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OVERLAND DISPERSAL OF AQUATIC INVASIVE SPECIES: A RISK ASSESSMENT OF TRANSIENT RECREATIONAL BOATING

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Abstract. Predictions of the geographic spread of introduced species are often limited by a lack of data on their mechanisms of dispersal. We interviewed boaters and inspected boating equipment at public boat launches on Lake St. Clair (Michigan, USA) to assess the potential for the zebra mussel, an invasive bivalve, to be dispersed overland to inland waters by transient recreational boating activities. Several mechanisms associated with recreational boating were found to be capable of transporting either larval or adult life stages. Larvae were found in all forms of water carried by boats (i.e., in live wells, bilges, bait buckets, and engines) but were estimated to be 40–100× more abundant in live wells than other locations. Dilution in receiving waters should, however, greatly reduce the risk of establishing new populations by the introduction of larvae. Contrary to common belief, mussel dispersal from these boat launches did not occur by direct attachment to transient boats. Rather, adult and juvenile mussels were transported primarily on macrophytes entangled on boat trailers and, less frequently, on anchors (5.3% and 0.9% of departing boats, respectively). Combining these data with estimates of survival in air and reported boater destinations, we predict that a maximum of 0.12% of the trailered boats departing these access sites delivered live adult mussels to inland waters solely by transport on entangled macrophytes. While this is a small probability, high levels of vector activity resulted in a prediction of a total of 170 dispersal events to inland waters within the summer season from the primary boat launch studied. Many other potential vectors remain to be assessed, but the dispersal of zebra mussels by trailered boats, particularly by ''piggybacking'' on macrophytes entangled on the trailers, must be controlled in order to limit further range expansion of the zebra mussel within North America.

Key words: aquatic weeds; biological invasions; Dreissena polymorpha; *exotic species; fouling; geographic spread; nonindigenous; zebra mussel.*

INTRODUCTION

After the intercontinental transport and introduction of a species by some human-mediated vector, further regional spread can occur through the action of additional mechanisms including both natural and human-mediated vectors. Ultimately, it is this secondary spread that will determine the scale of any ecological and economic impact of a biological invasion (Lodge et al. 1998). While it would be best to prevent initial introductions in the first place (e.g., through agricultural inspections or ballast water management), it is still critical to prevent further spread after initial establishment. Even efforts that only slow spread can provide the time needed to assess potential impacts and, if necessary, develop additional control strategies. Thus knowledge of the mechanisms of secondary dispersal of an introduced species can provide a basis for predicting its further spread (e.g., Ludwig and Leitch 1996, Schneider et al. 1998), and for effectively allocating resources towards preventing or slowing the spread.

Freshwater habitats offer a particularly tractable system for investigating the spread of exotic species, in that the habitats (e.g., lakes, streams) have well-defined borders and connections (Johnson and Padilla 1996). Dispersal between hydrographically isolated waters requires specific adaptations for overland transport and survival in inhospitable terrestrial environments or further assistance from human vectors. This phenomenon is well illustrated by the invasion of North America by the Eurasian zebra mussel (*Dreissena polymorpha*), a freshwater bivalve with many of the attributes of marine mussels (e.g., attachment by byssal threads to hard surfaces, a planktotrophic larval stage that spends 2–5 wk feeding in the water column before settling to the bottom). Since its introduction to North America in the mid-1980s, the zebra mussel has spread rapidly across a large portion of the continent (O'Neill and Dextrase 1994, Johnson and Carlton 1996). Most of this spread has been confined to interconnected waterways, aided by the natural downstream transport of planktonic larvae (Horvath et al. 1996); upstream spread has also occurred, most likely through the movement of adult stages fixed to the bottoms of ships or barges (Keevin

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et al. 1992). However, saltatory dispersal to isolated inland waters has resulted in the establishment of zebra mussel populations in a number of inland lakes in the regions surrounding the Great Lakes (Kraft and Johnson 2000). An understanding of the dispersal mechanisms available to this nuisance species is essential for predicting the rate and direction of its spread, as well as for implementing effective control strategies.

While overland dispersal of the zebra mussel can result from the actions of a wide variety of potential natural and human-mediated mechanisms (Carlton 1993), transient recreational boating is commonly perceived as the primary means by which the species is transported between unconnected bodies of water. This perception exists not only among researchers (e.g., Griffiths et al. 1991, Neary and Leach 1992, Carlton 1993, Schneider et al. 1998, Buchan and Padilla 1999), but also policy makers (OMNR 1991, Tyrus et al. 1994), outreach agencies (e.g., Kelch 1992) and the general public. As a result, costly boater education and boat cleaning programs have been implemented to prevent infestations and slow the spread. Transient boating activity has been invoked to explain distribution patterns of zooplankton (e.g., Yan et al. 1992, Havel et al. 1995), and the initial zebra mussel invasions of inland waterbodies in Wisconsin occurred almost entirely in those waterbodies used by boaters who also used waters with established populations of zebra mussels (Padilla et al. 1996). Recreational boating activity has previously been demonstrated as a vector for the unintentional overland transport of exotic aquatic macrophytes (Scales and Bryan 1979, Dove and Malcolm 1980, Dove and Wallis 1981, Dove and Taylor 1982, Johnstone et al. 1985, Joyce 1992), but only recently has its role in the transport of aquatic animals begun to be assessed (Johnson and Carlton 1996, Havel and Stelzleni-Schwent 2001). Thus, although intuitively appealing, the putative ability of recreational boats to disperse zebra mussels remains largely unexamined, and the mechanistic basis of any transport is known only from anecdotal observations (e.g., Griffiths et al. 1991, Janik 2001; but see Johnson and Carlton 1996).

