



Epiphytic refugium: are two species of invading freshwater bivalves partitioning spatial resources?

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Abstract

Enumeration of benthic (bottom dwelling) and epiphytic (attached to plants) zebra and quagga mussels (*Dreissena polymorpha* and *D. bugensis*, respectively) at Lake Erie near-shore sites in fall of 2000 revealed an unexpected prevalence of the zebra mussel on submerged plants. Even at Buffalo, New York, USA, where benthic dreissenids have been 92–100% quagga mussel since 1996, zebra mussels constituted 30–61% of epiphytes numerically. This may reflect a partitioning of settling space consistent with interspecific competition. A seasonal epiphytic refugium might allow the zebra mussel to persist even where the benthos is almost exclusively quagga mussel.

Introduction

The introduction in the 1980s of zebra and quagga mussels (*Dreissena polymorpha* Pallas and *D. bugensis* Andrusov, respectively) to the Laurentian Great Lakes ranks among the most dramatic biological invasions in history. Dreissenids now account for up to 90% of benthic secondary productivity in Lake Erie (Johannsson et al. 2000). Adverse economic (Ludyanskiy et al. 1993) and biological (MacIsaac 1996; Strayer 1999) effects of these biofoulers have been widespread.

The identity of the ‘quagga’ morphotype was at first uncertain, but was later established as *D. bugensis* by studies of allozyme variation (May and Marsden 1992; Spidle et al. 1994) and review of European systematic literature (Rosenberg and Ludyanskiy 1994). The two species do not appear to hybridize in nature (Spidle et al. 1995). The quagga mussel initially colonized

deeper lake zones and was suggested to be a cold-adapted, deep-water form (Mills et al. 1993). However, it is now replacing the zebra mussel through much of Lakes Erie and Ontario, including warm shallow sites previously harboring only zebra mussels (Claxton and Boulding 1997; Mills et al. 1999; Wilson et al. 1999; Baldwin et al. 2002). A similar trend has been observed within the quagga mussel’s Eurasian distribution, where it is supplanting the zebra mussel in rivers and reservoirs of the Ukraine (Grigorovich and Babko 1997; Mills et al. 1996) and southern Russia (Orlova and Shcherbina 2002).

In eastern Lake Erie, species composition of mussel collections (by KMS) from the principal Buffalo, New York (USA), municipal water intake (a masonry structure ~1.9 km offshore, from which mussels were collected 0.5–2 m below the surface) shifted from > 99% zebra mussel in 1991 to > 98% quagga by 1996 and onward. Asymmetrical interspecific competition

for algal resources is one mechanism that has been proposed to explain such a shift in the lower Great Lakes (Mills et al. 1999; Wilson et al. 1999). In this paper, we offer evidence of differential use of settling space by dreissenid species, with zebra mussels over-represented on submerged macrophytes (rooted plants) compared to nearby benthic populations. Further studies of interspecific dynamics should therefore investigate whether dreissenids also compete for space, and if macrophytes provide a refugium for the zebra mussel.

Materials and methods

We first noted a difference between epiphytic and benthic dreissenid populations in Presque Isle Bay, Pennsylvania (USA), in east-central Lake Erie. In September 2000, benthic samples were collected ~ 200 m southwest of the entrance to the bay, by a 15 × 15 cm Ponar grab in ~ 2 m of water. Our original intent was to obtain dreissenid mussels for a diet-choice study (Diggins et al. 2002) of the round goby *Neogobius melanostomus*, a benthivorous fish that recently invaded North America. A paucity of targeted 6–9 mm mussels in benthic grabs led us also to sample epiphytic mussels by collecting macrophytes from two nearby weed beds with a boat hook. One weed bed (east) was immediately adjacent to the site of benthic samples. The other (west) was ~1 km northwest, along the northern shore of the bay. Both were located in ~ 2 m of water.

An unexpected preponderance of epiphytic zebra mussels was visually obvious, so we collected additional macrophytes for enumeration of attached dreissenid species. We placed ~ 1 kg wet weight of plants from each weed bed in resealable bags, being careful not to dislodge mussels. We chose to count mussels attached to non-indigenous Eurasian water milfoil (*Myriophyllum spicatum*) because (1) this species was abundant in Presque Isle Bay, and we anticipated it would be common elsewhere in Lake Erie; (2) it was well colonized by dreissenids; and (3) it was collected effectively from a boat. Tugging sharply on hooked strands of milfoil typically broke the stem close to its base, or sometimes even pulled out roots.

