

The Quagga Mussel Invades the Lake Superior Basin

Igor A. Grigorovich¹, John R. Kelly^{2,*}, John A. Darling³, and Corlis W. West²

¹Wilson Environmental Laboratories, Inc
Duluth, Minnesota 55802

²U. S. Environmental Protection Agency
Office of Research and Development
National Health and Environmental Effects Research
Mid-Continent Ecology Division
6201 Congdon Boulevard
Duluth, Minnesota 55804

³U.S. Environmental Protection Agency
Office of Research and Development
National Exposure Research Laboratory
Molecular Ecology Research Branch
27 West Martin Luther King Blvd.
Cincinnati, Ohio 45268

ABSTRACT. Prior studies recognized the presence of a single dreissenid species in Lake Superior—the zebra mussel *Dreissena polymorpha*. However, taxonomic keys based on traditional shell morphology are not always able to differentiate dreissenid species with confidence. We thus employed genetic and morphological analyses to identify dreissenids in a major river-embayment of Lake Superior—the lower St. Louis River/Duluth-Superior Harbor—during 2005–2006. Our results revealed the presence of a second dreissenid species—the quagga mussel *D. bugensis* (alternatively known as *D. rostriformis bugensis*). Both species occurred in mixed clusters, in which zebra mussels outnumbered quagga mussels (20–160:1). The largest quagga mussel collected in 2005 was 26.5 mm long and estimated to be two years old, suggesting that the initial introduction occurred no later than 2003. Further monitoring is necessary to determine whether the quagga mussel will colonize Lake Superior. Our results indicate that the coupling of conventional morphological and molecular approaches is essential for monitoring dreissenid species.

INDEX WORDS: Quagga mussel, *Dreissena bugensis*, *Dreissena rostriformis*, identification, non-indigenous species, range expansion, dispersal, Lake Superior, Duluth-Superior Harbor.

INTRODUCTION

The zebra mussel *Dreissena polymorpha* (Pallas 1771) and the quagga mussel *Dreissena bugensis* (Andrusov 1897; alternatively known as *D. rostriformis bugensis*) are ecologically significant invaders in the Laurentian Great Lakes (Hebert *et al.* 1989, Vanderploeg *et al.* 2002). These mussels are endemic to the Ponto-Caspian region of Eurasia, which encompasses the Black, Azov, Caspian, and Aral Seas. Discovered in the late 1980s (Hebert *et*

al. 1989, May and Marsden 1992, Mills *et al.* 1993), both mussels have established large populations in all of the Great Lakes except Lake Superior, triggering wide-scale ecosystem changes (Vanderploeg *et al.* 2002).

Despite the importance of the quagga mussel in freshwater ecosystems, its taxonomy remains elusive. The mussel was first described from the Southern Bug River in 1890 by Andrusov (1897), and named as the new species *Dreissensia bugensis* (now a synonym with *Dreissena bugensis*). Since then, workers have treated *D. bugensis* as a full species or as a subspecies of *D. rostriformis* (re-

*Corresponding author. E-mail: kelly.johnr@epa.gov

viewed in Rosenberg and Ludyanskiy 1994). Traditional taxonomic classifications of *Dreissena* depend on a series of shell characters (Logvinenko and Starobogatov 1968, Skarlato and Starobogatov 1972, L'vova and Starobogatov 1982, Starobogatov 1994). However, efforts to classify dreissenid taxa using such an approach have had limited success (Rosenberg and Ludyanskiy 1994). The difficulty involving the identification of dreissenid mussels on the basis of morphology is due to their great intraspecific phenotypic variation and overlapping shell characters (Rosenberg and Ludyanskiy 1994; Claxton *et al.* 1997, 1998). Taxonomic keys discriminate *D. polymorpha* from *D. bugensis* primarily based on the presence or absence of the longitudinal carina or ridge at the ventro-lateral edge of the shell (Skarlato and Starobogatov 1972, Starobogatov 1994, Rosenberg and Ludyanskiy 1994). In *D. bugensis*, the carina is reported to be absent or confined to the umbonal region. This disagrees with Andrusov's (1897: pp. 285-286) description of *D. bugensis* as having an arched carina. Such diagnostic disagreements in classification of *Dreissena* species necessitate further morphological investigation of the variability in this character.

