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RESEARCH LETTER

Predicting the spread of zebra mussels (*Dreissena polymorpha*) to inland waters using boater movement patterns

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Abstract. Exotic species introductions are one of the major threats to biodiversity worldwide. Exotic species can be conspicuous, and their spread is often correlated with human activity. The rapidity of the *Dreissena* invasion in North America and its economic impacts provide a unique opportunity to study the invasion process. Trailered boating traffic may be the most important vector for the transport of zebra mussels among unconnected bodies of water. Therefore, knowing the activity patterns of boaters should allow us to predict the explicit regional-scale pattern of geographic spread. We used the results of a large boating survey conducted by the Wisconsin Department of Natural Resources to estimate the volume of boating traffic between waters known to contain zebra mussels (Great Lakes) and inland Wisconsin waterbodies. We found, (1) the most probable source of zebra mussels entering Wisconsin is Lake Michigan, (2) the most probable destinations are in eastern Wisconsin, and (3) geographic proximity to a source population and overall boater use are poor predictors of probability of invasion. Attention to human activity patterns may help predict the spread of other invading taxa.

Key words. Aquatic ecology, *Dreissena*, exotic species, geographic spread, invasion biology.

INTRODUCTION

Exotic species invasions are unplanned ecological experiments that can help us understand natural ecosystems. Historically, many such invasions received little or only superficial attention from ecologists during the process of invasion, and studies were hampered by difficulties of observing and quantifying the progress of the invasion. This has not been the case with the recent invasion of North America by zebra mussels (*Dreissena polymorpha* Pallas; Driessenidae). In anticipation of large ecosystem and economic impacts, attention has focused on this new invader. Documenting the spread of zebra mussels has been aided by the conspicuousness of this invader, and the detail with which the zebra mussel has been studied will make it possible to establish and measure the factors likely to be important in its spread.

The zebra mussel and the quagga mussel (*D. bugensis* Andrusov) were introduced into the Great Lakes through shipping traffic from Europe in the mid-1980s (Carlton, 1992). As of spring 1996, the zebra mussel has been reported from all of the Great Lakes, the Mississippi River, Ohio River, Illinois River, Hudson River and the St Lawrence. However, the quagga has only been confirmed from Lake Erie, Lake Ontario and portions of the St Lawrence. There are two (unconfirmed) sightings this spring from one location in Lake Huron and River Mile 289 (St Louis) of the Mississippi. Dreissenids are among the more formidable recent exotic invaders. They possess a suite of ecological and life history characteristics that are unusual for freshwater benthic species, including high rates of filter feeding, high fecundity, dispersible planktonic larvae, and attachment to hard substrates. *Dreissena* are economically important because they overgrow and clog underwater structures such as water intakes and turbines for power plants and municipalities (Nalepa & Schloesser, 1993 and references therein). *Dreissena* can colonize lakes with a wide range of physical and chemical

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properties (Ramcharan, Padilla & Dodson, 1992), and can have large direct and indirect effects due to their feeding and growth habits (Nalepa & Schloesser, 1993; Ludyanskiy, McDonald & MacNeill, 1993; Tucker *et al.*, 1993).

Zebra mussels have become the first invader into North America to foul municipal water systems and power plant plumbing; the cost of repair and remediation in the state of Wisconsin (USA) was estimated in 1994 at $4 million per year (C. Kraft, pers. comm.). In consequence of the large economic and ecological impacts of zebra mussels, most research has focused on the biology and impact of dreissenids, on the assumption that the invasion process itself would be brief. Although zebra mussels have spread rapidly through navigable waters, to date they have invaded few inland lakes.