The impressive biofouling ability of the zebra mussel has led to visions of boats departing infested waters with hulls encrusted with zebra mussels—certainly a worst-case scenario. However, in reality, there is a suite of mechanisms by which recreational boats might transport zebra mussels, including other mechanisms involving the transport of adults (e.g., on anchors or on entangled macrophytes) or larvae (i.e., in locations where water might accumulate such as live wells, bilges, bait buckets, and engine cooling systems).

The objectives of this study were to (1) determine the extent to which zebra mussels are transported by transient recreational boating; (2) identify precisely the mechanisms involved and evaluate their relative probability of transporting zebra mussels between unconnected bodies of water; and (3) illustrate a simple modeling approach for use in the risk assessment of these various mechanisms.

METHODS

To identify and estimate the relative importance of the mechanisms by which zebra mussels could be transported from infested waters, boaters were interviewed and boats and trailers were inspected and sampled at three public boat launches on the northwestern shore of Lake St. Clair (Michigan, USA), the body of water where zebra mussels were first reported in North America (Hebert et al. 1989). The two principal sites were the boat launches at the Ensign Public Access Site and the Metrobeach Public Access Site, with more limited sampling at the Selfridge Public Access Site. A total of 920 interviews were conducted on 24 different dates from 20 June to 4 September 1992: 617 at the Ensign launch on 21 dates, 280 at the Metrobeach launch on 11 dates, and 23 interviews at the Selfridge launch on one date. Of all the interviews, 99% were conducted during weekend periods (Friday noon until Sunday evening) and holidays and were usually conducted as boaters departed the access site (77%), a moment when they were more receptive to being interviewed. On any given date, interviews were usually conducted for a block of 5–7 h between 0900 and 2100 (local time), as initial observations indicated that boaters rarely departed before then. All departing boaters were solicited for interviews until the rate of departures exceeded the capacity of the interviewer, at which time the most recently retrieved boat was selected for the next interview. If no boaters were departing, then interviews were solicited from arriving boaters. Boaters rarely refused to be interviewed ($<3\%$), and most refusals were from boaters interviewed before. The interviews, which were part of a larger study aimed at documenting the habits and demography of boaters using waters infested by the zebra mussel, consisted of 25–30 questions and lasted an average of 5–10 min. Questions relevant to this study pertained to the duration of the outing, activities and devices associated with fishing, the use of anchors, and the anticipated time and location of the boat's next use (Table 1). The interview was modified over time as additional mechanisms of transport became apparent. These modifications and incomplete interviews produced sample sizes < 920 for certain types of information. During the summer, interviews were conducted by three people who rotated among these and other launches.

A visual inspection lasting 30–60 s was made of the boat exterior for any zebra mussels attached to the hull or motor, with particular attention paid to irregularities where zebra mussels were first likely to accumulate. During the course of the study, it became apparent that a previously unrecognized mechanism for the overland transport of zebra mussels existed: the transport of mussels attached to aquatic macrophytes entangled on boats or on boat trailers. Aquatic macrophytes often

TABLE 1. Survey questions asked of boaters departing public boat launches on Lake St. Clair (Michigan, USA).

1) How long were you out on the lake today? (number of hours, days or weeks)
2) Were you fishing today? (yes/no)
3) Were you equipped with a live well or similar device? (yes/no)
  If ‘‘yes,’’ then
    a) Did you use this device today? (yes/no)
    b) What was the fate of any water in it?
    (dumped in lake/dumped at ramp/taken from ramp/unknown)
4) What kind of bait did you use today? (minnows, worms, artificial, other)
  If minnows,
    a) Did you use a bait bucket today? (yes/no)
    b) What was the fate of any water it contained?
    (dumped in lake/dumped at ramp/taken from ramp/unknown)
5) Did you use your anchor today? (yes/no)
6) Where is your next planned use of this boat? (return here/other Great Lake launch/inland lake/unknown)
7) When do you plan to use this boat next? (Number of days or weeks/unknown)

Notes: For arriving boats, Questions 1–5 were framed in the present or future tense. Type of data or possible responses recorded are in parentheses.

fragment or become uprooted and then accumulate along the shoreline, where they can become entangled on boat trailers and equipment (Fig. 1; Johnstone et al. 1985). Zebra mussels can colonize macrophytes (Lewandowski 1982) and then be indirectly transported by boats when the macrophytes become entangled, i.e., ‘‘piggyback’’ dispersal. Thus, beginning in mid-July, we also examined departing boats and trailers for the presence of entangled aquatic macrophytes. Time and safety constraints permitted only the observation of entangled macrophytes on departing boats and not their examination for any attached zebra mussels. Therefore, to estimate the occurrence of macrophyte-associated zebra mussels (MAZM), we also examined empty boat trailers parked at these sites for the frequency of MAZM on entangled macrophytes. In addition, the percentage of parked trailers with entangled macrophytes was used as an independent estimate of the frequency of macrophyte entanglement. However, the inspection of parked trailers could underestimate this parameter, as macrophytes can also become entangled on the boat or motor or be caught between the trailer runners and the boat hull as the boat is placed on the trailer (Fig. 1). Boat trailers were inspected on 2–5 weekend dates (depending on the site) in August and early September, usually at midday, but occasionally at multiple times during the day. In the latter case, trailers were marked to avoid repeated sampling. The number of trailers sampled at any given launch on any given date ranged from 30 to 305. The quantity of macrophytes entangled was scored categorically as ‘‘None’’ (no plants visible), ‘‘Few’’ (1–5 separate plant strands), ‘‘Many’’ (>5 separate strands), or ‘‘Clumps’’ (1 or more masses of entangled fragments; Fig. 1 represents an extreme example of ‘‘clumps’’). Each strand or clump of macrophytes was removed from the trailer and macroscopically examined for attached zebra mussels (limit of detection near 2 mm in shell length), which were then counted and measured to the nearest 0.1 mm.

