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Habitat shift in invading species: zebra and quagga mussel population characteristics on shallow soft substrates

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Abstract

Unexpected habitat innovations among invading species are illustrated by the expansion of dreissenid mussels across sedimentary environments in shallow water unlike the hard substrates where they are conventionally known. In this note, records of population characteristics of invading zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels from 1994 through 1998 are reported from shallow (less than 20 m) sedimentary habitats in western Lake Erie. Haphazard SCUBA collections of these invading species indicated that combined densities of zebra and quagga mussels ranged from 0 to 32,500 individuals per square meter between 1994 and 1998, with *D. polymorpha* comprising 75–100% of the assemblages. These mixed mussel populations, which were attached by byssal threads to each other and underlying sand-grain sediments, had size–frequency distributions that were typical of colonizing populations on hard substrates. Moreover, the presence of two mussel cohorts within the 1994 samples indicated that these species began expanding onto soft substrates not later than 1992, within 4 years of their initial invasion in western Lake Erie. Such historical data provide baselines for interpreting adaptive innovations, ecological interactions and habitat shifts among the two invading dreissenid mussel species in North America.

Introduction

Exotic species are invading freshwater and marine ecosystems around the world at alarming rates. The extensive dispersal capacity and adaptive ability of invading species alone suggests that they can occupy a broader range of habitat types than in their native environments (Elton 1958; Carroll and Dingle 1996). Understanding these habitat shifts and adaptive innovations among invading species is central to implementing effective management strategies for the ecosystems which they can impact.

One of the most significant freshwater invasions in North America originated with the appearance of dreissenid mussels from Europe. Since its discovery in Lake St. Clair in the Great Lakes region of North America in 1988 (Hebert et al. 1989), the zebra mussel (*Dreissena polymorpha*) has spread northward into Canada, westward into the Mississippi River watershed, southward to the Gulf of Mexico and eastward to the New England seaboard (Ram and McMahon 1996). In 1992, the quagga mussel (*Dreissena bugensis*) also was discovered in the Great Lakes region (May and Marsden 1992; Mills et al. 1993; Spidle et al. 1994). However, unlike zebra mussels, quagga mussels only have been found in Lake Erie and Lake Ontario (Mills et al. 1996).

Dreissena polymorpha and *D. bugensis* both reproduce by external fertilization with large pools of broadly dispersing planktotrophic larvae that metamorphose into bysally-attached juveniles within weeks

(Borcherding 1992; Sprung 1992; Ackerman et al. 1994). Zebra mussels are best known for their extensive coverage of hard substrates (e.g. rocks, pier pilings, boat bottoms and intake pipes) in rivers and lakes with densities that commonly reach tens of thousands per square meter in North America (Nalepa and Schloesser 1992; Mellina and Rasmussen 1994). In contrast, congeneric quagga mussels are known to colonize soft substrates, commonly with high densities (tens of thousands per square meter) at depths greater than 30 m in the eastern basin of Lake Erie (Dermott and Munawar 1993; Dermott and Kerec 1997).

Recent studies also have revealed that high-density zebra mussels are expanding across shallow (less than 20 m depth) sedimentary habitats in Lake Erie (Coakley et al. 1997; Berkman et al. 1998). Documenting such habitat shifts is central to interpreting adaptive innovations and ecological patterns among invading species. The purpose of this note is to record previously unpublished data that can be used for establishing historical baselines of mixed zebra and quagga mussel populations in shallow sedimentary habitats in western Lake Erie near their point of origin in North America.

Materials and methods

Dreissena assemblages on sediments in the western basin of Lake Erie, which had been identified during remotely operated vehicle and side scan sonar surveys (Berkman et al. 1998), were haphazardly selected for *in situ* collections between 1994 and 1998 (Figure 1). In 1994, SCUBA was used for collecting dreissenid mussels 1 km north of Ballast Island at a depth of 13 m and on the east side of Rattlesnake Island at a depth of 10 m. Mussel assemblages were collected again from the Ballast Island site in 1995 and from a site 3 km north of Kelly's Island at 16 m depth in 1998. Bathymetric, substrate composition and dreissenid mussel characteristics in these areas are described in Haltuch (1998) and are available on a geographic information system CD-ROM (Haltuch and Berkman 1999).

At each site, patches of dreissenid mussels with areal coverages between 1 and 2 m^2 were selected. The small size of these assemblages was chosen to assess the presence or absence of underlying hard-substrate nuclei (e.g. native unionid mussel shells) that could have influenced dreissenid colonization. Collections came from three replicate patches at each of the 1994 sites, two replicate patches at the 1995 site and four replicate patches at the 1998 site.