Our goal was to use human behaviour to predict the spatial and temporal pattern of the geographic spread of dreissenids and other exotic taxa. Although aquatic taxa may be spread by a variety of mechanisms including migration of waterfowl, wind, surface water flow, and non-boating related human activity (Johnstone, Coffey & Howard-Williams, 1985), evidence suggests that recreational boaters are the dominant vectors of zebra mussel spread among inland, hydrologically isolated lakes (Carlton, 1992; Johnson & Carlton, 1996; Johnson & Padilla, 1996). We determined patterns of boater movement within the state of Wisconsin using results of a survey, conducted by The Wisconsin Department of Natural Resources (WI-DNR) (Penaloza, 1991). Based on these movement patterns and zebra mussel habitat requirements we predict which of Wisconsin's 15,000 lakes are the most probable sites of invasion from current dreissenid sources. We can use the ongoing invasion of dreissenids to test the importance of the role that humans play as vectors of exotic species on regional, as well as continental scales.

MATERIALS AND METHODS

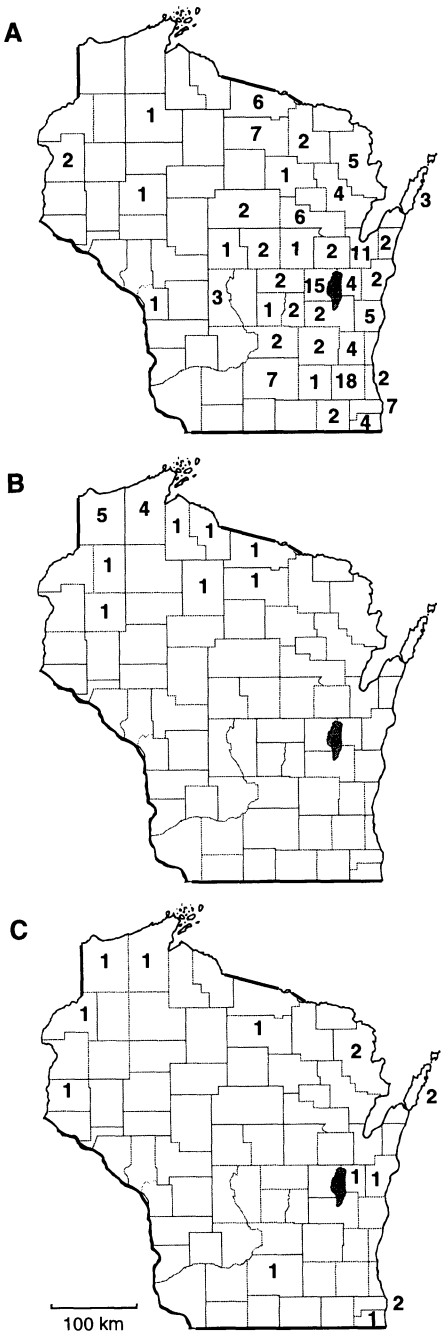
In 1989–1990, the WI-DNR conducted a randomized survey of boat use for the 482,336 boats licensed in Wisconsin. From each adjacent state (Illinois, Iowa, and Minnesota), an additional 5600 registered boaters were sampled from counties adjacent to Wisconsin and from the Chicago area, for a total sample size of 505,880. Survey data were collected by mailing a questionnaire to boat owners during twelve 2-week periods from May to October 1989 and two 2-week periods during April 1990. These data were collectively assumed to represent traffic during a single boating season. For each 2-week survey period, 4200 boat owners were selected at random (without replacement) from the state registration lists. The DNR estimated that each response to the survey represented approximately 243 trailered boating events (total sample/number of trailered vehicles), which could be used as a weighting factor to estimate the true amount of traffic.

Average survey response rate was 74%. By calculation, WI-DNR estimates that the survey results represented 6.2 million boat-days of activity in Wisconsin. 89% of the activity was on inland lakes or rivers (6,177,871 boater days), 9% boated on Lake Superior or Lake Michigan (620,860 boater days), and 2% boated on both inland waters and a Great Lake (138,750 boater days) (Penaloza, 1991).

