TEMPERATURE AS A DRIVER OF A SIZE-STRUCTURE SHIFT IN ZEBRA MUSSELS (*DREISSENA POLYMORPHA*) IN THE HUDSON RIVER

A Final Report of the Tibor T. Polgar Fellowship Program

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ABSTRACT

The introduction of zebra mussels to the Hudson River in 1991 caused strong impacts throughout the ecosystem. Since 2005, these ecosystem impacts have changed, likely as a result of a shift toward smaller-bodied mussels. Since this shift in size-structure has had a dramatic influence on the ecosystem, the cause of the size-structure is of interest in this project. Specifically, the role of temperature as a driver of the size-structure shift was studied using a combination of parameter estimations for a stage-structured matrix model based on long-term data, respiration differences among size classes at different temperatures (acute thermal effect), and the effect of increasing temperature on mortality (chronic thermal effect). The goal of this study was to test the following alternative hypotheses related to temperature: i) mortality increased in large mussels, favoring small-bodied mussels; ii) mortality increased in all size classes such that few mussels survive to a large size class; iii) high temperatures reduced growth rates, leading to smaller mussels. While the results from the analyses of the mechanism by which temperature affects size structure are not conclusive, they suggest that, based on the matrix model results and the acute thermal tolerance results, large mussels are not less thermally tolerant. Further, the experiments on chronic exposure to high temperatures indicated that there is a strong temperature effect on mussel survival, beginning at temperatures that frequently occur in the Hudson River during the summer. This means that high temperatures could be a significant source of mortality for zebra mussels in the Hudson River.

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INTRODUCTION

Zebra mussels (*Dreissena polymorpha*) first became abundant in the Hudson River in 1991, and their introduction led to dramatic changes to nearly every aspect of the ecosystem. The changes included an 80–90% reduction in phytoplankton (Caraco et al. 2006), a 70% reduction in zooplankton (Pace et al. 2010), a decrease in dissolved oxygen (Caraco et al. 2000), and increases in the deposition of organic matter (Roditi et al. 1997) and water transparency (Newell 2004). However, these impacts have not been constant over time. Zebra mussels exhibit strong cohort dynamics, which results in an oscillation between small- and large-bodied dominance in the population (Figure 1). When survivorship of adult mussels fell ~100 fold in 2005, there was a near elimination of large zebra mussels (Strayer et al. 2011) and zooplankton biomass recovered to pre-invasion levels by 2010, but phytoplankton biomass remained low (Pace et al. 2010). This suggests that the size-structure is a critical factor in the zebra mussels' impacts. This is expected because body size is important in many areas of ecology since it is closely related to physiological rates, interactions among organisms, and organisms' interactions with the environment. As a result, shifts in body size distributions often lead to shifts in ecological function

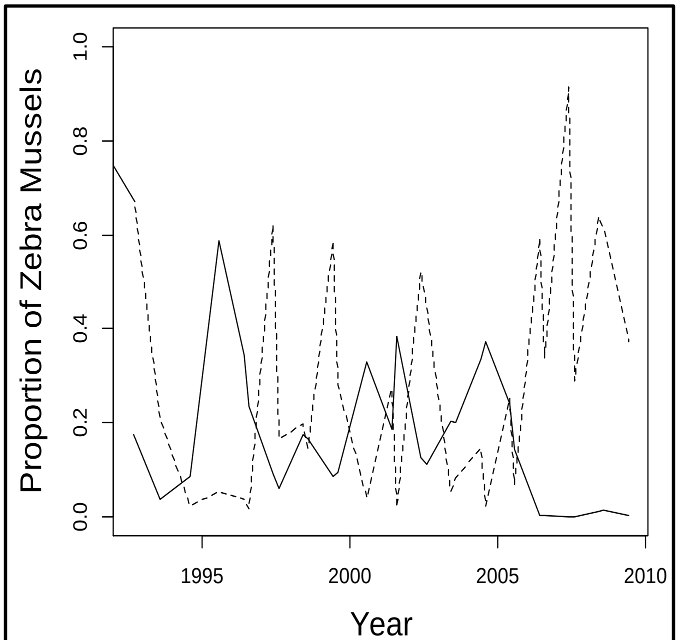

Figure 1: Proportion of zebra mussels belonging to the small (4–6 mm) size class (dashed line), and large (20–30 mm) size class (solid line) based on zebra mussel densities.