On six dates in August, water was sampled from areas where it might accumulate or be stored on a boat. Typically 5 to 15 samples were collected on any given day from boats chosen haphazardly. These included samples from live wells (containers designed to keep

FIG. 1. An extreme example of the entanglement of aquatic macrophytes on recreational boats and trailers. The photograph was taken at the boat launch area of the Ensign Public Access Site, Lake St. Clair, Michigan, USA, in the summer of 1993.

bait or captured fish alive, usually a built-in feature of the boat that pumps water directly from the lake, but sometimes simply an ice chest; $n = 54$), bait buckets ($n = 9$), bilge water (water that inadvertently accumulates between the hull and the floorboards; $n = 22$), and engine cooling water ($n = 2$). Sample volumes were 200–2000 mL, depending on the volume and time available for processing. Samples were concentrated using a 63-μm mesh (which retains the shelled larval stage of the zebra mussel; Marsden 1992) and stored on ice until returned to the laboratory where they were refrigerated pending examination. Samples were screened for the presence of larvae within 4 d using cross-polarized light microscopy (Johnson 1995). For a haphazardly selected subset of these samples, concentrations of larvae in the samples were also determined at the same time. To calculate the number of larvae transported by an individual boat (i.e., per event), these concentrations were multiplied by the volumes typical for these areas, which were estimated from observations or information from the manufacturers of boating and fishing equipment. Samples were also taken from the docks at the launches to document the presence of larvae in the lake. Using an 18-L bucket, 90–180 L of water were collected from the surface and filtered through a 63-μm mesh plankton net.

We also attempted to collect samples from the hulls of boats to look for mussel larvae that might have recently settled there. We used a rubber scraper (a squeegee, normally used for removing water from windows) but found that the hull usually dried too quickly, making it impossible to collect water in this manner. We therefore discontinued these efforts and assumed that, because zebra mussels have no dormant or resting phase, larvae transported on the external surfaces of boats, motors, and trailers could not survive aerial exposure during transit. The possibility remained that active settlement could have occurred in irregularities (e.g., seams, rivets), but the lack of a biofilm, which is used as a settlement cue for larvae (Wainman et al. 1996), would reduce this possibility.

To assess the risk of transporting zebra mussels associated with each mechanism, we estimated the probability that any randomly selected boat would transport zebra mussels away from the site ($P_{\text{transport}}$). This probability was calculated from the probability of a boat's ''exposure'' to a potential mechanism (P_{exposure}) multiplied by the conditional probability that zebra mussels were indeed being transported if exposed ($P_{\text{transport|exposure}}$). Estimates of P_{exposure} were calculated from interview data for anchors, live wells, bait buckets, and from inspections during the interview for entangled macrophytes. For example, if 40 of 100 boaters indicated that they had used their anchors during the voyage, P_{exposure} would be 0.40. An independent estimate of P_{exposure} to macrophyte entanglement was also calculated as the proportion of trailers with entangled macrophytes in parking areas. P_{exposure} for the exterior boat surfaces and engine cooling water systems was assumed to be 1 (=100%), because the use of any motorized boat in infested waters would, by definition, expose the hull to larvae in the water column and bring water with larvae into the cooling system. Bilges were difficult to inspect, and thus for gross comparative purposes we estimated the exposure at 80%, based on the observation that during almost any excursion some lake water either leaks in or is unintentionally brought aboard (e.g., while swimming, water-skiing, or fishing).

For both live wells and bait buckets, P_{exposure} does not simply depend on the presence of the device, but also on its use and the fate of any water it contained. Thus, P_{exposure} for these mechanisms was calculated from the proportion of boats equipped with the device (P_{equipped}), multiplied by the proportion of fishers who indicated that they had used the device during their outing ($P_{\text{used|equipped}}$) and intended to transport the water contained in the device away from the boat launch ($P_{\text{exposure|used}}$). In other words, if a boat's live well or bait bucket was not used or was emptied before leaving, the boat was not considered ''exposed'' with regard to this mechanism of transport. For example: if 200 of 300 boaters indicated that there was a live well on their boat, but only 60% indicated that they had used the device and half of those then indicated that they had dumped the water from their live well in the lake or at the launch, we would estimate $P_{\text{exposure}} = (200/300) \times 0.6 \times 0.5 = 0.02$.

$P_{\text{transport|exposure}}$ for each mechanism was estimated from the inspections of boat hulls and anchors of departing boats, from the inspections of parked trailers for entangled macrophytes, and from water samples of live wells, bait buckets, engine cooling systems, and bilges. Continuing with the above example, if zebra mussel larvae were found in 20 of 40 live wells sampled, $P_{\text{transport|exposure}}$ would be 0.5. Thus $P_{\text{transport}}$, the product of the two probabilities, would be $0.02 \times 0.5 = 0.01$ (or 1 out of any 100 departing boats).

Exportation of propagules from a source population involves only the first of a series of steps, each with an associated probability, that are necessary for the successful establishment of a new population. For the dispersal of zebra mussels on macrophytes, we were able to extend our simple probabilistic modeling approach to the two subsequent steps of the dispersal process: (1) the movement patterns of the vector (e.g., from infested to uninfested waters), and (2) the survival of propagules during transit. By combining the probability of transport ($P_{\text{transport}}$) calculated above with the probability of vector movement between source and target waterbodies (P_{move}) and survival of the life stage during transit to target waterbodies ($P_{\text{survival|move}}$), we estimated the maximum probability that a boat departing

TABLE 2. Probabilities of different steps in the dispersal of zebra mussels by various potential mechanisms of transport associated with transient recreational boating and fishing activities at public boat launches on Lake St. Clair (Michigan, USA).

