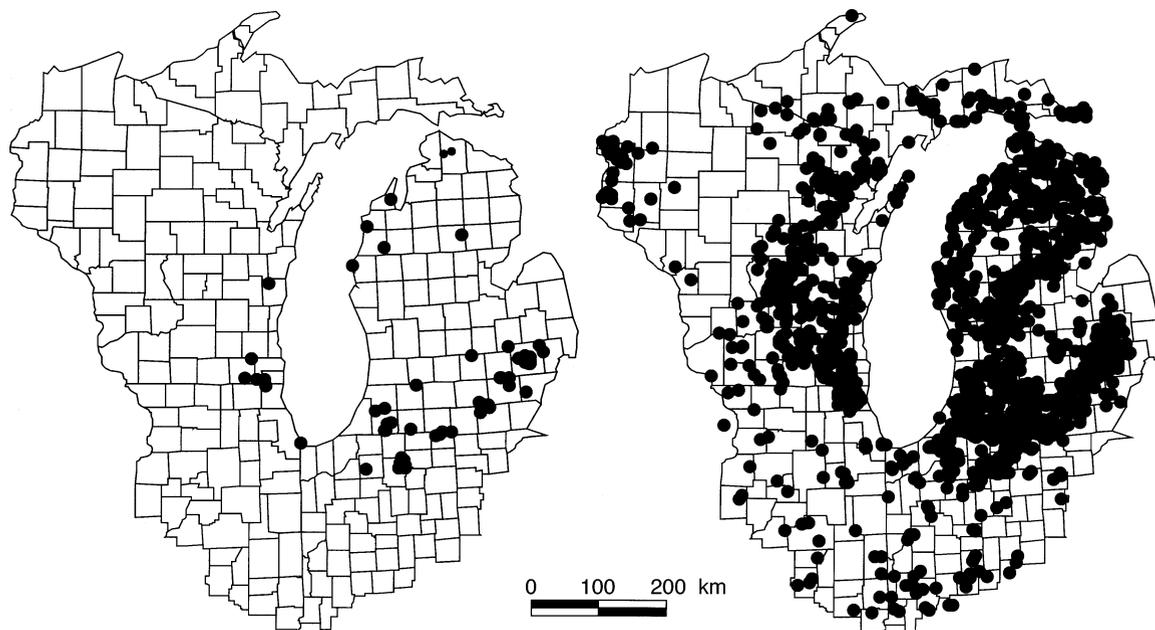


FIG. 2. Distribution of lakes invaded by zebra mussels in a four-state region of the United States (Kraft and Johnson 2000). Left panel: lakes invaded by zebra mussels. Right panel: lakes with suitable pH and Ca, not invaded by zebra mussels.

December 1997 (Fig. 2). Lake hydrography data were obtained from agency sources in Michigan and Wisconsin. Illinois, Indiana, and Ohio lake data were obtained from U.S. EPA River Reach Files (U.S. Environmental Protection Agency, Office of Water 1999). These data did not include complete information on connecting waterways.

Spatial pattern of invaded lakes was tested using Ripley's K (Ripley 1977), which evaluates the expected number of points within a Euclidean distance t of an arbitrary point within the area being evaluated. A circle of radius t is centered at each point and the number of neighbors within the circle is counted. For n individual points distributed in an area A , the density ($\lambda = n/A$) gives the mean number of points per unit area. The function $\lambda K(t)$ gives the expected number of further points within radius t of an arbitrary point within the landscape evaluated. If points are randomly distributed, the expected value of $K(t) = \pi t^2$.

The unbiased estimate of $K(t)$ for an observed spatial point pattern is

$$\hat{K}(t) = n^{-2} \sum_{i \neq j} \sum_{i \neq j} w_{ij}^{-1} I_i(u_{ij})$$

where n is the number of points in the landscape area (A); u_{ij} is the distance between points i and j ; $I_i(u)$, the counter variable, equals 1 if $u \leq t$ and 0 if $u > t$; w_{ij} is the proportion of the circumference of a circle centered at the point i with radius u_{ij} , which lies within A ; and the summation is over all pairs of lakes not more than t apart (Diggle 1983). $K(t)$ is a second-order statistic that provides an estimate of spatial variance and was estimated using S-Plus (Version 4.5; Venables and Ripley 1997).

