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Research Article

Estimating survival rates of quagga mussel (*Dreissena rostriformis bugensis*) veliger larvae under summer and autumn temperature regimes in residual water of trailered watercraft at Lake Mead, USA

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Abstract

On 6 January 2007, invasive quagga mussels [*Dreissena rostriformis bugensis* (Andrusov, 1897)] were discovered in the Boulder Basin of Lake Mead, Nevada, a popular site for recreational boating in the southwestern United States. Recreational watercraft are considered a primary vector for overland dispersal of quagga mussel veliger larvae between water bodies. Thus, effective decontamination of veligers in residual water carried by trailered recreation boats is critical to controlling this species' spread. The survival rate of quagga mussel veligers was measured during exposure to environmental temperature conditions mimicking those experienced in the residual water of trailered vessels during warm summer and cooler autumn months in the semi-arid southwestern United States. Under warm summer conditions, quagga mussel veligers survived approximately five days while under cooler autumn conditions they survived 27 days. When tested under autumn temperature conditions veliger survival times increased with increased level of larval development. The results suggested a greater likelihood of veliger transport in the residual water of trailered watercraft during autumn months. The results indicated that presently recommended vessel quarantine times to kill all externally attached juvenile and adult dreissenid mussels prior to launching in an uninfested water body should be increased to generate 100% veliger mortality in residual water unable to be fully drained from the internal areas of watercraft.

Key words: quagga mussel; *Dreissena rostriformis bugensis*; veliger; thermal tolerance; water temperature; watercraft management

Introduction

Invasive species and anthropogenically induced climate change are now considered the top two threats to our planet's biodiversity (Vitousek et al. 1997; Halpern et al. 2008). Zebra mussels [*Dreissena polymorpha* (Pallas, 1771)] and quagga mussels [*Dreissena rostriformis bugensis* (Andrusov, 1897)] arguably are the most serious nonindigenous biofouling pests introduced to North American freshwaters (LaBounty and Roefer 2007), and are among the world's most economically and ecologically damaging aquatic invasive species (Aldridge et al. 2006; Connelly et al. 2007). Following the appearance of zebra mussels in the Great Lakes in the 1980s, regional economic damages were estimated to be four billion US dollars over the first 10 years of introduction, largely from sport fishery losses (Roberts 1990). Prior to the discovery of quagga mussels in the western states, the combined economic losses due to zebra and quagga mussels were estimated to be as great as one billion US dollars annually (Pimentel et al. 2005). Estimates of the economic costs associated with mussel infestations of North American raw-water intake systems alone, have ranged from 100 million to one billion US dollars per annum (Pimentel et al. 2005 and Bidwell 2010). From 1989 to late 2004, the total economic cost for dreissenid fouling of electric generation and water treatment facilities in North America was estimated to be approximately US $267 million (Connelly et al. 2007).

Spread of aquatic invasive species, such as dreissenids, can occur unintentionally as a result of their temporary residence on vehicles, vessels, or in raw water transported by vessels between water bodies. Other aquatic invasive species have been spread intentionally as ornamental plants and animals, aquaculture organisms, and bio-control agents (Cohen 2011). Much of the ongoing dreissenid invasion of North American inland water bodies has been attributed to overland transport of mussel-infested watercraft (Schneider et al. 1998; Leung et al. 2006).

The veliger larvae of quagga and zebra mussels are believed to have been first introduced into the Great Lakes from the Black Sea region of the Ukraine in the 1980s by transport in the ballast water of commercial oceangoing vessels that was subsequently discharged in the western Lake Erie region of the lower Great Lakes (Carlton 2008). Quagga mussels are generally considered to have been subsequently carried to Lake Mead (and other isolated water bodies) through overland transport of mussel-fouled recreational boats (LaBounty and Roefer 2007; Wong and Gerstenberger 2011).

