Acclimation by invasive mussels: spatiotemporal variation in phenotypic response to turbidity

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Abstract: Increasing rates of invasion have led to shifts in dominance, and even replacement, of nonindigenous species. Shifts in invader dominance from the Zebra Mussel (*Dreissena polymorpha*) to a functionally similar and closely related species, the Quagga Mussel (*Dreissena rostriformis bugensis*), have occurred in several European and North American water bodies. We tested whether patterns of local dominance of these mussels in the St Lawrence River, a large heterogeneous system, could be explained by interspecific differences in morphological plasticity. We conducted field experiments across sites of contrasting turbidity (an important stressor for sessile filter feeders) to assess whether Zebra and Quagga Mussels grow at different rates, and whether such differences are related to variation in the morphology of their feeding organs (the palp-to-gill area ratio [PGR]) under different turbidity conditions. Turbidity had a small negative influence on the shell growth of both species, but Zebra Mussels were affected more severely. Across all sites, Zebra Mussels sustained reduced growth and greater mortality than Quagga Mussels. Spatial and temporal variation in PGR was observed for both species, but was more pronounced for Zebra Mussels. Reciprocal transplants suggested that these patterns reflect local acclimation rather than selection or genetic differentiation among local populations. Zebra Mussels exhibited significant shifts in PGR both across the growing season and after being transplanted from low- to high-turbidity conditions, whereas Quagga Mussels altered their PGR only while residing at, or after being transplanted to, a low-turbidity site. We propose that interspecific differences in morphological acclimation to low food conditions result in a competitive advantage for Quagga Mussels.
Key words: acclimation, bivalves, invasive species, phenotypic plasticity, reciprocal transplants, species replacement

Most studies of the ecological effects of invasions have been focused on interactions between the invading species and native species in the recipient community. As invaders accumulate within ecosystems (Ricciardi 2006, 2007), competitive interactions are expected to increase among the invaders themselves, with dominance shifts and species replacements becoming more prevalent (e.g., Lohrer and Whitlatch 2002, Russell et al. 2014, James et al. 2016). An ongoing example involves 2 closely-related Ponto–Caspian mollusks invading North American and European inland waters: the Zebra Mussel, *Dreissena polymorpha* (Pallas, 1771), and the Quagga Mussel, *D. rostriformis bugensis* (Andrusov, 1897). These species have similar morphology, life cycles, and functional ecology, but they exhibit contrasting invasion patterns. The Zebra Mussel is typically first to invade a lake or river, followed by the Quagga Mussel, which ultimately tends to dominate habitats where the Zebra Mussel was initially abundant (Mills et al. 1999, Orlova et al. 2005, Wilson et al. 2006, Zhulidov et al. 2010, Marescaux et al. 2015). Such events often involve concomitant declines in the Zebra Mussel population and impose consequences for contaminant cycling, the abundance and composition of benthic invertebrate communities, and system-wide food webs (Burlakova et al. 2014, Madenjian et al. 2015, Matthews et al. 2015). Proposed mechanisms of these dominance shifts include earlier spawning period, greater growth and survival rates, lower respiration rates, and more efficient food acquisition by Quagga Mussels (Mills et al. 1993, Stoeckmann 2003, Ram et al. 2012). None of these hypotheses explicitly considers the relative phenotypic plasticity of

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the 2 species, which could mediate their colonization and persistence in a heterogeneous environment (Davidson et al. 2011). For example, the Quagga Mussel exhibits distinct shell morphotypes in shallow- and deep-water habitats as a result of developmental plasticity, allowing it to more effectively use diverse substrates and, thus, to colonize a broader range of habitats than the Zebra Mussel (Peyer et al. 2010, 2011).

The sessile nature of suspension-feeding bivalves necessitates a capacity to adapt to changes in food quantity and quality, which vary seasonally and spatially in aquatic systems (Allan and Castillo 2007). Particle capture and processing depend on the size of the gills, which are primarily responsible for capture, and the labial palps, which are primarily responsible for particle sorting and rejection (Silverman et al. 1996, Baker et al. 2000, Bayne 2004). In many bivalves, the relative sizes of these organs can be adjusted to balance particle capture and sorting in response to varying concentrations of suspended particles across space and time. At high concentrations, inorganic particles reduce food quality, foul gill surfaces, and interfere with filtration, ingestion, and gas exchange across gill membranes (Aldridge et al. 1987, Madon et al. 1998), thereby imposing significant bioenergetic costs (Summers et al. 1996, Madon et al. 1998). To mitigate these effects, gills tend to become smaller and palps increase in size under conditions of high turbidity. The palp-to-gill area or mass ratio (PGR) of suspension-feeding bivalves varies with the ambient concentration of suspended sediment (turbidity) and the availability of food (e.g., Theisen 1982, Essink et al. 1989, Payne et al. 1995a, b, Barillé et al. 2000, Dutertre et al. 2009, Yoshino et al. 2013). For example, on the east coast of Australia both the native Sydney Rock Oyster, *Saccostrea glomerata*, and the invasive Pacific Oyster, *Crassostrea gigas*, exhibited changes in the relative masses of their gills and palps over time. However, *C. gigas* showed greater variation in PGR, suggesting greater flexibility in response to changing food resources, which could explain its higher growth rate compared to the native oyster (Honkoop et al. 2003). Zebra Mussels also appear capable of altering their PGR, at least spatially (Payne et al. 1995a, b). However, to our knowledge, seasonal variation in PGR has not been demonstrated for freshwater bivalves.

