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Notes

Contrasting shell/tissue characteristics of *Dreissena polymorpha* and *Dreissena bugensis* in relation to environmental heterogeneity in the St. Lawrence River

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ABSTRACT

The zebra mussel, *Dreissena polymorpha*, is widespread in the St. Lawrence River while the conspecific quagga mussel, *Dreissena bugensis*, is found only in the Lake Ontario outflow region of the river. This situation provided an opportunity to evaluate *in situ* environmental and interspecific heterogeneity in shell and tissue growth. Shell dry weight, carbon content, and shell strength of *D. polymorpha* from the four spatially discrete water masses differed significantly. For instance, *D. polymorpha* total and tissue mass increased over the summer in the shallow fluvial Lac Saint-Pierre but decreased in the upstream and downstream water masses. Standardized shell mass and strength of *D. polymorpha* was lowest where the mussels experienced salinity or low calcium. Although the response pattern of mass and glycogen content for *D. polymorpha* was spatially complex, mussels from the stressful oligohaline estuary population had the weakest shells and lowest glycogen content, even though their standardized tissue mass was the heaviest. This disparity in shell and tissue response suggests that some aspect of shell physiology alone may be limiting these mussels in estuarine environments. Tissue characteristics of *D. polymorpha* and *D. bugensis* were similar at the site where both were present, but the shell strength of *D. bugensis* was only equivalent to the weakest of *D. polymorpha*. We also conclude that lighter shells might make *D. bugensis* more susceptible to predation or mechanical damage but may also offer a bioenergetic advantage that is contributing to its rapid displacement of *D. polymorpha* where the two species co-occur.

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Introduction

The physiological requirements of dreissenid mussels are often thought of as constraints on their regional distribution (Whittier et al., 2008), but these requirements may also apply at smaller spatial scales within the heterogeneous environment in large rivers (Jones and Ricciardi, 2005). In the St. Lawrence, both the dreissenid mussels inhabit divergent local environments including the outflow of Lake Ontario, the Ottawa River plume which is limited to the north shore below Montreal, the southern tributary plume found along the south shore below Lac Saint-Pierre, to the oligohaline upper estuary downstream of the Quebec City (Thorp et al., 2005). For the zebra mussel (*Dreissena polymorpha*) and the quagga mussel (*Dreissena bugensis*), these water masses present divergent physiological challenges that include salinity, low calcium, and hypoionic conditions. Calcium in particular is essential during larval shell production and subsequently for protection of settled adults from predation and mechanical damage (Boles and Lipcius 1997, Thorp et al., 1998). Shell building in low calcium environments requires greater energy expenditure (Russell-Hunter et al., 1981). In addition, the osmotic challenge presented by fluctuating salinity negatively impacts all stages of *Dreissena*'s life cycle (Kilgour et al., 1994, Fong et al., 1995). However, variability in the spatial distribution of these physiological challenges within a single river has the potential to produce spatially distinct responses within an ostensibly continuous distribution of mussels. In this study, we compared shell and tissue traits of *D. polymorpha* from two physiologically challenging local environments, the low calcium Ottawa River plume and brackish upper estuary, with two sites more conducive to *Dreissena*, the Lake Ontario outflow and southern tributary plume. We hypothesize that if the low calcium and brackish upper estuary are more stressful for the mussels, then the shell and tissue traits should vary accordingly. Furthermore, although both dreissenid species are believed to have arrived in North America together, the zebra mussel initially spread much more quickly than the quagga mussel. However, despite their early dominance, zebra mussels now are being displaced by quagga mussels in many locations where they co-occur in the Great Lakes and St. Lawrence River (Mills et al., 1999, Ricciardi and Whoriskey 2004, Wilson et al., 2006).

Changes in shell length are often used as a surrogate for inferring change in total mussel biomass (Young et al., 1996, Chase and Bailey

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1999a). This is despite evidence that under temperature stress or food limitation, *Dreissena* differentially allocate energy to reproduction over somatic maintenance and growth (Chase and Bailey 1999b, Stoeckmann and Garton 2001). In fact, the loss of somatic tissue and/or shell mass, termed degrowth, is not uncommon in mollusks (*sensu* Russell-Hunter et al., 1981). If there is also degrowth in dreissenids, then biomass, growth, and condition may not be as tightly linked to shell length as commonly assumed. Thus, as part of the species and site comparisons, we also evaluated whether the allometric relationship also varied.

Materials and methods

Mussels used for the comparisons in this study were collected in June and October of 2002 at sites representative of each of the principal water masses of the St. Lawrence (Fig. 1). The sites most conducive to *Dreissena* are the Lake Ontario (LO, 44° 59′ 19″ and 74° 49′ 45″) and southern tributary (ST, 46° 12′ 02″ and 72° 49′ 48″) influenced water masses. The contrasting stressful water masses are associated with the low calcium Ottawa River plume (OR, 46° 16′ 35″ and 72° 41′ 40″) and that of the brackish upper estuary (Est, 46° 59′ 47″ and 69° 48′ 21″). More than 20 years of data have been used to discriminate among these four physically–chemically divergent water masses (St. Lawrence Centre, 1996, Thorp et al., 2005). This 20-year data set documents the consistent interannual character and distinctiveness of the water masses, particularly in terms of parameters known to affect mussel physiology such as salinity and calcium content (Table 1). Note that the designation LOQ indicates quagga mussels collected at the LO site. At each site, 25–40 individuals of each species from a single boulder-sized rock were collected to represent the full size range at each site; no attempt was made to include smaller juveniles (<5 mm) if present. We chose to compare changes between June and October because late summer is a physiologically stressful time of the year for dreissenid mussels, when the decline in food availability is compounded by the higher costs of both spawning and maintenance metabolism related to higher temperatures (Stoeckmann and Garton 2001).