Dreissenid mussels were collected within 0.25-m^2 quadrats placed over the replicate patches. Zebra and quagga mussels from each collection were identified, counted and measured with vernier calipers to the nearest 0.1 mm with a precision of ± 0.3 mm. These data were used for determining mussel densities, size–frequency distributions, and proportions of zebra and quagga species in each of the isolated patches on the sediments of western Lake Erie.

In addition, the sediments underlying each mussel collection to a depth of 5 cm were collected manually and then analyzed by dry sieving to identify any hard substrates for mussel attachment. Sediment grain-size distributions and their phi (ϕ) dimensions were based on the Wentworth sediment classification scheme (Gale and Hoare 1991): sand (2 mm to 63 μm, -1 to 4ϕ), silt (31.5–4 μm, 5–8ϕ) and clay (< 2 μm, $< 9\phi$) fractions. Phi means (M_ϕ), standard deviations (σ_ϕ) and skewness values (Sk_ϕ) were calculated to describe the sediment grain-size distributions (Trask 1955).

Results and discussion

Ecological interactions between invading zebra and quagga mussel populations as a function of their density, substrate type, depth and temperature are poorly understood (Mills et al. 1996). In this study, interacting assemblages of the two dreissenid species were interpreted from soft-substrate habitats in the western basin of Lake Erie at depths shallower than 20 m and above any permanent thermocline (Figure 1).

Sediments underlying all of the mixed mussel patches were predominated by silts and clays. In all cases, the sediment grain-size distributions were highly skewed toward the finer fractions, with 75–99% of the sediments by weight being smaller than 63 μm (Figure 2). Moreover, hard-substrate nuclei larger than the dreissenid mussels, such as stones or native unionid shells which are conventionally thought to facilitate zebra mussel recruitment in soft-substrate habitats (Lewandowski 1976; Schloesser et al. 1996), were not observed.

Zebra mussel densities are known to vary significantly with the size of their underlying hard substrates (Mellina and Rasmussen 1994). Similarly, areal coverage and expansion of dreissenid mussel beds