We limited our analysis to trailered boats, which are most likely to transport zebra mussels (98.6% of registered boats in the survey). We used data from survey questions that asked: (1) whether the boat was used during the preceding two weeks; (2) whether the boat was used in a Great Lake; (3) whether the boat was used in inland waters (i.e. other than Lake Michigan or Lake Superior); (4) in what inland counties the boat was used; (5) in what county containing Great Lake shoreline the boat was used; and (6) what single inland water body was most used. The answer to question (5) was used to identify which Great Lake was used. One hundred and twenty-three citations reported using both a Great Lake and an inland waterbody, and an additional forty-one citations reported use of a Great Lake and an inland county without naming a specific inland waterbody. To determine average distance traveled from a Great Lake to an inland waterbody, we measured the straight-line distance between the midpoint of the Great Lake county shoreline and approximate centroid of the corresponding inland waterbody for each record.

RESULTS

Of the respondents using a Great Lake, 81.7% reported using Lake Michigan, 8.8% reported using Lake Superior, and 9.5% did not report the specific Great Lake they used. The majority of Great Lake to inland waterbody boater connections were for waterbodies within counties bordering a Great Lake, especially Lake Michigan (Fig. 1). In the entire survey, boaters reported using more than 1162 inland waterbodies. Of 986 waterbodies within the counties visited by boaters who



used a Great Lake, only 8.4% (80 waterbodies) received boater traffic from a Great Lake user.

Waterbodies differed in how frequently they were used by boaters also using a Great Lake (Table 1). Only twenty of the eighty-three waterbodies identified as having boater links to a Great Lake were mentioned more than once in the survey. Of those twenty, almost half were in counties not adjacent to a Great Lake (Table 1, Fig. 2). Most boater traffic from a Great Lake moved only a short distance, to an inland waterbody in a county adjacent to a Great Lake. The distances between the most cited inland waterbodies and the centroid of the nearest Great Lake (estimated as the middle point of the shoreline in the cited county) averaged 118 km (SE = 87 km). The median distance was 91 km, and only 25% exceeded 175 km. Although the majority of the sixty waterbodies listed with a single boater connection to a Great Lake were concentrated in Eastern Wisconsin, many were found throughout the state (Fig. 1).

In the entire survey, the Mississippi River was the second most cited inland waterbody, receiving 4.8% of all citations. Of the boaters that used the Mississippi and visited another waterbody, only 1.8% used a waterbody not directly connected to the Mississippi. Only 2.8% (of 397) of Mississippi River boaters reported using a county not bordering the Mississippi.

DISCUSSION

Exotic species invasions can be viewed as special cases of range expansion (Hengeveld, 1992). However, exotic species are often both ecologically and phyletically very different from native taxa, and may establish and spread due to different life history characteristics or by exploiting resources differently from native organisms. The results of invasions can cause drastic changes in ecosystems (Hengeveld, 1989).

A variety of mathematical models, incorporating basic processes like advection, diffusion, and population growth, have been devised to explain or predict aspects of the invasion process (Skellam, 1951; Okubo, 1980;

Fig. 1. Numbers represent the number of citations of boaters using a Great Lake (A. Lake Michigan, B. Lake Superior, C. did not mention the name of the Great Lake), and a waterbody in that county. Of the 185 boaters reported using a Great Lake and an inland waterbody, most used waterbodies in counties close to, but not bordering, a Great Lake.

Table 1. Inland waterbodies and counties with the largest number of direct boater connections to a Great Lake, the greatest overall boater use and lakes which zebra mussels have invaded. Total boater use reflects all citations listed in the survey. Numbers next to waterbody name are ranks of Great Lake to inland waterbody use, and identify geographic location of waterbodies in Fig. 2.

Inland waterbody	Connections from a Great Lake	Total boater use	Zebra mussels
1. Lake Winnebago	14	363	
2. Fox River	7	112	
3. Wisconsin River	7	482	
4. Lake Mendota	6	202	
5. Pewaukee Lake	6	128	
6. Shawano Lake	5	109	
11. Elkhart Lake	2	20	Adults
16. Okauchee Lake	2	69	Veligers
17. Powers Lake	2	25	Veligers
21. Beulah Lake	1	48	Veligers
22. Silver Lake	1	28	Adults
23. Lake Geneva	1	206	Adults

