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In situ reciprocal transplants reveal species-specific growth pattern and geographic population differentiation among zebra and quagga mussels

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ABSTRACT

For bivalves, somatic growth is often inferred from shell measurements alone. However, shell growth may not always reflect changes in soft tissue due to confounding factors such as seasonal or ontogenetic asynchrony between shell and tissue, flexible energy allocation, or population differences. This study compares the relationship between shell growth, changes in soft tissue mass, and RNA/DNA ratio in the zebra mussel (*Dreissena polymorpha*) and quagga mussel (*Dreissena bugensis*) from contrasting riverine and brackish estuarine environments. Reciprocal transplantation indicated that shell growth in late summer was consistently lower for the estuarine source zebra mussels while the RNA/DNA ratio was highest for zebra mussels independent of either geographic source or destination. Shell growth of the river source quagga mussels was almost two times greater than zebra mussels at the river site, but both shell growth and final tissue mass were lower in the estuarine environment. While there were no differences in final RNA/DNA ratios between zebra and quagga mussels from the same source, the RNA/DNA ratio of zebra mussels from the estuary and transplanted to the estuary was higher than that of all other zebra mussel treatments. This study suggests that shell growth does not always accurately reflect tissue growth and that the shell and tissue growth of quagga mussels is greater than that of zebra mussels in fresh but not brackish waters, and that physiological plasticity can have a fixed geographic component.

Introduction

Growth integrates both internal and external factors, thus potentially reflecting a variety of ecophysiological constraints including food availability, food quality, ontogeny, or energy allocation to seasonal activities like reproduction. This means that measuring growth response of mollusks, arthropods, and other invertebrates to environmental constraints is complicated by the presence of two potentially contrasting compartments of overall animal growth: soft tissue and exoskeletal mass. In bivalve mollusks, growth of soft tissue is commonly estimated from an allometric relationship between shell length and soft tissue or total mass (Chase and Bailey, 1999; Gosling, 1992; Jokela and Mutikainen, 1995; MacIsaac, 1994; Smit et al., 1992; Stoeckmann and Garton, 2001; Young et al., 1996). However, many bivalves can vary the allocation of energy between shell and soft tissue growth depending on environmental conditions or life history needs (Hilbish, 1986; Jokela and Mutikainen, 1995; Stoeckmann and Garton, 2001), and in some instances shell and somatic growth can even be asynchronous (Gosling, 1992). For example, the zebra mussel, *Dreissena polymorpha*, commonly shows a seasonal decline in soft tissue mass of up to 40% in association with summer metabolic demands and spawning events without parallel change in shell dimensions or shell mass (Stoeckmann and Garton, 1997), similar to the seasonal asynchrony seen in marine mussels (Gosling, 1992). Thus changes in shell length can be an incomplete or misleading proxy for changes in soft tissue mass and subsequently physiological function like filtration and any resulting ecological impacts.

Zebra mussels and quagga mussels (*Dreissena bugensis*), both recent invaders of North American, are fast-growing freshwater bivalves that have quickly colonized a broad range of environments across the continent (McMahon, 2002; Thorp and Covich, 2001). When abundant, dreissenid mussels can have profound impacts on both structural and functional attributes of aquatic ecosystems depending on their population growth rates (Mills et al., 1999; Strayer et al., 1999), including large rivers (Ietswaart et al., 1999; Thorp and Casper, 2002, 2003; Welker and Walz, 1998). However, as they continue to spread across North America,

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dreissenid mussels will encounter significant constraints on their physiological abilities such as salinity and osmotic stress (Karatayev et al., 1998; McMahon, 2002). Although both dreissenid species are found in brackish environments in their native Ponto-Caspian range (Orlova et al., 2005; Son, 2007; Spidle et al., 1995), only zebra mussels have been found in the tidally brackish waters of the St. Lawrence to date (Mellina and Rassmussen, 1994, this study).

Zebra and quagga mussels are sympatric throughout much of their North American range and an initial reading of the literature often leaves readers with the inaccurate idea they are ecological equivalents. However in their native Ponto-Caspian range there is a much smaller overlap between the two (Son, 2007). In addition, a sub-set of studies in the recently invaded Great Lakes region has consistently noted a variety of potentially important species differences in food assimilation, physiology, and growth (Baldwin et al., 2002; Casper and Johnson, 2010; Stoeckmann, 2003; Wright et al., 1996). There is also field-based evidence from North America suggesting that species-specific differences may also be leading to a separation in the distribution of the two species similar to that seen in the Ponto-Caspian, notably that the quagga mussel is displacing the zebra mussel across much of their shared habitats in Great Lakes and St. Lawrence River basins (Mills et al., 1999; Ricciardi and Whoriskey, 2004; Wilson et al., 2006). A better understanding of species-specific differences in growth physiology may help explain the apparent differences in distribution and abundance.

Our purpose was to examine a set of related questions about the potential for the differential growth response of zebra and quagga mussel shell, somatic, and cellular physiology in divergent local environments. Our research hypotheses are: 1) that there are physiological differences between zebra and quagga mussels that explain differences in their distribution in fluvial estuary relative to riverine site, 2) that there will be geographically fixed shell and tissue attributes in mussels from the two divergent source environments, and 3) that only zebra mussel transplants can succeed in the oligohaline estuarine environments. These questions have implications for understanding the variability of growth, distribution, and dominance of the two mussels as they colonize diverse river systems of a new continent.