We first tested whether lakes with suitable pH and Ca for zebra mussels were aggregated in the Belarusian landscape by comparing their distribution with randomly chosen coordinates within the study area. For all estimates of $K(t)$, the centroid of each lake was designated as the point location representing each lake. A Monte Carlo simulation (1000 runs) of the distribution of 390 randomly chosen points was compared with the observed distribution of 390 suitable lakes. We compared $\lambda K(t)$ estimated for the observed lake sample population to the expected value of $\lambda K(t)$ for points randomly distributed throughout the landscape. A parallel analysis was conducted for U.S. lakes by comparing the observed distribution of 1756 suitable lakes to a Monte Carlo simulation (1000 runs) of the distribution of 1756 randomly chosen points.

To evaluate invaded lake distribution patterns without bias from the underlying lake distribution pattern, we compared the observed number of invaded Belarusian lakes found at a given distance from any invaded lake (estimated from $K(t) \times \lambda$) to 1000 Monte Carlo simulations randomly selecting 93 lakes (without replacement) from all of the 390 suitable lakes (those invaded as well as those not invaded). Parallel analyses

were conducted for U.S. lakes by comparing the spatial distribution of the observed 60 invaded lakes with 1000 Monte Carlo simulations that randomly selected sets of 60 lakes (without replacement) from among the 1756 lakes suitable for colonization. The observed number of invaded lakes in Belarus and North America (93 and 60, respectively) dictated the number of randomly selected lakes for each analysis.

Since many invaded Belarus lakes were connected via waterways that could serve as corridors for dispersal, we conducted two different one-dimensional analyses of connected lake distributions. Since these data were only readily available for Belarus, parallel analyses were not feasible for the U.S. data set.

Nearest invaded lake analysis.—Using the Belarus waterway network data, we compared waterway distances to the nearest invaded lake for both invaded and uninvaded lakes, thereby focusing on the single nearest invaded lake instead of lake aggregations (which were evaluated in our other analyses). To determine the likelihood that any observed pattern of distances to the nearest invaded lake could occur by chance, we conducted a randomization test. We started this analysis by evaluating each invaded lake that was not isolated, calculating the distance from that lake to the nearest invaded lake, up to distances of 200 km. Next, we calculated the same distance measures (i.e., distance to the nearest invaded lake) for a random distribution of lakes derived from 1000 Monte Carlo simulations in which invasions were randomly assigned (without replacement) to lakes that were not isolated. Finally, we compared the observed distribution of distances to the nearest invaded lake to the 1000 simulated distributions, using the upper 5% range of simulated distributions to determine statistical significance.

One-dimensional Ripley's K .—We evaluated the distances between zebra mussel-invaded lakes using distances along connected waterways, instead of Euclidean distance used above for the two-dimensional analyses. A one-dimensional version of $K(t)$ was used as the test statistic, as follows

$$\hat{K}(t) = n^{-1} \sum_{i \neq j} \sum_{i \neq j} I_t(u_{ij})$$

$K(t) = 2t$ for a random arrangement of points in one dimension. For clustered points, $K(t) > 2t$, and for segregated patterns, $K(t) < 2t$. Network distances between lakes were calculated using PC ArcInfo Version 8.0 (Environmental Systems Research Institute, Redlands, California). A network distance of 400 km was used as a maximum cutoff value, which exceeded the maximum east–west linear distance across Belarus (~ 300 km). $K(t)$ was calculated for invaded lakes using 4-km distance increment bins. This provided a measure of the average number of invaded lakes within 4-km intervals for the invaded Belarus lakes that were not isolated. $K(t)$ for 82 invaded (waterway-connected) lakes was then compared with the distribution of 1000

