Zebra/Quagga Mussel Veliger Transport Model Tarryall Reservoir to Cheesman

Reservoir

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1. INTRODUCTION

Zebra and quagga mussels are invasive aquatic species that have recently arrived in the western United States. Invasions of these small, 1-2 inch mussels have resulted in significant impacts to water providers, ecosystems, and recreationists. Zebra and quagga mussels differ from other mollusks in that 1) they can adhere strongly to surfaces via byssal threads, and 2) they are planktonic when they are in their larval stage (called veligers). Thus, they can travel far distances before they mature, settle and adhere to substrates.

The two most likely vectors for introduction into a reservoir are 1) recreational boats and 2) inflow from an infected upstream reservoir. Colonized lakes can serve as a source of zebra or quagga mussel veligers for downstream water bodies. Horvath, et al., 1996 found a significant positive association between zebra mussel presence in lakes and in the out-flowing streams.

Quagga mussel veligers were detected in October 2008 in Tarryall Reservoir, which is upstream of Denver Water's Cheesman Reservoir (Figure 1). Staff at Denver Water are concerned about the possible introduction of quagga mussels into their water system from Tarryall Reservoir via Tarryall Creek and retained AMEC to develop a veliger transport model to help determine potential risks.



Figure 1. Tarryall Reservoir, Cheesman Reservoir and the Flow Path between the Two Reservoirs (Tarryall Creek and the South Platte River)

Cheesman Reservoir is located approximately 32 miles downstream of Tarryall Reservoir. Mackie (1995) proposed a method to compute the theoretical dispersal distance of veligers in rivers. Initial computations for Tarryall Creek / South Platte River

between the two reservoirs result in a dispersal distance of much greater than 32 miles. Fortunately, the actual dispersal distance is less than the theoretical due to a number of possible factors. Field studies have shown that zooplankton densities decline with distance downstream of a lake or reservoir, possibly due to filtration of benthic filter-feeders (Armitage and Capper, 1976) or other forms of retention in the stream (Horvath, et al., 1996). In addition, turbulence (both the level of intensity and duration) have been suggested and studied as contributing to the mortality of veligers (Horvath and Lamberti, 1999; Rehmann, et al, 2003). Also, the presence of wetlands and vegetation can reduce veliger densities (Miller and Haynes, 1997). Thus, numerous factors need to be considered when investigating veliger transport and mortality.

Other factors to consider include 1) likely veliger densities and age distributions at the outlet of Tarryall Reservoir, 2) the potential for the establishment of intermediate populations between Tarryall Reservoir and Cheesman Reservoir that would act as a source of veligers, 3) the critical mass concentration that needs to enter Cheesman Reservoir in order for populations to establish, and 4) the range of hydrologic and operational conditions.

This report describes the development of a veliger transport model between Tarryall Reservoir and Cheesman Reservoir. The objective of this effort is to help determine the risk and timing of the potential establishment of quagga mussels in Cheesman Reservoir due to transport of veligers from Tarryall Reservoir. The probability of establishing a reproducing population in Cheesman Reservoir is related to the frequency with which the reservoir receives viable veligers and their ability to survive and reproduce in the reservoir. Note that the methodologies developed can be used on other portions of Denver Water's system in the future and should remain relevant. The invasion of zebra mussels in parts of Europe still continues 150 years after it began (Johnson and Carlton, 1993).

As described above, numerous factors must be considered during the development of a veliger transport model. The first section of this report focuses on general biology and factors possibly affecting veliger mortality in an advective system. This is followed by description of the setting and an assessment of water-quality conditions and possible limitations in the study area for the successful establishment of mussel populations. The development of the model and input data are then described along with a discussion of how random events and stochastic processes are considered. The report finishes with a discussion of the results, conclusions, and recommendations. Although quagga mussel (*Dreissena rostiformis bugensis*) veligers were detected in Tarryall Reservoir, most of the research has been conducted on zebra mussels (*Dreissena polymorpha*). The two species are considered to be very similar and the terms *Dreissena* or mussels are generally used interchangeably.

2. DREISSENA BIOLOGY AND FACTORS AFFECTING VELIGER MORTALITY

There are numerous detailed descriptions of the general biology of zebra and quagga mussels. Information that is important for modeling the transport of veligers is summarized below.

Life Stages and Growth Rates

Adult *Dreissena* can reproduce by the time they have an 8-10 mm shell length (Claudi and Mackie, 1994) which generally occurs at about 6-12 months. Reproduction is external (Franzen, 1983) and sexual – male and female gametes are released into the water (Baker, et al, 1994). The sex ratio of a population is generally 1:1 (Claudi and Mackie, 1994). Reproduction is initiated when water temperatures reach 12 °C and are maximized above 18 °C (Claudi and Mackie, 1994). A single spawning female can release tens of thousands to millions of eggs (Mackie, et al., 1989; Sprung, 1993; Mackie and Schloesser, 1996; Nichols, 1996).

Once fertilization occurs, Dreissena go through several life stages. Ackerman et al, 1994, describe the following stages. After fertilization, a **trochophore** larva develops (57-121 um, 6-96 hrs post fertilization). The trochophore is free swimming. It is during this stage that the velum is developed. The velum is a larval organ used for feeding and locomotion. The term veliger applies to all larval stages where a velum is present. The next stage occurs about 2-9 days post fertilization (dpf) when a D-shaped shell is secreted from shell glands. These larvae are referred to as **D-shaped** or straight-hinged veligers (70-160 um). The last free swimming veliger stage is referred to as the umboned veliger or veliconcha (120-280 um, 2-24 dpf). This life stage is round or clamlike in profile. Sometime after 10 dpf, the veliconcha develops a foot and associated byssal apparatus and becomes a **pediveliger** (167 um to 300 um). Upon receiving "proper cues", sometime between 18 and 90 dpf, a pediveliger can "settle" under the proper conditions and attach to an appropriate surface. Settling occurs in flow rates up to 5 ft/sec (Claudi and Mackie, 1994). Once settled and attached, Dreissena grow until they reach a sufficient size to reproduce. Claudi and Mackie (1994) report a life span for Dreissena of 1.5 to 2 years although Karatayev, et al., (2006) note reported longevities between 2 and 19 years.

Growth rates of post-larval mussels are variable and are a function of water temperature, season of the year, location in the water column, food availability, oxygen concentrations, water velocity, and various other environmental factors (Karatayev, et al., 2006).

Water Quality Requirements

The success of established *Dreissena* populations is a function of water temperature and water chemistry. Numerous authors have reported on specific ranges of waterquality constituents for mussel growth performance and reproduction. The constituents that appear to be most important are dissolved oxygen, water temperature, calcium, conductivity, pH, alkalinity, and total hardness (Table 1), although calcium, alkalinity and hardness are related. Note that the values in Table 1 are approximations. The lower lethal limit for dissolved oxygen at 18 °C is reported to be 4 mg/l (Sprung, 1987; McMahon, 1996).

