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Research Article

Settlement and growth of quagga mussels (*Dreissena rostriformis bugensis* Andrusov, 1897) in Lake Mead, Nevada-Arizona, USA

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Editor's note:
This special issue of *Aquatic Invasions* includes papers from the 17th International Conference on Aquatic Invasive Species held in San Diego, California, USA, on August 29 to September 2, 2010. This conference has provided a venue for the exchange of information on various aspects of aquatic invasive species since its inception in 1990. The conference continues to provide an opportunity for dialog between academia, industry and environmental regulators within North America and from abroad.

Abstract

Settlement and growth of quagga mussels *Dreissena rostriformis bugensis* were monitored in Lake Mead, NV, USA, where the first dreissenid occurrence was confirmed in the western United States. To measure the settlement rate of these invasive mussels, seven acrylonitrile butadiene styrene (ABS) pipes were attached to a line in shallow water (7.7 m below the surface) since November 23, 2007; eight ABS pipes were placed on another line in deep water (13.4 m below the surface) since January 3, 2008. Quagga mussels were sampled from these pipes on March 19, May 21, July 9, October 20, and December 19, 2008. Active settlement of veligers was recorded in all sampling events. The settlement rates of quagga mussels did not differ among the two lines and the highest settlement rate was found from October 20 to December 19. Three methods were used to estimate the growth of quagga mussels in Lake Mead: caged mussels, size distribution analyses on both natural populations and mussels attached to ABS pipes. Caged mussels were held in Las Vegas Boat Harbor from July 31, 2007 to March 19, 2008, where smaller mussels grew faster than larger ones. Size distribution data on two natural populations of quagga mussels collected from Sentinel Island and Indian Canyon in 2007 also showed that the growth rates decreased significantly as mussel size increased. Shell length data of cohorts collected from the ABS pipes were also used to estimate the growth of quagga mussels. The growth patterns of quagga mussels from the two lines were quite similar with the lowest growth rates detected from late summer to early autumn. The information on settlement and growth of quagga mussels from this study can help understand their population dynamics in the western United States.

Key words: invasive species, quagga mussel, settlement, growth, western United States

Introduction

The invasive quagga mussel (*Dreissena rostriformis bugensis* Andrusov, 1897) discovered in Lake Mead, Nevada-Arizona is a new invasive pest to the western United States (LaBounty and Roefer 2007; Stokstad 2007). This is the first known occurrence of an established dreissenid population in the western United States and the first known North American quagga mussel infestation of a large water body not previously infested by another dreissenid species, the zebra mussel (*Dresissena polymorpha* Pallas, 1771). Having spread throughout Lake Mead and other lakes and reservoirs in Arizona, California, Colorado, Nevada and Utah (Benson 2010), quagga mussels are now clogging water pipelines, attaching to boats, colonizing dam gates and fouling other substrates in the lower Colorado River Basin.

In the eastern United States, zebra mussels were discovered in the Hudson River in 1993 and were detected in Massachusetts in 2008. In the western United States, following their detection

Figure 1. Annual temperature profile and abundance of quagga mussel veligers in the Boulder Basin of Lake Mead, USA (Gerstenberger et al. 2011). The epilimion, metalimnion, and hypolimnion of Lake Mead range from 0-15 m, 15-35 m, and below 35 m in depth, respectively. The veliger samples were taken from the surface to 60 m in depth.

McMahon 2002; Strayer 2009; Lucy and Muckle-Jeffs 2010). Peer-reviewed publications on zebra/quagga mussels have increased exponentially in the past two decades; even the appearance of dreissenid mussels in North America helped to give birth to the study of invasion ecology (Padilla 2005; Strayer 2009). Both mussel species have similar geographic ranges and life-history. Their success on establishment in a new ecosystem depends on their capacity to adapt to the recipient environment. Lake Mead provides favorable environmental conditions to invasive quagga mussels, such as warm water, high calcium concentrations, hard substrates, suitable pH and sufficient dissolved oxygen (Cross et al. 2011). One major difference between quagga mussels in Lake Mead and temperate ecosystems is that the veligers are present year round in this subtropical reservoir, although densities are very low (e.g. <1.1 veligers/L) when the water temperature is below 13°C (i.e. January to March) (Figure 1). Therefore, the biology and ecology of quagga mussels in the southwestern U.S. may be different from those living in the Great Lakes and Europe. Since the quagga mussel is new to the western United States, basic biological information such as settlement and growth is still lacking and is needed for evaluating their environmental impacts and management (LaBounty and Roefer 2007; Wong and Gerstenberger 2011). We have monitored the settlement in the deep open water of the Boulder Basin, Lake Mead (Mueting et al. 2010). However, no data are available in the marina areas. As boats are important vectors for the spread of invasive species (Bossenbroek et al. 2001; Johnson et al. 2001; Leung et al. 2006), any recreation waters can be a potential preferred destination for quagga/zebra mussels, although the risk can be different among different systems (Gerstenberger et al. 2003). The quagga mussels in Lake Mead were assumed to be introduced by a recreational boat from the Great Lakes to the Boulder Basin of Lake Mead (LaBounty and Roefer 2007; Hickey 2010). The colonization rates and growth rates of quagga mussels need to be assessed in Las Vegas Boat Harbor as well as other shallow locations in Lake Mead. The present report describes our monitoring program on settlement and growth of quagga mussels in Lake Mead, the largest reservoir (by volume in its full capacity) in the United States (LaBounty and Burns 2005).