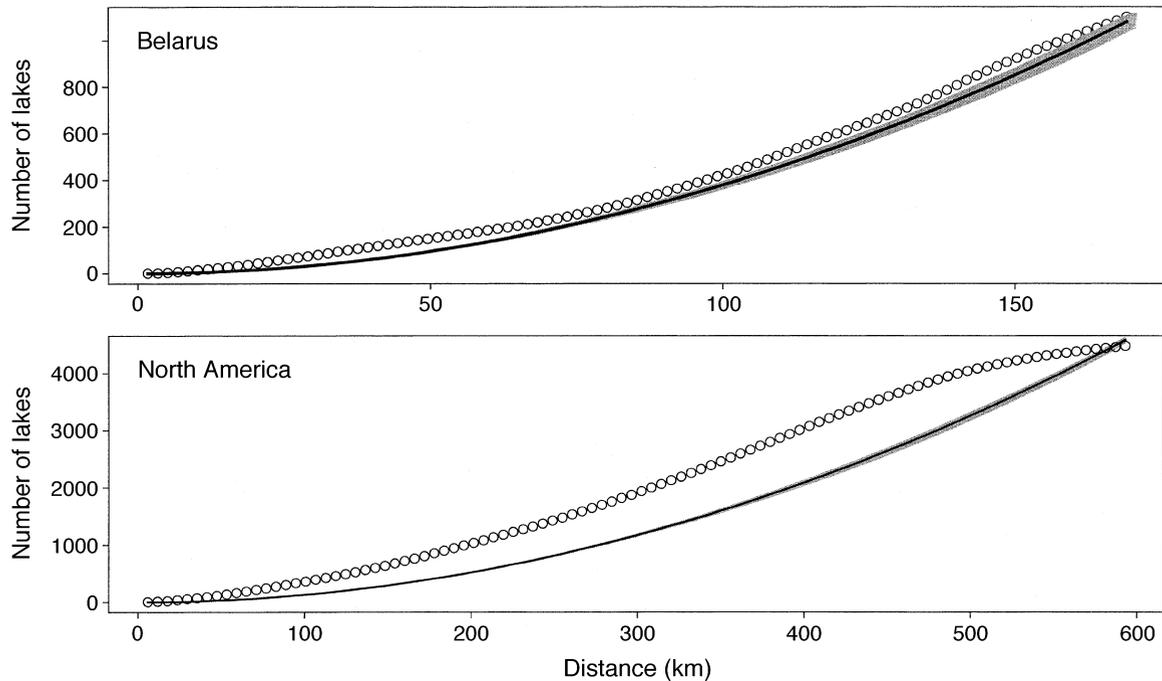


FIG. 3. (Top) Circles show the observed average number of lakes found at any given distance from any other lake within the Belarus landscape, based on Ripley's K statistic [number of lakes = $\lambda K(t)$] for 390 study lakes suitable for zebra mussels. The gray area shows the expected range of $\lambda K(t)$ based on 1000 Monte Carlo simulations, using random samples of 390 coordinates within the study area. (Bottom) Same as top panel, with data for 1756 suitable lakes from the U.S. study region.

Monte Carlo simulations of $K(t)$ in which 82 lakes were randomly selected (without replacement) from 396 lakes that were not isolated.

RESULTS

Results for the spatial pattern analysis of Belarus and North American lake distributions are shown in Fig. 3. The top panel compares $\lambda K(t)$, the average number of lakes at a particular distance interval from 390 study lakes with suitable pH and Ca, to 1000 Monte Carlo simulations of $\lambda K(t)$ for 390 randomly selected lake locations. At all distances <160 km, $\lambda K(t)$ for the observed lake distribution exceeded all simulated values of $\lambda K(t)$, indicating a significant aggregated spatial pattern. Lakes suitable for zebra mussels were aggregated at all spatial scales <600 km in the midwestern United States relative to randomly chosen coordinates (bottom panel, Fig. 3). Invaded lakes were similarly aggregated by comparison with randomly chosen coordinates (not shown).

Invaded lakes in Belarus and North America were both aggregated and segregated at different spatial scales, as compared to random distributions generated by Monte Carlo simulations constrained to lakes with suitable habitats (Figs. 4 and 5). In these figures, the bottom panel shows the proportional rank (by comparison with 1000 Monte Carlo simulations) of the average number of observed invaded lakes. Belarus invaded lakes were aggregated at distances <80 km since

for these distances, the proportional rank of $\lambda K(t)$ for observed invaded lakes exceeded 97.5% of the $\lambda K(t)$ values from 1000 Monte Carlo simulations of 93 randomly selected lakes with suitable pH and Ca (bottom panel, Fig. 4). At distances >120 km, invaded lakes were segregated. For these distances, the proportional rank of $\lambda K(t)$ for observed invaded lakes was smaller than 2.5% of $\lambda K(t)$ values from 1000 Monte Carlo simulations (bottom panel, Fig. 4).

Within the United States, invaded lakes were aggregated at all distances ranging up to 50 km (Fig. 5). Due to the small number of invaded lakes, relative to the large number of lakes in the data set, the Monte Carlo estimates were more variable for this region than for Belarus (Figs. 4 and 5). Although the values for $\lambda K(t)$ at greater distances were not significantly different from the random simulations (i.e., did not cross the 2.5% threshold, using $\alpha = 0.05$), there was a tendency toward segregation at distances of ~ 200 – 300 km (Fig. 5).