Materials and methods

Study site

The St. Lawrence is the second-largest river in North America with a 574,000 km^2 watershed, a basin that holds ~18% of the world's freshwater (>23,000 km^3), and a 655 km^3 mainstem with a mean annual discharge of 12,000 m^3/s into a 130 km long fluvial estuary that begins near Quebec City (Thorp et al., 2005). To provide contrasting conditions, we chose to reciprocally transplant mussels between divergent environments within the St. Lawrence River (Fig. 1): a site within the upper river (R; Robinson Bay near Massena, New York, USA: 44.987931° N and 70.823289° W) and a second located at the head of the turbid but oligohaline (0–2 psu; 100 NTU) fluvial estuary (FE; Saint-Francois on the eastern tip of Ile d'Orleans, Québec, Canada: 46.996525° N and 70.808397° W).

Experimental design

The mussels for the transplant experiment were collected from the upper surface of large rocks at a mean depth of 2 m^{-1} and within a roughly 3 m^2 area. Zebra mussels (standard size 26 mm based ANCOVA calculations) were reciprocally transplanted between the two sites, a distance of more than 600 km, using an experimental design with 2 destination treatments (R source to FE destination and FE source to R destination) and 2 source controls (R to R and FE to FE). Approximately 400 adult zebra mussels collected by hand from hard substrata at least 2-m deep were used to populate the 4 treatments of the reciprocal transplant design. The four treatments of the reciprocal transplant consisted of 100 zebra mussels collected from the R site and placed at the R site as a control, 100 collected at the R site and transplanted to the FE site as a treatment, 100 mussels collected from the FE site and placed at the FE site a control, and 100 collected at the FE site and transplanted to the R site as a treatment. Quagga mussels (standard size 18 mm based ANCOVA calculations) were not found in sufficient numbers at the fluvial estuarine site to be reciprocally transplanted. In fact, only 5 quagga mussels, all larger than 22 mm, were collected meaning that quaggas could only be moved from the upper river to the fluvial estuarine site (i.e. R to FE and R to R treatments). This meant that half the numbers of quagga mussels were involved in the experiment—approximately 200 and all from the R source population. During the transplantation process all mussels were held at 15 °C in the laboratory for a period of 24–72 h during which they were individually numbered with small plastic bee tags (3 mm diameter) glued to the shell. The initial shell length was measured to the nearest 0.01 mm using digital calipers. To obtain an estimate of measurement error for shell length, caliper measurements were repeated 10 times on 6 different individuals ranging in size from 14 to 26 mm in length. The initial soft tissue mass for each individual used in the experiment was estimated via regression of dry weight (DW) on shell length obtained from a separate sample of 20–30 individuals of a range of sizes from each source collected at the start of the experiment. Individual shell lengths were then measured and soft tissue removed from the shell and dried for 48 h at 60 °C and weighed. Transplanted mussels were placed in 20 × 25 cm envelope-shaped cages made of 1-cm^2 plastic mesh, which were then anchored to the river bottom by attaching them to the tops of cinder blocks (20 × 20 × 40 cm). Two cages were used at each site and all species-source combinations of zebra and quagga mussels were mixed together and then divided equally among those two cages. Thus the full experimental design used 50 local zebra mussels, 50 transplanted zebra mussels, and 50 local or transplanted quagga mussels in each individual cage (150 total). No cages were lost or damaged during this study. The experiment began in mid-July 2002 and ended 58 days later. Because growth and mortality could be strongly influenced by temperature, we measured water temperature every 30 min during the experiment using data loggers (Onset Stowaways, Pocasset, MA) placed inside the cages.

Data collection

After retrieval, surviving mussels were measured for one of the three complementary indicators of mussel growth: change in shell length, soft tissue mass, and RNA/DNA ratio. Shell growth is given as the total change in the maximum shell length of all surviving mussels after 58 days, standardized to a 26 mm zebra mussel and 18 mm quagga mussel for each treatment group (the standard size being a function of the ANCOVA calculations). Because of the large difference in standardized shell between the two species, separate ANCOVAs were conducted for each. This means that none of the statistical analysis makes direct interspecies comparisons. Instead analyses of the three indictors of growth are focused on testing whether there are intraspecific source population differences. Soft tissue dry weight (DW) was measured from a subsample of 20–30 individuals by removing soft tissue from the shell and drying it for 48 h at 60 °C. For analysis of RNA/DNA ratios, a separate subsample of 10 individuals from each treatment was frozen at −80 °C immediately after retrieval. The soft tissue was later dissected from the shell and homogenized in distilled water (5 times the volume/wet weight of the tissue). The extraction and purification procedure for nucleic acids was adapted from Buckley and Bulow (1987). In this procedure, the homogenized tissue was first treated with cold perchloric acid ($HClO_4$) to remove free nucleotides, amino acids, and other low molecular weight molecules. This step also precipitated the RNA, DNA, and proteins into a pellet for further analysis. The RNA fraction of duplicate samples of each individual sample was then solubilized in a