Recently, DNA-based identification has become a tool for the detection and monitoring of invasive species, and has been used to clarify species identifications in cases of equivocal morphological data (Darling and Blum 2007). For dreissenid mussels, the application of genetic techniques (allozyme studies, DNA restriction enzyme digests, and sequencing) over the past few decades have provided genetic markers, which have been used to examine the phylogeographic structure of dreissenid species and reevaluate their systematic relationships (Spidle *et al.* 1994; Stepien *et al.* 2002, 2003; Therriault *et al.* 2004; Gelembiuk *et al.* 2006; and references therein). Using DNA characters Therriault *et al.* (2004) argued that the quagga mussel is a freshwater race of *D. rostriformis*. However, other molecular systematic studies on *Dreissena* that employed additional DNA characters (Stepien *et al.* 2003) or greater sampling effort (Gelembiuk *et al.* 2006) treated *D. bugensis* as a full species. Since the nomenclature of the quagga mussel remains unresolved, we here refer to it as *D. bugensis* or the quagga mussel. Using the restriction analysis of the mitochondrial (mt) cytochrome *c* oxidase subunit 1 (COI) gene, Claxton *et al.* (1997) confirmed diagnostic importance of external shell characters in the discrimination between *D. bugensis* and *D. polymorpha*. L'vova and Starobogatov (1982) illustrated

differences among *D. bugensis*, *D. polymorpha*, and *D. stankovici* in the anterior and posterior muscle scars. Aleksenko (1994) used the anterior muscle scars on the myophore plate as a diagnostic character to discriminate *D. bugensis* from *D. polymorpha*. If phenotypically stable, such a character may prove useful for the separation of species when only umbonal shell sections are available. The present study employed the COI mt gene sequences to confirm the identity of dreissenid mussels in the Lake Superior basin and to determine if the anterior muscle scar characteristic can reliably separate *D. bugensis* and *D. polymorpha*.

We report the results of morphological and genetic surveys of dreissenid mussels in the Duluth-Superior Harbor and lower St. Louis River, including the first record of the quagga mussel in the Lake Superior basin. This study is part of a larger research project designed to develop an early detection monitoring program for vulnerable Great Lakes harbors and embayments. Our results indicate that *D. bugensis* has colonized sites throughout the harbor-river study area and dispersed into the adjacent shoreline in Lake Superior. We also discuss aspects of the quagga mussel range expansion in North America and Eurasia.

MATERIAL AND METHODS

Collection and Identification of Mussels

Collections were made during September 2005 and August-October 2006 at sites within the Duluth-Superior Harbor and St. Louis River using various sampling techniques (Table 1). During 2005, samples were collected with a standard Ponar (532 cm²; 1–3 grabs per site) in the harbor only (Zone 1, Fig. 1a). During 2006, samples were collected throughout the entire study area (Zones 1–3) using a petite Ponar (236 cm²; 1 grab per site). Samples were collected from depths of 0.2–13.6 m. Ponar sites (totaling 45 sites in both years) were selected using a spatially-balanced, random-probability design (Stevens and Olsen 2004). To supplement the Ponar collections, additional material was gathered using three qualitative sampling methods. Surface bottom sediments were sampled by sled dredge (width 0.38 m, mesh 500 μ m; two 50-m tows per site). Newly settling mussels (i.e., spat) were collected using Hester-Dendy traps (1 per site) deployed for about 6–8 weeks (July–August). A 500- μ m mesh sweep net (generally 1 per site) was used to gather sessile mussels attached to bottom substrata or submerged vegetation. These samples

TABLE 1. Summary of dreissenid collections examined for presence of *Dreissena bugensis* and *Dreissena polymorpha* in Duluth-Superior Harbor and lower St. Louis River in 2005–2006. Ponar sampling sites were selected by spatially-balanced, random probability design. 45 sites in Zone 1 were sampled with Ponar in both 2005 and 2006. In 2006, 11 subzones were intensively sampled using other sampling gears, providing an additional 44 samples system-wide. *Dreissena bugensis* was found in 6 of 11 subzones; *D. polymorpha* was encountered in 10 of 11 subzones.