in Lake Mead in January 2007, quagga mussel veligers were found in Sweetwater Lake in San Diego, California in December 2007. The distances between the two U.S. eastern sites and the two western sites are both about 500 km. The spread was faster in the U.S. than in Europe where quagga mussels were documented to spread at least 500 km northward in the Ukraine between 1964 and 1989 (Mills et al. 1996); in the U.S., the spread was faster in the West (i.e., 11 months) than in the East (i.e., 15 years). The presence of many artificial waterways for drinking water and irrigation along the Colorado River aqueduct in the western U.S. exacerbates the spread of quagga mussel veligers (Wong and Gerstenberger 2011).

Quagga/zebra mussels are both native species to Eastern Europe, and were accidently introduced into the Laurentian Great Lakes in North America in 1986 in ballast water (Hebert et al. 1989; May and Marsden 1992; Mills et al. 1993; Carlton 2008; Van der Velde et al. 2010). Because of these mussels' significance in ecology and economy, the research on dreissenid mussels' biology and their impacts are extensive (Nalepa and Schloesser 1993; MacIsaac 1996;

Figure 2. Colonization of quagga mussels on ABS pipes suspended in Lines 3 (L3: B-E) and 5 (L5: F-I). Photographs also demonstrate how the mussels were collected from each pipe: red arrows show where the mussels were taken from a measured area and transferred to a plastic bottle. Photographs by Wai Hing Wong.

Methods

Settlement of quagga mussels was monitored at Las Vegas Boat Harbor within the Boulder Basin of Lake Mead where quagga mussels were first discovered in the western United States (LaBounty and Roefer 2007; Hickey 2010). To measure the settlement rates of these invasive mussels, acrylonitrile butadiene styrene (ABS) artificial pipes were used as monitoring substrates (Figure 2A). Each pipe was 20.3 cm long, with outside and inside diameters of 6.0 and 5.1 cm, respectively. The outside surface area of each pipe was 385 cm^2. There were eight holes (1.3 cm in diameter) around the pipe and

one extra hole (0.9 cm in diameter) in the middle of the pipe for connecting the nylon rope (Figure 2A).

Seven ABS pipes were attached to a line (Line 3) in shallow water (from 6.4 to 8.2 meters, mean depth 7.7 meters below the water surface) since November 23, 2007. Additionally, eight ABS pipes were placed on another line (Line 5) in deep water (from 9.0 to 17.0 meters, mean depth 13.4 meters below the water surface) since January 3, 2008. Each line with a cement weight was suspended in the water in a boat docking slip in Las Vegas Boat Harbor (36°01′49.5″N; 114°46′13.1″W). All pipes were hung in a horizontal position to maximize water flow through them.

