

Exotic species replacement: shifting dominance of dreissenid mussels in the Soulanges Canal, upper St. Lawrence River, Canada

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Abstract. During the early 1990s, 2 Eurasian macrofouling mollusks, the zebra mussel *Dreissena polymorpha* and the quagga mussel *D. bugensis*, colonized the freshwater section of the St. Lawrence River and decimated native mussel populations through competitive interference. For several years, zebra mussels dominated molluscan biomass in the river; however, quagga mussels have increased in abundance and are apparently displacing zebra mussels from the Soulanges Canal, west of the Island of Montreal. The ratio of quagga mussel biomass to zebra mussel biomass on the canal wall is correlated with depth, and quagga mussels constitute >99% of dreissenid biomass on bottom sediments. This dominance shift did not substantially affect the total dreissenid biomass, which has remained at 3 to 5 kg fresh mass /m² on the canal walls for nearly a decade. The mechanism for this shift is unknown, but may be related to a greater bioenergetic efficiency for quaggas, which attained larger shell sizes than zebra mussels at all depths. Similar events have occurred in the lower Great Lakes where zebra mussels once dominated littoral macroinvertebrate biomass, demonstrating that a well-established and prolific invader can be replaced by another introduced species without prior extinction.

Key words: exotic species, zebra mussels, quagga mussels, *Dreissena*, biological invasion, biomass, competitive exclusion.

Few studies have documented the replacement of one exotic species by another. It is not known whether this situation reflects the rarity of such events or merely a lack of research attention. Most assessments of an invader's impact are concerned with its interactions with native biota (e.g., Ricciardi et al. 1996, 1997, Juliano 1998, Byers 2000, Kiesecker et al. 2001). Biotic resistance theory assumes that antagonistic interactions (e.g., competition) with incumbent species limit invasion opportunities for new arrivals (Case 1990, Vermeij 1991), although it is now recognized that facilitative interactions among exotic species occur frequently (Simberloff and Von Holle 1999, Richardson et al. 2000, Ricciardi 2001). Less information is available on species replacement or shifts in dominance among invaders (but see Dick and Platvoet 2000, Bachmann et al. 2001, Lohrer and Whitlatch 2002), in spite of the obvious implications these events have for community stability. We docu-

ment a dramatic shift in dominance between invasive aquatic invertebrates in a riverine habitat.

During the early 1990s, the St. Lawrence River was colonized by 2 closely related Eurasian mollusks, the zebra mussel *Dreissena polymorpha* and the quagga mussel *D. bugensis*. Quagga mussels were only recognized as a morphologically and genetically distinct species in 1991 (May and Marsden 1992). In 1991, both species were found attached to navigation buoys in the outflow of Lake Ontario, the source of the St. Lawrence River and, therefore, might have begun to colonize the river at about the same time (Mills et al. 1993). Within a few years, the zebra mussel formed dense populations of 10³ to 10⁴ individuals/m² at several locations along the river between Lake Ontario and Quebec City (Mellina and Rasmussen 1994, Ricciardi et al. 1996, 1997), whereas quagga mussel populations expanded at a much slower rate (Mills et al. 1993, Ricciardi et al. 1996). By 1991, a rapidly expanding zebra mussel population was established in the Soulanges Canal, an artificial waterway connected to the St. Lawrence River west of Montreal. In 1992, quagga mussels were dis-

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covered in the canal and remained at relatively low densities for several years (Ricciardi et al. 1996). We present data showing spatial and temporal patterns of change in exotic mussel biomass in the canal over the past decade.

Methods

The study area was the east section of the Soulanges Canal, which receives water from the St. Lawrence River at Lake St. Francois and empties into the lower Ottawa River at Pointe-des-Cascades, Quebec (lat 45°20'N, long 73°58'W). The depth of the canal is ~6 m and the bottom sediments are primarily mud with scattered cobble and woody debris. The canal walls are constructed from layers of timber with a top layer of cement. Water quality values measured from 1992 to 2003 were as follows: surface water temperature (May–October), 12 to 26 °C; mean calcium concentration [Ca^{2+}], 25.4 ± 1.7 mg/L; pH, 7.8 to 8.6; and mean dissolved oxygen (near the sediments), 6.1 ± 0.4 mg/L. Canal currents are sufficient to prevent thermal stratification and summer water temperatures usually varied by $<0.6^\circ\text{C}$ from surface to bottom.