Overall, 23% of all lakes studied in Belarus were isolated (not connected by waterways to other lakes), whereas only 11% of invaded lakes were isolated. This suggests that lakes connected to other lakes were more likely to be invaded. Invaded lakes were more likely than uninvaded lakes to be connected to another nearby invaded lake, since nearly all connected, invaded lakes were located within 15 km (along the waterway network) of another invaded lake (88%; Fig. 6). Almost

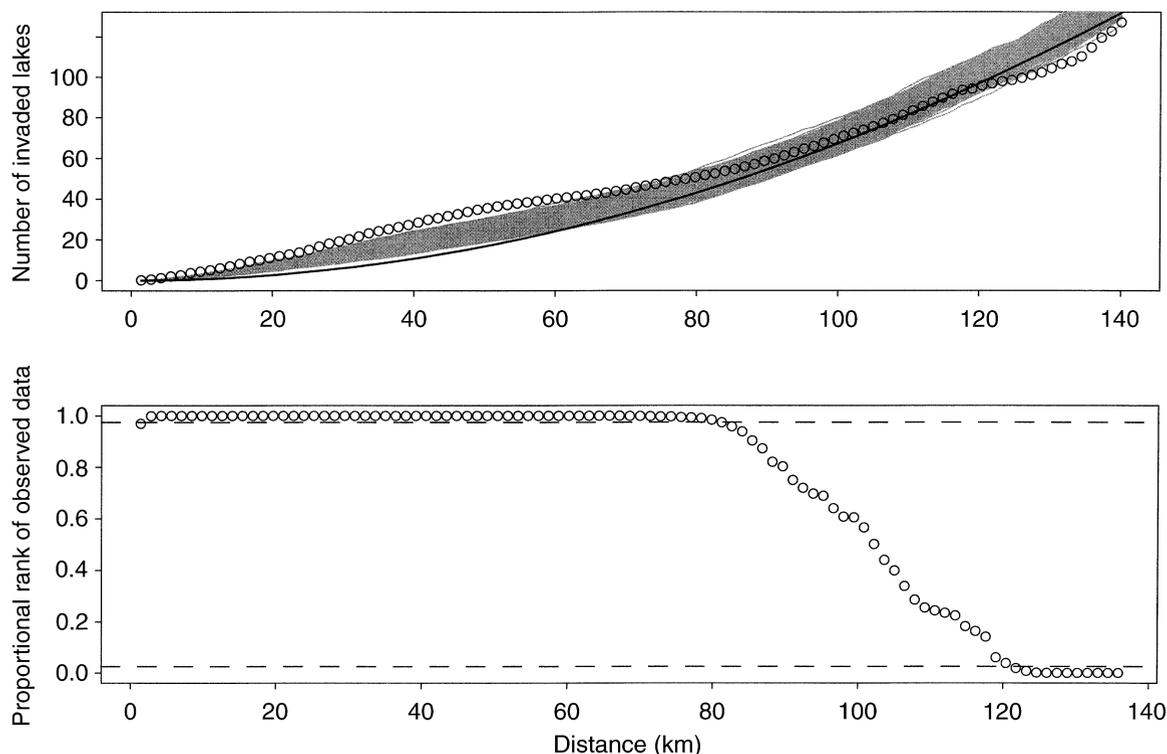


FIG. 4. Top panel: Circles show the observed average number of zebra mussel-invaded lakes found at any given distance from any other invaded lake within the Belarus landscape, based on Ripley's K statistic [number of invaded lakes = $\lambda K(t)$] for 93 invaded lakes. Gray lines show the expected range of $\lambda K(t)$ based on 1000 Monte Carlo simulations, using random samples (without replacement) of 93 lakes selected from 390 lakes with suitable pH and Ca for zebra mussel colonization within the study area. Bottom panel: proportional rank of observed number of invaded lakes by comparison with 1000 Monte Carlo simulations. Dashed horizontal lines show ranks at which values for observed data are $>97.5\%$ or $<2.5\%$ of values for simulated lake distributions.

one quarter (23%) of the uninverted lakes were also within 15 network km of an invaded lake, but a greater proportion of uninverted lakes were located at large waterway network distances (>100 km) from the nearest invaded lake (30%), whereas no invaded lake was >100 km from another invaded lake. A randomization test was used to determine the likelihood that this observed pattern of distances to the nearest invaded lake could occur by chance. For distances from 0 to 200 km, we compared the observed proportion of invaded lakes whose nearest neighboring invaded lake occurred within that distance to proportions estimated from 1000 Monte Carlo simulations. The observed proportions exceeded 95% of the simulations at distances ranging from 7 to 16 km, indicating that invaded Belarus lakes are more likely (by comparison with random occurrence) to be connected to another invaded lake within a waterway distance of 7–16 km.

For the one-dimensional Ripley's K analysis, $K(t)$ was not significantly different from random simulations for any distance (i.e., the observed invaded lake distribution was neither $>97.5\%$ nor $<2.5\%$ of $K(t)$ values from 1000 bootstrap simulations; Fig. 7).