It was apparent that quantifying the amount of milfoil collected in terms of lake bottom would be difficult late in the season, given this species' tendency to form long strands or mats along the water surface. Future studies of epiphytic dreissenids could therefore

quantify mussel settling in relation to wet weight of plant (Grigorovich and Babko 1997; Moore 2000) or length/number of stems (Brady et al. 1995). These densities might then be related to area of the weed bed.

Before macrophytes senesced, we collected dreissenids in similar fashion from additional sites in the eastern and western basins of Lake Erie. Two stations were sampled along the Buffalo waterfront in October 2000. At a southern station (near the entrance to the Union Ship Canal) benthic mussels were collected from ~ 6 m by trawl, while nearby macrophytes were hooked from ~ 2 m as in Presque Isle Bay. At a northern station (in the Black Rock Canal of the Niagara River, ~ 1 km south of the Peace Bridge to Canada) benthic samples were taken from ~2 m by 15 × 15 cm² Ponar, or were collected by hand from cobbles and bricks in < 1.5 m of water. Macrophytes were hooked from ~ 2 m water depth. Also in October 2000, mussels were sampled from Put-in-Bay, Ohio (USA), immediately west of Gibraltar Island, in western Lake Erie. Here, a diver collected mussel-colonized cobbles and macrophytes by hand from ~ 3 m.

Random sub-samples of epiphytic and benthic collections were enumerated by species into 2-mm length classes while still alive. Mussels were assigned to species based on shell morphology according to Pathy and Mackie (1993) and Claxton et al. (1997). Specimens < 4 mm in length were examined under a broad-field microscope at 7–20 × magnification. Degree of ventral flattening and presence or absence of a 'keel' were the primary discriminating features, and were readily discernable in collected specimens. Significant differences in species proportion between epiphytic and benthic samples were identified by 2 × 2 chi-squared contingency table analysis (Zar 1996).

Results and discussion

The majority of epiphytic mussels were observed on internodal stems of *Ceratophyllum demersum* (hornwort), *Potamogeton* spp. (pondweed), and *M. spicatum*. In the Black Rock Canal, Buffalo, leaf blades of *Valisneria americanum* (eel grass) were almost completely free of epiphytic dreissenids, although mussels were found attached to the base (first ~ 10 cm) of these plants.

Zebra mussels were consistently over-represented on Eurasian water milfoil stems relative to nearby benthic