Mechanism	Life stage	P_{exposure} (n)†	$P_{\text{transport}\mid\text{exposure}}$ (n)†	$P_{\text{transport}}$
1) Boat exterior (hull/motor)	ad/juv	1.0[a] (···)	0.0[b] (822)	0.0
2) Anchors	ad/juv	0.44[c] (149)	0.02[b] (49)	0.009
3) Entangled macrophytes	ad/juv	0.33[b] (535)	0.16[d] (383)	0.053
4) Engine cooling system	larvae	1.0[a] (···)	1.0[e] (2)	1.0
5) Bilge	larvae	0.8[f] (···)	0.64[e] (22)	0.51
6) Live wells (fishing only)	larvae	0.086[c] (835)	0.83[e] (54)	0.071
7) Bait buckets (fishing only)	larvae	0.024[c] (869)	0.44[e] (9)	0.011

Notes: ''Life stage'' indicates whether adults or juvenile (ad/juv) or larvae were transported. P_{exposure} is the probability of a boat's ''exposure'' to a particular mechanism, $P_{\text{transport}\mid\text{exposure}}$ is the conditional probability that zebra mussels are transported if the boat is exposed, and $P_{\text{transport}}$, the product of the two preceding probabilities, is the probability that any randomly selected departing boat would transport zebra mussels away from the site. $P_{\text{transport}\mid\text{exposure}}$ values for live wells and bait buckets are derived from Table 5 and include only cases in which water was taken from the boat launch. Numbers in parentheses are sample sizes.

†Sources of estimates: [a]By definition; [b]Inspection of departing boats; [c]Interviews with boaters; [d]Inspection of parked boat trailers; [e]Water samples; [f]Educated guess (see *Methods* for additional discussion).

the source waterbody will deliver living zebra mussels to source waters, P_{delivery}. Specifically,

$$P_{\text{delivery}} = (P_{\text{transport}})(P_{\text{move}})(P_{\text{survival}\mid\text{move}}).$$

Estimation of $P_{\text{transport}}$ is described above. P_{move} was estimated from information obtained during the interviews, specifically the intended location for the next use of the boat. $P_{\text{survival}\mid\text{move}}$ can be estimated here in two ways. The simpler method is to use the laboratory estimate of ≤5 d of aerial exposure for maximal survival time for mussels out of water under typical temperate summer conditions of 20°C and 50% relative humidity (Ricciardi et al. 1995), multiplied by the proportion of those boaters destined for inland waters who plan to use their boat within 5 d. A second, more conservative, method uses these same measurements of laboratory survival to estimate the probability that at least one mussel of a group of z mussels will survive the transit between infested and uninfested waters. In this case, $P_{s(d)}$, the probability of survival of a single mussel for d days out of water, can be used to calculate the probability that at least one mussel out of a group of z mussels will survive d days:

$$P_{s(d,z)} = 1 - (1 - P_{s(d)})^{z}$$

i.e., the probability of at least one mussel surviving is 1 minus the probability of all the mussels dying, which is the product of the probability of each individual dying. To then determine the conditional probability that any departing boat that is transporting zebra mussels will deliver at least one living mussel to uninfested waters,

$$P_{\text{survival}\mid\text{move}} = \sum (P_d)(P_z)(P_{s(d,z)})$$

where P_d = probability that a boat visiting inland waters will do so in d days, and P_z = probability that a boat will transport z mussels.

This approach assumes that (1) P_d and P_z are independent, which is reasonable, and (2) that the survivorship of individual mussels is independent of z (number of mussels transported), which is reasonable for small numbers of mussels.

TABLE 3. Duration in water of boats launched from public access sites on Lake St. Clair in summer 1992 (n = 799).

Duration	Frequency (%)
1–12 h (day trip)	88
13–36 h (overnight)	4
2–7 d	4
1–4 wk	1
1–3 mo	3

To convert these probabilities to estimates of the absolute numbers of dispersal events, data on the absolute numbers of boaters using these boat launches were obtained from the Michigan Department of Natural Resources (*unpublished data*) for the period 1988–1991. This extension of the probability model was only applied to transportation of zebra mussels on entangled macrophytes as the survival data on open-air desiccation is most applicable to this situation.

RESULTS

Zebra mussels were transported by all potential mechanisms except for the direct attachment to the hull (Table 2). The median time that boats were in the water was 6 h, and most boats (96%) encountered at these sites were in the water 1 wk or less (Table 3) and thus were not in the water long enough to be fouled. However, as discussed below, if a boat is left for a sufficient time (i.e., weeks) in the water, the direct attachment of zebra mussels could occur. Instead, the export of adults occurred most frequently on entangled macrophytes. Both the probability of exposure (i.e., how often macrophytes were entangled on boat trailers = P_{exposure}) and the proportion of macrophytes that harbored zebra mussels ($P_{\text{transport}\mid\text{exposure}}$) were extremely variable among dates and sites (Fig. 2). Overall 33% of the departing boats had entangled macrophytes (i.e., P_{exposure} = 0.33; Table 2), which is consistent with the observation of