Year	Location	Sampling effort	Depth range (m)	Frequency of occurrence (% of sample sites)		Mean density, <i>D. polymorpha</i> (#/m ²)	# dreissenids collected; (percent identified to species)
				<i>D. bugensis</i>	<i>D. polymorpha</i>		
2005	Zone 1 (Harbor)	70 Ponars	0.2–13.6	3	30	177	268 (95%)
2006	Zone 1 (Harbor)	45 Ponars	0.5–13.4	4	18	107	333 (84%)
	Zone 2 (mid-St. Louis River)	25 Ponars	0.5–12.0	0	24	88	153 (76%)
	Zone 3 (St. Louis River)	8 Ponars	0.9–5.4	0	0	0	0
	11 targeted subzones, excluding lakeside Minnesota Point	2 50-m sled tows, 1 Hester-Dendy trap, and 1 sweep net per subzone	Depends on subzone	20	64	not estimated due to qualitative sampling	101,156 including juveniles (7%)

were collected in 11 targeted subzones within the study area and one site on the Lake Superior side of Minnesota Point (Fig. 1a). Samples were preserved in 10% formalin or in 70% ethanol.

In the laboratory, mussels were separated from other material under a dissecting microscope, identified to species when feasible, and enumerated. Specimens were assigned to either *Dreissena polymorpha* or *D. bugensis* based upon the examination of shell characters: (1) presence/absence of the ventro-lateral carina, (2) degree of flatness of the shell at the ventral region, (3) overlap of valves, and (4) curvature and asymmetry of the ventral margin of valves (Skarlato and Starobogatov 1972, Pathy and Mackie 1993, Rosenberg and Ludyanskiy 1994, Claxton *et al.* 1997, Mackie 1999). Both external shell features and molecular markers were utilized to investigate the diagnostic usefulness of the anterior muscle scars. We examined the anterior adductor and anterior pedal retractor muscle scars on the myophore plate in 20 *D. polymorpha* and 3 *D. bugensis* individuals which were previously designated using external shell characters. The ages of quagga mussels were determined by shell sectioning (Hebert *et al.* 1989). Representative voucher specimens of *D. bugensis* were de-

posited in the Field Museum of Natural History, Chicago, Ill (Cat. #310454).

Genetic Procedures

Molecular methods were utilized to confirm initial morphological identifications of mussels collected in September 2005. One *D. bugensis* and five *D. polymorpha* individuals, and 20 additional dreissenids not subjected to morphological analyses, were processed for DNA-based identifications. Mussel tissues from these mussels were removed and analyzed using the DNeasy tissue kit (Qiagen). A 600 base pair (bp) fragment of the COI gene was amplified using the primers LCO1490 and HCO2198 as described by Folmer *et al.* (1994). PCR cycling parameters consisted of an initial denaturation step at 94° for 5 min, followed by 35 cycles of 30 s at 94°C, 60 s at 50°C, and 60 s at 72°C, with a final extension of 15 min at 72°C. Bi-directional sequencing was performed directly on PCR products using amplification primers. Comparisons with published GenBank sequences of *Dreissena* were made based on 476 bp of the COI gene using the Basic Local Alignment Search Tool (BLAST). Sequences obtained in this study were submitted to GenBank: accession numbers are EU484436 for