9

The horizontal distance between these two lines was 5.0 meters. Quagga mussels were sampled from these pipes on March 19, May 21, July 9, October 20 and December 19, 2008. For each sampling event, mussels from a small area (usually $3 - 4$ cm^2) of each pipe were collected with a scraper. Photos from each sample pipe (with a scale indicated) were taken to quantify the area and calculate the density of colonized mussels (Figure 2I). The mussels were placed in the freezer (-20°C), quantified and measured in University of Nevada Las Vegas' Environmental Health Laboratory. For mussels equal or smaller than 3 mm, their shell length was measured with the AxioVision 4 Image Analysis Software set up for an AxioCam (Carl Zeiss Inc.), which connects a computer to a cross-polarized stereomicroscope (Carl Zeiss SteREO Discovery.V8, Toronto, Ontario, Canada). An electronic caliper was used to measure mussels with shell length larger than 3 mm. All samples collected on March 19, 2008 were newly settled mussels. For samples collected on May 21, July 9, October 20 and December 19, 2008, the newly settled mussels were from cohorts that were not detected from the previous sampling date (Figure 3). The new cohorts were estimated using the modal progression of Fish Stock Assessment Tool II (FiSAT II). FiSAT is the official program used by United Nations' Fisheries and Aquaculture Department to estimate population dynamics of finfish and shellfish. FiSAT II applies the maximum likelihood concept to separate the normally distributed components of size-frequency samples, allowing accurate demarcation of the component cohorts from the composite polymodal population size of finfish or shellfish (Food and Agriculture Organization of the United Nations 2010). Settlement rates (mussels/m^2/month) and abundance of mussels (mussels/m^2) on the experimental ABS pipes were calculated for each inspection date.

There are multiple approaches used to evaluate quagga/zebra mussel growth and it is recommended that monitoring marked mussels under natural conditions provides the most reliable data, though it is the least used method (Karatayev et al. 2006). In Lake Mead, it is not suitable to use this method as high predation can make the experiment difficult to implement as the top two fish species are common carp and gizzard shad (almost 75% of the fish community in terms of biomass in 2010) (Herndon 2010), which are both voracious consumers on dreissenid mussels and other benthic organisms