Before its discovery in the Boulder Basin of Lake Mead (Nevada, USA) on January 6, 2007, the quagga mussel was primarily restricted to the Great Lakes region. The 2007 Lake Mead observation provided evidence of the first confirmed introduction of a dreissenid species in the western United States, and it was also the first time that a large ecosystem was infested by quagga mussels without previous infestation by zebra mussels (Labounty and Roefer 2007; McMahon 2011). Lake Mead is the largest reservoir by volume in the United States (LaBounty 2008), and provides municipal and irrigation water for approximately 25 million people in the western U.S. (Holdren and Turner 2010). Lake Mead's recreational uses are managed by the National Park Service's Lake Mead National Recreation Area, which received 6,396,682 visits in 2011 (National Park Service 2012). During the summer months, the average number of vessels on Lake Mead at any given time is approximately 3,000; on holiday weekends, it rises to 5,000 vessels (Zegers 2008).

Although Lake Mead is located in the arid desert southwest, where daily high air temperatures can surpass 37ºC during the summer, it has been shown that quagga mussels can spawn and survive several weeks above 30ºC (AWWA 2008). It is also well documented that quagga mussel veligers are present in Lake Mead throughout the year; sometimes reaching densities of 29 veligers/L (Gerstenberger et al. 2011). It has been estimated that there were 320 trillion quagga mussel veligers in Lake Mead in 2011 (Brean 2012). Accordingly, there is concern that quagga mussel veligers and adults could be transported from Lake Mead by recreational watercraft to water bodies in California and other western states (AWWA 2008). Since dreissenid colonization of inland lakes is considered to have occurred primarily by overland transport on recreational boats (Leung et al. 2006), Lake Mead and the infested water downstream such as Lake Pleasant, Lake Mojave and Lake Havasu have been identified as a major source for further spread of quagga mussels when departing boats have not been properly decontaminated including decontamination of veliger larvae in internally held residual water. In order to better assess the potential for quagga mussel veliger larvae to be transported in watercraft residual water, the present study assessed veliger survival times under water temperature conditions mimicking those of residual water in trailered recreational watercraft leaving Lake Mead during both warm summer and cooler autumn months.

Dreissenid larval development occurs over four stages (Figure 1): the trochophore, straight-hinged veliger (also known as the D-Shaped veliger), umbonal veliger, and pediveliger (Ackerman et al. 1994; Nichols and Black 1994). During larval development, shell material is continuously secreted, thickening and strengthening the shell, thus providing increased protection against some environmental impacts. Therefore, we also tested the hypothesis that more developed veliger stages would have higher survival rates under similar thermal conditions relative to less developed larval stages. The information generated is likely to be of value in the reassessment of the quarantine times required to decontaminate adult, juvenile and larval dreissenid mussels in or on watercraft including all mussel veliger larvae retained in residual water not capable of being drained before transportation to an uninfested water body from Lake Mead.

Methods

On August 25, 2011, quagga mussel veliger samples were collected from the Boulder Basin of Lake Mead by 12 m vertical plankton tows with a Wisconsin Plankton Net (63 -µm mesh

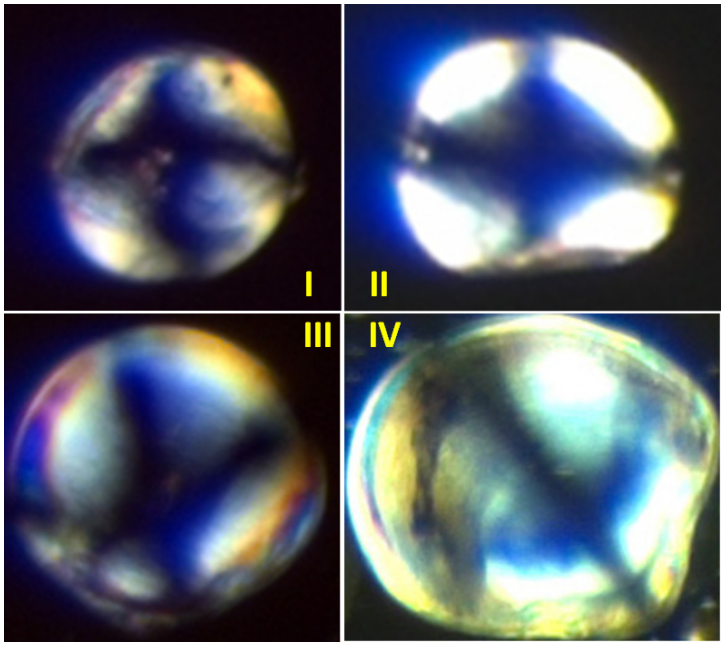

Figure 1. Photomicrographs of four stages of quagga mussel veligers in Lake Mead. I) trochophore, II) straight-hinged veliger, III) umbonal veliger, and IV) pediveliger (Photos by WH Wong).