	No Survival		Poor Growth		Mod. Growth		Good Growth		Best Growth
	From	То	From	То	From	То	From	То	
Alkalinity (mg CaCO₃/I)	0	17	18	35	36	87	88	122	>122
Calcium (mg/l)	5	6	10	11	25	26	35	>35	
Total Hardness (mg CaCO ₃ /I)	0	22	23	41	43	90	91	125	>125
Conductivity (µS/cm)	0	21	22	36	37	82	83	110	>110
рН	0	6.8	6.9	7.4	7.5	7.8	7.9	8.0	>8.0
Temperature* (°C)	<-2	>40	0-8	28-30	9-12	25-27	13-17	21-24	18-20

 Table 1: Water-Quality Constituents Impacting Growth Performance of Dreissena

 (From Claudi and Mackie, 1994)

*Temperature should be interpreted with caution here because it affects mussels at both high and low values. For example, there is no survival at temperatures below -2 or above 40 °°C but there is survival between these temperatures; there is poor growth both between 0-8 C and 28-30 °C but moderate to best growth between these extremes; etc.

Critical Mass

In order to reproduce, some type of critical mass needs to exist in order for external fertilization to occur. Sperm and eggs are diluted in the water column and are subject to local hydrodynamics, decreasing the chances of fertilization occurring. Critical mass depends on the population's size, sex ratio, spatial distribution, physiological stress endured during transport, environmental conditions in the receiving water body, and a host of other considerations. According to Johnson and Carlton (1993) regarding the size of a critical mass, "the short answer is we simply do not know."

Potential Causes of Veliger Mortality in Advective Systems

Since young *Dreissena* are planktonic, they can be transported from one reservoir to another via a river or canal. Veligers can be advected and dispersed in the downstream direction, depending on the flow regime in the river. Field studies have shown a decrease in the number of live veligers downstream of a reservoir outlet (Horvath and Lamberti, 1999). Numerous factors can affect the overall mortality rate of veligers as they are transported downstream. Some of these factors are discussed below.

Inability to Settle on Suitable Substrate before Reaching Next Life Stage

Depending on 1) the age of the veliger as it enters a stream system, 2) travel time, 3) stream velocities, 4) water-quality conditions and 5) the presence of suitable substrate, a veliger may not be able to successfully settle and attach before it reaches the next non-planktonic life stage. Thus, the veliger may perish before it reaches the end of the stream segment.

Starvation

Mussels can die due to lack of food. Although a starving mussel may be weakened, mortality due to starvation may not be an issue for advective systems with short travel times. According to Horvath and Lamberti (1999), citing Sprung (1989), "veligers can survive for 1-2 weeks without food."

Predation

Predation of veligers has been noted in the literature. Eggs and larvae can be consumed by zooplankton, micro-crustaceans and post-larval fish (Hayward and Estevez, 1997). Predation by zooplankton is described in Stanczykowska (1977) and predation by adult *Dreissena* is addressed in MacIsaac, et al. (1991). Predation is considered a possible mechanism for veliger mortality but data on the actual role in a natural system are lacking.

Turbulence

Dreissena veligers are sometimes noted as being "fragile" and several authors have investigated the possible role of turbulence on the mortality of veligers. In 1999, Horvath and Lamberti (1999) reported on a field study on Christiana Creek in Michigan. Samples of zebra mussel veligers showed an exponential decrease in the number of live veligers over the 18 km section of the river. The authors surmised that veligers may be "highly susceptible to damage by physical forces (e.g. shear), and therefore, mortality in turbulent streams could be an important mechanism limiting zebra mussel dispersal to downstream reaches." This was supported by the appearance of veligers collected in the creek in that they appeared to be pulled open during transport. Empty but unbroken veliger shells were frequently observed. When veligers feed, the shell must be open to allow the velum to sweep food particles. This may make them more vulnerable to hydrodynamic forces during feeding. For Christiana Creek, the gradient was approximately $5x10^{-4}$, the maximum water velocities were >1.0 m/s, the travel time was 16 hours, and the daily survival rate was approximately 34%.

The results from a laboratory study also indicated a relationship between veliger mortality and small-scale turbulence (Rehmann, et al., 2003). Veligers were subjected to turbulence and the rate of dissipation of turbulent kinetic energy (ϵ) was measured. The impacts were quantified through the use of a term, d^* , which is the ratio of the shell size to the Kolmogorov length (the size of the smallest eddy in the velocity field). The laboratory results showed that mortality increases when d^* exceeds 0.9. This is when the size of the veliger is comparable with or larger than the smallest eddy. When veligers are small (compared to the size of the smallest eddy), then the veligers are essentially flushed through the system, unimpaired. Questions regarding the necessary length of time that turbulence needed to be endured in order to cause mortality were raised. In addition, the work did not address how varying levels of turbulence impacted veligers, once d^* exceeded 0.9.

A third study was reported in 2007 (Jessopp, 2007) where field measurements of a variety of larvae were taken above and below a "rapids" in a marine environment in an effort to take concurrent measurements of turbulence and mortality under natural conditions. Again, the necessary length of time in turbulent conditions was not addressed. There was a significant effect of turbulent transport for some taxa but not for

others. The taxa most closely resembling *Dreissena* were *Mytilus* spp., a bivalve veliger. Data for this taxa show that 54% survive after being transported through the rapids. The size of the veligers was not reported – nor was the travel time through the rapids.

A final study focusing on how turbulence impacts *Dreissena* veligers was conducted by Crane and Horvath (2007) in the laboratory. An orbital shaker was used at different levels of turbulence and for different periods of time to look at the relationship between hydrodynamic forces and veliger mortality. There was little difference in the level of mortality between the controls and the treatments for all of the combinations, with the exception of the highest intensity (400 RPM) at the longest length of time (48 hours). Under these conditions, approximately 45% of the veligers survived. The authors did not report any information upon which the dissipation rate could be calculated.

Mortality Due to Vegetation

There is little in the literature describing the impact of vegetation and wetlands on veliger mortality. Miller and Haynes (1997) described creeks where one would expect zebra mussel colonies, yet none existed. They hypothesize that retention of veligers by a wetland could be the reason for non-establishment. Bodemer and Bossenbroek (2008) conducted a field study to pursue this line of thinking. These authors concluded that wetlands can cause rapid decreases in veliger abundance, although veliger populations were not reported.

3. ENVIRONMENTAL SETTING

Tarryall Reservoir (Figure 2) is located in Park County in central Colorado at an elevation of 8,860 feet. The 175 acre reservoir is owned and operated by the Colorado Division of Wildlife (CDOW) and is open for fishing and boating. Water can be released from the reservoir over a spillway (Figure 3) or through two 48-inch valves at the base of the dam, which are the river outlets (Figure 4). Currently, the river outlets are not being operated (Englemann, 2009a), although this may be changing in the future (Englemann, 2009b). Discharges from the reservoir generally range from 20 to 800 cfs.