Sampling of mussel populations began in October 1991 and continued during the summers (and occasionally the spring and autumn) of 1992 to 1995, 2002, and 2003. Dreissenid densities were estimated by the removal of mussels from substrates within $25 \text{ cm} \times 25 \text{ cm}$ (0.0625 m^2) polyvinylchloride quadrats by a SCUBA diver; 3 to 5 quadrat samples were taken randomly at each of 3 depths (surface = 1.5–2 m, middle = 2.5–3.0 m, bottom = 3.5–4.6 m) along the canal wall, all from the timber sections. Five quadrat samples were also taken randomly from the bottom sediments starting at least 2 m from the base of the wall. Mussels were scraped from the canal wall with a knife, and were collected from bottom sediments by manual removal of all hard (>1 cm) objects to a depth of 5 cm within the quadrat. The objects were taken to shore, where all mussels attached to these objects were removed with a scalpel and a bristle brush; this procedure extracted mussels >2 mm in size, but excluded recently settled juveniles.

Mussels were bagged, placed on ice in a cooler, and transported to a lab within 3 h of collection. Upon arrival, they were sorted to their respective species, blotted on tissue paper, and

weighed to the nearest 0.1 g fresh mass (wet mass including shells). Shell lengths were measured to the nearest mm using digital calipers. Mussels were identified to their respective species based on a combination of morphological characters (Pathy and Mackie 1993, Claxton et al. 1997).

Results

An incipient quagga mussel population (mean \pm SE = 11 ± 2 g/m²) was first observed on the canal walls in August 1992 (Fig. 1). Within 2 y, it increased by more than an order of magnitude, but still contributed $<4\%$ of the total dreissenid biomass. From 1991 to 1995, zebra mussels contributed $>96\%$ of the dreissenid biomass in the canal, dominating at all depths on the wall and on all available bottom substrates, including the shells of living and dead unionid mussels. No sampling was done between 1996 and 2002, but during this time quagga mussel biomass increased by a factor of 30. By 2002, quaggas constituted 79% of the total dreissenid biomass on canal walls.

Biomass of both species varied significantly with depth on the canal wall (Figs 2, 3). The upper limit of mussel patches began at 1 to 1.5 m below the water line. Zebra mussel biomass in the surface zone exceeded that of quaggas (Fig. 2) and constituted 70% of the total dreissenid biomass in August 2003, compared with ~40 to 50% in the previous year (Fig. 3). However, quaggas dominated dreissenid biomass at lower depths, and their shells were significantly larger than those of zebra mussels at all depths (Table 1). Shell lengths of zebra mussels were largest in the shallow zone ($F_{2,2} = 274.8$, $p < 0.038$), whereas those of quagga mussels did not differ across depths. For both species, shell size varied independently of biomass on the canal wall (zebra mussels: $p > 0.05$; quagga mussels: $p > 0.29$).

Species replacement on the bottom of the canal was nearly complete in 2003. Zebra mussel biomass declined by 4 orders of magnitude since 1994, when it had peaked at 936 g/m², whereas quagga mussel biomass increased to a similar amount (831 ± 194 g/m²) and constituted $>99\%$ of the total dreissenid biomass on bottom substrates in August 2003 (Fig. 4). Remarkably, only 2 living zebra mussels were collected from canal bottom at this time.