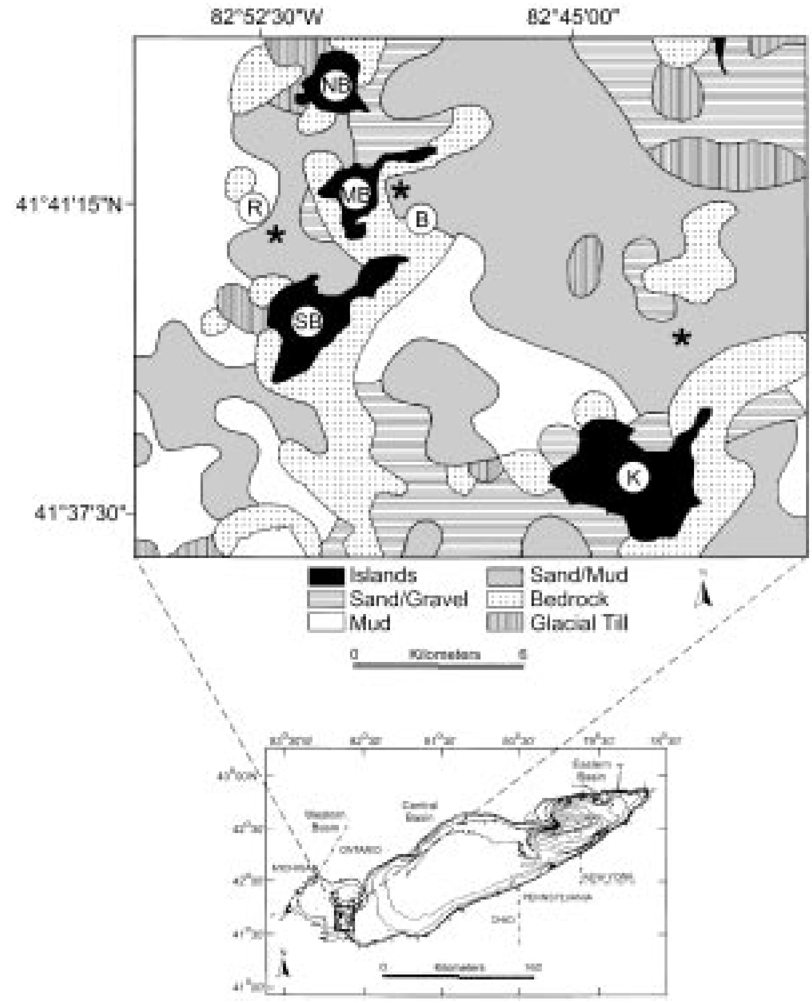

Figure 1. Collection sites of dreissenid mussel species and sediments in the western basin (upper panel) of Lake Erie (lower panel). Distribution of sediment types are shown in the western basin at different latitudes and longitudes near Rattlesnake Island (R), North Ballast Island (NB), Middle Bass Island (MB), Ballast Island (B) and Kelly's Island (K). SCUBA collection sites (asterisks) of dreissenid mussel species and sediments were offshore from Ballast Island at 10 m depth in 1994 and 1995; Rattlesnake Island at 14 m depth in 1994; and Kelly's Island at 16 m depth in 1998. Boundaries of adjacent states and provinces are shown along with 5-m depth contours at different latitudes and longitudes in Lake Erie at a 1 : 1,650,000 scale. Universal Transverse Mercator projections of sediment types and bathymetric contours in Lake Erie were based on geographic information system analyses (Haltuch 1998; Haltuch and Berkman 1999).

have been shown to vary directly with underlying sediment grain sizes in soft-substrate habitats in Lake Erie (Berkman et al. 1998). In this study, dreissenid mussel densities further were shown to vary with the size of their soft substrates, decreasing significantly as sediment grain sizes became skewed toward the smaller fractions (Figure 3).

Microscopic examination of sieved sediments from these dreissenid assemblages revealed sediment conglomerates composed of zebra and quagga mussels less than 5 mm in length attaching their byssal threads to sand grains (Figure 4). This ability of larval or juvenile dreissenids to attach directly to sediment particles (Berkman et al. 1998) is well known for marine bivalves (Stanley 1972). Moreover, expansion of dreissenid mussels across Lake Erie sediments (Dermott and Munawar 1993; Coakley et al. 1997; Berkman et al. 1998) may be analogous to the positive-feedback development of oyster reefs in coastal marine habitats where "*. . . soft muddy bottoms may be gradually converted by the oysters themselves into oyster banks or reefs. . .* " (Galtsoff 1964).

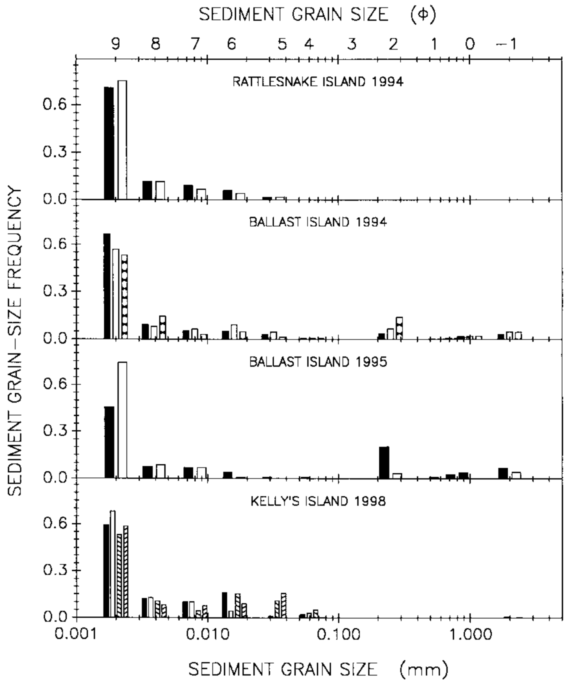

Figure 2. Sediment grain-size distributions from collection sites in western Lake Erie (Figure 1). The mean phi (M_ϕ) and phi skewness of the sediments from these sites were: Rattlesnake Island 1994 ($M_\phi = 5.03$, $\sigma_\phi = 0.36$, $Sk_\phi = 5.20$, $n = 2$); Ballast Island 1994 ($M_\phi = 5.02$, $\sigma_\phi = 0.33$, $Sk_\phi = 3.04$); Ballast Island 1995 ($M_\phi = 5.02$, $\sigma_\phi = 0.38$, $Sk_\phi = 2.04$, $n = 2$); and Kelly's Island 1998 ($M_\phi = 5.03$, $\sigma_\phi = 0.33$, $Sk_\phi = 5.52$, $n = 2$). Sediments collected with SCUBA at Rattlesnake Island, Ballast Island and Kelly's Island correspond with the overlying dreissenid mussel assemblages described in Figures 5 and 6.