Figure 2: Tarryall Reservoir (photo by R. Blair Hanna, AMEC)

Very few water-quality measurements have been taken in the reservoir. Three profiles were taken in 2007 (June, July, and August) for temperature, pH, and dissolved oxygen (DO). Samples were also taken of Secchi-disk depth, chlorophyll *a*, and total phosphorus on those dates. Samples for mussels were taken in 2008 and 2009 according to recently developed protocols (CDOW, 2009). Results for mussel testing in 2008 are shown in Table 1. On the date when a positive identification was made, only one quagga mussel veliger was detected. Samples collected in 2009 did not result in the positive identification of veligers.



Figure 3: Tarryall Reservoir Spillway (photo by R. Blair Hanna, AMEC)



Figure 4: Tarryall Reservoir River Outlets (photo by R. Blair Hanna, AMEC)

Tarryall Reservoir releases water into Tarryall Creek (Figure 5). This meandering river (Figure 6) flows for about 25 miles between the reservoir and confluence with the South Platte River (Figure 1). There are two small impoundments located downstream of the reservoir. The one to the west is referred to in this report as "Camp Pond" and the one to the east is Bayou Salado Reservoir (Figure 8). Both appear to be on private land.

The section of the South Platte River between the confluence and Cheesman Reservoir is about 6 miles. Flows in the South Platte River upstream of Cheesman Reservoir range from about 50 cfs to over 2,700 cfs. Estimates of channel slope in the riverine portions of the study area are shown in Figure 7. Note that the highest slopes occur in Tarryall Creek, just upstream of the confluence with the South Platte River.

Sample Date	Location	Result	
6/16/2008	Dam	No Veligers	
8/13/2008	Dam	No Veligers	
9/11/2008	Dam	VELIGER FOUND	
10/10/2008	East Dam PT 2a	No Veligers	
10/10/2008	East Dam PT 2b	No Veligers	
10/10/2008	Main East boat ramp PT 6a	No Veligers	
10/10/2008	Main East boat ramp PT 6b	No Veligers	
10/10/2008	Mid Dam PT 1a	No Veligers	
10/10/2008	Mid Dam PT 1b	No Veligers	
10/10/2008	Mid Res PT 5a	No Veligers	
10/10/2008	Mid Res PT 5b	No Veligers	
10/10/2008	Out from dam PT 3a	No Veligers	
10/10/2008	Out from dam PT 3b	No Veligers	
10/10/2008	West Ramp PT 4a	No Veligers	
10/10/2008	West Ramp PT 4b	No Veligers	
10/10/2008	West Ramp PT 4c	No Veligers	

 Table 1: Sampling Results for Tarryall Reservoir in 2008

Data Source: E. Brown, CDOW, July 13, 2009 email



Figure 5: Tarryall Creek Downstream of Tarryall Reservoir (photo by R. Blair Hanna, AMEC





Figure 6: Tarryall Creek between Tarryall Reservoir and the South Platte River



Figure 7: Channel Slope for Tarryall Creek and the South Platte River between Tarryall Reservoir and Cheesman Reservoir



Figure 8: Bayou Salado Reservoir (photo by R. Blair Hanna, AMEC)

There are very few water-quality measurements in Tarryall Creek although there are more in the South Platte River as it enters Cheesman Reservoir. Sites with any available water-quality samples are noted in Figure 9. Sampling for zebra or quagga mussels has not occurred in Tarryall Creek or the South Platte River. Cheesman Reservoir (Figure 10) is owned and operated by Denver Water, situated at an elevation of 6,842 feet above mean sea level. Shoreline fishing is allowed at this 875-acre reservoir. Denver Water collects some water-quality data in the reservoir.



Figure 9: Locations with Water-Quality Data



Figure 10: Cheesman Reservoir (photo by Jackie Shumaker)

The available water-quality data were analyzed and compared to conditions required for successful *Dreissena* populations to exist. Note that the locations and types of data are sparse in some cases, making a thorough assessment difficult. In addition, localized conditions may not be evident from the data. Of the numerous types of water-quality constituents, there are four that appear to be key for determining the risk of a future infestation – temperature, conductivity, calcium, and dissolved oxygen. An assessment using the available data for these variables is described below.

<u>Temperature</u>

Dreissena can live in a wide range of temperatures (Table 1). Lethal temperatures occur below -2 °C and above 40 °C. Temperatures of 12 °C or more are needed for spawning to occur (Cohen, 2001).

Temperature profiles in 2007 (June-August) in Tarryall Reservoir indicate a temperature range of 9-19 °C, decreasing with depth during the summer stratified period. All temperatures are at least 12 °C or above in the top 5.5 meters of the reservoir. Thus, reproduction of adult *Dreissena* should not be limited by temperature in the upper regions of the reservoir. Note that zebra mussels have been observed spawning at temperatures as low as 2.5°C (Walz 1978) but this is not considered typical.

The only temperature data in the riverine section of the study domain is at the inlet into Cheesman Reservoir. Temperatures vary between 0 °C and 23 °C. During the summer months (June to September), temperatures are 11 - 23 °C. Thus, South Platte River temperatures should not limit veliger survival. There are no temperature data for Camp Pond or Bayou Salado Reservoir on Tarryall Creek.

Cheesman Reservoir temperature profiles near the South Platte inlet indicate a temperature over 12 °C for the entire water column in July through September.

In summary, temperature does not appear to be a limiting factor for the establishment of a *Dreissena* population, although spawning may be limited to the upper regions (closer to the surface) in Tarryall Reservoir. Both Tarryall Reservoir and Cheesman Reservoir

reach optimal spawning temperatures in the summer and temperature conditions in Cheesman Reservoir are better than in Tarryall Reservoir, since they are warmer.

<u>Calcium</u>

There are a wide variety of required calcium concentrations for *Dreissena* survival and reproduction. In general, studies in Europe indicate the need for at least 25 mg/l calcium for establishment. In North America however, colonies have been established at lower concentrations (about 7-15 mg/l) (Cohen, 2001). Most studies of potential zebra mussel distribution have used values of 12 or 15 mg/l as the minimum calcium threshold below which the establishment of a population is unlikely, though threshold values of 2, 7, and 9 mg/l have also been used (Cohen, 2001). Cohen and Weinstein (2001) report very little evidence to support the view that *Dreissena* can become established at calcium concentrations below 20 mg/l.

Note that calcium concentrations within a reservoir can vary with depth and in horizontal directions. Despite low overall calcium concentrations in Lake George, New York, zebra mussels have reproduced in areas of the lake with elevated calcium concentrations (Nierzwicki-Bauer, 2009).

