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POST-ESTABLISHMENT SPREAD IN LARGE-SCALE INVASIONS: DISPERSAL MECHANISMS OF THE ZEBRA MUSSEL *DREISSENA POLYMORPHA*[1]

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INTRODUCTION

Although numerous reports have documented the "patterns of spread" of nonindigenous species, we have virtually no detailed studies regarding the mechanisms of spread for any large-scale invasion. The zebra mussel offers a unique opportunity to dissect out the importance of different mechanisms because the invasion is proceeding at a rapid, but tractable, pace. The pattern of spread has been relatively well documented due to the zebra mussel's conspicuous nature and economic importance. Moreover, this invasion is limited to aquatic environments, which have discrete boundaries and well-defined connections. This attribute permits clear distinctions between gradual "diffusive" spread (e.g., within a lake), "advective" spread (e.g., within a watershed), and "saltatory" jumps in distribution (e.g., between watersheds). In this paper we review the likely mechanisms by which the zebra mussel *(Dreissena* spp.) is spreading through North America.

HIGH DISPERSAL AND AN "EMPTY NICHE" CREATE A SUCCESSFUL INVASION

Of the invaders of North American freshwaters, the zebra mussel *Dreissena polymorpha* has been one of the most dramatic due to its rapid range expansion and immediate economic impacts (Roberts 1990, Ludyanskiy et al. 1993, Nalepa and Schloesser 1993). When abundant, this invader can have dramatic ecological effects, ranging from the displacement of unionid clams (e.g.. Mackie 1991, Haag et al. 1993) to large-scale community and ecosystem changes as energy and nutrient flows are redirected by the mussel's filter-feeding (Mackie 1991).

The successful invasion of the zebra mussel appears to be due to a combination of traits that fill an ecological role previously unknown in North American freshwaters, i.e., an "empty niche." Byssal threads, which allow for attachment to the stable surfaces (e.g., rocky reefs, aquatic plants) of the productive littoral zone, are not found in the adults of other freshwater bivalves. As a long-lived species capable of actively pumping the water it filters, the zebra mussel is better suited than shorter-lived, passive filter-feeders (e.g., insect larvae) to exploit the resources of calmer lacustrine habitats. Models strongly suggest that this active filtering can greatly exceed the combined filtering activities of the zooplankton (MacIsaac et al. 1992, Bunt et al. 1993). The production of planktotrophic larvae (veligers) permits higher potential fecundity by further exploitation of the planktonic food resources of the photic zone (MacIsaac et al. 1992). Taken together, these traits make the zebra mussel a uniquely effective harvester of planktonic primary productivity.

The traits that provide zebra mussels an advantage in exploiting food resources are also the key to its ability to disperse quickly by both natural and human-mediated mechanisms. Planktotrophic larvae require weeks of development in the plankton, thereby ensuring the widespread dissemination of offspring by currents and wind-driven advection. Likewise, juveniles and adults can disperse by fouling submerged objects

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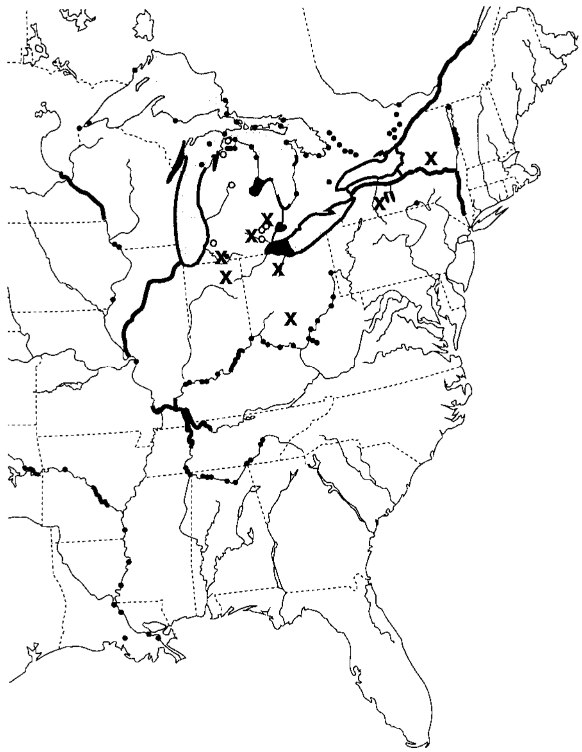