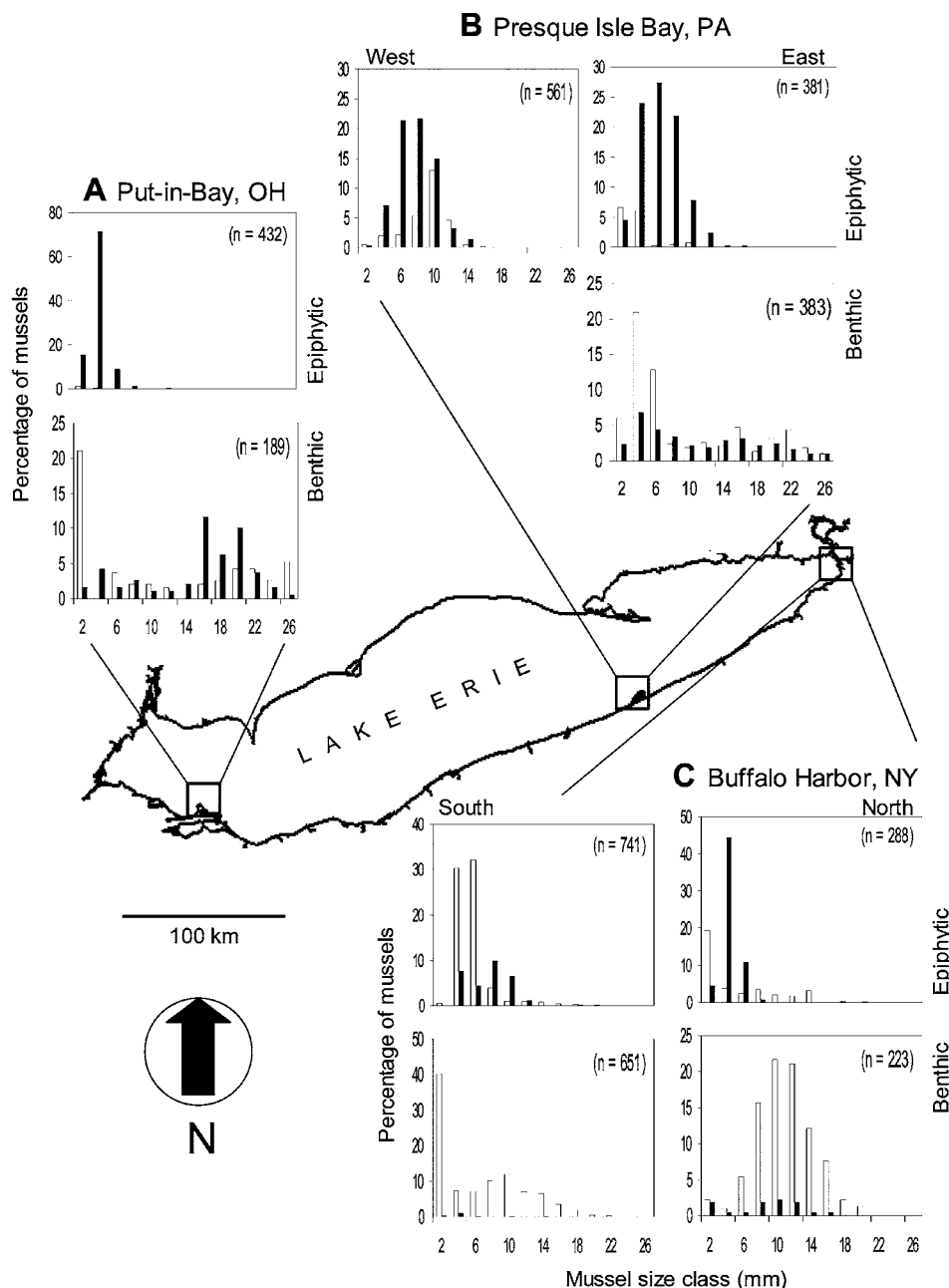


Figure 1. Species composition of epiphytic and benthic dreissenid mussel communities at: (A) Put-in-Bay, Ohio, USA, (B) Presque Isle Bay, Pennsylvania, USA, and (C) Buffalo, New York, USA. Data are percentage of sample comprised of zebra mussels, *Dreissena polymorpha* (solid bars), and quagga mussels, *D. bugensis* (open bars). Sample sizes given for each plot. X-axes of histograms denote upper size limits of 2-mm length classes. Note that ordinate scale varies among graphs.

populations (Figure 1). Comparisons of epiphytic and benthic samples at each collection station reveal a highly significant difference in species proportions in all cases (Table 1, $\chi^2 > 79.1$, $P < 0.001$).

At Put-in-Bay (Figure 1A) benthic mussels were nearly evenly distributed between species in terms of total abundance, although newly recruited quagga (< 2 mm) were very abundant. In contrast

Table 1. Results of contingency table chi-squared analysis comparing quagga/zebra mussel species proportions from epiphytic and benthic samples.

	χ^2	<i>P</i>
Put-in-Bay, OH	232.0	< 0.001
Presque Isle Bay, PA		
West	89.1	< 0.001
East	179.3	< 0.001
Buffalo, NY		
North	130.7	< 0.001
South	180.3	< 0.001

epiphytes were 99% zebra mussel. At Presque Isle Bay (Figure 1B) quagga mussels represented 61% of benthic mussels numerically, while epiphytic samples from the west and east weed beds were 70% and 86% zebra mussel, respectively. At the southern Buffalo site (Figure 1C) benthic mussels were > 98% quagga mussel, but epiphytic mussels were 30% zebra mussel. At the northern Buffalo site (Figure 1C) benthic mussels were 92% quagga, while epiphytic mussels were 61% zebra mussel.

Median length of epiphytic zebra mussels ranged from 3 mm (midpoint of length class) at Put-in-Bay and the northern Buffalo site, to 7 mm at the western Presque Isle Bay weed bed and the southern Buffalo site (Figure 1). The largest epiphytic zebra mussels exceeded 8 mm at the southern Buffalo site and both Presque Isle Bay weed beds.