There are no available calcium data for Tarryall Reservoir. Samples taken above the reservoir in May of 2002 show a calcium concentration of 20 mg/l. A grab sample taken below Bayou Salado Reservoir on Tarryall Creek in 2009 indicates a concentration of 22 mg/l calcium. These numbers suggest an expected level of moderate growth. The inflow into Cheesman Reservoir ranges from 23 to 40 mg/l calcium, with a mean concentration of 33 mg/l. Higher concentrations of calcium occur here due to the impact of South Platte flows, which appear to have higher calcium levels than Tarryall Creek. There are no calcium data for Cheesman Reservoir, although concentrations may be similar to the inflow. This would suggest an expected level of good growth.

In summary, calcium concentrations do not appear to be a limiting factor for *Dreissena* establishment. Conditions in Cheesman Reservoir are more conducive to growth than in Tarryall Reservoir, however.

Conductivity

Conductivity above 110 μ S/cm is suggested as providing optimal growth conditions for *Dreissena* (Table 1). The only locations with conductivity data in the study area are at the inflow to Cheesman Reservoir (mean = 350 μ S/cm) and Cheesman Reservoir (mean = 250 μ S/cm). Therefore, it appears that conductivity is not a limiting factor for this system.

Dissolved Oxygen

As noted above, the lower lethal limit for dissolved oxygen at 18 °C is reported to be 4 mg/l (Sprung, 1987; McMahon, 1996). Dissolved oxygen profiles for Tarryall Reservoir in 2007 (Figure 11) show less than 4 mg/l DO at depths of two meters or more in August (although the temperatures are around 14 °C in this region, less than 18 °C). If the 2007 profiles are typical, DO could place a limitation on *Dreissena* establishment in Tarryall Reservoir, by providing appropriate habitat only in the top two meters.



Figure 11: Dissolved Oxygen in Tarryall Reservoir

The inflow into Cheesman Reservoir always has a dissolved oxygen concentration of above 4 mg/l. Dissolved oxygen profiles in Cheesman Reservoir show concentrations above 4 mg/l throughout the water column in June through August. By the end of September, concentrations below 30 meters deep drop below the threshold. This would provide a very large area for establishment in Cheesman Reservoir.

In summary, dissolved oxygen may be a limiting factor for a large portion of Tarryall Reservoir. Populations may be confined to the top two meters and available substrate in this area may be limited. Dissolved oxygen conditions should not be problematic for *Dreissena* populations in Cheesman Reservoir however.

Water-Quality Assessment Summary

In general, water-quality conditions in Tarryall Creek and the South Platte River should not impact the mortality of veligers as they are transported downstream. Conditions in Tarryall Reservoir are less than optimal, especially with respect to dissolved oxygen concentrations. This is based on three profiles taken over one summer. Calcium concentrations are also lower but suggest a moderate level of growth. For Cheesman Reservoir, water-quality conditions should not result in limitations for the establishment of *Dreissena*.

5. MODEL DEVELOPMENT

In order to investigate the probability of mussels establishing a population in Cheesman Reservoir, a model was developed to quantify veliger population movement and integrate many of the processes described above. The model is based on a particle tracking approach. A set of particles, each one representing a number of veligers, moves with the flow from Tarryall Reservoir, through two small impoundments, to Cheesman Reservoir. The characteristics of each particle are tracked through time. These include information such as: age, size, state of movement with flow, settled or attached.

Tarryall Creek and the South Platte River between Tarryall Reservoir and Cheesman Reservoir are characterized as 104 0.5 km segments in the model. Tarryall Reservoir is the upstream end of the reach. Cheesman Reservoir is simulated as one 20-km segment at the downstream end. Two intermediate impoundments exist along the Tarryall Creek -- "Camp Pond" and "Bayou Salado Reservoir (Figure 12).



Figure 12. Model Segmentation Schematic

Physical characteristics of each segment are based on data from the National Hydrographic Data (NHD) Plus spatial database (EPA, 2009). This dataset provides physical characteristics of stream length, slope and average hydrologic data for each segment, where a segment is defined as a section of river bounded by tributary inflows. The NHD provides data for 19 segments between Tarryall Reservoir and the South Platte River and 6 segments in the South Platte between the Tarryall confluence and Cheesman Reservoir.

The NHD provides hydrologic characteristics for each segment and includes a calculation of annual average discharge. This discharge was calculated as a function of spatial watershed parameters and an average annual set of precipitation. Annual average discharge values are provided for all river segments in the spatial database. Using these discharge values, a relationship between the flow in the upstream segment and all downstream segments was developed. This relationship accounts for tributary gains throughout the watershed. The upstream discharge (release from Tarryall Reservoir) for each simulation period is set and the resulting downstream flows are

computed from the upstream value. Tarryall releases are based on historical flow data from 1974 – 2009.

Veligers are simulated as a particle moving through the set of segments. Information about each veliger is stored, such as the location, age, size, if moving with the flow, settled or attached and if it is reproducing. Although it is known that *Dreissena* can reenter the water column after settling, this mechanism is assumed to play a minor role in veliger transport and is not included in the model. A schematic of the processes included is presented in Figure 13.



Figure 13. Particle Process Schematic

Particles undergo processes of movement, aging, settling, attachment or death. Death can occur by vegetative filtering, turbulence, old age and by random chance. We assume that mortality due to starvation and predation is insignificant. Many of the processes considered can only occur at certain ages or life stages. The zebra mussel life stages and their characteristics assumed in the model are described in Table 2. It is important to keep track of each life stage since some processes affect some life stages differently than others (e.g., settling, turbulence, ability to free-flow, etc.). This is a simplified view and assumes that a specific age corresponds to a specific life stage and size. It is understood that in reality, there are large overlaps in sizes among the larval stages (Ackerman, et al., 1994). In addition, the influence of certain environmental factors on the growth rate is ignored in the model.

The age distribution for the population of particles that flow out of Tarryall Reservoir follows a triangular distribution specified by a minimum, maximum and mode (age of highest frequency). Particles are all assumed to be in free-flowing life stages that leave Tarryall Reservoir.

The model simulates a two year period using a one-hour time step, each with twelve monthly periods with average conditions. It is assumed that there are no *Dreissena* in the system at the start of the simulation.

Age (days)	Life Stage	Size (um)	Growth rate (um/day)	Processes
<= 2	trochophore	89	10	Free-flowing; Can not settle nor attach
2 - 6	D-shaped veliger	115	11.34	Free-flowing; Can not settle nor attach
6 - 13	veliconcha	200	0.85	Free-flowing; Can not settle nor attach
13 - 28	pediveliger	235	0.85	Can settle; Can attach
> 28	plantigrade	329	28.5	Can settle; Can attach

Table 2. Modeled Life Stage Characteristics

The processes that the particles undergo are summarized as follows:

Each veliger:

- Can age and grow in size over time
- Is moved by velocity in segment
- If free-flowing, can die as a function of turbulence, which is a function of veliger size, channel characteristics, and velocity
- If free-flowing, can die if randomly filtered by vegetation
- Can die randomly at any time
- Can die of old age
- Can settle in selected low-velocity segments
- If settled, can be randomly attached or die
- During June September, if a veliger is attached and the segment-specific minimum density of attached particles is satisfied, female individuals can randomly produce new offspring

Additional mussel-specific data are provided for each segment in the domain.