Both dreissenid mussel species became established in the St Lawrence River (SLR) in the early 1990s, and the Zebra Mussel rapidly became abundant along the length of the river (Ricciardi and Whoriskey 2004). Consistent with patterns observed elsewhere, dreissenid populations in areas of the river that were previously dominated by Zebra Mussels are now composed largely of Quagga Mussels (Ricciardi and Whoriskey 2004, Farrell et al. 2010). To gain insight into whether interspecific differences in phenotypic plasticity can account for this shift in dominance, we compared growth rates and variation in PGR of the 2 species across sites of contrasting turbidity in the SLR. The Quagga Mussel thrives in a broader range of food quantity and quality conditions (Baldwin et al. 2002, Orlova et al. 2005), including the deep waters of the Great Lakes where food is relatively scarce (Mills et al. 1993, Nalepa et al. 2009) and the SLR at sites far downstream of Lake Ontario where phytoplankton biomass is lower and suspended sediment is higher (Hudon et al. 1996). Moreover, Quagga Mussels have lower respiration rates than Zebra Mussels (Stoeckmann 2003), and this difference is more pronounced under the stress of increased turbidity (Summers et al. 1996). Lower respiration rates translate into lower energetic costs, leaving more energy available for somatic growth and perhaps a greater capacity for morphological plasticity. Therefore, we predicted that the Quagga Mussel has a more variable PGR than the Zebra Mussel. We conducted field experiments to test the following hypotheses: 1) Turbidity has a stronger negative affect on Zebra Mussel growth than on Quagga Mussel growth. 2) The PGR of each species will vary through the growing season in relation to fluctuating turbidity. 3) For each species, mussels established at high-turbidity sites will have a higher PGR than conspecific individuals at sites of lower turbidity. 4) Either species transplanted to a site of contrasting turbidity will show a change in PGR, but the magnitude of this change will be greater in the Quagga Mussel.

METHODS

Mussel survival, growth, and PGR were examined at 8 SLR sites situated between Port Lewis (PL) and St-Laurent-de-l'Île-d'Orléans, Quebec (SL) (Fig. 1). Site selection was based on published reports (Frenette et al. 1989, Rondeau 1993, Rondeau et al. 2000) and an exploratory survey (by JO-P) that indicated that these sites had contrasting turbidity conditions, contained both mussel species in sufficient abundance (>100/m^2), and possessed artificial structures (floating docks) that could facilitate the deployment of growth cages and sediment traps. Experiments were deployed in marinas to reduce differences in flow and depth across sites. We avoided selecting sites of increasing turbidity along a downstream gradient to limit confounding covariation with stream position.

Shell-growth experiment

We conducted a field experiment to evaluate intra- and inter-specific differences in growth in relation to ambient variation in turbidity (hypothesis 1). We used modified fishing-tackle boxes (27 × 17 × 4 cm) as growth cages with each mussel isolated in its own compartment (4.4 × 2.5 × 4 cm), thereby allowing for successive growth measurements on the same individual. Each cage had 6 compartments on the long axis and 5 on the short axis (total of 30) and was ballasted to stand vertically in the water column (Fig. S1). The 2 broad faces of the cages (originally the top and bottom panels of the tackle boxes) were open and cov-

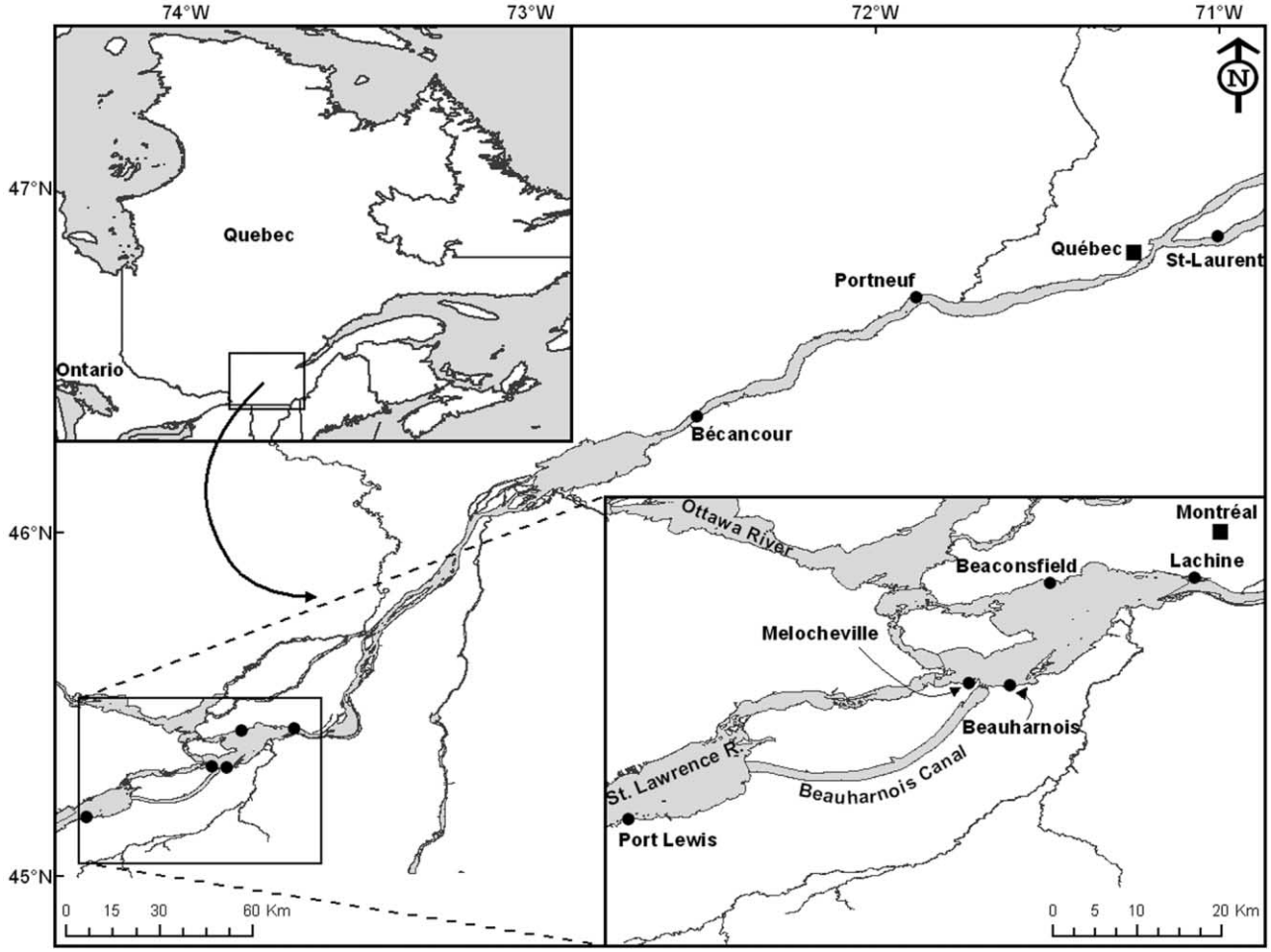

Figure 1. Location of sampling sites along the St Lawrence River.

ered with 4-mm plastic mesh secured with cable ties to permit the flow of water through the compartments (see Tuchman et al. 2004, Salazar and Salazar 2005).