FIG. 1. Known distribution of the zebra mussel Dreissena polymorpha in North America as of 31 December 1993. "X"s represent adult populations thought to be established by overland dispersal, open circles represent sitings (larval or adult) during a detection program in Michigan, black circles and thick lines represent other sitings. This latter group consists primarily of sitings in the Great Lakes and connected waterways but also includes inland sitings of adult populations downstream from established inland populations or sitings of only larval stages. Modified from New York Sea Grant 1993 (printed with permission of the New York Sea Grant Institute).

that subsequently drift (e.g., aquatic macrophytes). Thus, zebra mussels are quite capable of natural dispersal within a body of water or downstream into other streams, rivers, or lakes. However, the transport by aquatic birds or other aquatic animals (e.g., turtles, muskrats) is the only likely natural mechanism for colonizing upstream areas, maintaining populations in fast-moving lotic systems lacking upstream source populations, or dispersing overland.

Unfortunately, the potential human-mediated dispersal mechanisms are almost limitless (Carlton 1993). Essentially, any activity that can move water (which can contain larvae) or submerged objects (which can be fouled by juveniles or adults) within or between bodies of water can greatly accelerate the spread of this species, especially upstream or overland.

The current distribution of the zebra mussel (Fig. 1) demonstrates the rapid spread of this species and suggests the importance of certain mechanisms of dispersal (see O'Neill and Dextrase [1994] for a detailed time course of the range expansion). Although the precise time and place of the establishment of the first zebra mussels in North America is not known, the evidence suggests that larvae in discharged ballast water established the first population in Lake St. Clair (Michigan; USA/Ontario; Canada) in the mid-1980s (Hebert et al. 1989). The spread downstream was rapid, and by 1991 the mussels were found in the Hudson River (New York) and the St. Lawrence River (Quebec). Although much of this spread was due to the dispersal of larval stages, "gaps" in the distribution (e.g., along the Erie Canal) suggest that adults were also being dispersed, most likely as fouling organisms on boats, barges, or ships.

During this period substantial upstream dispersal was also occurring. Initial detections occurred in the port areas of the upstream Great Lakes, and by 1992 mussels entered the Mississippi watershed via the Chicago Sanitary and Ship Canal and then spread throughout the major rivers of this system (Fig. 1). The mechanism by which initial adult populations have been established appears to be transportation by commercial shipping. The current distribution of zebra mussels (Fig. 1) closely matches the commercially navigable waters of the Great Lakes and Mississippi basins (McMahon 1992, Geraghty et al. 1973: Plate 19), and anecdotal observations indicate that commercial barges carry adult mussels along these waterways for over 1000s of kilometres (Keevin and Miller 1992).

COULD FURTHER GEOGRAPHIC SPREAD BE LIMITED BY DISPERSAL OPPORTUNITIES?

Models based on physiological parameters suggest that the zebra mussel has the potential to colonize most of the United States and southern Canada (Strayer 1991, McMahon 1992). However, the rapid range expansion of the zebra mussel may be misleading when naively extrapolated to the remaining uncolonized areas. Almost all the current range of the zebra mussel is within lakes, rivers, and waterways that are directly connected. Further expansion will require overland dispersal into upstream waters or uncolonized watersheds. Although range expansion, especially downstream, is likely to be rapid once an initial population is established within a watershed, the difficulty of dispersal between unconnected watersheds may greatly constrain the rate of range expansion of the zebra mussel.

At first glance, the range of the zebra mussel appears almost entirely restricted to the Great Lakes and the connecting rivers and canals (Fig. 1). By the end of 1993 zebra mussels were distributed from Quebec to Louisiana, yet in all of North America, adult mussels had only been found in eight isolated inland lakes (i.e., lakes without navigable connections with infested waters and with no reported populations of zebra mussels upstream). However, this apparent slow overland spread of the zebra mussel may be misleading. The above discoveries were all made inadvertently. When research efforts have been directed towards detection of zebra mussel populations, the number of overland invasions increases considerably. In Michigan we detected populations (either larval or adult mussels) in 7 of 27 inland lakes that we considered at high risk of invasion due to their large size, high degree of public access, and proximity to established populations of zebra mussels in the Great Lakes (L. E. Johnson, P. Marangelo, and J. T. Carlton, *unpublished data).* Thus part of the explanation for the apparent slow overland spread of the zebra mussel is that less effort has been directed at looking for them in inland waters.