(Young 1996). Since changes in size-structure can dramatically alter ecosystem impacts, the cause of the shift toward small-bodied mussels is of interest.

The size-structure shift likely resulted from increased mortality, with an observed drop in survivorship of approximately 100-fold (Strayer et al. 2011). This increase in mortality has partially been attributed to blue crab (*Callinectes sapidus*) predation (Carlsson et al. 2011). Blue crabs migrate into the freshwater portion of the Hudson River during the summer, and Carlsson et al. (2011) tested whether blue crabs were the source of the increased mortality in the Hudson River using exclosure experiments. Higher mortality was observed where blue crabs were not excluded, indicating that blue crabs are a source of mortality for the zebra mussels. However, this did not entirely explain the change because mortality rates in both the control and experimental sites were higher than those previously observed from 1993 to 2008 (Carlsson et al. 2011). Further, higher mortality rates were observed in both the control and the exclosure before blue crabs arrived at the site. Another potential source of mortality is high temperature. Simulation and experimental evidence suggest that zebra mussels may be adversely impacted by warming temperatures and the Hudson is warming (Seekell and Pace 2011). Experiments have also provided evidence for decreased growth rates and increased mortality in large zebra mussels at high temperatures (Allen et al. 1999).

The effect of water temperature in well-mixed riverine systems like the Hudson, is likely more dramatic than in lake or reservoir systems where bottom-dwelling mussels experience lower temperatures. In the Hudson, when water temperatures exceed 25ºC, as they do in summer, even mussels at depth are exposed to this high temperature because of uniform temperatures over depth (Limburg et al. 1986). Further, the highest number of days observed above threshold temperatures over the range 25 to 28 degrees all occurred in 2005, the same year as the size-structure shift in the zebra mussel population (Figure 2, data from USGS).

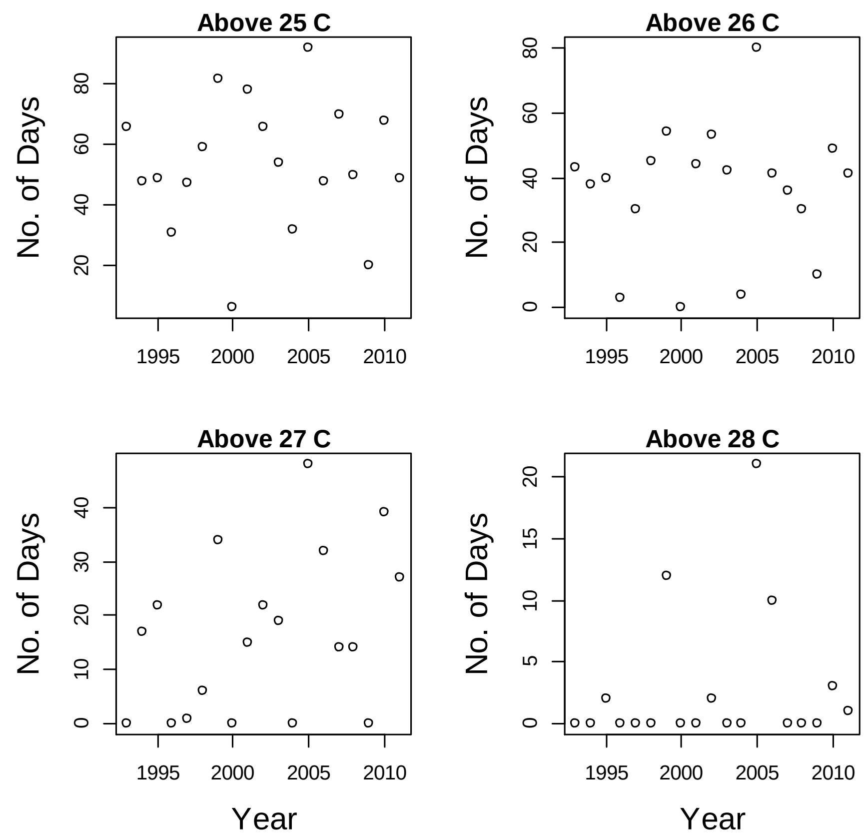

Figure 2: Plots of the number of days reaching temperatures above 25°C, 26°C, 27°C, and 28°C for each year since the zebra mussel invasion. Additionally, there was one day in 2005 that reached a temperature above 29°C.