Mussels used in experiments were selected from dreissenid clusters removed manually from docks or nearby rocks at each sampling site. Individuals of each species were carefully separated from the clumps and measured. To obtain detectable growth increments, we selected individuals of a size range typical of mussels <2 y of age: the mean, minimum, and maximum shell lengths were 17.9, 11.0, and 25.0 mm, respectively. We deployed 4 cages at each site, with 15 mussels of each species placed individually in compartments of each cage (total = 120 mussels per site). Depth can affect mussel growth rates (Garton and Johnson 2000, Karatayev et al. 2006), so we standardized cage depth by suspending cages from floating docks at 0.5 to 1.0-m depths at sites subjected to tidal regimes (floating docks were not used at PL, which is unaffected by tides).

We deployed cages in mid-May 2012, near the beginning of the growing season. We cleaned the cages and measured shell lengths of all mussels every 5 wk until the end of the growing season (early October). We measured and discarded dead mussels, and left their compartments empty. On the final visit, we transported mussels to the laboratory in individual plastic tubes and stored them in a freezer at –16°C for <3 mo, and we recorded the final shell length and dry mass of each mussel.

PGR measurements

We tested hypotheses 2 and 3 as follows. At 5-wk intervals coinciding with measurements taken during the growth experiment, we collected mussels from large stones or docks ≤~10 m from the cages at each site and transported them to the laboratory in 70% ethanol for soft-tissue measurements. On each occasion, we chose 20 Zebra Mussels and 20 Quagga Mussels similar in size to those used in the growth experiment. After an average preservation time of 6 wk (range: 8–64 d), we dissected the soft tissues of these mussels, laid them flat on a microscope slide, and photographed

them. We completed these tasks rapidly to avoid excessive drying. The areas (mm^2) of both labial palps (PA) and the right inner and outer demibranch gills were measured from the photographs with ImageJ (version 1.47f; Abramoff et al. 2004) calibrated with a stage micrometer. The combined area of the measured sides of the 2 demibranchs was multiplied by 4 to obtain the total gill area (GA) of the mussel (Barillé et al. 2000). The same procedure was used for the labial palps, except that the measured area was multiplied by 2 because their nonciliated inner surfaces are not involved in particle acquisition. PGR was calculated as 100 × PA/GA. Last, soft-tissue dry mass (STDM; palps, gills, and the remaining soft parts; dried at 60°C for ≥48 h) was measured for each mussel. We inspected correlations between shell length and STDM for both species to ensure that PGR was consistent across the size range of mussels used in our study.

Total suspended sediment measurements

We measured total suspended sediment (TSS) as a surrogate for turbidity by deploying a sediment trap at each site. The trap was cylindrical (94 cm long, 7.6 cm in diameter), one end was completely open (aperture size = diameter), and the other end had a removable collection cup. We deployed each sediment trap such that its aperture was at the same depth as the growth cage. Prior to deployment, we filled collection cups with ~5% formalin (volume/volume) and local SLR water (pre-filtered using a 20-μm mesh) in the field. We deployed sediment traps at the same time as the growth experiment (May 2012), and we collected sediment from the traps every 5 wk coincident with inspection of the growth cages. During each sampling event, we collected all sediment from the collection cup and refilled the cup with formalin and local SLR water before redeploying the sediment traps. We returned the sediment samples to the laboratory on ice and stored them at ~8°C in the dark. We later measured dry mass (TSS) of each sample (Appendix S1).

Reciprocal-transplant experiment

We conducted a reciprocal-transplant experiment between 2 sites of contrasting turbidity to compare the change in PGR of Zebra and Quagga Mussels (hypothesis 4) and to test whether observed differences were the result of phenotypic plasticity or genetic differentiation among isolated mussel populations. We collected mussels (mean shell length ± SD = 19.85 ± 1.62 mm) in mid-June from a low-turbidity site, PL, and a high-turbidity site, SL (see Fig. 2A, B for seasonal changes in ambient turbidity during the study period for these and other sites). We transported the mussels to the laboratory in coolers at <10°C, housed them in aquaria at 8°C, and fed them dehydrated algae (*Chlorella* sp.) for up to 2 d before returning them to the river. We deployed 6 cages identical to the ones used in the growth experiment at each

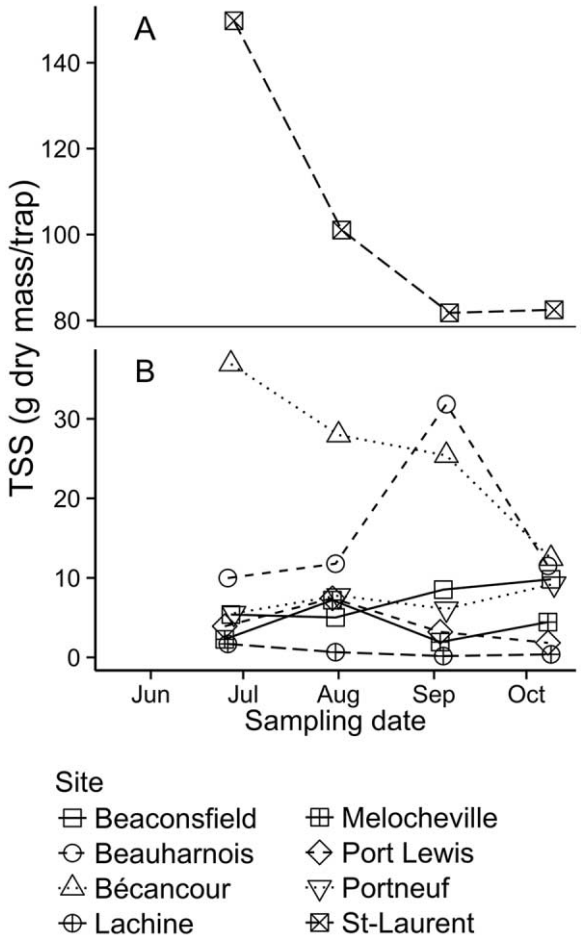

Figure 2. Dry mass of total suspended sediments (TSS) estimated from sediment traps at St Laurent (A) and 7 other sampling sites (B). Points represent sediments accumulated over 5 wk.

transplant site. In total, we randomly assigned 28 mussels to individual compartments in each cage according to their species and origin (i.e., 7 individuals of each species from PL and SL, respectively). We preserved additional mussels from each site in 70% ethanol for initial PGR measurements. We deployed cages at the 2 sites following the same procedure as for the growth experiment, except that mussels were retrieved and measured only at the end of the experiment. Field logistics were planned so that all mussels experienced the same travel time out of the water (Wong and Cheung 2003). We retrieved all mussels in October, after a 16-wk exposure time in the river.