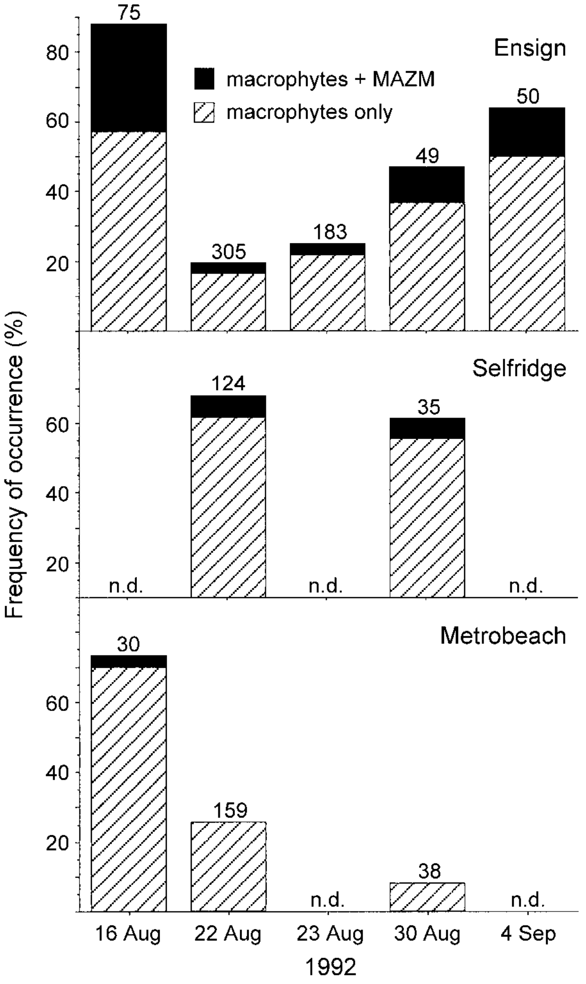

FIG. 2. Occurrence of entangled macrophytes and macrophyte-associated zebra mussels (MAZM) on boat trailers parked at three public access sites (Lake St. Clair, Michigan, USA) sampled in summer 1992. The hatched portion of each bar represents the percentage of trailers with only entangled macrophytes, whereas the solid portion of each bar represents percentage of trailers with entangled macrophytes and MAZM. Sample sizes (number of trailers) for each date are indicated above each bar; n.d. = no data.

36% of trailers in the parking areas having entangled macrophytes (Table 4). Macrophyte-associated zebra mussels (MAZM) were found on 16% of these trailers (i.e., $P_{\text{transport|exposure}} = 0.16$), which leads to an estimate that 5.3% of boats leaving these boat launches had MAZM on their trailers (i.e., $P_{\text{transport}} = 0.053$). MAZM were found disproportionately more often on trailers with greater amounts of entangled macrophytes (Table 4; $P < 0.001$; $G = 20.5$, $n = 61$; G test). There was a mean of 2.3 mussels per trailer (range 1–8; $n = 55$); the number did not vary with the quantity of macrophytes entangled on the trailer (Table 4). The average zebra mussel length was 4 mm and 13 mm for the two cohorts apparent from the size frequency (data not shown).

TABLE 4. Occurrence and abundance of macrophytes on trailers and zebra mussels on macrophytes (macrophyte-associated zebra mussels = MAZM) in parking areas of boat launches (n = 1053 trailers).

Macrophyte abundance	Trailers with macrophytes (%)	Macrophytes with MAZM (%)	MAZM/trailer (mean ± 1 SD) (n)
Absent	64	···	···
Present	36	16	2.3 ± 1.8 (55)
Few	24	8	2.1 ± 1.8 (21)
Many	10	31	2.4 ± 2.0 (27)
Clumps	2	39	2.1 ± 1.1 (7)

Note: See *Methods* for definitions of abundance.

Anchors were used frequently by boaters ($P_{\text{exposure}} = 0.44$), but mussels were found on anchors only once out of 49 inspections. Neither the abundance nor size of mussels on the anchor was recorded.

Larvae were found in all areas where water accumulated on the boats (Table 2). P_{exposure} in these areas ranged from 0.024 to 1.0 and was particularly low for mechanisms associated with fishing (i.e., live wells and bait buckets) due to (1) low frequencies of boats equipped with these devices (P_{equipped}), and (2) the low probability of taking water away from the site even when the device was used ($P_{\text{exposure|used}}$; Table 5). Thus, $P_{\text{transport}}$ was much lower for activities associated with fishing than for more general mechanisms transporting larvae. The highest estimates of $P_{\text{transport}}$ were found for engine cooling water and bilge water due to high values for both P_{exposure} and $P_{\text{transport|exposure}}$ for these mechanisms (Table 2). Although these parameters are based on either low sample sizes ($P_{\text{transport|exposure}}$ of engine cooling water) or qualitative observations (P_{exposure} of bilge water), precision is not important in these cases (i.e., both would remain the most likely methods of transport even if estimates of both parameters were reduced by 50%). However, as discussed below, the number and survival of larvae transported by these means will influence the importance of these mechanisms.

The concentration of larvae in these areas ranged from 5.9 to 19 larvae/L, but was highly variable (Table

TABLE 5. Use of live wells and bait buckets and the fate of any water they might contain by recreational boaters using public boat launches on Lake St. Clair in summer 1992.

Device	P_{equipped} (n)	$P_{\text{used/equipped}}$ (n)	$P_{\text{exposure/used}}$ (n)	P_{exposure}
Live wells	0.39 (835)	0.65 (242)	0.38 (138)	0.086
Bait buckets	0.11 (869)	1.00 (68)	0.22 (68)	0.024

Notes: P_{equipped} is the probability of a boat being equipped with the device; $P_{\text{used|equipped}}$ is the conditional probability of a boat equipped using the device during that day's outing; $P_{\text{exposure|used}}$ is the conditional probability that any device used is carrying water as it departs the launch site (as opposed to being dumped in the lake or at the launch). P_{exposure} is then the product of the preceding probabilities; n = sample size.

TABLE 6. Estimates of the numbers of larvae transported in water accumulated in various locations on recreational boats using public boat launches on Lake St. Clair (Michigan, USA) in August 1992.

Location (*n*)	Volume† (L)	Concentration (larvae/L)‡	Larvae transported per event	Likelihood of survival§
Engine cooling system (2)	1	16 ± 1	16	high
Bilge (13)	2	5.9 ± 13	12	low
Live well (38)	65	19 ± 34‖	1230	moderate
Bait bucket (3)	4	7.8 ± 8.4	31	moderate

Notes: Larvae transported per event is the product of the estimated volume and the measured concentration of larvae; *n* is the sample size of water samples used for determining concentrations.