This study provides a stage-structured matrix model to consider the parameters which most likely led to the observed change in dynamics based on long-term population data by testing the following alternative hypotheses related to temperature: i) mortality increased in large mussels, favoring small-bodied mussels; ii) mortality increased in all size classes such that few mussels survive to a large size class; iii) high temperatures reduced growth rates, leading to smaller mussels. To experimentally test the first hypothesis, acute thermal stress differences among zebra mussel size classes were studied by comparing respiration rates of individual mussels at temperatures between 18 and 24°C. To test the temperature at which chronic effects on mortality would occur, the number of dead mussels were counted daily in tanks held at 18 (control), 25, 27, and 29°C.

METHODS

STUDY SITE AND ZEBRA MUSSEL SAMPLING

Zebra mussel population data was collected in the freshwater, tidal zone of the Hudson River, extending from Troy at river kilometer 248 (measured from the Battery in Manhattan) to Newburgh at river kilometer 100 (Figure 3). The Hudson's freshwater tidal reach is 900m wide and 8.3 m deep on average (Strayer and Malcolm 2006). The water is turbid, moderately hard, and nutrient rich (Strayer and Malcolm 2006). Water temperatures reach 25–28°C during the summer (based on USGS data). Since the Hudson River is well-mixed, temperature is generally uniform with depth (Limburg et al. 1986).

From 1993 to 2012, demographic data was collected on the zebra mussel populations by sampling 6–7 rocky sites throughout the Hudson River. These rocky sediments were sampled by collecting 10 rocks (15–40 cm in dimension) using a diver. In the laboratory, all mussels >2 mm long were removed from the rocks and counted. The area of each rock was estimated by tracing the outline of the rock. Subsamples of zebra mussels were saved for measurement of shell length (approximately 300 mussels per site, when possible) to determine the size-structure of the population. Only rocky areas were used for demographic information because these samples contained a large enough number of mussels to study population demographics, and >75% of the population in the middle estuary is represented by rocky areas (Strayer and Malcolm 2006). Sampling was conducted and the resulting data was provided by David Strayer's laboratory at the Cary Institute of Ecosystems Studies. Data was provided in the format of estimates of the density of small (4–6 mm), medium (12–18 mm), and large (20–30 mm) zebra mussels each year for late June to early July, and mid-August to early September.

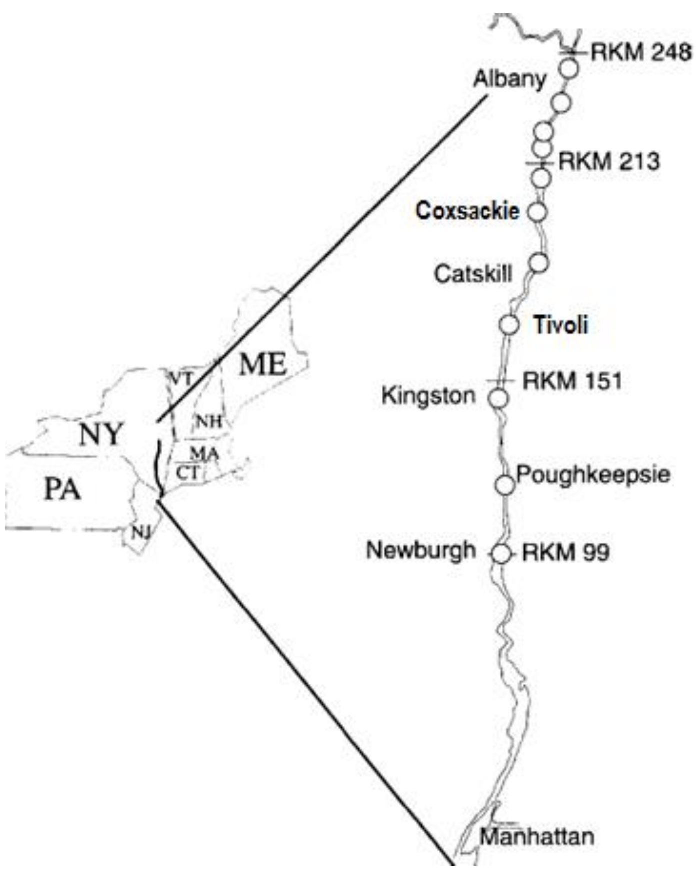

Figure 3: A map of sampling locations used to determine zebra mussel population size and size-structure (circles), and the two locations where experimental organisms were collected. Map is modified from Strayer and Smith 1996.