Table 1
Select chemical characteristics illustrating heterogeneity among the four St. Lawrence River water masses.

Parameter	Water mass			
	LO	OR	ST	Est
Conductivity (μS/cm)	305	80	272	244
Turbidity (NTU)	1–6	3–28	2–35	80+
Hardness [$CaCO_3$ (mg/L)]	123	61	104	95
Ca (mg/L)	36	18	31	28
Na (mg/L)	10	7	11	10
NO_2/NO_3 (mg/L)	0.24	0.27	0.32	0.26
Total P (mg/L)	0.01	0.08	0.052	0.043

Values are compiled from 20+ years of monitoring (St. Lawrence Centre, 1996). *Dreissena* (LO = Lake Ontario; OR = Ottawa River; ST = southern tributaries; Est = upper estuary).

Size, mass, and glycogen

All values presented are standardized to the grand mean of mussels in the study, 22 mm, unless otherwise noted. The lengths of all shells were measured to the nearest 0.01 mm with digital calipers. Measurement error for shell length, calculated by repeating measurements 10 times on six individuals ranging from 14 to 26 mm in length, was consistently small with a mean standard deviation of 0.075 mm and mean standard error of 0.048 mm. The soft body tissue was dissected from shell for a randomly chosen sub-sample of at least 24 individuals per site and the dry weight (DW) of both the shell and soft tissue was measured after subsequently drying the sample for 48 h at 60 °C. A separate sub-sample the soft tissue of 10 individuals per site by date combination was kept frozen until analyzed for glycogen content using a modified acid hydrolysis-phenol method (*sensu*;

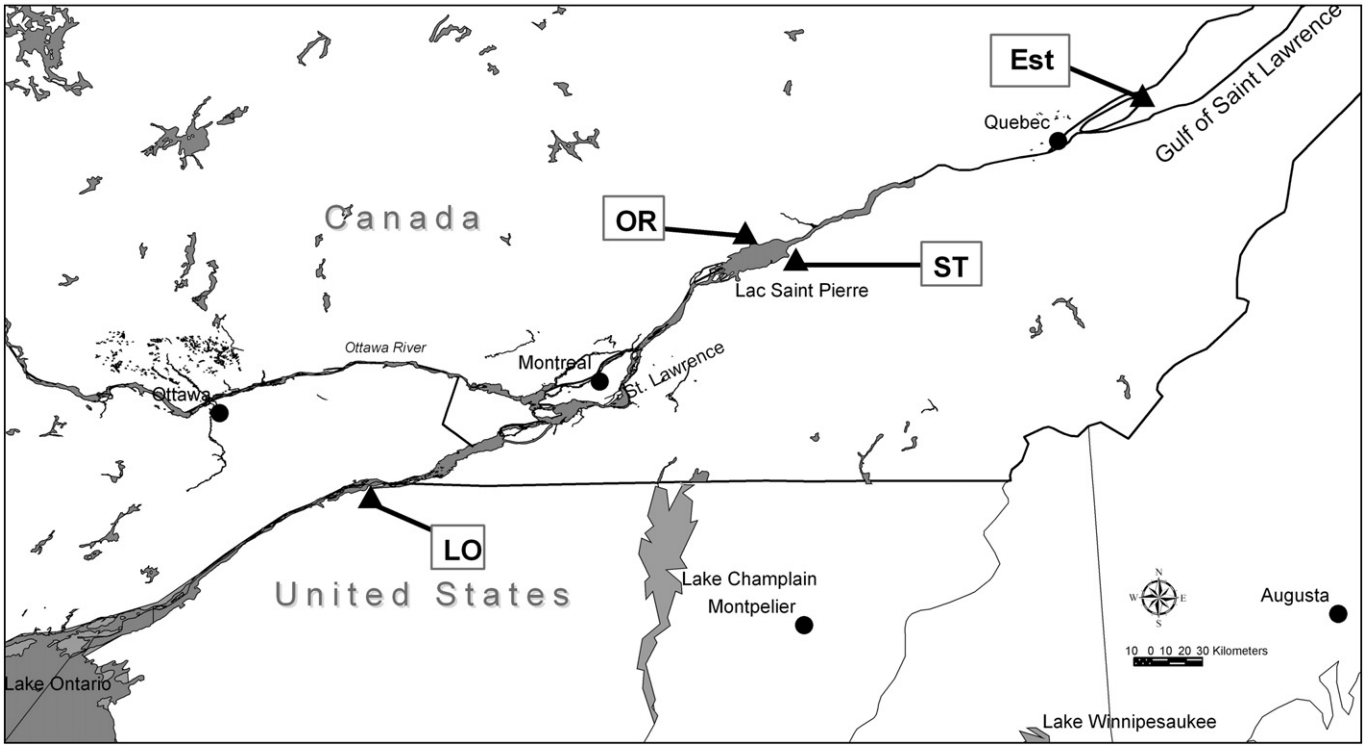

Fig. 1. Map of the St. Lawrence river-estuary system with the general location of sample sites are indicated. LO for the Lake Ontario water mass near Massena, NY; OR for the Ottawa River water mass along the north shore of Lac Saint-Pierre; ST for the southern tributary water mass along the south shore of Lac Saint-Pierre; and Est for the upper estuary at the eastern tip of Île d'Orléans, Québec.