We preserved mussels from both experiments, including the additional wild mussels collected from each site, on site in individual plastic tubes in 70% ethanol and later dissected them for PGR measurements as described previously. At each site, we measured wild mussels to calculate an independent PGR predictor variable for use in the PGR and growth models.

Statistical analyses

We conducted all statistical analyses with R (version 2.15.3; R Project for Statistical Computing, Vienna, Austria). To test factors affecting mussel shell growth, we developed a linear mixed model using the *lmer* function (*lme4* package, version 0.999999-2; Bates et al. 2013) appropriate for the nested experimental design (i.e., mussels clustered in cages within sites). This model accounted for within-mussel, within-sampling period, and within-sampling site growth correlations (Weisberg et al. 2010). We calculated the response variable, shell-length growth, as the difference in shell length between each sampling event (i.e., 0–5, 5–10, 10–15, and 15–20 wk) denoted Time5, Time10, Time15, and Time20, respectively. We retained negative growth measurements in the data set because negative mussel shell growth has been observed elsewhere (Downing and Downing 1993), and measurement errors with digital calipers could either under- or overestimate growth (Smith et al. 2010). Predictor variables were previous shell length (i.e., shell length at the beginning of the previous 5-wk period), species identity (ID), TSS during the 5-wk period, mean PGR of locally collected wild mussels (see PGR measurements), time (i.e., Time5, Time10, etc.), and sampling site. Although sampling sites were chosen subjectively, we treated this variable as a random effect for the purpose of evaluating general spatial patterns within the river. The relatively large number of sites and their even distribution supports viewing them as representative of the river as a whole and, hence, as a random effect. Mussel ID number and cage ID also were included as random effects.

We selected the final growth model following a 2-step approach in which we chose the best model's random effects component and then the best model's fixed effects component (Zuur et al. 2009). To determine the best random effects component, we fitted different models with the same fixed effects structure (i.e., all investigated variables and interaction effects including species ID) and varied the random component based on a combination of variables (i.e., sampling site, cage ID, and mussel ID). We selected the best random effects component by comparing these models according to the sample-size-corrected Akaike information criterion (AICc), the residual sum of squares (RSS), and Akaike weight (ω_i). The model having the smallest ΔAICc and the largest ω_i was the one chosen for the 2nd step in model selection. Models having ΔAICc > 2 were not considered plausible candidates for the best model (Burnham and Anderson 2002).

Following identification of the best random component, we used a similar procedure to select the best fixed structure of the growth model. Using the optimal random structure identified in the first step, we fitted several models with different combinations of the predictor variables. We then selected the best fixed structure based on the same procedure as for the random structure. After having found the model with the best random and fixed effects components, we calculated *p*-values for the fixed variables by applying Markov Chain–Monte Carlo (MCMC) simulations using the *pvals.fnc* function (*languageR* package, version 1.4; Baayen 2013).

We used a similar approach to evaluate models explaining factors related to PGR, but did not consider cage ID and mussel ID because they were not part of the experimental design. Predictor variables investigated for PGR were species ID, TSS, and time. We had PGR data for Time0, but these data were not included in the analysis because TSS measurements were not taken before that sampling event. We used the *glht* function (*multcomp* package, version 1.2-17; Hothorn et al. 2008) to conduct Tukey post hoc tests on the levels of categorical predictor variables of both the growth and PGR experiment models to identify pairwise significant differences. We present only the final models for both experiments (see Tables S1–S4S4 for details of alternative random and fixed-effect model components).

We analyzed the reciprocal transplant experiment with an analysis of variance (ANOVA) with main effects origin (O), destination (D), and species (S); all three 2nd-order interactions; the 3rd-order interaction; and the nested term, cage. The response variable was the observed change in PGR (ΔPGR), calculated for each mussel as the difference between PGR_{final} (the transplanted mussel's PGR at the end of the experiment) and $PGR_{initial}$ (the mean PGR of locally collected mussels at the beginning of the experiment). We performed post hoc Tukey tests with the *glht* function, and we used Welch's *t*-tests to evaluate whether changes in treatment groups' PGR were driven by adjusting their palps or gills.

RESULTS

Survivorship in experiments

Zebra Mussels sustained higher mortality than Quagga Mussels in the growth and reciprocal transplant experiments (Table 1, Fig. 3). In the growth experiment, Zebra Mussel survivorship was low at all sites except PL. At the end of the experiment, mean and median survival across all sites were 15 (7.3, omitting PL) and 5%, respectively. Mean and median Quagga Mussel survivorship across all sites were 77.5 and 78.5%, respectively. In the transplant experiment, mean survivorship across all 4 origin–destination groups was 33.5% for the Zebra Mussel and 69.5% for the Quagga Mussel. In an inventory of mussels collected from docks during the final sampling event, Zebra Mussels made up, on average, 94% of recently dead dreissenids (recency indicated by intact and uneroded shells) across all 8 sites, indicating that this species was differentially vulnerable to a system-wide stressor. Most Zebra Mussel mortality occurred during weeks 5 through 15 when temperatures were elevated (Figs 3, S2). Quagga Mussel mortality showed no clear temporal pattern.

Table 1. Percent survival of Quagga (Q) and Zebra (Z) Mussels after 20-wk growth and 16.5-wk transplant experiments. PL = Port Lewis (low turbidity), SL = St Laurent (high turbidity).