Zebra mussels used in laboratory studies were collected by divers in mid-June near Coxsackie, NY, and in mid-July near Tivoli, NY (Figure 3). Rocks with zebra mussels attached were brought back to the laboratory, where the mussels were removed by cutting the byssal threads with a razor blade. The shells were cleaned using a toothbrush, and the mussels were placed in 10 gallon tanks with untreated well water, held at 18–19°C in a climate controlled room. The water was oxygenated using air stones and pumps in each tank. Mussels were fed 0.32g of green algae (*Chlorella* sp.) per 100 animals each day. The water in the holding tanks was changed one to two times per week. In temperature treatment tanks, 2L of water was removed from each tank daily and replaced with new untreated well water so as not to substantially alter the temperature.

POPULATION MATRIX MODEL

A stage-structured population matrix was developed to study which parameters most likely led to the observed change in dynamics. Parameters for the period before the size-structure shift (1993–2005) were compared to those after the size-structure shift (2006–2010). Long-term population size data from the Hudson River was used to fit the following three stage matrix model:

$$\begin{bmatrix} \mathrm{Xsm},\ t+1 \\ \mathrm{Xmd},\ t+1 \\ \mathrm{Xlg},\ t+1 \end{bmatrix} = \begin{bmatrix} (\mathrm{Fsm} + \mathrm{Ssm} - \mathrm{Csm}) & (\mathrm{Fmd} - \mathrm{Cmd}) & (\mathrm{Flg} - \mathrm{Clg}) \\ (\mathrm{Gsm}) & (\mathrm{Smd}) & 0 \\ 0 & (\mathrm{Gmd}) & (\mathrm{Slg}) \end{bmatrix} \begin{bmatrix} \mathrm{Xsm},\ t \\ \mathrm{Xmd},\ t \\ \mathrm{Xlg},\ t \end{bmatrix},$$

where F is the fecundity (per mussel), S is the proportion of mussels remaining in same size class, C is the cannibalism of veligers (per mussel), G is the proportion of mussels growing to next size class, and X is the abundance of mussels in small (sm), medium (md), and large (lg) size classes. The fecundity minus cannibalism term will be referred to as “net fecundity.” Parameter estimations were calculated in MATLAB (R2012a) using a least squares method described in Caswell (2000). Since the changes in parameters could have been caused by factors other than temperature, temperature as the cause of the shifts in parameters was then explored experimentally.

OXYGEN CONSUMPTION AMONG SIZE CLASSES

To measure acute thermal stress differences among the zebra mussel size classes, oxygen consumption rates were measured on three individual mussels from each size class, and an empty control at 18, 22, 26, 30, and 34°C. Untreated tap water, which was filtered through a 0.2 μm filter and kept oxygenated with an air stone, was used during the experiments. Each mussel's shell was cleaned with a toothbrush, before it was placed in a 60 ml biological oxygen demand (BOD) bottle. An optical dissolved oxygen probe (YSI ProODO) was inserted into the BOD bottle, and the bottle was then placed into a water bath. The water in the bottle was allowed 15 minutes to reach the experimental temperature before data was collected. Oxygen consumption rates were determined either over a 2 hour period or until the animal expired, with the level of dissolved oxygen (mg O_2/L) recorded every 5 minutes. The slope of the least squares regression line for the level of dissolved oxygen over time was used to determine the oxygen consumption rate (mg O_2/L/hr). Oxygen consumption rates were averaged to create a plot for the three size classes at the five experimental temperatures. Metabolism speeds up with increasing temperature to a point, and then the animal begins shutting down its metabolic processes. The temperature at which the decline in oxygen consumption begins after the initial increase was taken as a measure of the thermal stress point. This thermal stress point was then compared among size classes.

ZEBRA MUSSEL SURVIVAL AT INCREASED TEMPERATURES

To study the effect of chronic exposure to high temperatures, mussel survival was monitored in tanks with experimental temperatures of 18 (control), 25, 27, and 29°C. Zebra mussels were brought to the experimental temperatures by raising the water temperature by 1°C per day using an aquarium heater. Tanks were observed daily and dead mussels were removed. This experiment was conducted twice, first using 20 medium mussels per tank, and then using 40 medium mussels per tank.