† The engine cooling system volume was estimated by determining the mean of the manufacturers' specifications for a 35-horsepower outboard, a 100-horsepower outboard, and a 100-horsepower inboard/outboard (1 horsepower = 746 W). Bilge volume ranged from 0 to 20 L (L. E. Johnson, *personal observation*). The live well volume was determined by the mean of the two most common sizes (56.8 and 75.7 L) encountered at various internet listings (*n* = 10 locations). The bait bucket volume was an estimate based on bait buckets sold at fishing supply stores and L. E. Johnson (*personal observation*).

‡ Mean ± 1 SD.

§ Predictions based solely on presumed water quality in each location (see *Discussion*).

‖ Incorrectly reported as 111 (222) larvae/L in Johnson and Carlton (1996) due to calculation error.

6), due perhaps to the use of different locations within the lake. As larval densities usually peak earlier in the season, these samples probably underestimated the density of larvae for the entire season. The range of values is consistent with measurements of larval abundance in water collected at the boat launches (mean ± 1 SD = 25 ± 22 larvae/L; *n* = 4). Using the estimated average volumes of lake water that could accumulate in each area and the observed larval concentrations, live wells had the potential to export 40–100 times more larvae on a per-trip basis than did other mechanisms, due both to the large volume of this structure and to higher concentrations of larvae (Table 6). While the probability of transport of zebra mussel larvae in engine cooling water is very high (probably near 100%), the small volume of the cooling system severely limits the total number of larvae transported per event.

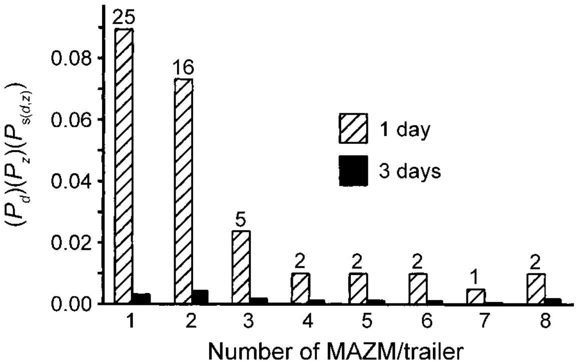

FIG. 3. Values of $P_dP_zP_{s(d,z)}$, the component of the conditional probability of survival if moved between infested sites and inland lakes, for different numbers of macrophyte-associated zebra mussels (MAZM) and for different transit times (1 and 3 d). Numbers above the pairs of bars indicate the absolute number of times that number of MAZM was observed. These numbers were used to calculate values for P_z, the probability of transporting z mussels.

Based on the reported next use of boats, P_{move}, the probability of boat movement between these infested waters and inland lakes (which at the time were not known to be infested) was 0.089 (68 of 766). Of the boaters destined for inland waters, 27% intended to use their boats within 1 d or less, 25% within 2–5 d, 37% within 5–10 d, and 12% in > 10 d. From Ricciardi et al. 1995, $P_{s(d)}$ (the survival of an individual mussel surviving *d* days out of water) for mussels 10–18 mm in length is $P_{s(1)} = 0.73$, $P_{s(3)} = 0.03$, and $P_{s(5)} = 0$. Thus, for the simpler estimate, $P_{\text{survival|move}} = (0.27 + 0.25) = 0.52$, i.e., the proportion of boats intended to be used in inland lakes within 5 d after their use in infested waters. This estimate assumes that at least one mussel will survive for periods up to 5 d, an unlikely assumption given the low numbers of MAZM per boat (Table 4) and low survival after a 3-d exposure. For the more complex model, $P_{\text{survival|move}} = 0.25$, which is influenced by the much higher survival rates for the 1-d period and the low number of mussels carried by individual boats (Fig. 3). Combining this latter, more realistic, value with the probabilities of transport ($P_{\text{transport}}$; Table 2) and movement (P_{move}, above), we can estimate the maximum probability that an individual boat might deliver a live zebra mussel on aquatic macrophytes to inland waters as $P_{\text{delivery}} = (0.053) \times (0.089) \times (0.25) = 0.0012$. In other words, we estimate that a maximum of 12 of every 10 000 boaters who used these Great Lakes boat launches transported live (juvenile and adult) zebra mussels on entangled macrophytes to inland waters.

What does this mean in absolute terms of overland dispersal? An annual average of 96 800 boaters used the Ensign launch during the period 1988–1991 (Michigan Department of Natural Resources, unpublished data). Based on the above model and data specific to that site (i.e., 7.6% of departing trailers with MAZM and 8.8% of departing boaters destined for inland waters; thus $P_{\text{delivery}} = (0.076) \times (0.088) \times (0.25) = 0.0017$), we predict that this site alone was the source of 170 ($= 0.0017 \times 96\,800$) events having the potential to transport a live zebra mussel into inland waters within that single season. Clearly, the data for MAZM were variable between public boat launches (Fig. 2), and care is needed in extrapolating results from this one site. For example, applying the model to data from the Metrobeach launch (i.e., 0.4% of departing trailers with MAZM and 7.8% of departing boaters destined for inland waters), gives an overall probability of an individual boat delivering live mussels to inland waters that is less than 5% that for the Ensign launch ($P = 0.00008$ vs. $P = 0.0017$, respectively). Still, these public access sites represented only a fraction of the transient boating activity on Lake St. Clair, suggesting that hundreds and perhaps thousands of dispersal events have occurred each year within this region.