size) from an open dock in the Lake Mead Marina, Nevada, (Lat. 36.0292°, Long. -114.7713°) (Gerstenberger et al. 2011). The net was pulled up at < 1 meter/second to prevent veliger damage with care taken to prevent collision with submerged structures. Veliger larvae retained in the net's sample bucket water were carefully transferred to a 15 l plastic water container (Coleman Water Carrier 5GL, The Coleman Company Inc, Wichita, KS) which had been previously filled with 15 l of Lake Mead water. This procedure was repeated for each of 15 containers, which were then carefully transported within an hour to the Environmental Health Laboratory (EHL) at the University of Nevada, Las Vegas. On arrival at EHL, one of the 15 containers was randomly chosen for veliger viability testing (as described below), which indicated that 100% of mussel larvae were alive. The same procedure for veliger collection was repeated for 30 containers on 5 November 2011.

All 15 summer and 30 autumn veliger samples in 15-liter plastic water containers were placed under a table (53 cm × 183 cm) outside of EHL where exposure to direct sunlight was limited. These conditions mimicked the environmental temperature conditions of retained lake water transported by watercraft. The containers were individually covered with black plastic bags during the course of the experiment to prevent direct exposure to sunlight. The lids (diameter of 1.75 cm) of all containers were open to the atmosphere to allow air exchange.

Temperature measurement

Water temperature was monitored in two, randomly-selected containers with individual temperature probes (Pace-Scientific Model XR440 pocket Datalogger with four temperature probes, Mooresville, NC). Two other probes were used to monitor air temperature. Both air and water temperatures were recorded every 30 min by a computer connected to the datalogger. The average temperature value of the two probes in water or air was calculated to represent *in situ* temperature. In addition, during the autumn trials, the oxygen concentration of water in containers was determined daily with an YSI oxygen meter (YSI Inc, Model YSI 85, Yellow Springs, OH).

Veliger enumeration and counting

During the experimental periods [i.e., summer from August 25 to September 2, 2011 (192hr) and autumn from November 5 to December 5, 2011 (720 hr), the survival of veligers was assessed in a randomly selected water container at 24-h intervals. Monitoring consisted of

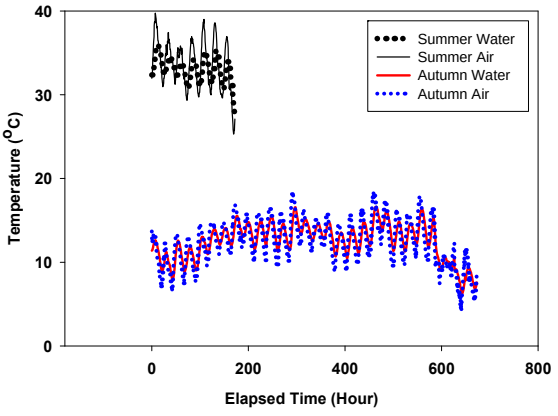

Figure 2. The water and air temperatures in containers holding quagga mussel larval stages during summer and autumn 2011 temperature simulation experiments.

pouring the 15 l of water in a selected container slowly through the 63-µm mesh sample bucket of the Wisconsin Plankton Net. The final concentrated veliger sample retained in the sample bucket was 100 ml, which was stored in two 50-ml centrifuge tubes. A 1-ml sample of concentrated veligers was taken from the 50-ml centrifuge tube with a pipette (Oxford® BenchMate™, Nichiryo America pipette, Japan) using tubes with tips cut to an internal diameter of 2.5 mm. Before the 1-ml sample was taken, the 50ml centrifuge tube was vertically rotated three times to randomize veliger distribution. The 1-ml sample was observed under a stereo microscope (SteREO Discovery V8, Carl Zeiss Inc, Germany) at 40× for veliger viability. Multiple 1-ml samples were examined until the viability of 50 veligers was determined. Live veligers were easily distinguishable from dead veligers by ciliary movement during a two-minute observation period (Britton and Dingman 2011) and/or by movements of their internal organs (Watters 2011).