RESULTS

The parameter estimations based on long-term zebra mussel size data showed a decrease in survival and growth parameters for medium- and large-bodied mussels (Table 1). Medium mussels went from an estimate of 74% surviving without growing into the next size class, to 0%, and large mussels went from 51% surviving to 30% surviving. Growth from the medium size class to the large size class also decreased from 6% to 0%. The results also showed a decrease in net fecundity for medium mussels by 0.13 veligers/mussel, but an increase for large mussels by 10.44 veligers/mussel. For small-bodied mussels, net fecundity plus survival, and growth parameters both increased. Related to the hypotheses, these results show a decrease in growth and survival for medium and large mussels, but an increase in both for small mussels.

Parameter	1993-2005	2006-2010	Change
$F_{sm} + S_{sm} - C_{sm}$	0.00	0.06	0.06
G_{sm}	0.00	0.49	0.49
$F_{md} - C_{md}$	0.13	0.00	-0.13
S_{md}	0.74	0.00	-0.74
G_{md}	0.06	0.00	-0.06
$F_{lg} - C_{lg}$	0.33	10.77	10.44
S_{lg}	0.51	0.30	-0.21

Table 1: Parameter estimations for the 3x3 stage-structured population matrix, where F is the fecundity (per mussel), S is the proportion of mussels remaining in same size class, C is the cannibalism of veligers (per mussel), and G is the proportion of mussels growing to next size class.

The oxygen consumption rate comparison among size classes at 18, 22, 26, 30, and 34°C did not provide support for the hypothesis that large mussels are more adversely affected by high temperatures than smaller mussels. In fact, it appears that small mussels are less thermally tolerant, with the thermal stress point where oxygen consumption begins to decline after initial increase occurring at 22°C in small mussels, and at 26° in large mussels (Figure 4).

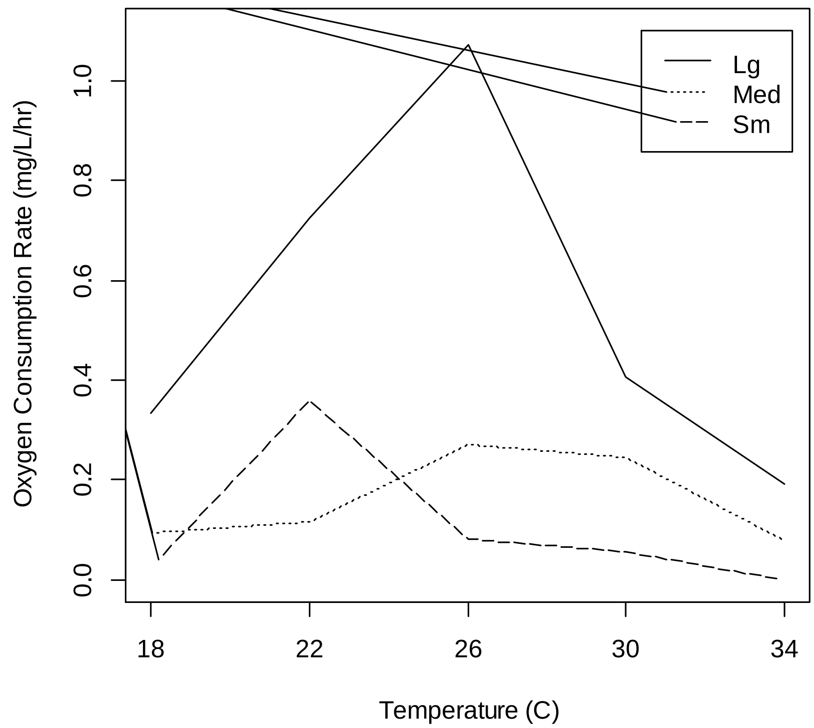

Figure 4: Average oxygen consumption rate at five experimental temperatures for each size class.

Mortality rates for medium mussels at 18, 25, 27, and 29°C could not be compared because too few mussels remained by the time the tanks reached their experimental temperatures. For example, only 3 of the 60 individuals survived to 29°C. The proportion of mussels surviving as the temperature was raised by 1°C per day shows a rapid decrease in survival between 23 and 25°C, while the reference tank (held at 18°C) experienced a very high survival rate (Figure 5).