Unfortunately, little is known about the rates of overland spread and the relative roles of the various potential overland dispersal vectors, both in terms of their ability to transport mussels and the frequency at which they move between isolated bodies of water. Given this dearth of information, policy makers and water managers must instead rely on their intuition, which has led to two conflicting schools of thought. The first is that recreational boating and its associated activities will rapidly spread zebra mussels among isolated inland waters. The second is that natural vectors, especially aquatic birds, will spread zebra mussels to inland waters. Both positions have some empirical basis: recreational boating has been implicated in the spread of nonindigenous aquatic plants (Johnstone 1985), and various aquatic organisms have been found on aquatic birds (e.g., Darwin 1878, Maguire 1963). It is essential that we determine the relative importance of these two mechanisms-boats vs. birds-in order to assess which policies might be effective in limiting the dispersal of the zebra mussel. For example, attempts to restrict boating activities would be senseless if aquatic birds were a more effective dispersal mechanism.

A variety of approaches can be taken to investigate mechanisms of dispersal, including directly observing transport, comparing the characteristics of invaded and non-invaded lakes, predicting patterns of invasions based on vector activity, or experimentally manipulating the vectors of interest (Johnson and Padilla 1996). With regards to determining the relative roles of recreational boating and aquatic birds, we presently only have information on the ability of these vectors to carry zebra mussels overland.

Aquatic birds

Observations on the potential for aquatic birds to disperse zebra mussels were made by examining the ability of mallard ducks *(Anas platyrhynchos)* to carry veliger and juvenile stages either internally or externally (L. E. Johnson, M. Furman, and J. T. Carlton, *unpublished data).* Internal transport by the ingestion and defecation of juvenile mussels or veligers was examined by allowing captive ducks to consume mussels or concentrated suspensions of veligers and then examining the resulting fecal material. As observed in similar studies (Thompson and Sparks 1977) no animals survived passage through the gut, presumably due to a combination of the high body temperatures of the ducks, the crushing action of the gizzard, and the action of digestive enzymes. External transport was examined by permitting ducks to swim in a lake containing veligers (Lake St. Clair, Michigan, USA) or in 2-m-diameter wading pools containing enhanced concentrations of veligers or juveniles and then directing them overland (2.5 m) into target pools of tap water. Water from the target pools was then examined for zebra mussels. Zebra mussels were transported under all situations, but at very low numbers, usually <0.5 mussel per duck per trip. The enhanced zebra mussel densities, the extremely short distances involved, and the fact that the ducks walked rather than flew to the target pools suggest that these rates of transfer overestimate the ability of waterfowl to transport zebra mussels overland.

Recreational boating

Recreational fishing and pleasure boats were inspected and sampled at public boat ramps in the summer of 1992 as they departed the zebra-mussel-infested waters of Lake St. Clair (L. E. Johnson and J. T. Carlton, *unpublished data).* We identified seven different mechanisms by which these boats could transport zebra mussels overland: (1) adults attached to exterior boat or motor surfaces, (2) adults attached to anchors or material snagged by the anchor, (3) adults attached to aquatic macrophytes entangled on the boat trailer during retrieval of the boat, (4) larvae in bilge water, (5) larvae in engine cooling water, (6) larvae in bait buckets, and (7) larvae in live wells.