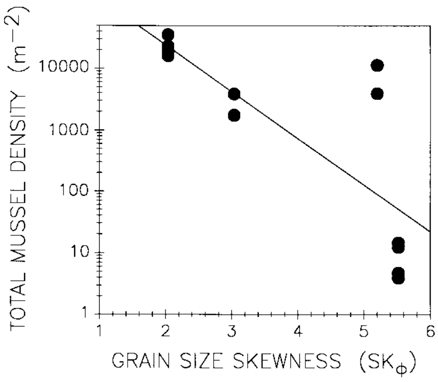

Figure 3. Log-linear plot indicating that the combined densities of zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels exponentially decreased as the distribution of sediment grain sizes (Figure 2) became skewed toward smaller fractions ($F = 5.91$; d.f. 1, 12; $P < 0.03$).

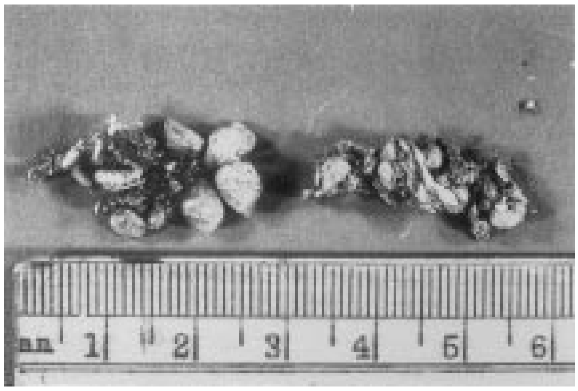

Figure 4. Photo of sand grains between 65 μm and 2.0 mm in dimension, collected from the western basin of Lake Erie, which were bound into a conglomerate by byssal threads of juvenile zebra mussels (*Dreissena polymorpha*) less than 5 mm in dimension.

Shell size–frequency distributions indicate that zebra mussels were significantly smaller than quagga mussels at all of the sites (Figure 5). Offshore from Rattlesnake Island in 1994, shell lengths of the zebra mussels peaked around 7 and 17 mm, representing at least two cohorts. Bimodal size–frequency distributions also were encountered with zebra mussels near Kelly's Island in 1998 and with quagga mussels at all sites in 1994, 1995 and 1998.

Size–frequency data have been used previously to interpret that zebra mussels invaded the Great Lakes region in 1986, two years before they were first observed (Griffiths et al. 1991). In the same manner, the presence of two or more zebra mussel cohorts on the lake sediments in 1994 (Figure 5) suggests that they were colonizing these soft-substrate habitats by at least 1992.

Timing of this initial sediment colonization by dreissenid mussels in western Lake Erie is corroborated by an independent remotely operated vehicle survey from 1990 which revealed that *"SSS (side scan sonar) records interpreted to be coarse gravel proved to be zebra mussel infestations"* (McQuest Marine Sciences Ltd. 1991). Observations from commercial sand-dredging areas in Lake Erie (Liebenthal 1988) further indicate that *Dreissena*-sediment conglomerates have been clogging industrial screens since 1990 (R. Kight, Erie Sand & Gravel Company, personal communication, April 1997). Together these data and observations demonstrate that dreissenid species were