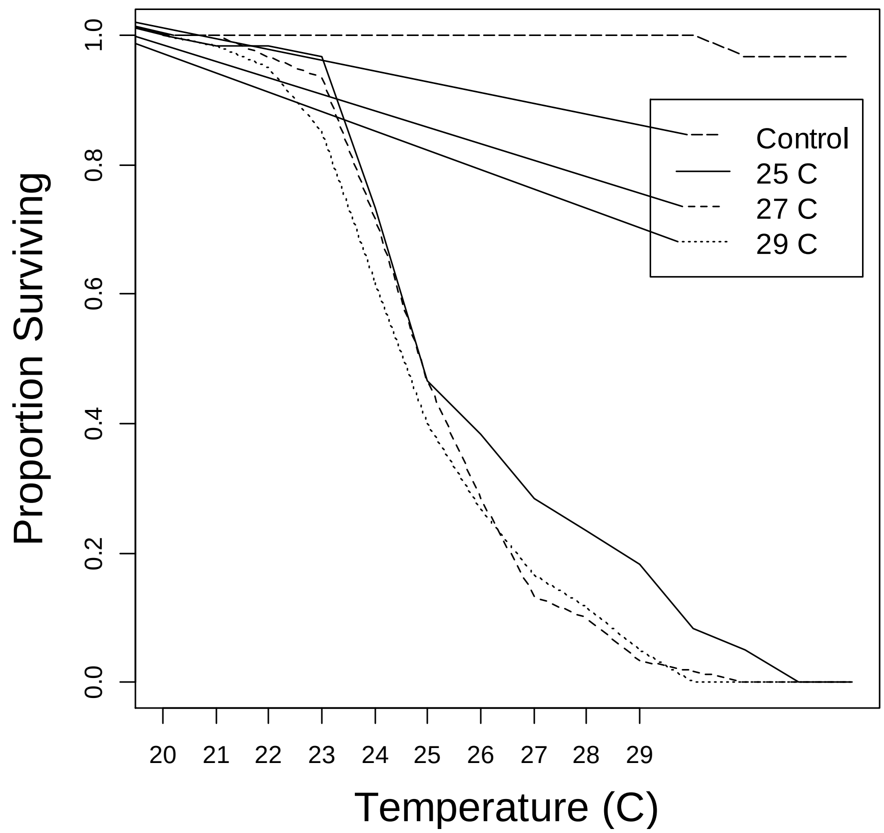

Figure 5: A plot of the proportion of mussels surviving as the temperature was raised 1°C per day to the experimental temperature. After the experimental temperature was reached, the tank was kept at that temperature for each day as the other tanks continued to be raised to their experimental temperatures. The control tanks were kept at 18°C on all days.

DISCUSSION

The results from these analyses were not conclusive in determining the most likely mechanism by which temperature leads to a shift in size-structure. The results do suggest that it is unlikely that large mussels are less thermally tolerant based on the matrix model results and the acute thermal tolerance results. However, the changes in parameter estimates from before the size-structure shift to after do not all seem reasonable. For example, none of the parameters are likely to be zero in either time period, and it seems unlikely that net fecundity would decrease for medium mussels (by

0.13 veligers/mussel), but increase in large mussels (by 10.44 veligers/mussel). The parameter estimation may be improved in the future by including biologically relevant constraints, and using maximum likelihood methods instead of a least squares approach. Studying the nonlinear dynamics of the model would also provide insight into how shifts in parameters could lead to different size-structures.

The acute thermal tolerance results suggest that small mussels are less thermally tolerant than large mussels, but since the experiment only focused on respiration, conclusions are limited because there are other physiological parameters relevant to thermal stress. These results do motivate further experiments using a scope for growth (SFG) approach. SFG provides a measure of an organism's stress by measuring the energy acquisition (feeding and digestion) against energy expenditure (metabolism and excretion) (Widdows et al. 1995). Further work using this approach would be valuable.

The experiments on chronic exposure to high temperatures indicated that there is a strong temperature effect on mussel survival, beginning at temperatures much lower than expected. The effect of temperature on mortality became clear between 23 and 25°C, temperatures that the Hudson River frequently reaches during the summer. Even mussels at depth are exposed to these temperatures because the Hudson River is well-mixed with uniform temperatures over depth. Therefore, high temperatures could be a significant source of mortality for zebra mussels in the Hudson River.

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