Submerged macrophytes are well known as a substratum for zebra mussels in both North America (Brady et al. 1995; Horvath and Lamberti 1997; Moore 2000) and Europe (Grigorovich and Babko 1997; Karatayev et al. 1998). However, no attempt has been made previously to compare epiphytic quagga and zebra mussel populations, or to compare epiphytic species proportions to those in the benthos. In Lake Erie's Long Point Bay, Ontario (Canada), Jarvis et al. (2000) noted that zebra mussels seemed unexpectedly prevalent on macrophytes, but they were unable to collect nearby samples of benthic mussels due to ice scouring during the previous winter.

Species competing for a limiting resource must either partition that resource or one of them will be excluded. Evidence from eastern Lake Erie (Mills et al. 1999) indicates the replacement of zebra mussels by quagga mussels in the benthos here is very nearly total. Mills et al. (1999) and Wilson et al. (1999) have suggested this represents a competitive exclusion. Our examination of epiphytic populations suggests settling

space may be partitioned between dreissenid species, and could be the object of competition. Macrophyte stems appear to provide zebra mussels an alternate attachment surface that they utilize more effectively than do quagga mussels. Plant stems might also allow modest but significant numbers of zebra mussels to persist, even where the quagga mussel dominates the benthos, as at Buffalo.

Fate of mussels after yearly senescence of water milfoil is unknown, but Brady et al. (1995) found that zebra mussels epiphytic on bulrush (*Scirpus americanus*) stems in Saginaw Bay, Lake Huron, could survive, over-winter, and spawn after loss of their substratum plants. Attachment to macrophytes has been implicated in the spread of zebra mussels both by drift (Horvath and Lamberti 1997) and overland transport on boat trailers (Wilson et al. 1999; Johnson et al. 2001). If zebra mussels are proportionally more abundant than quagga mussels as epiphytes they might better exploit this dispersal mechanism than would the quagga mussel.

While differential use of settling space could be consistent with interspecific interference competition, it would be naïve to dismiss hastily exploitation competition for phytoplankton resources. Both dynamics can operate simultaneously. However, some recent experimental results counter a hypothesis of asymmetrical exploitation of phytoplankton. Interspecific comparisons of filtering ability (the mechanism by which these organisms procure food) have yielded either a modest advantage for quagga mussels, significant only among larger individuals (Diggins 2001), or no difference at all (Ackerman 1999; Baldwin et al. 2002). Additionally, a reciprocal transplant study conducted in Lake Erie (MacIsaac 1994) failed to reveal growth or mortality differences between zebra and quagga mussels moved from the western basin to the eastern basin, where the dreissenid community shifted first, and most completely (Mills et al. 1999). If zebra mussels were losing to quagga mussels in a competition for phytoplankton in the eastern basin, transplanted zebra mussels should have fared poorly compared with quagga mussels. Transplanted mussels were held 1.5 m from the lake bottom, however, so exploitation competition within a narrower benthic boundary zone (MacIsaac et al. 1992) cannot necessarily be ruled out.

Both dreissenid species pose serious ecological and economic risks to North American waters, but it is increasingly apparent their invasion dynamics are not equivalent. Interspecific differences in distribution

(Mills et al. 1993, 1999), dispersal (Wilson et al. 1999), growth (Baldwin et al. 2002), and possibly competitive ability (Mills et al. 1999; Wilson et al. 1999) suggest two concurrent but asynchronous invasion processes. We hypothesize that evidence of substratum partitioning presented here may indicate interspecific competition for spatial resources. The existence and/or relative importance of such competition can be assessed experimentally, as could the contribution of possible mechanisms such as differences in growth rate or reproductive output. We also hypothesize that submerged macrophytes may provide the zebra mussel a refugium, traditionally envisioned (e.g., Ricklefs 1997) in ecology as ‘... (allowing) a species or community to persist in the face of environmental change over the remainder of its distribution’. In this case, the environmental change has been the increasing dominance of the benthos by the quagga mussel. Mechanisms responsible for differential use of submerged macrophytes are not known, but might include: (1) interspecific differences in veliger distribution, with zebra mussel larvae proportionally more abundant up in the water column or in weed beds; (2) greater ability of zebra mussel post-veligers to settle on plant stems and leaves; (3) a tendency for juvenile zebra mussels to migrate up vertical surfaces, including macrophyte stems; or (4) superior ability of newly recruited zebra mussels to persist and grow on plants. Testing these and other hypotheses of dreissenid interspecific dynamics should expand our understanding of the ecology of these species where they are sympatric, and may yield predictions for where they do yet interact.

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