DISCUSSION

As most bodies of water connected to the Great Lakes have been colonized by the zebra mussel, further range expansion will largely occur through interbasin dispersal, and thus should be determined by the availability and effectiveness of overland transport mechanisms. Overland dispersal has already occurred (Kraft and Johnson 2000), and although there are a myriad of vectors with the potential to transport zebra mussels overland (Carlton 1993), recreational boating has generally been assumed to be the primary vector of dispersal (Padilla et al. 1996, Schneider et al. 1998, Buchan and Padilla 1999). The results of this study clearly demonstrate the potential for recreational boating to transport zebra mussels away from infested waters. However, the mere existence of a vector does not assess its importance relative to other potential vectors (e.g., Johnson and Carlton 1996). Other vectors, including other classes of recreational boats (see following paragraphs), may also be operating and should be similarly assessed.

Our results clearly demonstrate that recreational boating must be considered as a suite of mechanisms that can be categorized according to the stage of the life cycle transported (i.e., larvae vs. attached stages) or by specific human activities (e.g., fishing vs. other recreational activities). Overall, larvae appear to be more commonly transported than adults due to their occurrence in the lake water that accumulates in a variety of places on boats. Although engine cooling water may be the most likely means in which larvae are transported, live wells may present a greater overall risk due to their larger volume and thus larger number of larvae transported (Table 6 and below). However, boaters who took lake water away from boat launches in the live well often indicated that they intended to empty or clean it (typically at home) before the next use of their boats. Thus, our calculation of the probability of export is likely to be an overestimate of the transport of water in live wells and bait buckets between lakes.

Contrary to expectations, adults were not found on the boat hull itself, but instead only on aquatic macrophytes entangled on the boat trailer or on the anchor. Given the short duration that most recreational boats spent in the water (Table 3), this result is not surprising, as there was insufficient time for the development of the biofilm necessary as a settlement cue for larvae (Wainman et al. 1996). Moreover, most boaters who use public boat launches store their boats out of water (e.g., in a driveway), and neither larvae nor recent metamorphosed juveniles are adapted for living out of water. The domain of this study, namely recreational boats using public access sites, did not, however, include ‘‘resident boats,’’ those boats that are seasonally moored in infested waters. Although these boats are unlikely to be transported between unconnected bodies of water, they have a tremendous potential for transporting large numbers of juvenile and adult mussels, for example when their owners change residences. All of the infested boats intercepted at California inspection stations appear to have been resident boats commercially hauled from the Midwest (Janik 2001), suggesting this type of dispersal may be especially important at larger spatial scales.

The entanglement of macrophytes occurred frequently, either on 33% or 36% of the trailers, depending on the assessment method used. These estimates are consistent with those from New Zealand (27%; Johnstone et al. 1985), but much higher than those found in British Columbia, Canada (3.9%; Dove and Malcolm 1980, Dove and Wallis 1981, Dove and Taylor 1982). This latter study, however, only examined one species of aquatic macrophyte, underestimating the general phenomena, and included many nontrailered boats (e.g., canoes) which were less likely to entangle macrophytes. As with our data, there was substantial variation among boat launches in these studies, presumably due to differences in macrophyte abundance and distribution, location of the launches, and species characteristics (e.g., propensity to fragment). Not surprisingly, the probability of transporting MAZM increased with the amount of macrophytes entangled, but it is not clear why the number of MAZM per trailer did not follow the same pattern (Table 4). The low numbers of MAZM per strand may reflect low colonization levels of macrophytes or a propensity of more heavily colonized plants to sink and thus not accumulate near launches.

Identification of the relative importance of the mechanisms in which zebra mussels are transported is critical both for modeling the geographic spread of zebra mussels and for control strategies. Past modeling efforts (Neary and Leach 1992, Schneider et al. 1998, Buchan and Padilla 1999) have treated all boating activity as equivalent in terms of the abilities of boats to transport zebra mussels. Our results demonstrate that boats can vary in this capacity depending on the exact activity (e.g., fishing, use of anchors) and can vary substantially in space and time (e.g., macrophyte entanglement; Fig. 2). As stressed by Schneider et al. (1998), data on vector movement and probabilities of transport are needed for developing models of invasion risk. For example, given the data available at the time, Schneider et al. assumed a probability of export of 1%, which likely underestimates this parameter (Table 2). Further information is also needed on the demographic conditions needed for establishing new populations.

Knowledge of the details of transportation is also needed for preventing or delaying the further spread of zebra mussels. For example, early guidelines for boaters included measures aimed at sterilizing the exterior surfaces of boats with chlorine solutions, hot water, or long periods out of water (e.g., Kelch 1992). Given that these procedures were both inconvenient and voluntary, compliance rates were undoubtedly quite low. Moreover, as no mention of the removal of aquatic plants was made, boaters were directed away from the more likely mechanism of transport. Detailed information about dispersal mechanisms, especially their relative frequency of occurrence, can help guide the development of such programs.

This study primarily addressed transport from infested waters. Survival during transit is the next key aspect. Unfortunately, there are only limited survival data for these mechanisms. Maximum survival of adults in air is estimated at ≈3 wk under conditions that minimize desiccation (low temperature [<5°C], high humidity [≥95% relative humidity], and no wind; McMahon 1996). At more typical summer outdoor conditions (20°C, 50% relative humidity) survival is likely to be 3–5 d (Ricciardi et al. 1995), but desiccation of adult zebra mussels might be reduced when they are attached to moist macrophytes. Conditions in the small volumes of water transported in recreational boats (e.g., temperature, pH, dissolved oxygen) are likely to differ from natural conditions, and we hypothesize that survival rates of larvae will be low (Table 6). Conditions in bait buckets and live wells are likely to be degraded by fish excretions, and may even be worse in bilge water where other contaminants (e.g., fuel) accumulate. Thus water trapped in the intake of the engine cooling system, where temperatures are not elevated, is likely to be the most suitable, and on one occasion we found a living larva in engine cooling water collected from a boat that had been recently used in zebra mussel-infested waters (Lake Erie) as it was preparing to launch in an uninfested inland lake (L. E. Johnson, *personal observation*). Still, the small volumes involved suggest the absolute number transported per event is low (Table 6).