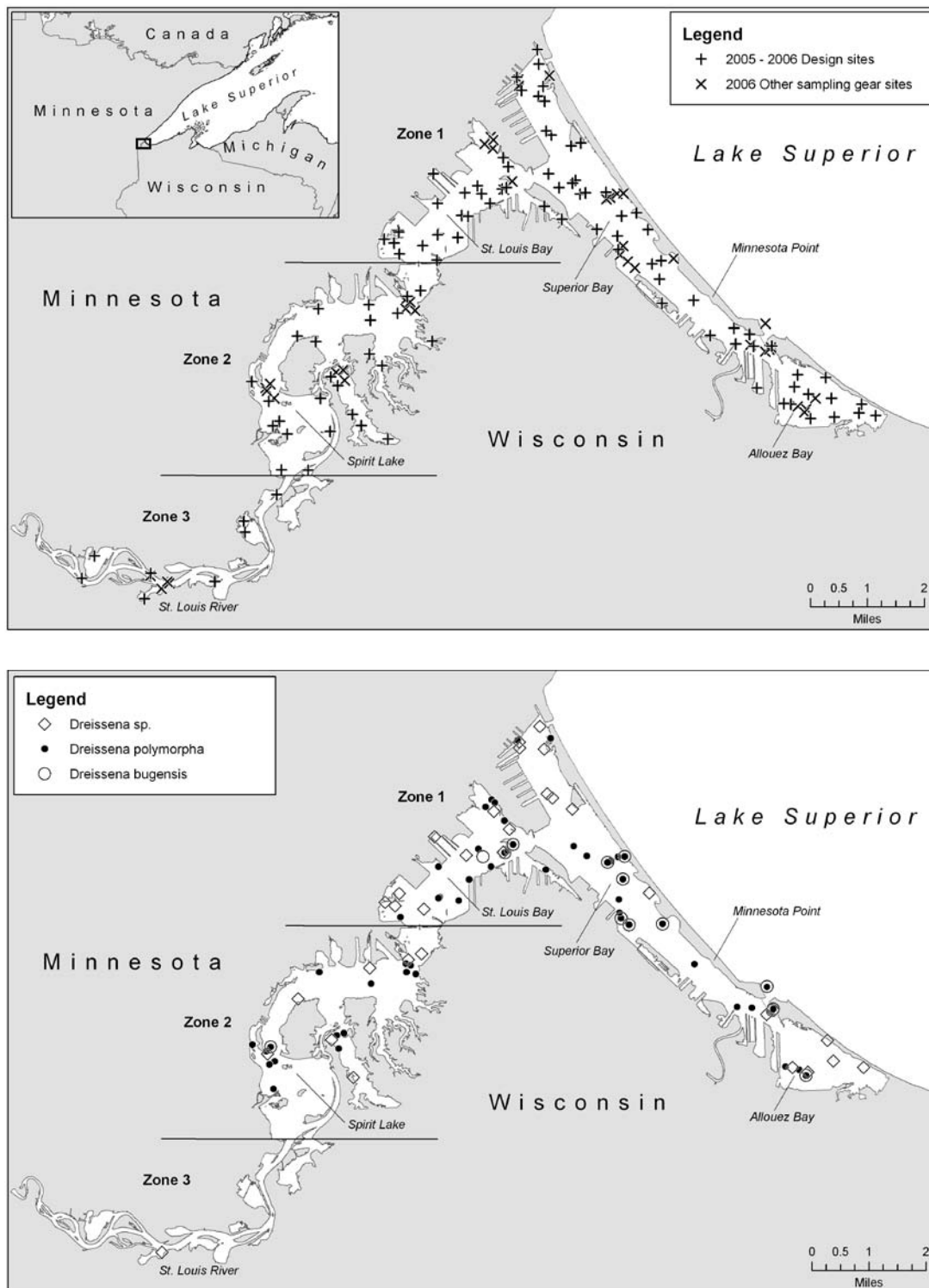


FIG. 1. a) Map showing sampling sites in 2005–2006. Design sites were sampled exclusively with Ponar. In 2006, additional sites were sampled in 11 subzones using other sampling gears (dredge, sweepnet, artificial substrates). b) Map showing localities of *Dreissena bugensis*, *D. polymorpha*, and unidentified (mostly juvenile) individuals of *Dreissena* (only shown where no species-level identifications were made).

Dreissena bugensis, EU484431-EU484435 for morphologically-identified *Dreissena polymorpha*, and EU484437-EU484456 for *D. polymorpha* specimens that were not morphologically identified prior to genetic analysis.