(Judge 1973; Molloy 1998). Therefore, in the present study, the following methods were used: 1) shell length monitoring on caged mussels; 2) size-frequency analysis on mussels collected from natural environments; and 3) size-frequency analysis on mussels colonized in suspended ABS pipes in the aforementioned settlement experiment. For the caged-mussel study, 12 mussels from 2.0 to 9.0 mm were placed in individual cages. The 12 cage unit was constructed using a 635 mm × 127 mm × 48 mm (Length × Width × Height) section of "ChoiceDek" Composite Decking and a matching piece of 4.8 mm Plexiglas (Figure 4A). Twelve 54-mm diameter holes were drilled through the material creating the individual compartments. Matching holes were drilled in the Plexiglas. A 1.6-mm nylon mesh was adhered to one surface of the decking and one side of the Plexiglas. The Plexiglas was used as a cover for the compartments and was held in place by two eyebolts that were also used to suspend the unit. The eyebolts were screwed into T-nuts making it very fast and easy to open the cages. The unit was suspended at a 45° angle to maximize water flow through the cages. Cages were placed in Las Vegas Boat Harbor on July 31, 2007 at a depth of 7.5 meters. The shell length of each mussel was recorded on September 8 and December 11, 2007, and January 30 and March 19, 2008. For each observation, cages were taken out of the water and kept in a tray filled with lake water; the cages were kept out of the water as little time as possible to prevent potential damage or trauma to the mussels from the heat. Natural populations of quagga mussels were collected from rocks by divers about 10 meters below surface water from two locations: Sentinel Island (36°03′33.7″N; 114°44′48.3″W) and Indian Canyon (36°06′53.3″N; 114°36′50.2″W). Mussels were collected by divers from Sentinel Island on February 25 and March 30, 2007, and from Indian Canyon on February 25, and June 22, 2007 at about 20 m below the water surface. The shell length of mussels was measured to the nearest 0.1 mm with a caliper. The size distribution was analyzed and cohorts were identified with FiSAT II (Food and Agriculture Organization of the United Nations 2010). For each cohort identified, mean shell length with standard deviation was computed to calculate growth rate of the same cohort living in the natural environment. A Von Bertalanffy growth model was used to estimate the maximum mussel shell length in Sentinel Island and Indian Canyon
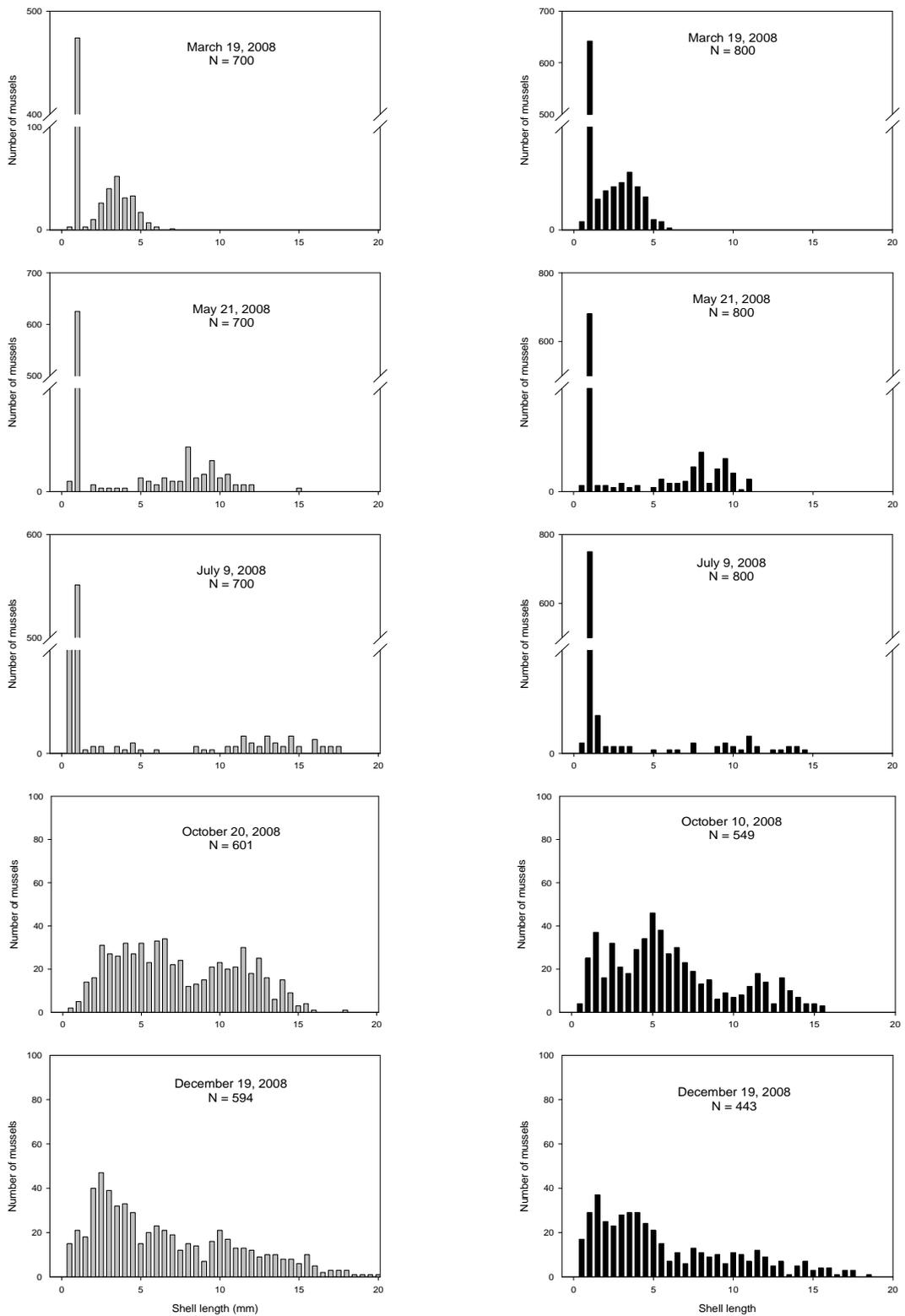
Figure 3. Shell length distributions of the mussels from Line 3 (7.7 m, left panel) and Line 5 (13.4 m, right panel) in Las Vegas Boat Harbor.
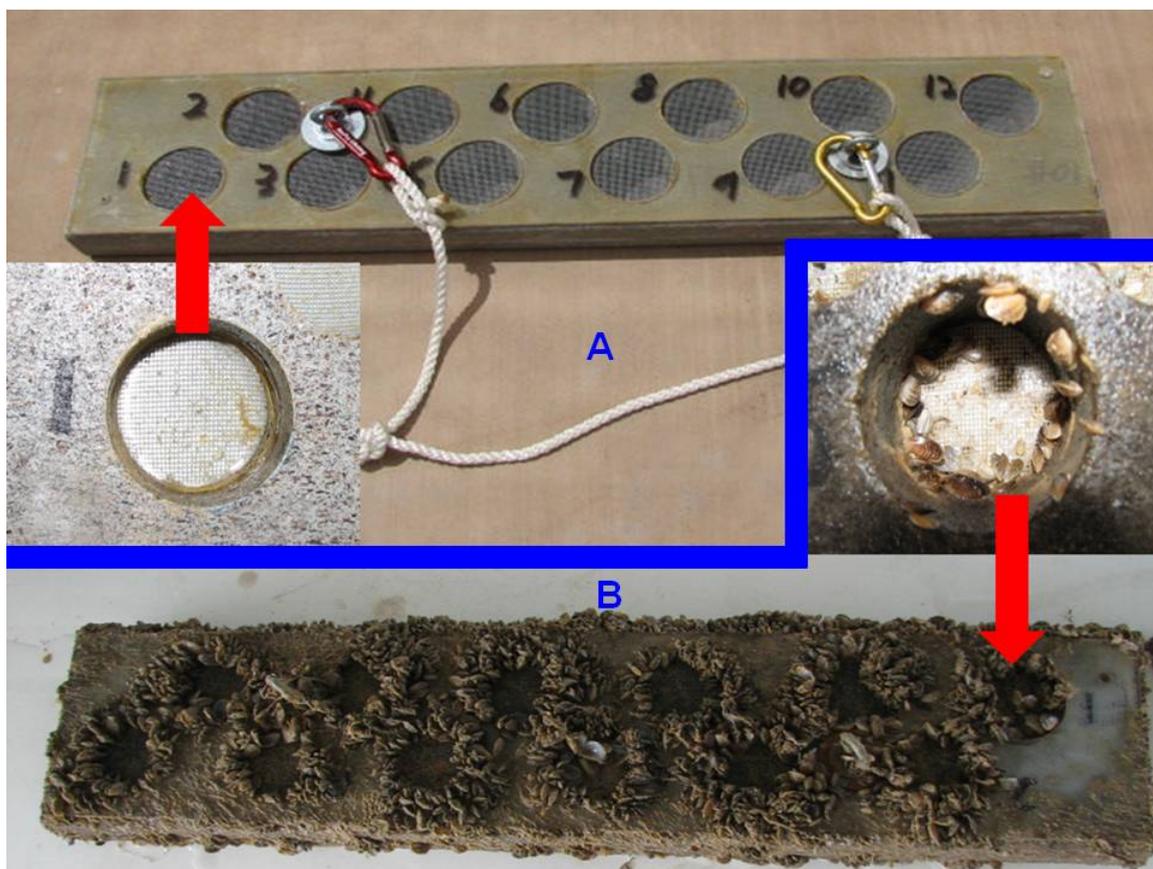
Figure 4. Individual cage design for monitoring quagga mussel growth (**A**) and colonization of non-experimental mussels outside and inside of the cage (**B**). Photographs by Wen Baldwin.