The details of each of the processes are outlined below.

Random Processes

Many of the processes describing movement or death of veligers have a random component. These are driven by a variable describing the percent chance of a process occurring. Within the model code, the uniform random number generator is used and the random number compared against the percent chance as follows:

random_number is a real number [0 - 1) chosen from a uniform distribution between 0 and 1 (greater than or equal to 0, less than 1).

If (random_number < the_chance) then Occurred by chance Else Did not occur by chance

Endif

Triangular Distributions

Values for veliger ages and flow velocity are chosen randomly based on a triangular frequency distribution. The distribution is described by minimum, mode and maximum. The minimum and maximum values are the lowest and highest values possible in the population (Figure 14). The mode is the value that is most frequent. The distribution does not have to be symmetric.



Figure 14. Triangular Distribution Schematic

Advective and Dispersive Transport

Empirical relationships (Jobson, 1996) were incorporated into the NHD Plus dataset to calculate the travel time velocity for each segment. These velocities correspond to the velocity of the center of mass (peak concentration) of a dispersive cloud. The center of mass velocity is the most frequent flow velocity encountered in the reach. The velocity of the leading edge of the dispersive cloud (the fastest particle) and the trailing edge of the cloud (the slowest particle) are also calculated based on empirical relationships developed from travel time/dye tracer studies in over 60 rivers throughout the U.S.

The relationship for the velocity of the center of mass is presented below. This velocity is considered the most frequent velocity in a segment.

$$V_{center} = 0.094 + (0.0143 * D_a^{(0.919)} * Q_a^{(-0.469)} * S_0^{(0.159)} * \frac{Q}{D_a})$$

where:

$$D_a^{'}$$
 = dimensionless drainage area = $(D_a^{1.25} * g^{0.5}) / Q_a$

- $Q_a^{'}$ = dimensionless relative discharge = Q/Q_a
- Q = segment discharge (m³/s)
- Q_a = mean annual discharge in the segment (m³/s)
- D_a = drainage area of the segment (m²)
- g = acceleration due to gravity (m/s²)

 S_0 = segment slope (m/m)

For segments with low to no slope (Camp Pond, Bayou Salado Reservoir, Cheesman Reservoir), an empirical relationship not including slope is used, as presented below.

$$V_{centernoslope} = 0.02 + (0.051 * D_a^{,0.821} * Q_a^{,-0.465} * \frac{Q}{D_a})$$

The velocity of the leading edge is related to the velocity of the center of mass as presented below. This velocity is the highest flow velocity expected in the segment.

$$V_{leadingedge} = \left(\frac{1}{0.89}\right) V_{center}$$

The velocity of the trailing edge of the cloud is presented below. This is the velocity of particles in the trailing edge of the dispersed cloud where the concentration is 10% of the peak. This velocity is considered the slowest expected flow velocity in a segment.



where Δx is the length of the segment (500 m in the model).

The velocity of a particle in a segment is chosen randomly during the simulation from a triangular distribution with minimum velocity (trailing edge) and maximum velocity (leading edge) and a mode (most frequent) velocity (center of mass). If a veliger is settled or attached, the velocity is set to zero.

<u>Settling</u>

For each segment in the model, the veliger can flow through or settle as specified by a segment-specific binary settling value. The ability to settle is life-stage specific, only pediveligers and plantigrade life stages can settle. If settling can occur in a segment, then when a veliger of the minimum size enters, the veliger settles.

<u>Attachment</u>

Only settled veligers can attach. There is a random chance of the veliger attaching once settled. The probability of attachment is a simulation variable. If a settled veliger does not attach by chance, the veliger dies. This process models the possibility of a settled veliger attaching to inadequate substrate or attaching in a location of poor water quality (e.g., low dissolved oxygen) so that the zebra mussel does not continue to grow once attached.

Death by Old Age

The life span of a veliger is assumed to be 2 years (Claudi and Mackie, 1994). The variability in this life span is represented by a mean and standard deviation of the life span. These are variables input to the model. If a veliger's age is greater than the mean plus one standard deviation, the veliger dies.

Random Death

During any life stage a zebra mussel can die randomly. This process includes such events like predation or illness. The chance is set via a random death rate applied to all living veligers, used for the model simulation.

Death Due to Vegetation Filtering

If a veliger is moving with the flow, there is a chance that vegetation along the stream bank can filter the veliger from the flow. The chance of filtering the veliger, essentially killing it, is a segment-specific probability. This process is included in the model as a random chance for all non-settled and non-attached veligers in segments. Since the level of vegetation in Tarryall Creek and the South Platte River is low, the chance of filtering is set to be low.

Death Due to Turbulence

Information from the laboratory and field studies reviewed in Section 2 above was used to determine a method for computing the impact of turbulence on veliger mortality. Following Rehmann, et al. (2003), we used a dimensionless number d^* - the ratio of the veliger shell size (*d*) and the Kolmogorov length scale (L_k). The Kolmogorov length scale

is the smallest scale in the velocity field and is a function of the dissipation rate of turbulent kinetic energy:

$$d^* = \frac{d}{L_k} = \frac{d}{\left(\frac{v^3}{\varepsilon}\right)^{\frac{1}{4}}}$$

where:

 ε = dissipation of turbulent kinetic energy (m²/s³)

$$d =$$
veliger size (μ m)

v = kinematic viscosity of water at 20 °C = 1.004 x 10⁻⁶ m/s

The authors hypothesized that turbulence will affect mortality when $d^* \ge 1$. If d^* is << 1, the eddies are large in relationship to the veliger and the veliger is transported with the flow. If, on the other hand, d^* is ~1 or more, turbulence would be at a scale sufficient to "toss and turn" the veliger enough to increase the rate of mortality. Thus, a smaller veliger would require more intense turbulence for mortality to occur. The rate of energy dissipation can be measured in a laboratory or estimated in a natural setting. One method to estimate the value of energy dissipation averaged over a channel depth has been suggested by Rehmann, et al, (2003):

$$\varepsilon = 8 \frac{\left(gR_h S_0\right)^{1/2}}{v}$$

where:

g = acceleration due to gravity = 9.8 m/s²

 S_0 = channel slope

 R_h = the hydraulic radius of the flowing channel.

Using the wide rectangular channel assumption, R_h = depth

y = channel depth (m)

All of the information required to compute d^* for each veliger within a segment is computed in the model, although the value of d^* needs to be tied to some type of chance of survival. For this, we turned to the results from the two field studies that provided enough information to compute the dissipation rate and collected veliger data to compute mortality. The results should show that the higher the d^* , the greater the chance of mortality.