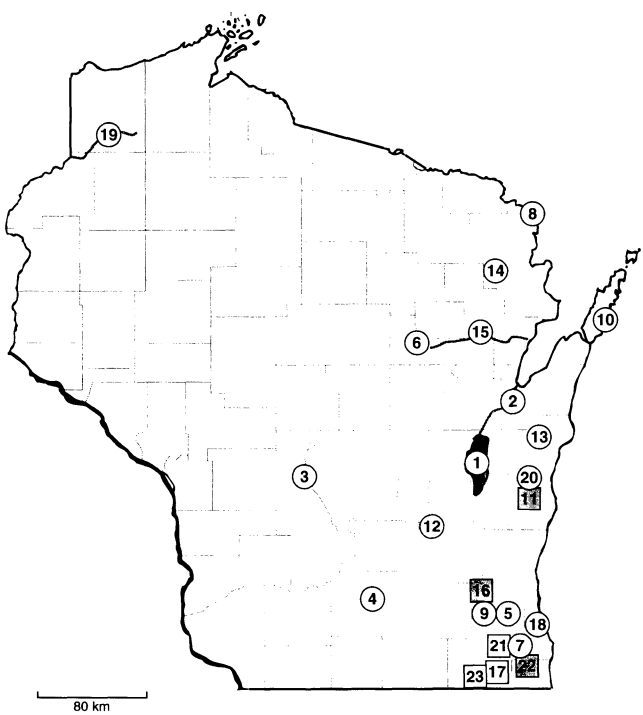


Fig. 2. Map of Wisconsin showing the locations of inland waterbodies that were most frequently cited by boaters who also reported use of a Great Lake. Numbers reflect the relative rank order of waterbodies with regard to the number of boaters using that waterbody and a Great Lake. All connections, except the St Croix River (19) are between Lake Michigan and an inland waterbody. Open circles have not been invaded. Shaded squares were invaded in 1994, and open squares were invaded in 1995.

Vandenbosch, Metz & Dickmann, 1990; Mollison, 1991; Cantrell & Cosner, 1991; Hanski, 1994). Although these models can be successful at describing continental wide range expansion (Okubo, 1980; Hengeveld, 1989, 1993; Renshaw, 1991; Liebhold, Halverson & Elmes, 1992), they do not perform well when geographical variation and patterns of dispersal vector movement are complex, especially at regional spatial scales (Johnson & Padilla, 1996). Unfortunately, these are the conditions under which managers and conservation biologists usually operate, and must anticipate or act to control the spread of an exotic.

The Laurentian Great Lakes region is an important example of this problem. The Great Lakes have been a major focal point for the introduction and subsequent spread of aquatic exotics into North America. At least 139 species, including fishes, molluscs, crustaceans, vascular plants, and algae have successfully invaded since the early 1800s through a variety of mechanisms, particularly through the activities of humans: thirteen species have had large ecological and economic impacts (Mills *et al.*, 1993).

The pattern of geographic spread of an invading species will depend on the overlap between the movement of dispersal propagules and suitable habitat (Ramcharan *et al.*, 1992; Koutnik & Padilla, 1994; Johnson & Padilla, 1996). However, just knowing that propagules have the potential to access suitable habitats is insufficient to predict patterns of spread. Attempts have been made to predict which waterbodies in North America have suitable conditions to support zebra mussel populations (Ramcharan *et al.*, 1992; Koutnik & Padilla, 1994) or potential access to lakes which can support zebra mussels (Neary & Leach, 1992), but, predicting the actual pattern of invasion has not been possible. Zebra mussels appear to spread quickly through connected, navigable waters, but less quickly across land. Human behaviour plays an important role in determining the pattern of invasion of aquatic taxa across the landscape (Johnstone *et al.*, 1985). As recreational trailered boat traffic is likely to be the main avenue of spread, the patterns of lake use and choices of waterbody visited by boaters will affect which waterbodies are most likely to be invaded. Preferences for timing and location of boating are affected by a variety of factors, only some of which are correlated with other factors traditionally considered in the spread of invading species (e.g. distance from a road or source, Neary & Leach, 1992). Although there are a large number of registered boaters in Wisconsin, few use both a Great Lake and an inland waterbody within a time scale appropriate for the transport of live mussels (2 weeks). This may be part of the explanation for the slow initial invasion of inland waterbodies. Although zebra mussels have been in Lake Michigan since 1989, inland lakes of Wisconsin were only invaded in 1994. Adult zebra mussels were found in Okauchee Lake, Elkhart Lake, Silver Lake and Racine Quarry in the late summer and early fall of 1994. In the summer of 1995 several lakes were targeted for monitoring of zebra mussel invasion, based in part on our recommendations of lakes most likely to be invaded because of high boater visitation from Lake Michigan (C. Kraft, personal communication). Veligers were found in two of those lakes, Powers and Beulah, and by the fall of 1995 adults were found in Lake Geneva (Fig. 2).