Of these mechanisms, transportation on entangled macrophytes and in live wells appears to be the most common means of transporting adult and larval zebra mussels, respectively. Depending on the day and site, anywhere from 0 to 31% (7.8 ± 9.2 [mean ± 1 SD]; n = 9 ramp inspections) of the trailers at public boat ramps had entangled vegetation with 1 to 8 adult mussels attached (2.7 ± 2.0 [mean ± 1 SD]; n = 49 trailers with zebra mussels on entangled vegetation). On the receiving end (i.e., ramps at uninfested inland lakes), zebra mussels were observed entangled in macrophytes on 1 of 275 trailers inspected. The potential of this mechanism depends on the densities of mussels on the plants. Zebra mussel densities of > 1000 mussels/m stem length (L. E. Johnson, *personal observation)* suggest a much greater potential than the above numbers might indicate (i.e., hundreds to thousands of mussels per trailer). Vast numbers of adult mussels can also occur on the hulls of "resident boats" (i.e., those boats that are continually moored in infested waters). Although no adult mussels were seen on the hulls of the > 1800 boats included in our survey, the rare overland transport of resident boats may also be important in establishing new invasions.

Larvae were found in all places that lake water was stored or accumulated in boats. However, because of the different volumes involved, the transport in live wells has the greatest potential for carrying larval stages overland. Larvae were found in 43 of the 52 live wells sampled (83%) and the densities of larvae in a subset of these samples ranged from 0.5 to 157 larvae/L (111 ± 222 [mean ± 1 SD]; $n = 37$ live wells containing larvae). Thus, a boat equipped with a typical 38-L live-well system had the potential to transport an average of 4200 larvae.

Other considerations

This preliminary comparison of the two most widely suspected overland dispersal mechanisms demonstrates that the transport of zebra mussels by waterfowl is relatively low and thus of minor concern. On a per trip basis, recreational boats are capable of transporting far more zebra mussels than are waterfowl. However, this is only the initial component of the dispersal process-a complete comparison must also include the frequency of movements between infested and uninfested waters and the survival of mussels during transit. Comparable data are not available in this case, although in the Great Lakes region, recreational boating activity and the concomitant movement of boats between bodies of water are usually greatest in the summer and early fall when veligers are present in the water and aquatic plants are most abundant. Movements by waterfowl are usually limited during this period due to nesting, molting, and pre-migration feeding. Thus waterfowl also appear much less likely to move between bodies of water than recreational boats.

The demographic conditions necessary for establishing new populations also argue against the role of waterfowl as vectors of zebra mussel dispersal because they are unlikely to introduce more than a few mussels at a time. Zebra mussels are dioecious, and reproduction in zebra mussels occurs through external fertilization of gametes shed into the water. Dilution of gametes will decrease fertilization rates (Denny and Shibata 1989) although the synchronous spawning observed in zebra mussels (Haag and Garton 1992, Nichols 1993) should help mitigate some of the effects of dilution. Given this life history, the sessile nature of adult mussels suggests that founding populations must be either very large or quite spatially aggregated. The introduction of larvae is unlikely to lead to either condition due to the dispersion of individuals after introduction. Indeed, if it were not for the large volumes of water discharged as ballast from commercial vessels (Carlton and Geller 1993), it would be hard to imagine how zebra mussels were first established in the Great Lakes. In contrast, introductions of adults are likely to remain spatially aggregated and therefore capable of high fertilization rates. However, post-fertilization dispersion of offspring may still present problems in establishing the density needed for perpetuating the population.

The zebra mussel's dramatically successful invasion of North America is certainly partly due to an underexploited (or perhaps "empty") niche and an ability to disperse rapidly. The interesting feature of this invasion is the extent to which the mussel's geographic spread has been channeled primarily along connected waterways. This pattern raises the possibility that future range expansion may be limited by dispersal opportunities. Evidence in favor of this hypothesis can be found in Europe where the zebra mussel spread rapidly along connected waterways but then spread much more slowly into unconnected waters (e.g., 80% of the suitable lakes in Belarus remain uncolonized by zebra mussels; Karataev and Burlakova 1995). Our perspective on invasions tends to take post-establishment dispersal for granted and rarely recognizes that barriers to dispersal can constrain an expanding range. Yet the field of biogeography routinely considers dispersal barriers as important to demarcating biogeographic zones. We believe that studies of contemporary invasions must recognize the potential role of dispersal barriers and focus on the mechanisms of dispersal in order to understand the means by which we can predict and possibly control the geographic spread of invading species. For example, by discounting the role of waterfowl in the overland dispersal of zebra mussels, we can now weigh the costs and benefits of interventions aimed at human-mediated mechanisms of dispersal.

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