(Von Bertalanffy 1938). Growth rates of the mussels collected from ABS pipes were estimated based on shell length for each cohort identified by FiSAT II.

Analysis of covariance (ANCOVA) was used to evaluate any significant difference in settlement rate or abundance for mussels collected from the two lines using collection date as the covariate for the settlement experiment. Since no significant difference was found in settlement rates and abundance between the two lines (see Figure 5 in the results), analysis of variance (ANOVA) and post-hoc multiple comparisons (Student-Newman-Keuls) were used to assess the differences among seasons. Correlation analysis was used to determine if there was any relationship between sample depth and settlement rate or abundance of mussels. ANCOVA was used to

assess differences in growth among different seasons for mussels collected from ABS pipes suspended in Las Vegas Boat Harbor by using the initial length of each cohort as a confounding factor. Simple linear regression was used to assess the relationship between initial shell length and growth rate. ANCOVA was also used to test if the two lines (growth vs. initial shell length) for caged mussels and mussels collected from Sentinel Island and Indian Canyon was different in slope and elevation (Zar 1996). T-tests were used to determine significant difference on maximum individual shell length between these two lines collected from each observation. SAS 9.1 (SAS Institute Inc. Cary, NC) was used to perform all the statistical analysis. All tests utilized the significance levels of $\alpha = 0.05$ and $\alpha = 0.01$.

Results

Settlement

Active settlement of quagga mussel pediveligers was recorded in all sampling events (Figures 2B–2H and 3). ANCOVA showed that the settlement rates of quagga mussels did not differ among the two lines (P > 0.05), but a significant difference was found among seasons (P < 0.01). The average settlement rates for the five observations were 133,348, 180,538, 337,462, 11,086, and 2,740,516 mussels/m^2/month (Figure 5A), with significantly higher values recorded in December 19, 2008 (ANOVA, P < 0.01). Similar to the results of settlement rates, ANCOVA demonstrated that the abundance of mussels did not differ between the two lines (P > 0.05), but a significant difference was found among seasons (P < 0.01). The highest density was found on December 19 (ANOVA, P < 0.01) while no difference was found among other observations. The abundances for the five observations were 397,308, 416,568, 606,908, 103,079 and 10,945,056 mussels/m2, respectively (Figure 5B). The correlation between settlement rate or abundance of mussels and depth was not significant (P > 0.05).