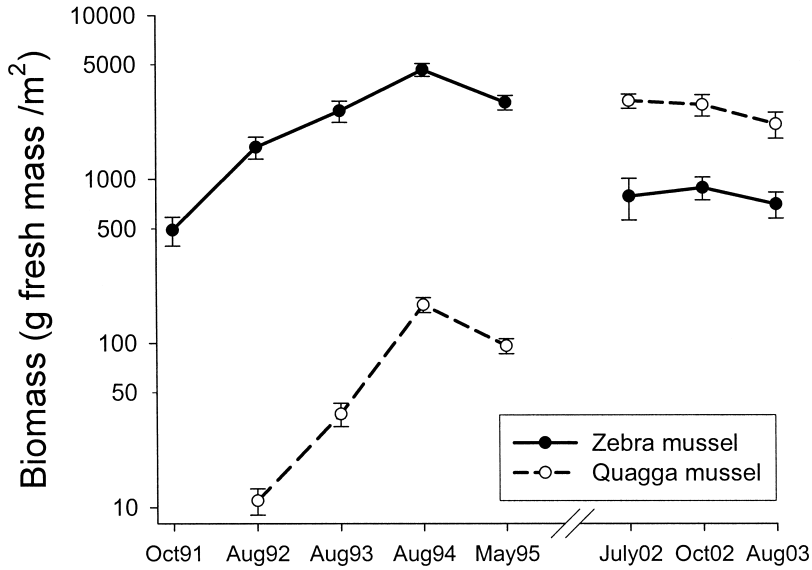


FIGURE 1. Mean (\pm SE) dreissenid biomass from all samples on the wall of the Soulanges Canal since 1991.

Discussion

Zebra mussels heavily colonized the shells of both living and dead unionid mussels in the Soulanges Canal during the 1990s, but quagga mussels contributed only a small proportion (<10%) of fouling biomass on unionids (Ricciardi et al. 1996). Unionids were extirpated from the canal by 1995 (Ricciardi et al. 1996).

Consequently, even empty unionid shells have become scarce (only 3 were found in 5 bottom quadrats in 2002 and none were found in 2003). Interestingly, zebra mussels rarely colonized quagga mussels on the bottom of the canal. We speculate that the disappearance of unionids partly contributed to the decline of zebra mussels on muddy sediments in 2 ways: 1) filtration currents created by living unionids may have

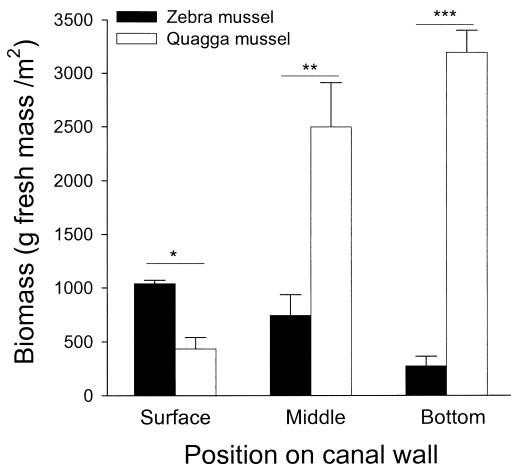


FIGURE 2. Mean (\pm SE) dreissenid biomass versus position on the canal wall, August 2003. Comparisons at each position were made using 2-sample *t*-tests on log-transformed data. * = $p < 0.05$, ** = $p < 0.005$, *** = $p < 0.0001$.

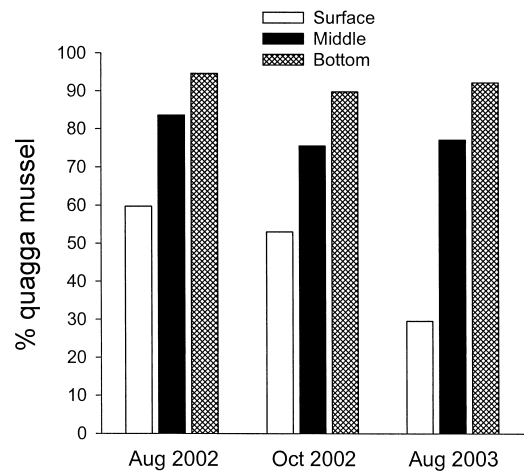


FIGURE 3. Percentage of dreissenid biomass represented by the quagga mussel at the surface (1.5–2 m), middle (2.5–3.0 m), and bottom (3.5–4.6 m) zones of the wall of Soulanges Canal, 2002 to 2003.

TABLE 1. Shell lengths of zebra and quagga mussels collected in August 2003 from the wall of the Soulanges Canal at 3 depths: surface = 1.5 m, middle = 3 m, and bottom = 4.6 m. Comparisons between species were made using *t* tests. *n* = sample size.