Although not all lakes with zebra mussels are in counties on the shore of Lake Michigan, all of these waterbodies were identified in the DNR survey as having boater connections to Lake Michigan (Table 1). The only exception was Racine Quarry which is not accessible by boats, but is known to have a large volume of recreational divers. The lakes with zebra mussels all rank in the top 80 of most-used lakes by boaters, and Lake Geneva is the 4th most used lake in Wisconsin.

Although Lake Michigan, Lake Superior and the Mississippi River could act as sources of zebra mussels for inland lakes, Lake Michigan is most important because it has a large source population and a large volume of trailered boater use with the broadest geographic distribution. Other research (Ramcharan *et al.*, 1992) has suggested that Lake Superior will not support viable populations of zebra mussels because of low calcium concentrations, and is therefore an unlikely source of invading mussels. Indeed, after initial detection in Duluth Harbor, few zebra mussels have been found in Lake Superior. Although a large number of boaters use the Mississippi, they tend to travel locally, mainly visiting flowages connected to the river. Therefore, although zebra mussels are in the Mississippi, the river is also unlikely to be an important source for the spread to inland lakes.

The timing and pattern of spread of zebra mussels will depend on several variables, including dispersal and survival to form new populations which can act as sources for future spread. Of the lakes with the highest potential to receive zebra mussels through trailered boating (>1 record of Great Lake to inland lake use), only Harpt Lake has conditions which will not support zebra mussels (Koutnik & Padilla, 1994). Lakes with many boater connections to Lake Michigan and high overall boater use (Table 1) are likely to be the most

important sources for the spread of zebra mussels to other inland waterbodies. Of the lakes with zebra mussels, Lake Geneva is the second most used lake in the state, and the fourth most used waterbody with an estimated 50,000 boaters per year. Therefore, as soon as zebra mussel populations are large (3–6 years from initial invasion; A. Karatayev, personal communication), Lake Geneva will be the most important new source for the spread of zebra mussels. Other lakes with zebra mussels also have high use, ranking in the top 8% of all lakes in the survey (Table 1), and will soon become sources for the spread of zebra mussels. Lakes with high overall volume of boat use and Great Lake connections (Table 1) are likely to become the most important sources for inland invasion. However, overall boater use is not necessarily a good predictor of initial invasion. The nineteen waterbodies cited more than once as being visited from a Great Lake ranked 3–460th in overall use. Therefore, using overall boat use alone would overestimate the probability of initial invasion by zebra mussels.

Our study represents the first attempt to predict the specific pattern of spread among waterbodies of an aquatic invading species via human activity on a regional scale. Koutnik & Padilla (1994) found that many lakes, especially in southeast Wisconsin are suitable for zebra mussels, however many more lakes will support zebra mussel growth than will receive propagules. Therefore, knowledge of the spatial patterns of dispersal vector movement (e.g. boaters) increases our ability to predict both spatial and temporal patterns of invasion. As humans are the major vector for the spread of exotic aquatic species, knowing patterns of human movement is most important for predicting invasion patterns. Unlike other dispersal vectors, humans can be sampled in large numbers and asked about their behavior. The Wisconsin boater survey has given us a unique opportunity to anticipate the invasion pattern of zebra mussels, and target specific waterbodies for monitoring and management to prevent future spread.

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