The first study took place on Christiana Creek (Horvath and Lamberti, 1999). For this study, 52% of the veligers survived the 16 hour "ride" over 18 km. Fitting this information to a first-order rate equation, the hourly chance of survival is 96%. For this same study, Rehmann, et al. (2003) estimated a range of d^* between 0.51 and 1.27. The mid-point of this range is 0.9. Therefore, for the Christiana Creek study, there was a 96% hourly chance of survival and an approximate d^* of 0.9.

The second field study took place on the "rapids" at the Lough Hyne Marine Nature Reserve (Jessopp, 2007). For this study, values of the rate of dissipation were reported along with veliger mortality rate. The author reported that 54% survived after going over

the rapids. It is estimated that the rapids are 100 meters in length. Using the reported velocity and the estimated length, a travel time was estimated. The hourly chance of survival in this situation was computed to be 1.6E-12%. The dissipation rate for this study was almost five times that of the Christiana Creek study. A d^* of approximately 2.5 for the "rapids" study was estimated. The results of this work did not clearly separate the effect of turbulence from other possible causes of mortality. We attributed about one-third of the mortality to turbulence. Using that conservative adjustment, the number that may have survived the turbulent ride was 85%. This adjustment results in an hourly chance of survival of 0.02%.

Using the two data points from the two studies, a relationship was developed between values of d^* and the chance of survival. Not having any additional information, a line was fit between the two data points (Figure 15). Below a d^* value of about 0.8, we assumed there would be no mortality due to turbulence. As d^* increases, the chance of survival decreases and the chance of dying due to turbulence increases. At a d^* equal to 2.5, the chance of survival is 0.02%. At d^* above 2.5 the chance of survival is set to zero.



Figure 15. Relationship between *d** and the Hourly Chance of Survival

Reproduction

Only mature attached veligers can reproduce given adequate density on the channel bed. Veligers must be mature with a minimum size of 8 mm (Claudi and Mackie, 1994). The minimum populations in Camp Pond, Bayou Salado Reservoir, and Cheesman Reservoir are input variables. It is assumed that spawning can only occur during warm weather in this system (June – September) and that peak spawning is associated with the warmest month (August).

The reproduction rate is assumed to vary as a function of the minimum population required for viable reproduction. The chance of reproducing is 95% at the required density and decreases linearly to 10% at 20% of this requirement. This rate relationship is shown in Figure 16.

It is assumed that reproduction can occur once a mussel is at least 8 mm in size. It is also assumed that mussels can spawn four times in their lives and only during the period June to September, when temperatures are at least 12 °C.

If conditions are right, there is a random chance that the females of the population (50% are assumed to be female) can produce a set of offspring. The number of offspring produces is a simulation variable. The ages of all the offspring are set to zero days and are released into the flow at the location of the parent. These new particles are then tracked in the simulation.



Figure 16. Reproduction Rate as a Function of Minimum Required Population

Model Simulation

The model simulates two identical years of monthly average conditions using an hourly time step. Yearly time series of monthly conditions are provided as model variables describing the releases from Tarryall and populations of veligers released at the start of each month. The values of the simulation variables (Table 4) are set for each model simulation.

Model Output

At the end of the two year simulation, the following information is output from the model:

- Total number of individuals discharged from Tarryall Reservoir;
- Total number of offspring produced;
- Total number of deaths by vegetation;
- Total number of deaths by turbulence;
- Total number of deaths by old age;
- Total number of deaths by random death;
- Total number of deaths by non-settling;
- Ending population throughout Tarryall Creek and the South Platte River;
- Population in Cheesman;
- Total population that are settled;
- Total population that are attached; and
- Total population that are reproducing.

Other simulation data are available for all particles such as:

- Current location;
- Current life stage and size;
- Cause of death and location of death; and
- Current level of turbulence for particle (if dead, level of turbulence at death).

Variable Name	Unit	
12 monthly discharges	cfs	
12 monthly populations released	Number of veligers	
Age distribution min	Days	
Age distribution max	Days	
Age distribution mode (most frequent value)	Days	
Random death rate	Percentage	
Age of natural death mean	Days	
Age of natural death stdev	Days	
Chance of attaching if settled	Percentage	
Min pop for reproduction: Camp Pond	Number of veligers	
Min pop for reproduction: Bayou Salado Reservoir	Number of veligers	
Min pop for reproduction: Cheesman	Number of veligers	
Chance of reproduction if adequate density	Percentage	
Number of offspring per female	Number of veligers	

Table 4. Variables in the Simulation

6. MODEL RESULTS

A variety of model runs were made initially to explore the impacts of various factors on mortality. The results are described below.

Conservative Simulation

The model was initially used making conservative assumptions in order to investigate the potential death of veligers due to turbulence in Tarryall Creek. After computing d^* values for Tarryall Creek and the South Platte River, it was evident that mortality due to turbulence would be a dominant factor. The level of turbulence in this study area is much higher than levels in the two field studies described above (the average d^* is >2.5). Therefore, the first simulation was conducted conservatively, adjusting some variables to minimize d^* . A simulation was run using the lowest discharges, the smallest veliger sizes, and with the population released from Tarryall Reservoir increased by a factor of ten. The spillway was also removed (thus simulating flow through the river outlets) to reduce the initial level of turbulence. In addition, the random-death rate was set to zero.

The results for this conservative run are shown in Figure 17. The y-axis represents the number of veligers (dead or alive) by distance from Tarryall Reservoir. Note that all veligers perished, mostly due to turbulence (99.8%) and a few due to vegetative filtering. A few veligers made it past Camp Pond but died before reaching Bayou Salado Reservoir. Thus, it is apparent that turbulence plays a very large role in the fate of veligers for the Tarryall Creek / South Platte River system.



Figure 17. Results from the Initial Model Test (Conservative Simulation)

Base Case Simulations

Simulations were run using the most likely variables and parameters, with and without the spillway at Tarryall Reservoir. Note that due to the segmentation of the model (each segment is 0.5 km), the slope of the first segment is an average over the entire segment. Thus, the actual change in elevation at the spillway is more drastic than the model characterization. The results are shown in Figures 18 and 19. With the spillway, all of

the veligers perish before reaching 7.5 km downstream. Without the spillway (releasing the water through the river outlets), all veligers perish before reaching 9.0 km. Essentially all veliger mortality is due to turbulence.