Experiment	Site	Start date (2012)	End date (2012)	% survival		
				Q	Z	Combined
Growth	Beaconsfield	22 May	09 October	87	0	43
	Beauharnois	23 May	08 October	72	2	38
	Bécancour	23 May	09 October	78	2	39
	Lachine	22 May	09 October	79	5	41
	Melocheville	21 May	08 October	83	5	43
	Port Lewis (PL)	21 May	08 October	75	69	73
	Portneuf	24 May	10 October	83	12	48
	St-Laurent (SL)	24 May	10 October	63	25	44
Transplant	PL→PL	16 June	10 October	83	43	63
	PL→SL	16 June	10 October	62	29	26
	SL→SL	16 June	10 October	52	31	42
	SL→PL	16 June	08 October	81	31	56

Shell growth experiment

The best shell growth model included the random effects of site and mussel ID and the fixed effects of previous shell length, species ID, TSS, mean PGR, time, and all 2-way interactions involving the main effect of species ID (Table 2). TSS had a negative, but small effect on shell growth, and the interaction between TSS and species identity was marginally significant ($p = 0.079$), suggesting that Zebra Mussel growth is slightly more affected by TSS than is Quagga Mussel growth.

Small mussels of both species grew more rapidly than large mussels. However, a marginally significant interaction between species and previous shell length ($p = 0.069$) suggests that this effect was more pronounced in Quagga Mussels. Growth rates of both species declined through the growing season. Quagga Mussels grew faster than Zebra Mussels early in the growing season at Time5 (species ID, $p = 0.053$) and Time10 (species ID × Time10, $p = 0.011$), but growth rates of both species converged by Time15 (indicated by the nonsignificant interactions of Time15 and Time20 with species ID; Table 2). Mean PGR had a significant negative effect on shell growth and interacted with species ID such that Quagga Mussels were disproportionately affected. For every 1% increase in the mean PGR, the growth increment was reduced by 0.03 mm for Zebra Mussels (the difference in the effect sizes of mean PGR and its interaction with species) and 0.36 mm for Quagga Mussels (Table 2).

PGR model

Mean PGR was not correlated with shell length or dry tissue mass for either species (Fig. 4A, B). PGR was higher for Zebra Mussels than for Quagga Mussels. Zebra Mussel PGR increased gradually throughout the study after week 5, but Quagga Mussel PGR was temporally invariant (Fig. 5A). PGR showed no clear longitudinal pattern within the river. For both species, PGR was highest at the 3 sites with the highest TSS (SL, Bécancour, and Beauharnois; Fig. 2A, B). The best PGR linear mixed model included the random effect of site and the fixed effects of species ID, TSS, time, and all 2-way interactions involving the main effect of species ID (Table 3). The linear mixed model also supported higher PGR for Zebra than Quagga Mussels, and significant interactions between species ID and Time15 and Time20 showed that this difference increased throughout the growing season (supporting hypothesis 2; see also Fig. 5A). In

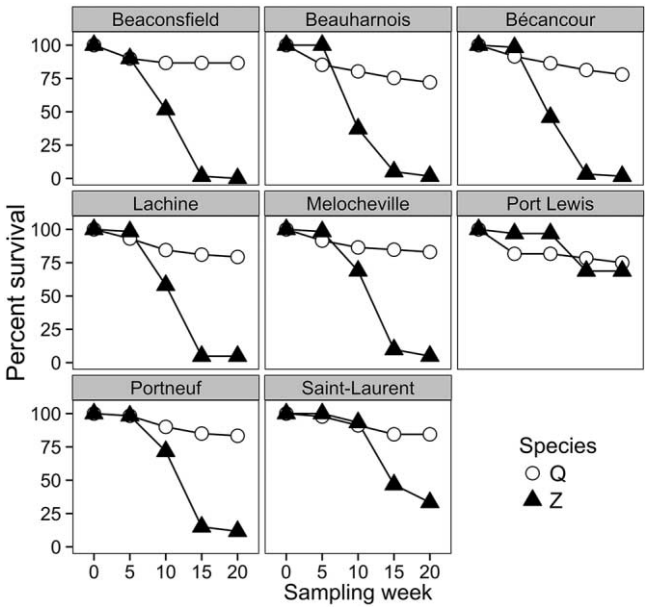

Figure 3. Percent survival for Quagga (Q) and Zebra (Z) Mussels used in the growth experiment over the study period and for each sampling site.

Table 2. Description of the best linear mixed model (LMM) (random structure = site + mussel identifier [ID]) for the growth experiment. SL_previous = mussel shell length at the beginning of the growth period, species = Quagga (baseline) and Zebra (Z), TSS = total suspended sediments, PGR_mean = mean palp-to-gill area ratio, time (sampling week) = 5 (baseline), 10, 15, or 20.

Variable	Coefficient	Standard error	p
Intercept	8.945	0.316	0.0001
SL_previous	−0.341	0.010	0.0001
SpeciesZ	−0.860	0.366	0.0530
TSS	−0.006	0.001	0.0001
PGR_mean	−0.360	0.105	0.0001
Time10	−0.286	0.040	0.0001
Time15	−0.580	0.047	0.0001
Time20	−0.422	0.051	0.0001
SpeciesZ × PGR_mean	0.325	0.104	0.0001
SL_previous × SpeciesZ	0.035	0.015	0.0694
SpeciesZ × TSS	−0.001	0.001	0.0790
SpeciesZ × Time10	−0.306	0.061	0.0108
SpeciesZ × Time15	−0.168	0.093	0.4188
SpeciesZ × Time20	−0.323	0.111	0.9168

spite of the high PGR observed at some high-turbidity sites (Fig. 5B), mean TSS/trap had a small overall negative effect on PGR that was more pronounced in Quagga than in Zebra Mussels (species ID × TSS interaction; Table 3).

Reciprocal-transplant experiment

The ΔPGR observed at the end of the reciprocal-transplant experiment was best explained by destination and species, which interacted with origin (Table 4). The 3-way interaction between destination, species, and origin was marginally significant. This interaction is demonstrated by the strong plastic response of Zebra Mussels transplanted from the low-turbidity site (PL) to the high-turbidity site (SL) (mean ΔPGR ± 95% CI = 1.13 ± 0.51; Fig. 6), which was driven by a disproportionate increase in palp area (initial mean = 11.4 ± 1.9 mm^2, final mean = 18.1 ± 4.5 mm^2) (Welch's $t_{14.68}$ = 4.8047, $p < 0.001$; Table S5). The PGR of Zebra Mussels transplanted from PL to SL increased such that it became similar to that of wild Zebra Mussels at SL and significantly higher than that of wild mussels at PL at both the beginning (T_0) and end (T_f) of the experiment (Fig. 7), as would be expected if observed changes in PGR reflected a plastic response to local environmental conditions. Zebra Mussels exhibited a greater change in PGR than Quagga Mussels only when transplanted from PL to SL, a result suggesting that both origin and destination influenced PGR.