The viability of 50 veligers from a container was counted at each 24-h time interval. The experiment was terminated when 100% veliger mortality was recorded on four consecutive days. An examined container was then cut into six pieces to determine whether any juvenile mussel settlement had occurred on its internal surfaces. During the autumn experiment, live veligers were classified by developmental stage (i.e., trochophore, straight-hinged veliger, umbonal veliger, and pediveliger) according to the scheme of Nichols and Black (1994). Samples were safely disposed of by adding 10% ethyl alcohol to the centrifuge tubes to destroy any remaining viable veligers.

Data analysis

Analysis of covariance (ANCOVA) was conducted to examine the difference in survival rates between the two experimental seasons (i.e., summer vs. autumn) with experimental time as a covariant. ANCOVA was also used to test for any significant differences in survival rates among the four different veliger stages in autumn with experimental duration as a covariant. The significance criterion was set at $\alpha = 0.05$ and the highly significant criterion was set at $\alpha = 0.01$. All statistical analyses were performed using SAS 9.2 (SAS Institute Inc, Cary, NC, U.S.).

Results

Temperatures

In summer, the highest air and water temperatures recorded were 40°C and 36°C, and the lowest, 25°C and 27°C, respectively (Figure 2). On average, both air and water temperatures in experimental containers generally exceeded 30°C (day and night). In autumn, the highest air and water temperatures recorded in containers were 18°C and 16°C, and the lowest, 6°C and 8°C, respectively (Figure 2).

Quagga mussel veliger survival

During the summer trial, the number of surviving veligers declined rapidly with experimental time. In contrast veliger mortality rate was reduced during the autumn trial (Figure 3). Summer survival was significantly lower than in the autumn (ANCOVA, $F_{3,54} = 62.00$, $P < 0.01$). During summer, it took approximately 120 h (≈ 5days) to attain 100 % veliger mortality compared to approximately 648 h (≈ 27days) during autumn (Figure 3). No veliger settlement was observed in containers during the course of either the summer or autumn trials.

Survival of different stages of veligers

During the autumn trial, time to 100% mortality was positively correlated with developmental stage, being 384 h for trochophores, 480 h for

to 41°C) and autumn (6 to 23°C) at Lake Mead (National Park Service 2012).

Veliger survival rate was significantly different between the summer and autumn trials, with veligers experiencing 100% mortality after 5 days under summer temperature conditions, and after approximately 27 days under autumn temperature conditions. The key difference between the two trials was water temperature, being generally higher than 30°C in summer trials, maximally reaching 36°C while remaining around 12.5°C in autumn trials, which appeared to favor veliger survival. For *D. polymorpha*, 18°C is reported to be the optimum temperature for larval development (Sprung 1987), with veligers unable to survive at > 35°C (Craft and Myrick 2011). However, the results of this study indicated that veligers of *D. rostriformis bugensis* from Lake Mead can survive short exposures to 35°C or higher. The difference in the results of these two studies may be due to variation in experimental design. In our study, veligers were retained in the same water and container throughout the experimental period allowing gradual acclimation to changing temperature regimes. In contrast, Craft and Myrick (2011) directly transferred *D. rostriformis bugensis* veligers into water at 35°C without prior acclimation. It has been demonstrated that prior acclimation to elevated temperatures can increase acute thermal tolerance in zebra mussels) (McMahon and Ussery 1995). Similarly, quagga mussels acclimated to 5°C have a reduced tolerance of elevated temperature relative to specimens acclimated to 15 and 20°C (Spidle et al. 1995).