RESULTS AND DISCUSSION

Occurrence and Identification

Both the mitochondrial gene COI sequence and morphological analyses of bivalves from the western Lake Superior basin confirmed the presence of two species of *Dreissena*: *D. polymorpha* and *D. bugensis*. The former was previously known to occur in Lake Superior (specifically, Duluth-Superior Harbor), whereas the latter is a new species record for the basin. We collected over 100,000 *Dreissena* mussels (Table 1). Of those identified to species, more than 99% were *D. polymorpha*. The zebra mussel was distributed throughout the harbor and the lower St. Louis River, reaching as far up-river as Spirit Lake (Fig. 1b). The quagga mussel was initially discovered in September 2005, when single individuals (ranging in length from 4.5 to 26.5 mm) were identified among *D. polymorpha* druses in Superior Bay, and Allouez Bay near the Superior entry (the specimen confirmed by DNA analysis). In the following year, the quagga mussel was detected in the same areas, as well as in St. Louis Bay and in Spirit Lake (Fig. 1b). In 2006, it was collected in six of the 11 sampled subzones, and each sampling gear type yielded quagga mussels. In addition, it was found on the Lake Superior side of Minnesota Point in 2006 (Fig. 1b). The probability of detecting the quagga mussel increased by supplementing quantitative Ponar sampling with other, more qualitative collection methods (Table 1). These methods included sampling over large areas and across various bottom types with sled dredges, collecting settling mussels with Hester-Dendy traps, and intensive sweeping of dense macrophyte stands with dip nets.

Deep- and shallow-water phenotypes of *D. bugensis* have been described from the lower Great Lakes (Dermott and Munawar 1993, Claxton *et al.* 1998). Mussels we collected matched the description of the shallow-water phenotype.

The ventro-lateral carina has been used as the key character in the separation of *Dreissena* species (Skarlato and Starobogatov 1972, Pathy and Mackie 1993, Starobogatov 1994, Rosenberg and Ludyanskiy 1994). *Dreissena bugensis* shells from Lake Superior possessed the ventro-lateral region varying

from broadly rounded to strongly arched (Fig. 2). The carina, when present, was confined typically to the proximal 1/3 of the shell length, becoming obsolete posteriad. One *D. bugensis* individual from the harbor possessed a rather strong carina that extended posteriad, sloping downward (Fig. 2D). *Dreissena polymorpha* was identifiable by having a pronounced carina at the ventro-lateral edge of the shell, running the entire shell length. These results suggest that traditional assignments of *Dreissena* specimens to *bugensis* or *polymorpha* based primarily on the presence/absence of carina could result in incorrect identifications.

The ventral region of *D. bugensis* bulged ventrally in end view, while that of *D. polymorpha* was truncated to concave (Fig. 2B, E) (e.g., Mackie 1999). The valves of *D. bugensis* overlapped at the posterior region and sometimes along the ventral margin of the shell (Fig. 2B), although this overlap often was more apparent in juveniles (< 5 mm) than in adults (Claxton *et al.* 1997). The valves of *D. polymorpha*, joining together in a midventral line of the shell, were more symmetric than those of *D. bugensis* (Fig. 2B, E).

L'vova and Starobogatov (1982) proposed discriminating between *D. bugensis* and *D. polymorpha* on the basis of the anterior adductor and anterior pedal retractor mussel scars on the myophore plate. *Dreissena bugensis* was reported to possess an elongated scar outline nearly twice as long as wide (Fig. 2C), whereas that of *D. polymorpha* was characterized by more even dorsal and ventral aspects (Fig. 2F). We established that the shape of the anterior muscle scars varied markedly among *D. polymorpha* individuals (Fig. 2F, G) and was discordant with the external shell features and COI gene sequences. Specifically, of the five morphologically designated *D. polymorpha* individuals, whose identity was verified by DNA sequence analysis, two clearly exhibited anterior muscle scar features described for *D. bugensis* (Fig. 2G). We conclude that the shape of anterior muscle scars has limited, if any, diagnostic utility for these two taxa.