Depth	Species	<i>n</i>	Shell length (mm)				<i>p</i>
			Mean	SE	Min	Max	
Surface	Zebra	98	25.6	0.31	13.5	32.0	0.031
	Quagga	26	27.0	0.43	19.8	31.3	
Middle	Zebra	143	22.6	0.16	16.8	27.9	<0.0001
	Quagga	264	26.6	0.14	14.7	33.2	
Bottom	Zebra	63	18.9	0.29	14.3	27.1	<0.0001
	Quagga	229	25.8	0.15	16.4	31.5	

facilitated feeding by attached zebra mussels, offsetting their apparent energetic disadvantage with quaggas, and 2) unionid shells provide stable substrates for zebra mussels, which are poorly adapted to colonizing very fine sediments (Mellina and Rasmussen 1994). In contrast, during 2002 and 2003, quagga mussels not only dominated the remaining scattered cobble and wood debris, but also formed aggregations of 10 to 20 clumped, living mussels unattached to the fine sediments. A similar phenomenon involving dreissenid mussels occurs in Lake Erie (Botts et al. 1996). Our observations are consistent with European data that indicate quagga mussels are more abundant than zebra mussels

on silty substrates (Pligin 1984, Mills et al. 1996). In Lake Erie, zebra mussels remain dominant on fine sediments in the western basin, but have been replaced by the quagga mussel in the central and eastern basins (Jarvis et al. 2000).

The zebra mussel dominates only at shallow depths on the walls of the Soulanges Canal and a few other sites in the upper St. Lawrence River (AR, unpublished data), possibly because it has a higher upper thermal tolerance (Domm et al. 1993, Spidle et al. 1995) and survives longer periods of aerial exposure than the quagga mussel (Ricciardi et al. 1995). These physiological factors are important given that water levels in the canal may vary during the year by as much as

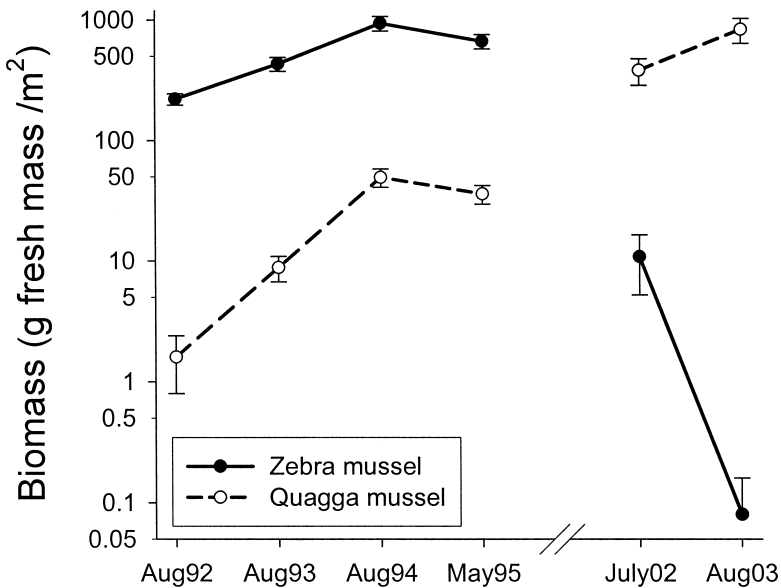


FIGURE 4. Mean (\pm SE) dreissenid biomass on bottom substrates in the Soulanges Canal since 1992.

1 m, thus potentially exposing mussels on the upper walls. The quagga mussel was initially abundant only at deep sites in the lower Great Lakes, so it was thought to be a cold-water species (Mills et al. 1993). However, over the past several years it has become increasingly common in littoral areas and survives in relatively warm waters (MacIsaac 1994, Mitchell et al. 1996, Mills et al. 1999, Jarvis et al. 2000).

The shift in dominance from quagga mussels to zebra mussels in the Soulanges Canal parallels similar events in the lower Great Lakes (Mills et al. 1999, Jarvis et al. 2000) and in the Dnieper River, Ukraine (Pligin 1984, Mills et al. 1996). Patterns of colonization of several Dnieper River reservoirs suggests that the zebra mussel rapidly invades newly formed habitats and dominates benthic biomass prior to the arrival of the quagga mussel. The quagga mussel typically colonizes the deeper areas of a reservoir before expanding into shallower depths occupied by the zebra mussel, coinciding with a decline in abundance of the latter species (Pligin 1984, Mills et al. 1996). In the Kiev reservoir, this species shift occurred within 8 y of quagga invasion (Mills et al. 1996), similar to the length of time in which quaggas became dominant in the Soulanges Canal (5–10 y; a precise estimate is unavailable as a result of the interruption in sampling during the late 1990s). The pattern was repeated in Lake Erie and Lake Ontario within 5 to 6 y (Mills et al. 1999, Jarvis et al. 2000).