DISCUSSION

We found that zebra mussel-invaded lakes are not randomly located across the landscape, but are aggregated at spatial extents <80 km in Belarus and <50 km in the United States. In addition, invaded lakes are segregated at spatial extents >120 km in Belarus and are tending toward segregation at scales >200 km in the United States. This type of aggregation and segregation pattern suggests that neither zebra mussel invasion has taken place solely as a radiating, diffusion front, but has occurred as a series of long-distance dispersal events that subsequently led to local spread. Thus, as previously suggested (Johnson and Padilla 1996, Buchan and Padilla 1999), reaction-diffusion models are not always appropriate for predicting the geographic spread of aquatic invaders across heterogeneous landscapes.

Although processes responsible for aggregation and segregation patterns cannot be definitively inferred from spatial pattern analysis, possible scenarios for the invasion process can be compared to the observed spatial patterns. Segregation at extents >120 km is consistent with the idea of long-distance overland dispersal

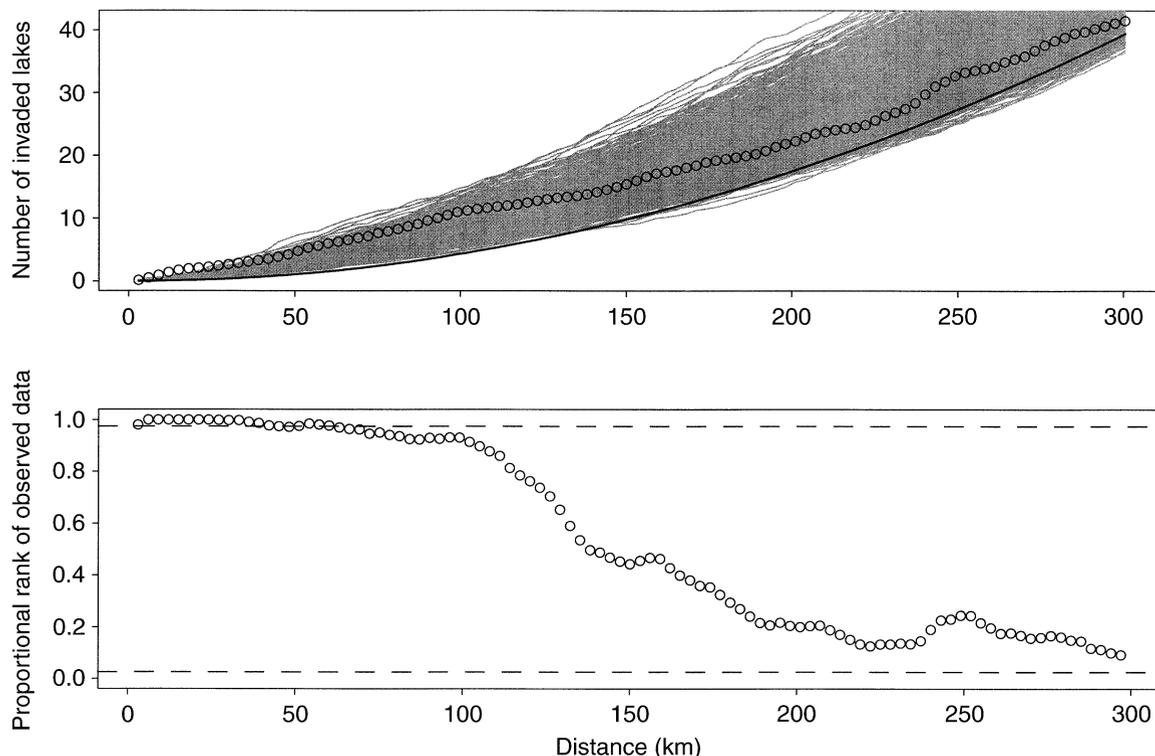


FIG. 5. Top panel: Circles show the observed average number of zebra mussel-invaded lakes found at any given distance from any other invaded lake within the U.S. study region, based on Ripley's K statistic [number of invaded lakes = $\lambda K(t)$] for 60 invaded lakes. Gray lines show the expected range of $\lambda K(t)$ based on 1000 Monte Carlo simulations, using random samples (without replacement) of 60 lakes selected from 1756 suitable lakes within the study area. Bottom panel: proportional rank of observed number of invaded lakes by comparison with 1000 Monte Carlo simulations. Dashed horizontal lines show ranks at which values for observed data are $>97.5\%$ or $<2.5\%$ of values for simulated lake distributions.