In spite of the dominance of mechanisms transporting larvae (Table 2), adults are hypothesized to have a greater potential to establish new populations (Johnson and Padilla 1996). Gamete dilution, which decreases fertilization rates of benthic invertebrates in marine systems (Levitan et al. 1992), requires that introduced populations must be either very large or spatially aggregated to become established. Thus, the incidental release of small numbers of larvae by recreational boats is not likely to meet these conditions, as larvae will become diluted and suffer high mortality (Sprung 1993). We concur that interbasin range expansion from transient recreational boating is most likely to continue by the dispersal of adult or juvenile stages, especially those attached to entangled macrophytes.

The simple probability model developed here predicted that hundreds to thousands of potential dispersal events occurred during the period of the study. How does this estimate of ‘‘propagule pressure’’ (sensu Ricciardi and MacIsaac 2000) compare with subsequent patterns of inland invasion in adjacent areas? As of 1997, zebra mussel populations had been found in 11 of the 36 lakes >50 ha in area within the four-county region of Michigan bordering Lake St. Clair (Kraft and Johnson 2000), but six of these were most likely the result of secondary dispersal of zebra mussels downstream (L. E. Johnson and C. E. Kraft, *unpublished data*). Given the abundance of lakes in this region, this number is surprising low considering the number of potential colonizing events. This discrepancy can be explained in a number of ways. First, we only made observations as boats and trailer were leaving infested waters, and not as they arrived at inland lakes. Although MAZM have been observed arriving at uninfested inland lakes (Johnson and Carlton 1996), we do not know the proportion of MAZM that fall off en route, that are removed by boat owners, or that are not released upon arrival (i.e., that are retained on the trailer). Second, individual inoculations may often fail to found new populations (the ‘‘Noah Fallacy,’’ Johnson and Carlton 1992), or multiple deliveries may be required to attain a minimum viable population. Indeed, for modeling purposes, Schneider et al. (1998) chose a threshold of 2000 visitations by infested boats to establish new populations of zebra mussels. Last, boaters do not visit lakes randomly (Johnson and Padilla 1996, Padilla et al. 1996, Buchan and Padilla 1999), and thus invasions may be more likely for popular lakes. However, it is not the overall use of recreational boats on a given a lake, but rather the frequency of ‘‘promiscuous’’ behavior (i.e., the sequential use of multiple waterbodies by boaters) that will likely determine the likelihood of invasion, all other factors being equal (Padilla et al. 1996).

The presence of adult zebra mussels on trailered boats, coupled with a high frequency of multilake usage by boaters (Gunderson 1994, Padilla et al. 1996, Buchan and Padilla 1999; this study), suggests that transient recreational boating activities may play an important role in the colonization of isolated inland lakes (but see the previous comments concerning resident boats). Recreational boating has already been implicated in the spread of exotic macrophytes (Dove and Taylor 1982 and references therein, Johnstone et al. 1985, Joyce

1992). Because zebra mussels attach frequently to submerged macrophytes (Lewandowski 1982, UWSGI 1993, Lewandowski and Ozimek 1997, Horvath and Lamberti 1997) and macrophyte abundance is predicted to increase in lakes infested with zebra mussels (Griffiths 1993), we contend that the interbasin transport of macrophytes entangled on boat trailers and equipment (e.g., motors, propellers) must be targeted to prevent or slow the further invasion of inland waters. Fortunately, the importance of removing macrophytes from boats and trailers, both to prevent the spread of zebra mussels and the macrophytes themselves, is beginning to be integrated into educational efforts (e.g., MSG 2000). Guidelines for the control of zebra mussels and other epiphytes must emphasize the potential interaction between macrophytes and boat trailers, not only for the obvious danger of dispersing exotic macrophytes, but also for dispersing associated exotic animals including, but not limited to, the zebra mussel. Although we focused specifically on the further regional expansion of the zebra mussel, our results are applicable to the dispersal of other aquatic species, including the past, present and future invaders of North American inland waters (Mills et al. 1993, Ricciardi 1998, Ricciardi and Rasmussen 1998). Besides the obvious relevance to the dispersal of macrophytes and any associated fauna and flora, the transport of small quantities of water could play a major role in the spread of species possessing planktonic life stages, particularly those capable of parthenogenetic reproduction, e.g., the invasive cladocerans *Bythotrephes cederstroemi* (Yan et al. 1992) and *Daphnia lumholtzi* (Havel et al. 1995, Havel and Stelzleni-Schwent 2001).

This study examined in detail the diverse mechanisms of dispersal associated with one vector, namely transient recreational boating, but our approach is widely applicable to other vectors and other invasive species. Dispersal can be inherently difficult to study even in a qualitative manner, and thus the vectors of dispersal are often ignored by researchers who instead focus on the ecological and economic impacts of invaders. Still, as we have demonstrated here, one can make the key observations needed to demonstrate that a suspected vector is indeed capable of transporting the species in question. Beyond this basic requirement, one can then compare different mechanisms by which organisms can be transferred and ideally make comparisons among different vectors (Johnson and Carlton 1996). Finally, the overall risk of any particular mechanism can be assessed by quantifying the various probabilities associated with each step in the process of dispersal. For the case of the zebra mussel, intuition and anecdote have served in the absence of any formal risk assessment as the only basis for policy decisions and educational efforts (e.g., the 100th meridian project; Tyrus et al. 1994). Quantitative approaches to dispersal and geographical spread can help develop a more rigorous science on which to base these decisions.

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