Figure 18. Results from the Base Case Simulation (Release over Spillway)



Figure 19. Results from the Base Case Simulation (Release through River Outlets)

Constant-Turbulence Simulations

Since the simulations using the turbulence model described above resulted in 100% mortality, several simulations were conducted using a constant chance of mortality due to turbulence, versus making turbulence mortality a function of veliger size, slope, and flow. This was done to obtain simulations that resulted in development of populations in Cheesman in order to evaluate the importance of other parameters and variables. The first constant-turbulence simulation used the turbulence computed for the Michigan field study (Horvath and Lamberti, 1999). The hourly chance of survival for this study was approximately 96%. Thus, we essentially applied the level of turbulence in Christiana

Creek to the Tarryall Creek / South Platte River system consistently over the study area. The results are shown in Figure 20. This simulation shows the establishment of a population in Cheesman Reservoir. The population in Cheesman is assumed to be uniformly distributed in the upstream end of the reservoir, hence the flat-line population indicated in the figure. Of the veligers that died, 82% died from turbulence, 10% from not being able to attach once settled, 7% from random death, and <1% from vegetative filtering.



Figure 20. Results from the Constant-Turbulence (hourly chance of survival of 96%) Simulation (Release through the River Outlets)

Simulations were also run to determine what minimum hourly chance of survival was needed to prevent a population from establishing in Cheesman Reservoir. It was determined that an hourly chance of survival due to turbulence of 80% or more will more than likely result in a population establishing in Cheesman Reservoir. An hourly chance of survival of 65% or less would more than likely result in a population not establishing in Cheesman Reservoir. The *d** ratio would need to be less than 1.5 for this to occur, using the turbulence model described in Figure 15. The average *d** for the Tarryall Creek / South Platte River system is greater than 2.5 predominantly due to higher channel gradients.

Monte Carlo Analysis

A set of 100 simulations was performed to investigate the relationship between the system variables and the chance of a population of *Dreissena* establishing in Cheesman reservoir. A range is established for each of the simulation variables. For each of the 100 simulations, values for each variable are chosen from the allowable range using a uniform distribution (Table 5). Ranges of variables and parameters are based on the best available data and professional judgment. Minimum and maximum values used for discharge are based on historical flow data from 1974 – 2009. The average monthly discharges from Tarryall are used to choose the set of discharges for each realization. The average monthly values (Table 6) are scaled as a set to represent inter-annual variability of flow using a factor chosen from a uniform random distribution between 0.25 and 2. For these runs, it was assumed that Tarryall Reservoir releases occurred at the river outlets and a constant turbulence model was used (96% hourly chance of survival).

Variable Name	Minimum	Maximum
Jan population released	0	0
Feb population released	0	0
Mar population released	0	0
Apr population released	0	0
May population released	0	0
Jun population released	0	500
Jul population released	0	500
Aug population released	0	1000
Sep population released	0	500
Oct population released	0	100
Nov population released	0	0
Dec population released	0	0
Age distribution min	0 days	13 days
Age distribution max	13 days	28 days
Age distribution mode (most frequent value)	2 days	10 days
Random death rate	0	1/10,000 per hr
Age of natural death mean (set constant)	730days	730 days
Age of natural death stdev	0 days	0 days
Chance of attaching if settled	50%	90%
min pop for reproduction: Camp Pond	100 attached	500 attached
min pop for reproduction: Bayou Salado Reservoir	100 attached	500 attached
min pop for reproduction: Cheesman	500 attached	1000 attached
Chance of reproduction f(population)	10%	90%
number of offspring per female	0	100
Mortality due to turbulence method	1 – constant 0.04%	1 – constant 0.04%

Table 5. Simulation Variable Set

Variable Name	Average (cfs)
Jan discharge	35
Feb discharge	35
Mar discharge	35
Apr discharge	115
May discharge	165
Jun discharge	425
Jul discharge	140
Aug discharge	115
Sep discharge	55
Oct discharge	35
Nov discharge	35
Dec discharge	35

Table 6. Average Monthly Discharges from Tarryall Reservoir

The majority (87%) of the simulation runs result in populations being established in Cheesman Reservoir. For the veligers that perished, turbulence is the leading cause of mortality.

7. LIMITATIONS AND UNCERTAINTY

This analysis relied on as much of the available information on the biology of *Dreissena* as we could find. However, even the large amount of published and un-published information available to us contained very little information relevant to understanding the survival and viability of *Dreissena* in the environment of Tarryall Reservoir, Tarryall Creek, the South Platte River and Cheesman Reservoir. In particular, we relied on two field studies in order to develop a model of *Dreissena* mortality due to turbulence, and we had to infer or estimate some aspects of both of these studies. There simply is not much information that is directly relevant to this analysis, and even those laboratory and field studies that we have found are all flawed in some important way.

Factors other than turbulence can influence the mortality or viability of *Dreissena* and we had even less quantitative information about these factors than we had about turbulence. In formulating the model we relied on professional judgment to synthesize the body of research as the basis for estimates of plausible ranges of parameters and variables.

In addition, we note that each 0.5 km segment in the model is treated as having a homogeneous slope. In reality, the meandering section of Tarryall Creek below the Tarryall Reservoir, in particular, is interspersed with areas with and without riffles. There may be some areas with localized conditions conducive to settling and attachment. If this is the case, some reproduction could occur. Note however, that the resultant

intermediate population would need to be high in order to withstand the steep sections of Tarryall Creek above the confluence with the South Platte River.

8. CONCLUSIONS AND RECOMMENDATIONS

When the model is run using realistic parameters, 100% mortality occurs and no populations are established in Chessman Reservoir. The overwhelming reason for the mortality is the high level of turbulence in the Tarryall Creek / South Platte River system. This occurs for both of the release scenarios – releases over the spillway and releases through the lower river outlets. Visual and regression analyses were conducted to determine the relative importance of causes of mortality other than turbulence. These analyses were based on a constant hourly chance of survival from turbulence of 96%. No clear pattern was evident.

Based on our analysis, subject to the limitations set out above, we believe that there is a low likelihood that *Dreissena* populations will be introduced into Cheesman Reservoir via Tarryall Creek. The limited information available to us indicates that turbulence will cause a very substantial mortality to *Dreissena* in Tarryall Creek. Given the apparent magnitude of this effect, we have a reasonable degree of certainty in our conclusion.

Other conclusions include:

- Based on the available data, water-quality in the Tarryall Creek / South Platte River system and Cheesman Reservoir should not limit the establishment of *Dreissena* in Cheesman Reservoir.
- Due to low dissolved oxygen concentrations below 2 meters in Tarryall Reservoir, water-quality could limit the amount of suitable habitat for establishment in Tarryall Reservoir.
- Although numerous samples have been taken in Tarryall Reservoir over two years, only one veliger has been detected thus far. This is a very low number.
- Settling is possible at two intermediate locations in the Tarryall Creek / South Platte River system if viable veligers reach either location. These are Camp Pond and Bayou Salado Reservoir.