In situ veliger development is potentially impacted by multiple environmental stressors (e.g., thermal stress, hypoxia, bacterial and viral infection, and UV radiation, among others) (Penchenik 1999). During the autumn trial, the lowest recorded dissolved oxygen level in containers was 7.8 mg O_2 l^{-1} with an average level of 8.0 mg l^{-1} which was 79.4% of the full air O_2 saturation value of 10.08 mg l^{-1} at the average 12.5°C container water temperature. This level of O_2 concentration was well above the minimal O_2 concentration of 2.27 mg O_2 l^{-1} (i.e., 24.4% of full air saturation) required for maximal veliger larva survival and development to settlement in *D. polymorpha* (Sprung 1987). Although not recorded during the summer trial, the lack of extensive variation in and relatively high levels of O_2 concentration recorded during the autumn trial suggested that similar conditions would have prevailed during the substantially shorter summer trial. Lake Mead is a dynamic, oxygen-rich water body with annual DO in the epilimnion (< 25 meter surface water) varying between 7.9 and 8.9 mg O_2 l^{-1} from 2000 to 2008 (Chris Holdren, unpublished data). Therefore, it is unlikely that the O_2 concentration of container water impacted veliger mortality during either trial.

The autumn chlorophyll *a* concentration in Lake Mead is only about 50% of summer values (Wong et al. 2013). Although there may be some shift in phytoplankton composition between seasons, food quantity should be more critical than food quality due to the oligotrohic status of Lake Mead (< 2 µg/L chlorophyll) (Wong et al. 2010). Therefore, the high mortality recorded during the summer trail was unlikely to have been caused by the lack of food. Thus, the significant difference in veliger mortality between seasons recorded in this study appeared to be mainly a result of differing water temperature regimes.

Temperature also impacts the shell morphology of quagga mussels: maintenance at higher temperatures (18–20°C) induces a morphotype typical of wild shallow water specimens while maintenance at lower temperatures (6–8°C) leads to that of wild deep water mussels (Peyer et al. 2011). It has also been shown that more fully developed molluscan veligers have an increased tolerance of stressors (Dame 2011). The present study produced results consistent with these findings: the most developed pediveliger stage was best able to survive autumn temperature conditions while the least developed trochophore stage was least able to survive them.

In Lake Mead, the settlement rate of quagga mussels is positively correlated with temperature over 11.9 to 22.6°C (Chen et al. 2011). Juvenile and adult dreissenid mussels have a broad temperature tolerance ranging from -2°C to 32°C (Karateyev et al. 1998). Low growth rates occur from 0 to 8°C or 28 to 30°C, with maximal growth rates occurring between 18 to 20°C (Claudi and Mackie 1994).

Based on a study of the impacts of air temperature and relatively humidity on emersion tolerance in zebra mussels (McMahon et al. 1993), the 100th Meridian group (http://www.100thmeridian.org/emersion.asp) recommends that watercraft be quarantined after hauling from

Lake Mead or other nearby water bodies for 1 to 2 days during summer (i.e., June to August), or 2 to 5 days during autumn (i.e., September to November) prior to launching in another water body. These proposed minimum drying times to kill dreissenid mussels are based on the assumption that all sources of standing water in a boat have been drained. However, most areas inside a boat (except live wells and bait wells) cannot be fully drained since the drain openings are above than the lowest level of the bilge, ballast tank, or other internal water containment areas. Even when an opening is at the bottom of the tank, there is still a flange on the inside of the tank that can prevent complete drainage. If a multi-use watercraft (e.g., fishing, water skiing, etc.) were to be efficiently drained but not dried of residual water, an estimated 8 l of water may be retained on board based on the vessel decontamination experience of Utah's Aquatic Invasive Species Biologists for more than 30,000 inland boats (Personal communication, L. Dalton, Utah Division of Wildlife Resources). Any veligers retained in undrained residual water could then be released after launching and starting a boat in a new water body.