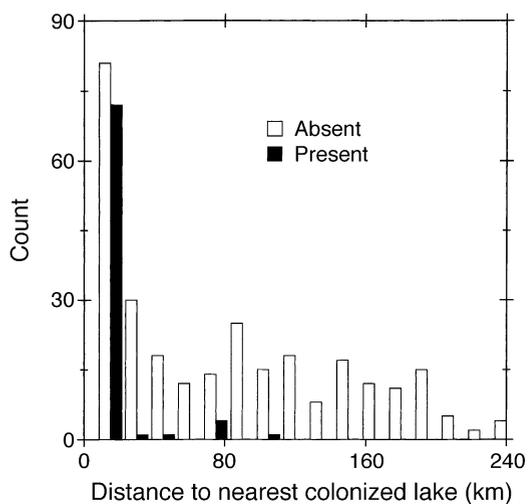


FIG. 6. Distance to nearest zebra mussel-invaded lake for all lakes within the Belarus study region. Number of invaded lakes within 15-km distance increments are shown for lakes in which zebra mussels were either present or absent.

events from source populations (Buchan and Padilla 1999). These apparently rare events could establish nascent foci from which local dispersal occurs, due to short-distance overland dispersal and/or waterway dispersal of larvae or adults (Horvath et al. 1996, Horvath and Lamberti 1997; also Fig. 6).

Our results have several important management implications. First, our results support other studies indicating that dispersal is the primary factor limiting zebra mussel expansion into novel environments (Allen and Ramcharan 2001, Bossenbroek et al. 2001). Second, the spatial pattern analysis indicates that extensive lake regions with suitable pH and Ca remain uncolonized in both Belarus and North America. Third, our findings suggest that waterway connections to nearby colonized lakes greatly enhance the likelihood of invasion. Taken as a whole, these results provide guidance regarding the potential for a particular lake to become invaded by zebra mussels, given its spatial proximity and connectedness to other invaded lakes. This information can be used to target programs designed to interrupt zebra mussel dispersal. In general, the analytical methods outlined in this study provide a way to evaluate the spatial extent of similar dispersal processes for other nuisance invaders.