The PGR of Quagga Mussels decreased when transplanted to PL from both PL (mean ΔPGR ± 95% CI = −0.40 ± 0.16) and SL (ΔPGR = −0.29 ± 0.16). The magnitudes of these changes were less than those of the changes observed for Zebra Mussels (Fig. 6). The decline in PGR of Quagga Mussels from PL to PL was driven by an increase in gill area (initial mean ± SD = 453.0 ± 70.3 mm^2, final mean = 541.0 ± 91.0 mm^2; Welch's $t_{63.92}$ = 4.525, $p < 0.001$), whereas individuals transplanted from SL to PL exhibited a marginally significant increase in gill area (initial mean = 461.9 ± 59.5 mm^2, final mean = 488.1 ± 66.9 mm^2; Welch's $t_{65.11}$ = 1.710, $p = 0.093$) and reduction in palp area (initial mean = 9.6 ± 0.8 mm^2, final mean = 8.8 ± 2.4 mm^2; Welch's $t_{39.52}$ = −1.879, $p = 0.068$).

No other treatment groups exhibited significant changes in PGR during the transplant experiment, but Quagga Mussels from both SL and PL grew their palps and gills at SL, indicating overall significant somatic growth (Appendix S1).

DISCUSSION

Why did Zebra Mussels suffer higher mortality?

The high mortality observed for Zebra Mussels within the growth and transplant cages is intriguing because this pattern was observed at all sites, suggesting that turbidity was not the principal stressor. We suspect high water tempera-

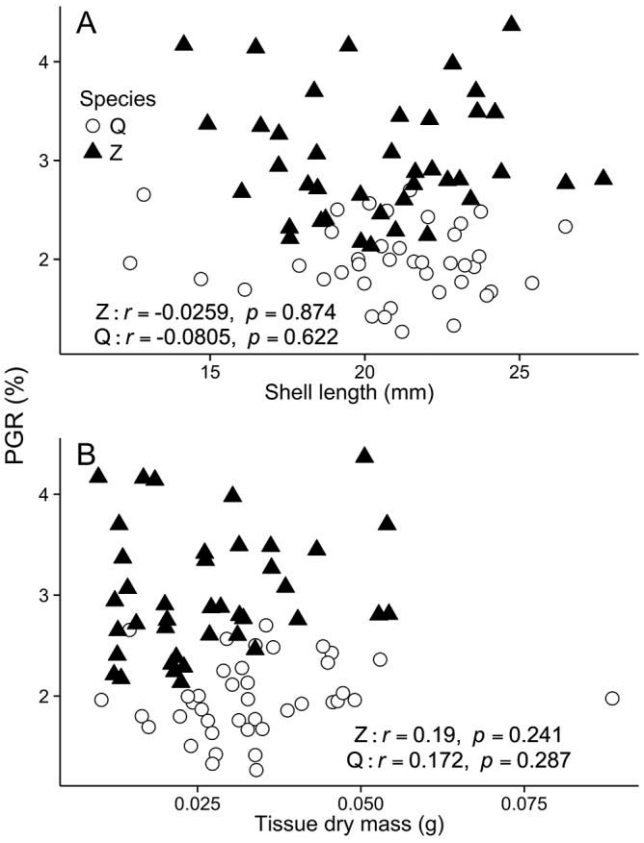

Figure 4. Palp-to-gill area ratio (PGR) vs shell length (A) and tissue dry mass (B) for Zebra and Quagga Mussels. Each data point represents the mean PGR and mussel shell length or tissue dry mass (n = 20 individuals) for a species at a particular site and sampling week.

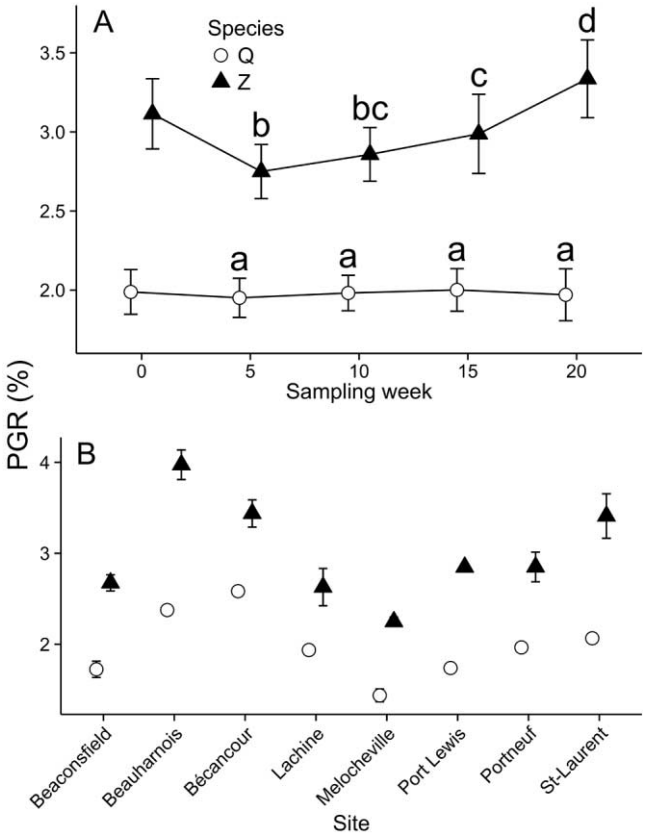

Figure 5. Mean (±SE) palp-to-gill area ratios (PGR) by sampling date (A) and site (B) along the St Lawrence River. Symbols are grand means of 8 and 5 data records, respectively, each being the mean of 20 measured specimens. Bars with the same letters are not significantly different (Tukey post hoc test, $p > 0.05$).

ture (Fig. S2) as a likely cause of mortality, but we have no data for this factor apart from point measurements taken on sampling days. The literature is contradictory regarding which dreissenid species is more thermally tolerant (Spidle et al. 1995, Mills et al. 1996, Mitchell et al. 1996, Thorp et al. 1998). Upper temperature thresholds of ≥30°C have been reported for Zebra Mussels from short-duration laboratory studies, but a heat-induced summer mass die-off was observed in a lake following chronic exposure to temperatures >25°C (White et al. 2015). Interspecific differences in seasonal mortality also may arise from Zebra Mussels spawning in warmer temperatures, and hence later in the year, than Quagga Mussels (Claxton and Mackie 1998, Stoeckmann 2003, Ram et al. 2011). The stress of spawning during peak summer temperatures could have produced a die-off, as has been observed for a marine mussel species (Myrand et al. 2000).