Genetic analysis revealed that the quagga mussel from the Lake Superior basin was genetically identical at the COI gene to other *D. bugensis* populations from the Great Lakes and Europe (e.g., corresponding to GenBank accession number DBU47651 of Baldwin *et al.* 1996; AF096765 of Claxton *et al.* 1998, AF510504 of Theriault *et al.* 2004, and DQ840132 of Gelembiuk *et al.* 2006). Our mitochondrial gene COI sequences of *D. polymorpha* were 100% identical to previously pub-

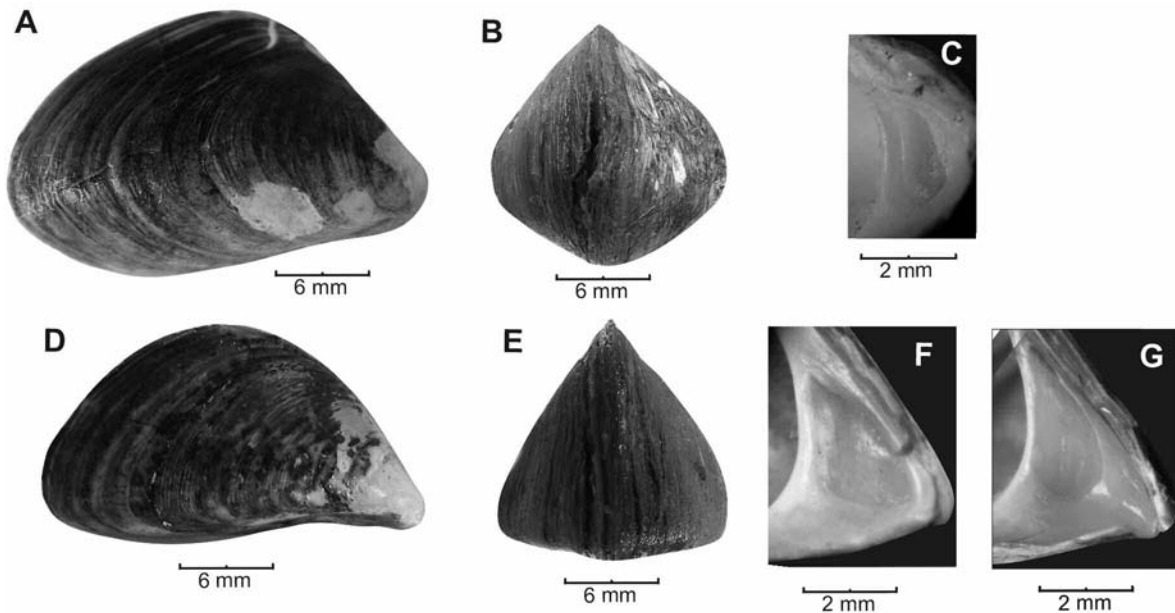


FIG. 2. *Dreissenidae* of the Lake Superior basin. *Dreissena bugensis*: non-carinate shell, lateral view (A); non-carinate shell, end view (B); carinate shell, lateral view (D); and anterior adductor and anterior pedal retractor muscle scars (C). *Dreissena polymorpha*: end view (E) and anterior adductor and anterior pedal retractor muscle scars (F, G). Logvinenko and Starobogatov's (1968) figure of *Dreissena rostriformis pontocaspica* from the Caspian Sea resembles carinate *D. bugensis* from the Lake Superior in overall shell morphology.

lished GenBank haplotypes of Gelembiuk *et al.* (2006), all of which were reported from the Great Lakes.

Population Characteristics

During 2005, the largest quagga mussel collected was 26.5 mm long and estimated to be at least 2 years old, suggesting that the initial introduction of *D. bugensis* occurred no later than 2003. During August–September 2006, our *D. bugensis* collections were dominated by small individuals with shell sizes up to 3 mm long (Fig. 3). The largest quagga mussel shell collected in 2006 was 30.5 mm long.