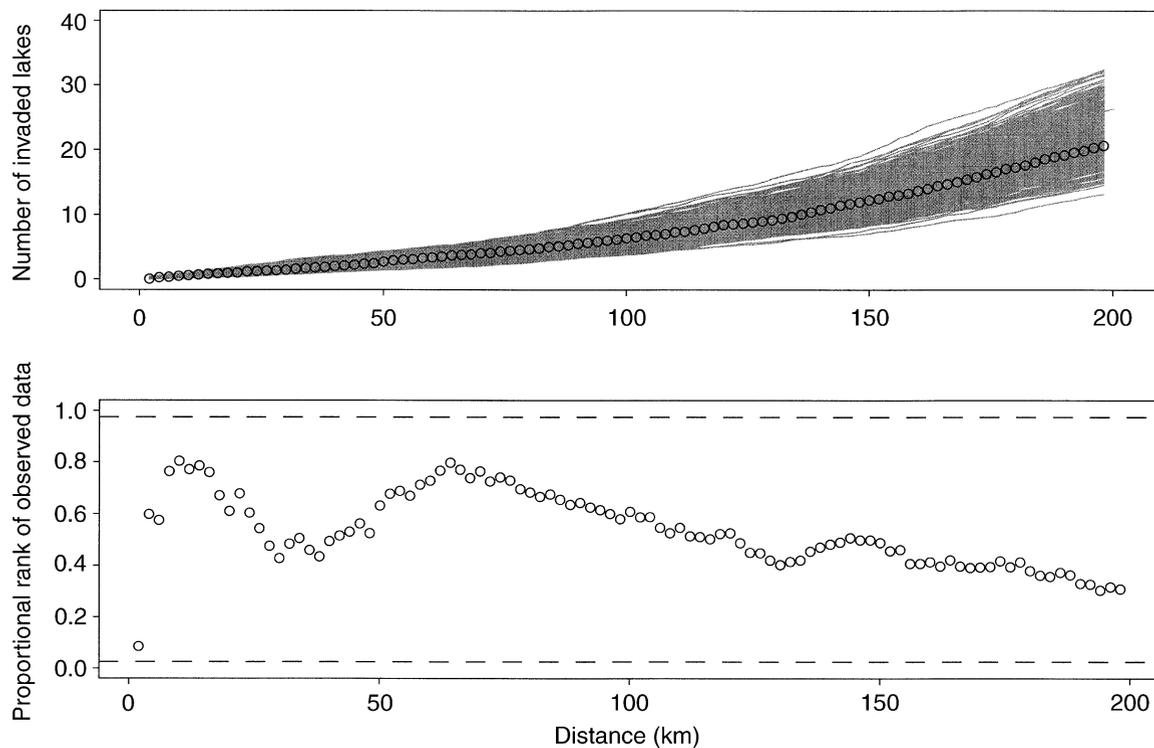


FIG. 7. Circles show the observed average number of zebra mussel-invaded lakes found at a given distance from any other invaded lake within the Belarus study region, based on a one-dimensional version of Ripley's K statistic, using linear distances between connected lakes (396 of 522 lakes). Gray lines show the expected range of $K(t)$ based on 1000 Monte Carlo simulations, using random samples (without replacement) of 82 lakes selected from 396 connected lakes. Bottom panel: proportional rank of observed number of invaded lakes by comparison with 1000 Monte Carlo simulations. Dashed horizontal lines show ranks at which values for observed data are $>97.5\%$ or $<2.5\%$ of values for simulated lake distributions.

Previous applications of Ripley's K to spatial pattern analysis in ecology have compared observed distribution patterns to random patterns of simulated distributions, using all possible locations within the landscape as available habitat (Haase 1995, Coomes et al. 1999). Such applications have thereby implicitly assumed the availability of homogeneous suitable habitat, or suitable habitat gradients. Our analysis clearly demonstrates that inland lakes, the principal potential habitat for zebra mussels, are not randomly distributed across the landscape but are instead aggregated at a broad range of spatial scales. Lake-dwelling aquatic organisms colonize aggregated and discrete habitats that, due to their disjunct nature, confound processes responsible for the appearance of species distribution gradients (e.g., particularly dispersal). Thus we invoked an alternative model, in which we constrained our comparison of observed vs. random distributions to locations within the landscape that satisfy basic zebra mussel habitat requirements. Similar comparisons could be implemented for other organisms in which spatial patterns of distribution are clearly limited by underlying habitat factors. This analysis also avoids the error of mistakenly identifying spatial patterns of distribution that reflect availability of suitable habitat

(e.g., lakes; Fig. 3), rather than some other biotic mechanism.

The similar extent of aggregation of invaded lakes from two distinctly different landscapes is unexpected, given that the timing of the Belarus and U.S. invasions and potential vectors of dispersal are markedly different. Regions without invaded lakes can be distinguished within both landscapes, and our analyses demonstrate that these areas do not simply indicate regions of lakes without suitable pH and calcium conditions. Given the zebra mussel's reputation as an invasive species (Ludyanskiy et al. 1993), it is surprising that this organism has not colonized all such suitable lake habitats in Belarus, and the segregated distribution pattern at large spatial scales (>120 km) shows that smaller scale aggregations have not coalesced over the 200-yr period of invasion. Instead, this result suggests that dispersal limitations have prevented suitable lakes from becoming invaded, and supports previous suggestions that nonhuman-mediated zebra mussel vectors provide a very limited ability for range expansions to occur over time scales on the order of decades and centuries (Johnson and Carlton 1996). Although a significant pattern of segregation was not seen among North American lakes, we suggest that our data indicate a tendency

toward segregation at 200–300 km distances (Fig. 5). Future, updated spatial analyses of North American invaded lake distributions can be used to evaluate the significance of this pattern and contrast the North American spread of zebra mussels to European patterns of spread.

The observed spatial patterns reported in this study could have been produced by limiting habitat conditions other than pH and Ca, despite the fact that pH and Ca have been previously used to identify lakes suitable for zebra mussel colonization (Neary and Leach 1992, Ramcharan et al. 1992). In this event, our analysis has identified spatial pattern in underlying lake habitat conditions that has not been recognized in previous studies.

Habitat corridors have recently received attention as potential avenues for the spread of aquatic invasive species (Hrabik and Magnuson 1999), including zebra mussels (Neary and Leach 1992, Horvath et al. 1996). Our Belarus one-dimensional analysis evaluated spatial patterns along a waterway network, which effectively serves as a network of habitat corridors throughout the aquatic landscape. Several aspects of our Belarus analysis show that, within the waterway network, the relative proximity of a lake to a single invaded lake influences the likelihood of invasion. First, invaded lakes were more likely to be located within the river network (i.e., were not isolated) than would be expected by chance. Second, 88% of invaded lakes were located within 15 km of another invaded lake. Third, more lakes were observed to be invaded, at distances to the nearest invaded lake ranging from 7 to 16 km, than in 95% of Monte Carlo simulations. However, the likelihood of invasion was not enhanced by proximity to an aggregation of invaded lakes, which was the measure evaluated using the one-dimensional Ripley's K analysis. The result of this one-dimensional analysis therefore shows no spatial aggregation along the waterway network, which contrasts with the strong aggregation observed throughout the two-dimensional landscape. This suggests that the network (one-dimensional) and areal (two-dimensional) results were produced by different dispersal processes, though we have not thoroughly explored the extent to which pairs of connected infested lakes could be responsible for regional aggregations of infested lakes. Our results support observations by Horvath et al. (1996) that invaded lakes serve as sources for small stream (<30 m wide) zebra mussel populations at distances up to 10 km.