Abiotic and intrinsic factors affecting mussel growth

Early in the growing season, Quagga Mussels achieved higher growth rates than Zebra Mussels. Moreover, unlike Zebra Mussels, Quagga Mussels exhibited tissue growth at both sites during the transplant experiments. Previous studies comparing Zebra and Quagga Mussel growth in the laboratory and in the field have yielded disparate results depending on factors, such as temperature, season, and shell length (Baldwin et al. 2002, Karatayev et al. 2010, MacIsaac 1994, Thorp et al. 1998, 2002). In the SLR, turbidity had a negative but small effect on the growth of both species, but a marginally significant interaction between species ID and turbidity suggested that Quagga Mussels may have a small advantage at more turbid sites. Like us, investigators found only marginal effects of the influence of turbidity on the growth of dreissenid mussels in 2 previous field studies (Thorp et al. 1998, Allen et al. 1999). In contrast, investigators have demonstrated that high turbidity can limit growth potential in laboratory studies (Madon et al. 1998, Schneider et al. 1998).

Variation in PGR among species, seasons, and sampling locations

The PGR of Zebra Mussels was higher than that of Quagga Mussels at all sites. Zebra Mussels had proportionally larger labial palps and smaller gills than Quagga Mussels, regardless of ambient conditions (Fig. S3). If labial palps have a comparatively smaller role in particle sorting by Quagga Mussels (as seen in some other bivalves; e.g., Ward et al. 1998), then an investment of more energy into gill area (thereby lowering the PGR) might provide more efficient particle capture and ingestion capacity under low food concentrations. Quagga Mussels residing at or transplanted to the low-turbidity site decreased their PGR over time. Transplanted mussels reduced their palp area while increasing their gill area, whereas resident mussels increased their gill

Table 3. Description of the best linear mixed model (LMM) (random structure = site) for the palp-to-gill area ratio (PGR) experiment. Species = Quagga (baseline) and Zebra (Z), TSS = total suspended sediments, PGR_mean = mean palp-to-gill area ratio, time (sampling week) = 5 (baseline), 10, 15, or 20.

Variable	Coefficient	Standard error	p
Intercept	2.124	0.200	0.0001
SpeciesZ	0.695	0.070	0.0001
TSS	−0.006	0.002	0.0006
Time10	−0.007	0.066	0.9620
Time15	−0.002	0.066	0.9734
Time20	−0.049	0.068	0.5124
SpeciesZ × Time10	0.100	0.092	0.2772
SpeciesZ × Time15	0.222	0.092	0.0162
SpeciesZ × Time20	0.607	0.093	0.0001
SpeciesZ × TSS	0.004	0.001	0.0002

Table 4. Analysis of variance for the mussel transplant experiment.

Model	df	SS	MS	*F*	*p*
Origin (O)	1	0.34	0.337	0.787	0.3764
Destination (D)	1	8.97	8.975	20.966	<0.0001
O × D	1	0.97	0.966	2.256	0.1352
Species (S)	1	11.24	11.235	26.245	<0.0001
O × S	1	2.44	2.438	5.695	0.0182
D × S	1	0.54	0.544	1.271	0.2614
O × D × S	1	1.34	1.344	3.139	0.0784
Cage	9	6.70	0.7444	1.738	0.0846
Error	156	66.78	0.428		

area (Table S5). This shift may be a response to changing food availability at the end of the summer.

Our model suggested a small inverse relationship between PGR and turbidity, contrary to our prediction (hypothesis 3) and earlier work on other bivalves. Theisen (1982) and Dutertre et al. (2009) found positive correlations between turbidity and PGR, but their TSS data were collected prior to and not concurrent with their study. Essink et al. (1989) found a positive relationship between palp area and turbidity based on instantaneous measurements of TSS from grab samples taken concurrently with the mussel samples used for palp measurements. Most previous investigators of this relationship categorized turbidity as low or high based on long-term observations (e.g., Theisen 1982, Mettam 1992, Payne et al. 1995a, b, Barillé et al. 2000, Dutertre et al. 2009, Yoshino et al. 2013). Sediment traps should provide a time-averaged representation of turbidity conditions, but they may not capture incidental events that might influence PGR. In our model, TSS had a small negative effect on the growth and PGR of both species, but mussels exhibited higher PGR at sites that had consistently high turbidity (i.e., Beauharnois, Bécancour, and SL; see Frenette et al. 1989, Rondeau 1993, Rondeau et al. 2000). This pattern is further reinforced by the observed increase in the PGR of Zebra Mussels transplanted to SL. However, mussels collected from SL had only a moderately higher PGR than mussels at most other sites (and lower than at Beauharnois and Bécancour), in spite of exposure to an order-of-magnitude higher level of turbidity. Changes in PGR could conceivably reflect responses to other context-dependent factors (e.g., food quality, temperature) not explicitly considered in our study. The linear mixed model accounts for interacting variables, such as time, that are not captured in Fig. 5A, B.

Mussel acclimation in the reciprocal transplant experiment

The reciprocal transplant experiment provided further evidence that the seasonal differences in PGR were linked to responses to environmental conditions. Both species acclimated to new local conditions rapidly (in ~114 d), similar to morphological acclimations observed in marine bivalves (120–150 d; Essink et al. 1989, Wong and Cheung 2003, Drent et al. 2004). Quagga Mussel PGR declined at the low-turbidity site for both resident and transplanted individuals. Transplanted individuals exhibited reduced palp size and increased gill area, both predictable adjustments to low particle concentrations. Resident individuals increased their gill area while keeping their palp area constant, which could be explained as an adjustment to low food availability in the autumn. In contrast to Quagga Mussels, Zebra Mussels transplanted to a high-turbidity site exhibited a pronounced change in PGR, whereas no change was observed in Zebra Mussels transplanted to what could be considered less stressful conditions (i.e., low turbidity). A similar asymmetric response in the morphology of reciprocally transplanted sponges was interpreted as an adaptation to risk by Palumbi (1984). He hypothesized that exposure to sudden, more stressful physical conditions requires rapid acclimation, whereas exposure to more benign conditions does not warrant a rapid response that would be counterproductive in a fluctuating environment (Palumbi 1984). Assuming that Zebra Mussels are more sensitive to turbidity than Quagga Mussels, as indicated by our model results, then Zebra Mussels transplanted to high-turbidity conditions would need to adjust their PGR rapidly, but those transplanted in the opposite direction could retain their existing morphological arrangement as a precaution against sudden turbidity changes.