Recommendations for future work include:

- Sample all or a measured fraction of the outflow of Tarryall Creek over the spillway for a sustained period in order to establish the rate of introduction of veligers into Tarryall Creek and their age and size distribution. This should be incorporated into a regular monitoring program.
- Collect samples from the two impoundments below Tarryall Reservoir (using both vertical tows and artificial substrates).
- Monitor dissolved oxygen concentrations and calcium in Tarryall Reservoir to better understand typical conditions.
- Continue to take preventative measures at Tarryall Reservoir

- Conduct further modeling studies to develop better models for the causes of mortality other than turbulence
- Conduct laboratory turbulence studies. Carefully designed studies would provide data that could be used in engineering risk assessment studies that would provide much more precise estimates of the likelihood of *Dreissena* reaching Cheesman Reservoir through Tarryall Creek.

8. REFERENCES

- Ackerman, J.D., B. Sim, S.J. Nichols, and R. Claudi. 1994. A review of the early life history of zebra mussels (*Dreissena polymorpha*): comparison with marine bivalves. Can. J. Zool. 72:1169-1179.
- Armitage, P.D. and M.H. Capper. 1976. The numbers, biomass and transport downstream of micro-crustaceans and Hydra from Cow Green Reservoir (Upper Teesdale). Freshwater Biology. 6:425-432.
- Baker, P., S. Baker, and R. Mann. 1994. Criteria for Predicting Zebra Mussel Invasions in the Mid-Atlantic Region. Virginia Institute of Marine Science.
- Bodamer, B.L. and J.M. Bossenbroek. 2008. Wetlands as barriers: effects of vegetated waterways on downstream dispersal of zebra mussels. Freshwater Biology. 53:2051-2060.
- CDOW. 2009. State of Colorado Aquatic Nuisance Species Sampling Procedures. Colorado Department of Wildlife and Colorado Department of Natural Resources. Last updated February 10, 2009.
- Claudi, R. and G.L. Mackie. 1994. Practical Manual for Zebra Mussel Monitoring and Control. Lewis Publishers.
- Crane and Horvath. 2007. The effects of hydrodynamic forces on zebra mussel (*Dreissena polymorpha*) veliger mortality in a laboratory setting. <u>http://www.oneonta.edu/academics/biofld/PUBS/ANNUAL/2007/zebra%20musse</u> <u>l.pdf</u>
- Cohen, A.N. 2001. A Review of Zebra Mussels' Environmental Requirements. California Department of Water Resources.
- Cohen, A.N. and A. Weinstein. 2001. Zebra Mussel's Calcium Threshold and Implications for its Potential Distribution in North America. San Francisco Estuary Institute. June 2001.
- Englemann, C. 2009a. Colorado Department of Water Resources. Personal communication. May 18, 2009.
- Englemenn, C. 2009b. Colorado Department of Water Resources. Letter to Grady McNeill. September 23, 2009.
- EPA. 2009. NHDPlus User Guide. Environmental Protection Agency and the U.S. Geological Survey. January 20, 2009.
- Horvath, T.G. and G.A. Lamberti. 1999. Mortality of Zebra Mussel, *Dreissena polymorpha* Veligers during Downstream Transport. Freshwater Biology. 42:69-76.

- Horvath, T.G., G.A. Lamberti, D.M. Lodge, and W.L. Perry. 1996. Zebra mussel dispersal in lake-stream systems: source-sink dynamics? J. N. Am. Benthol. Soc. 15(4):564-575.
- Jessopp, M.J. 2007. The quick and the dead: larval mortality due to turbulent tidal transport. J. Mar. Biol., Ass. UK. 87:675-680.
- Johnson, L.E. and J.T. Carlton. 1993. Counter-productive public information: the "Noah Fallacy" and mussel myths. *Dreissena polymorpha* Information Review. 3(3):2-4.
- Jobson, H.E. 1996. Prediction of Traveltime and Longitudinal Dispersion in Rivers and Streams. U.S. Geological Survey. Water-Resources Investigations Report 96-4013.
- Karatayev, A.Y., L.E. Burlakova, and D.K. Padilla. 2006. Growth Rate and Longevity of Dreissena polymorpha (Pallas): A Review and Recommendations for Future Study. J. of Shellfish Research. 25(1):23-32.
- Mackie, G.L. and D.W. Schloesser. 1996. Comparative biology of zebra mussels in Europe and North America: An overview. *American Zoologist.* 36: 244-258.
- Mackie, G.L., W.N. Gibbons, B.W. Muncaster and I.M. Gray. 1989. The Zebra Mussel *Dreissena polymorpha*: A Synthesis of European Experiences and a Preview for North America. A report for the Ontario Ministry of the Environment, Water Resources Branch, Great Lakes Section, Queen's Printer, Toronto.
- MacIsaac, H.J., W.G. Sprules, and J.H. Leach. 1991. Ingestion of small-bodied zooplankton by zebra mussels (Dreissena polymorpha): Can cannibalism on larvae influence population dynamics? Canadian Journal of Fisheries and Aquatic Sciences. 48:2051-2060.
- McMahon, R. 1996. The physiological ecology of the zebra mussel, *Dreissena polymorpha*, in North America and Europe. *American Zoologist* 36: 339-363.
- Miller, S.J. and J.M. Haynes. 1997. Factors Limiting Colonization of Western New York Creeks by the Zebra Mussel (*Dreissena polymorpha*). J of Freshwater Ecology. 12(1):81-88.
- Nichols, S.J. 1993. Spawning of zebra mussels (*Dreissena polymorpha*) and rearing of veligers under laboratory conditions. Pages 315-329 in: *Zebra Mussels: Biology, Impacts, and Control*, Nalepa, T.F. and D.W. Schloesser (Eds.), Lewis Publishers, Boca Raton, FL.

Nierzwicki-Bauer, S.A. 2009. Darrin Freshwater Institute. Personal communication.

- Rehmann, C.R., Stoeckel, J.A., and Schneider, D.W. 2003. Effect of turbulence on the mortality of zebra mussel veligers. Canadian Journal of Zoology, 81:1063-1069.
- Sprung, M. 1987. Ecological requirements of developing *Dreissena polymorpha* eggs. *Arch. Hydrobiol. (Suppl.)* 79:69-86.

- Sprung, M. 1989. Field and laboratory observations of *Dreissena polymorpha* larvae: abundance, growth, mortality, and food demands. Archiv fur Hydrobiologie, 115:537-561.
- Sprung, M. 1993. The other life: an account of present knowledge of the larval phase of *Dreissena polymorpha*. In: *Zebra mussels: biology, impacts, and control,* T. Nalepa and D. Schloesser, (Eds). Lewis Publishers. Ann Arbor, MI.
- Stanczykowska, A. 1977. Ecology of *Dreissena polymorpha* (Pall.) (Bivalvia) in lakes. Poldkie Archiwum Hydrobiologh, 24:461-530.
- Walz. N. 1978. The energy balance of the freshwater mussel *Dreissena polymorpha* Pallas in laboratory experiments and in Lake Constance. II. Reproduction. Arch. Hydrobiol. 55 (Suppl.): 106-119.