Ripley's K has been most frequently used in ecological studies to evaluate spatial patterns in plant communities (Haase 1995, Coomes et al. 1999), and this technique has rarely been applied to evaluate animal distributions (for an exception, see O'Driscoll 1998). Data for plant distribution studies are usually conducted using rectangular sampling units. Several Ripley's K edge correction methods have been developed to deal with the difficulty of estimating the number of

neighbor points in the vicinity of a sample point near the edge of a sampling area (Haase 1995), and these methods assume that the sampling unit is rectangular. The S -Plus function used to estimate Ripley's K in our study also assumed rectangular sampling areas (Venables and Ripley 1997), although both the Belarus and U.S. study areas were not rectangular. However, since our analysis evaluated the spatial pattern for a specific set of points among which all randomizations were conducted, traditional concerns with edge effects, e.g., situations where spatial pattern is being evaluated over all possible locations within a two-dimensional landscape (Haase 1995), should have limited influence on our results. Furthermore, the correspondence of our results with the visual appearance of our lake data indicate that these results are robust. Still, the application of Ripley's K to nonrectangular sample areas is a subject that merits further investigation.

Only one previous application of Ripley's K has attempted to use this statistic in a one-dimensional analysis (O'Driscoll 1998). For our analysis, network distances >400 km were excluded, and no edge correction was applied to Ripley's K estimates. Some bias is inherent in our one-dimensional estimates of $K(t)$ because some individuals may lie at distances < t from the ends of the river network, which extends beyond the study area into neighboring countries. This bias will increase as t increases (Ripley 1981). Since the lack of an edge correction influences all inter-lake comparisons greater than half the maximum distance calculated (400 km), we only evaluated one-dimensional distances shorter than 200 km.

Lake-dwelling organisms colonize discrete habitats. Such distributions are common, even within terrestrial landscapes, and our method of spatial point pattern analysis can be applied to address other ecological issues in biogeography and conservation biology (Nekola and Kraft 2002). The ability to expand analyses of spatial patterns of species distribution from the realm of plant ecology to studies of invasive species, or biogeographical studies, in general, is a key lesson from our effort. Spatial point pattern analyses have been widely applied by ecologists to evaluate plant species distributions and competition (Haase 1995, Coomes et al. 1999). Real and McElhany (1996) also evaluated spatial pattern in plant disease given an underlying plant distribution spatial pattern, yet such techniques have been rarely applied to animal populations (Davis et al. 2000). Processes responsible for producing spatial patterns of distribution include the initial distribution of colonists, dispersal ability, history of disturbance, the underlying heterogeneity of the abiotic environment, extinction of isolated populations, and ecological interactions between species. We hope that our study stimulates broader applications of such analyses in the realm of invasive species biology and biogeography.

The most important result of our study is to have demonstrated the use of spatial pattern analysis of zebra

mussel distributions as a method to distinguish key dispersal characteristics of this nuisance invader. Since experimental transplants of such invasive species are often illegal and usually unethical, spatial pattern analysis provides a general approach for evaluating dispersal limitations of such organisms. Although we cannot conduct the types of experimental manipulations that plant ecologists have often used to more conclusively determine mechanisms responsible for observed species distribution patterns, simulation models can be developed to evaluate likely dispersal processes (Bossonbroek et al. 2001). These models can also be evaluated according to the extent to which they produce distribution patterns that correspond to observed spatial patterns of aggregation and segregation.

We have shown that short-distance overland and/or waterway dispersal events are primarily responsible for inland lake colonization by zebra mussels, suggesting that zebra mussel dispersal prevention efforts can be most productively focused in regions with colonized lakes. Long-distance dispersal certainly plays a role in establishing segregated regions with multiple lake zebra mussel populations, but such events are rare by comparison with new lake colonization events that occur within short distances of colonized lakes. This contrast in colonization between rare, long-distance events and more frequent short-distance events effectively calls for two types of dispersal prevention efforts, operating at different spatial and temporal scales. Most significantly, we have demonstrated that the zebra mussel invasion of inland lakes has not saturated either the Belarus or North American lake landscapes, thereby justifying the continuation of dispersal prevention efforts potentially discouraged by public or published perceptions that zebra mussels will colonize all suitable habitats within a decade of their North American discovery (see Ludyanskiy et al. 1993).

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