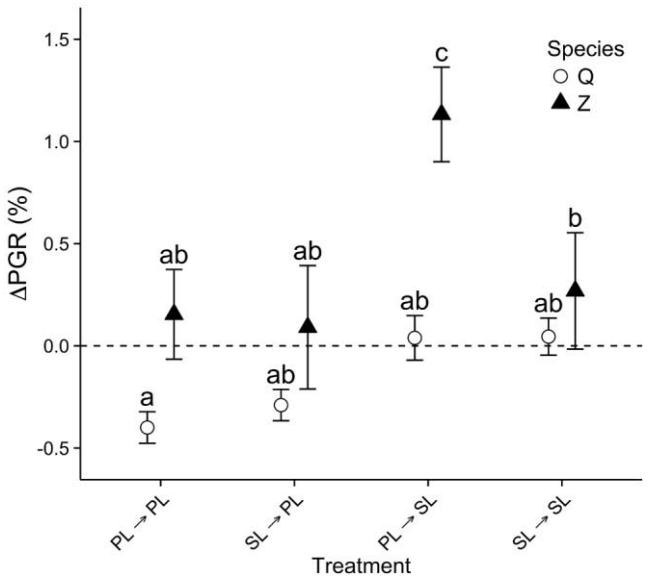

Figure 6. Mean (±SE) % change in palp-to-gill area ratio (ΔPGR) following a ~16.5-wk reciprocal transplantation experiment. Port Lewis (PL) and St-Laurent (SL) are sites of low and high total suspended sediments, respectively. Points with the same letters are not significantly different (Tukey post hoc test, $p > 0.05$).

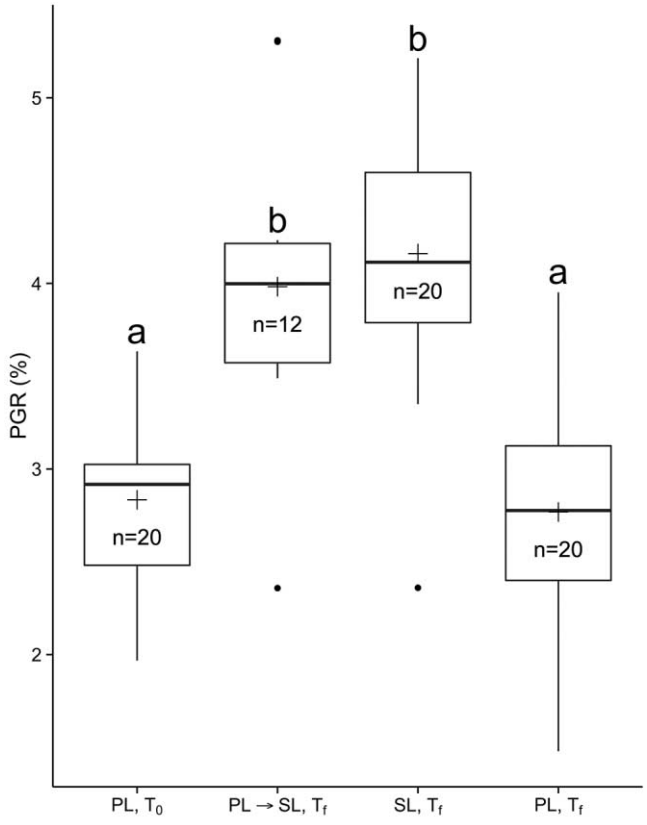

Figure 7. Box-and-whisker plots showing the absolute palp-to-gill area ratios (PGR) of Zebra Mussels transplanted from Port Lewis (PL; low turbidity) to St-Laurent (SL; high turbidity) in comparison to local mussels. Crosses are means, lines in boxes are medians, box ends are quartiles, whiskers are the 1.5 inter-quartile range, points are outliers. T_0 and T_f are initial and final samplings, respectively. Plots with the same letters are not significantly different (Tukey post hoc test, $p > 0.05$).

Does phenotypic plasticity mediate dreissenid mussel replacements?

The long-standing hypothesis that phenotypic plasticity promotes invasion success has received mixed support from observational and experimental studies (e.g., Davidson et al. 2011, Godoy et al. 2011, Palacio-López and Gianoli 2011, González-Suárez et al. 2015). Flexibility in feeding morphology might be advantageous for sessile species in seasonally heterogeneous environments. In the case of suspension-feeding bivalves, temporal variation in PGR has been observed in the field and was interpreted as an adaptation to changing environmental conditions that affect sediment resuspension and food availability (Honkoop et al. 2003, Drent et al. 2004, Yoshino et al. 2013). However, such flexible feeding carries metabolic costs, and the trade-offs are potentially complex (Bayne 2004). The Zebra Mussel's more pronounced acclimation to higher turbidity should involve costs associated with rapid production of filtration organs best suited to ambient conditions and maintenance of sensory and regulatory mechanisms involved in this adjustment (DeWitt et al. 1998). Conceivably, these added costs could contribute to a competitive imbalance between the Zebra Mussel and the Quagga Mussel under the stress of higher turbidity. In contrast, the plasticity of feeding organs in Quagga Mussels appears to be promoted by exposure to low food supply. Under these conditions, Quagga Mussels exhibit a greater capacity than Zebra Mussels to adjust their palps and gills for greater particle capture. Results of previous experiments suggest that Quagga Mussels can maintain higher filtration rates than Zebra Mussels of similar size regardless of season (Diggins 2001) and appear better able to process food that is diluted by suspended inorganic particles (Baldwin et al. 2002, Stoeckmann 2003). Our results are consistent with the view that interspecific differences in bioenergetics and efficiency of food acquisition promote the dominance of Quagga Mussels, and they can help explain why Quagga Mussels frequently replace Zebra Mussels in habitats where food resources have become progressively depleted.

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