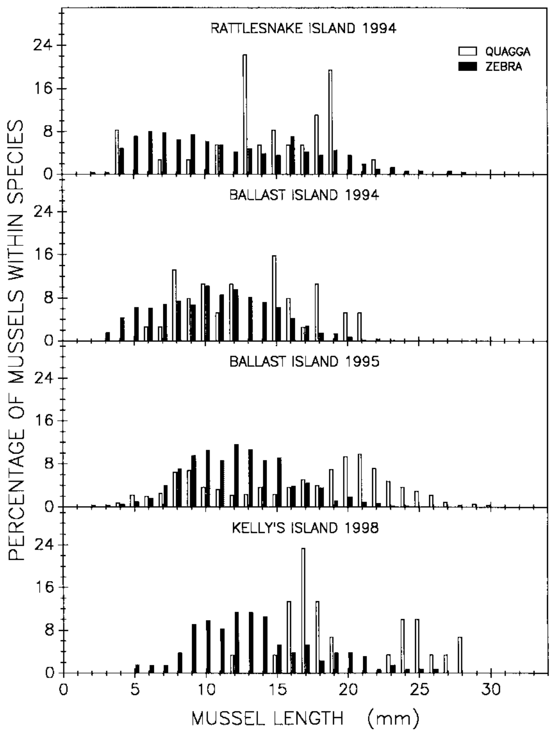

Figure 5. Percentages of dreissenid mussels within different size classes from sampling sites in western Lake Erie (Figure 1). Size means and standard errors for the zebra mussels (*Dreissena polymorpha*) were: Rattlesnake Island 1994 (12.3 ± 0.2 mm, $n = 557$); Ballast Island 1994 (11.1 ± 0.1 mm, $n = 951$); Ballast Island 1995 (12.8±0.1 mm, $n = 1355$); and Kelly's Island 1998 (13.9±0.4 mm, $n = 133$). Size means and standard errors of the quagga mussels (*Dreissena bugensis*) were: Rattlesnake Island 1994 (14.9±0.7 mm, $n = 37$); Ballast Island 1994 (13.5 ± 0.7 mm, $n = 38$); Ballast Island 1995 (17.0 ± 0.3 mm, $n = 537$); and Kelly's Island 1998 (20.4 ± 0.8 mm, $n = 30$). Size comparisons between the dreissenid mussel species in 1994 ($F = 20.92$; d.f. 1, 1581; $P < 0.001$) and in 1995 ($F = 341.01$; d.f. 1, 1890; $P < 0.001$) indicate that the quagga mussels were significantly larger than the zebra mussels.

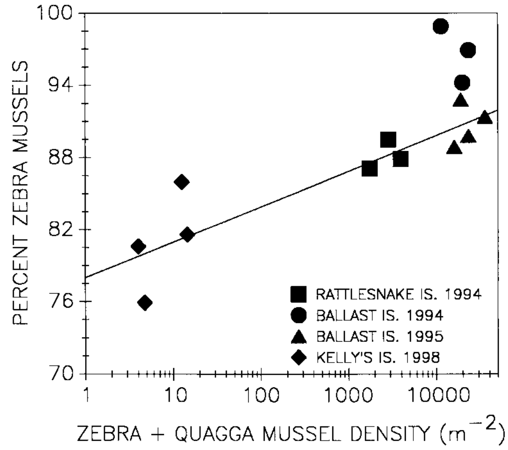

Figure 6. Log-linear plot comparing the combined densities of zebra (*Dreissena polymorpha*) and quagga (*Dreissena bugensis*) mussels to the percentage of zebra mussels in samples from sedimentary habitats in western Lake Erie (see Figures 1, 3 and 5 for collection site information, underlying sediment characteristics and relative mussel size–frequency profiles). These data indicate that total dreissenid mussel densities ranged from less than 50 m^{-2} to greater than 32,000 m^{-2} on the fine-grain sediments, with *D. polymorpha* accounting for greater than 75% of the mussels in each sample. Zebra mussel percentages increased significantly with total mussel densities in these mixed dreissenid assemblages ($F = 8.64$; d.f. 1, 12; $P < 0.01$).

expanding across sedimentary habitats in western Lake Erie by 1992, less than four years after their well-documented invasion on hard substrates began in the Great Lakes.

Dreissenid mussels from the fine-grain sedimentary habitats in western Lake Erie (Figure 2) had densities ranging from a few per square meter to 32,500 m^{-2} (Figure 3). These high mussel densities in soft-substrate habitats were comparable to their well-documented densities on rocks, pier pilings and other hard substrates. Proportions of the two dreissenid species in these mixed assemblages indicated that *D. polymorpha* dominated *D. bugensis* by nearly an order of magnitude at all sites. Moreover, the proportion of zebra mussels increased significantly with total dreissenid mussel density (Figure 6).

Dreissenid mussel assemblages are expanding across hundreds of square kilometers in soft-substrate habitats across Lake Erie (Coakley et al. 1997; Berkman et al. 1998). Like oyster reefs in coastal marine systems, these dreissenid beds have the potential for altering: (1) sediment characteristics and near-bottom flow dynamics; (2) nutrient exchange between the benthos and overlying water; (3) benthic communities; (4) contaminant mobility and uptake; and (5) the distribution of hard-substrate dependent species within the ecosystem. Historical data on mixed assemblages of zebra and quagga mussels provide baselines for interpreting the development, persistence and ecosystem impacts of expanding dreissenid mussel beds on shallow soft substrates in Lake Erie and potentially other sedimentary habitats which are being invaded across North America.

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