Because it is impossible to drain all sources of standing water in many recreational boats without extreme effort, the risk of survival of veligers in retained water is high whether during summer or autumn. For example, based on our results, veligers, especially pediveligers, under autumn temperature conditions could survive long periods in a small amount of residual water. The average abundance of veligers in Lake Mead from August to November is approximately 18 veligers l^{-1} (Gerstenberger et al. 2011). Therefore, a total of 144 quagga mussel veligers could be left in 8 l of residual water retained in a drained boat during this time of the year. Thus, if boat residual water is not completely dried or decontaminated, these veligers could be transported to another water body. Based on the veliger survival rates recorded in this study, launching a boat in a mussel-free water body two days after being on Lake Mead, could result in release of 98 (summer months) to 144 (autumn months) living veligers into that water body.

Lake Mead is a popular water recreation area that can be accessed from several interstate and major state highways including I-15 and US-93. Through these and other highways, boaters can reach Arizona, California, and Utah within a day and quagga mussel-free states such as Oregon, Washington, Idaho, Montana, as well as southern British Columbia and southern Alberta within two days. Quagga mussel veligers may even survive overland transport in the residual water of trailered boats during transport to any location in the continental 48 states that could be reached within <5 days during summer and <27 days during autumn. Therefore, the presently recommended boat quarantine times of 1–2 d (summer) and 2–5 d (autumn) to kill externally attached juvenile and adult dreissenids before re-launching from Lake Mead into another water body (100th Meridian group, http://www.100thmeridian.org/emersion.asp) may have to be extended to > 5 days and > 27 days, respectively, in order to kill veliger larvae in residual water if not decontaminated by other physical or chemical means.

Many state and federal agencies have proposed that watercraft and watercraft trailers should be cleaned with a pressurized hot-water spray exceeding 60°C for 10 sec to kill and remove mussels attached to external surfaces and readily accessible internal areas (Morse 2009; Zook and Phillips 2009; Comeau et al. 2011). In order remove all dreissenid veligers, it is recommended that internal water should be drained to the extent possible, followed by application of a hot-water decontamination treatment protocol (Zook and Phillips 2009).

Veligers are too small to be viewed with the naked eye and thus can be readily overlooked even during the most careful of boat inspections (Zook and Phillips 2009) making them potentially the most likely dreissenid life cycle stage to be dispersed by overland vessel transport. Survival times for adult quagga mussels attached to external vessel surfaces at Lake Mead have been estimated to be 0.5 d in summer and 3 d in late winter and early spring (Kappel 2012). Based on the results of this study, these adult survival times are, respectively, 10 to 9 times shorter than the quarantine times required to kill quagga mussel veligers in vessel residual water. Thus, the longer survival times and difficulty of detection and decontamination of dreissenid veligers suggests that they are the more likely to be transported on watercraft than fouling adults and juveniles exposed directly to the atmosphere. Thus, if all water inside a boat cannot be completely drained or decontaminated by other means, recommended quarantine times prior to re-launch should be extended to assure that dreissenid veligers are not transported in residual water.

Conclusions

Veligers collected from Lake Mead and subjected to environmental temperature conditions mimicking those of retained water in recreational watercraft survived longer under cooler autumn temperature regimes than under warmer summer regimes. In addition, later veliger developmental stages had longer survival times. Veligers are present in Lake Mead throughout the year, and can survive on any wet or damp portions of a boat if all areas and spaces in and on the boat cannot be completely dried prior to overland transport to another water body. Therefore, after draining, recreational watercraft from quagga or zebra mussel infested water bodies should be quarantined long enough to kill veligers in any retained residual water before launching in another water body, particularly during cooler seasons if residual water cannot otherwise be decontaminated.

Invasive quagga and zebra mussel veligers are potentially a greater threat than adult mussels to uninfested waters, as they are invisible to the naked eye and can be transported in even small volumes of retained water in trailered watercraft. The results of this study indicate that all water must be expelled from a vessel prior to being trailered to and launched a new water body or that portions of a vessel retaining water should be decontaminated by other means (i.e., thermal treatment, chlorination, other molluscicide treatment, or adequate quarantine times prior to re-launching) in order to prevent the further spread of invasive zebra and quagga mussels in North America.

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