The quagga mussel occurred at an extremely low density < 1 individual m⁻² at all sites. Five individuals were identified from 2005–2006 Ponar samples, whereas other sampling gears yielded another 57 individuals. Based on repeated Ponar sampling at 45 sites in Zone 1, there was no difference in the overall frequency of occurrence at these sites between years (Table 1). This 1-year comparison using repeated sites indicates a rapid expansion was not occurring in the harbor (Zone 1) between 2005 and 2006. In 2006, the more spatially-extensive

sampling documented a wider presence of the quagga (Fig. 1b); however, no repeated sampling is available to characterize time trends across the whole study area. To date, all results suggest the quagga mussel is likely at an initial colonizing stage. In comparison, *D. polymorpha* population has spread throughout Zones 1 and 2 (Fig. 1b) since its discovery in the Duluth-Superior Harbor in 1989, and its density during 2005–2006 averaged at least two orders of magnitude higher than the quagga mussel (Table 1). At the later stages of invasion in the lower Great Lakes, *D. bugensis* has become the dominant dreissenid species, replacing *D. polymorpha* (Mills *et al.* 1999, Vanderploeg *et al.* 2002).

Dispersal

Since the early 1940s, the geographical range of the quagga mussel has expanded from the Southern Bug River and estuary in the northwestern Black Sea coast to major Ponto-Caspian drainages, Western Europe, and the Great Lakes of North America (Zhuravel 1967, Starobogatov 1994, Therriault *et al.* 2004, Karatayev *et al.* 2007, Molloy *et al.* 2007). The quagga mussel has been far slower in its

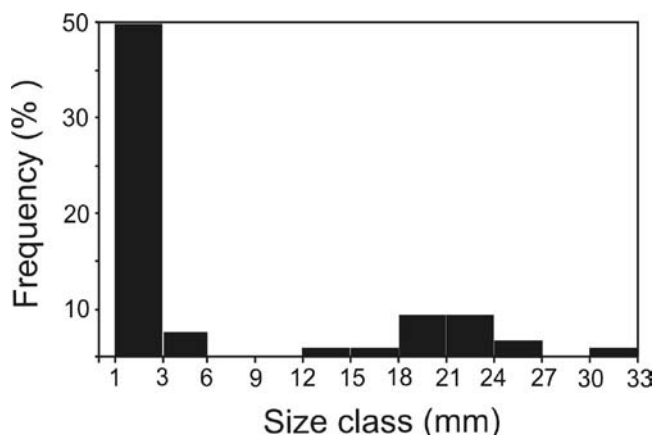


FIG. 3. Length-frequency distribution of *Dreissena bugensis* from the St. Louis River estuary in August–September 2006. $n = 59$.

range expansion within the Great Lakes basin compared to *D. polymorpha*. Discovered in 1988, the zebra mussel extended its distribution explosively, invading all the Great Lakes by 1990 and reaching the Illinois, upper Mississippi, and Hudson Rivers the following year (Hebert *et al.* 1989, Benson *et al.* 2007). In contrast, the quagga mussel was first collected in 1989 and has since been slowly colonizing the lower Great Lakes and St. Lawrence River system (Mills *et al.* 1993, 1999; Benson *et al.* 2007). Its appearance in Lake Michigan was recorded nearly a decade after the first detection in the Great Lakes basin (Mills *et al.* 1993, Nalepa *et al.* 2001). Our new record for *D. bugensis* extends its distribution to all the Laurentian Great Lakes.

The chronology of discoveries of the quagga mussel may not accurately reflect the true pattern of its introductions. In habitats where the zebra mussel resided, *D. bugensis* has been not been detected early in its colonization. For example, the quagga mussel has cryptically colonized major river drainages of Europe. In reservoirs on the Volga and Dniester Rivers in Eastern Europe, the quagga mussel was undetected or misidentified as *D. polymorpha* for at least 6 years (Antonov 1993, Shevtsova and Grigorovich 1998). In the Danube and Don River drainages, it was overlooked for up to 17 years (Grigorovich and Afanasiev 1996, Zhulidov *et al.* 2004). One of us (IAG) was unable to find *D. bugensis* in 2001 in two areas in the western Lake Superior basin near where this species was present in 2005–2006 (Grigorovich *et al.* 2003). The quagga mussel may have been introduced into the Lake Superior basin after 2001, in concordance with the age

of the mussels we collected. Alternatively, *D. bugensis* simply may have been missed in previous surveys. The present study included more intensive sampling and used molecular markers in cases where few morphological characters were available for classification of the species.

Results from this study show that the coupling of conventional morphological and molecular approaches is essential for early-detection monitoring of quagga mussel invasions.

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