Hypothesized mechanisms of species replacement

At least 3 hypotheses could explain the shift in dreissenid abundance in the Great Lakes–St. Lawrence River system. First, it may result from a differential competitive ability to exploit changing food regimes. Quagga mussels are more efficient filter-feeders (Diggins 2001) and are better adapted to acquiring food resources when food is scarce or when food quality is low (Baldwin et al. 2002). This hypothesis could explain why quagga mussel populations continued to increase in the upper St. Lawrence River while chlorophyll *a* levels declined in Lake Ontario throughout the 1990s (Johannsson et al. 1998, O. Johannsson, Department of Fisheries and Oceans, Canada, personal communication), although competition between these 2 species

for food has not been demonstrated (MacIsaac 1994, Baldwin et al. 2002).

Second, the shift may be a succession of *r*- and *K*-selected species. Zebra mussels have a typical *r*-selected life history (McMahon 2002). They release more eggs and devote a greater proportion of body tissue to reproduction than quagga mussels, which have lower respiration rates and larger body size (Stoeckmann 2003). Quaggas also settle at a larger size than zebra mussels, possibly because of a prolonged period of development in the plankton or a higher larval growth rate (Martel et al. 2001). A comparison of life-history traits in several closely related thiarid snails that invaded Martinique revealed that those species that produce numerous small offspring were successful during early invasions, whereas those that produce fewer, but larger, offspring were more successful as later invaders (research by B. Facon discussed in Hänfling and Kollman 2002). Moreover, the relative size of their invaded range, both in North America and Europe, suggests that zebra mussels are better dispersers than quagga mussels (Mills et al. 1999, New York Sea Grant 2003). All these factors indicate that the quagga mussel is more of a *K*-selected species compared with its congener. Therefore, the quagga mussel may be less adapted to colonizing disturbed habitats than the zebra mussel, possibly explaining why the latter still dominates the shallow strata of the Soulanges Canal walls, which are subject to annual ice scour (AR and FGW, personal observations).

Third, the recent expansion of quagga mussels into shallow, warm-water habitats could simply reflect genetic adaptation to these environments. As noted by Mills et al. (1996), because dreissenid mussels are genetically variable (Stepien et al. 2002) and can produce up to 1 million larvae per spawning event (Sprung 1991), rare alleles could rapidly increase in frequency with each generation. This process might be expedited by the particularly high variability in exotic dreissenid populations, which is similar to Eurasian populations and is probably the result of multiple introductions (Stepien et al. 2002).

Regardless of the mechanism, the ongoing species replacement in the Great Lakes–St. Lawrence River system demonstrates that even a prolific, well-established invader can be replaced by another invader without the latter re-

quiring prior extinction to gain a foothold. We did not sample from 1996 to 2001, but it is unlikely that zebra mussels went extinct and reappeared later in the canal during that period, given that their densities have remained high at local upstream sites in Lake St. Francois (AR, unpublished data). In fact, quaggas began to increase, by an order of magnitude, in the early 1990s while zebra mussels were reaching peak densities. This pattern seems to challenge biotic resistance theory, which suggests that undisturbed communities of competitive dominants inhibit invasion by species requiring similar resources (Diamond and Veitch 1981, Vermeij 1991). However, our observations are consistent with biotic resistance theory if the zebra mussel is (as we argue) not competitively dominant in the presence of its bioenergetically advantaged congener.

Our study provides the first evidence of species replacement between invasive mussels in a riverine habitat. In North America, the St. Lawrence is the only major river containing both zebra mussels and quagga mussels, and was the first major river to be invaded by either species. A dominance shift to quagga mussels could have significant ecological consequences if it occurs throughout the river. In Lake Erie and Lake Ontario, the quagga mussel has been implicated in the precipitous decline of the native deep-water amphipod, *Diporeia*, presumably through resource competition (Dermott 2001). If quagga populations exert greater filtration pressure than zebra mussels, then their expansion will further alter nutrient and contaminant cycling (cf. Endicott et al. 1998, Vanderploeg et al. 2002), as well as the downstream export of primary production. Changes in particle export might ultimately affect the ecology of the freshwater-saltwater transition zone in the St. Lawrence estuary, one of the most productive sections of the river (Vincent and Dodson 1999).

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