Growth

For the caged study, all mussels showed significant growth from July 31, 2007 to March 19, 2008 (Figure 6A); however it is evident that larger mussels grew slower and smaller mussels grew faster (Figure 6B). Based on this growth pattern of the 4 small individuals (2–3 mm), it is estimated that it takes about 4 months for a mussel to grow from 2.5 mm to 10.0 mm. Caged mussels at 7.5 m depth in Las Vegas Boat Harbor in Boulder Basin of Lake Mead were also used to estimate the growth of quagga mussels. Size distribution on the population of quagga mussels from Sentinel Island showed that there were four and three distinct cohorts on February 25 and March 30, 2007, respectively (Figure 7). The computed mean shell length of the four cohorts on February 25 was 0.6 mm, 6.7 mm, 12.4 mm, and 18.4 mm, respectively (Figure 7A); while shell length for the three cohorts on March 30 was 2.9 mm, 7.7 mm, and 13.6 mm, respectively (Figure 7B). These three cohorts on March 30 were derived from the three smaller cohorts on February 25, while the cohort with the largest size was indistinct on March 30. For the mussels
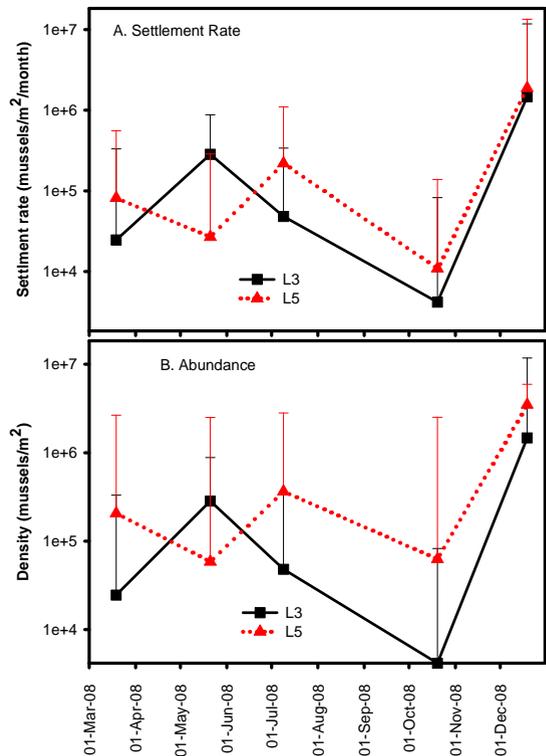
Figure 5. Settlement rates and abundance of quagga mussels in Las Vegas Boat Harbor at two depths (ABS pipes attached to L3 and L5 are 7.7 m and 13.4 m below water surface; Y-Axes were plotted on a log scale).

in Indian Canyon, there were four cohorts on each sampling date. The shell length for the four cohorts on February 25 was 4.5 mm, 11.4 mm, 16.3 mm, and 18.5 mm, respectively (Figure 7C), while the shell length for the four cohorts on June 22 was 0.4 mm, 9.7 mm, 14.1 mm, and 19.2 mm, respectively (Figure 7D). The cohort with the smallest size on June 22 was a new recruitment while the cohort with the largest size on February 25 was not recognizable on June 22. The calculated growth rates (mm/day) for these two natural populations showed similar growth pattern to that of caged mussels. Growth rates decreased significantly as mussel size increased and the size-specific growth rate was comparable (Figure 6B). ANCOVA showed no significant difference in growth rate for these two groups of mussels; only initial size is the major factor to determine their growth rate. Based on the Von Bertalanffy growth model (Von Bertalanffy

13

1938), the maximum mussel shell length in Sentinel Island and Indian Canyon Cove was calculated as 22.7 and 25.8 mm, respectively. These theoretical values agreed well with the field observed maximum shell length, which was 22.0 mm in Sentinel Island and 24.0 mm in Indian Canyon.

The computed shell length of each cohort for mussels colonizing on the ABS pipes at different sampling dates is shown in Figure 8. The growth patterns of quagga mussels from the two lines were similar. The computed mean size of the oldest cohort was 19.9 mm (standard deviation 1.6 mm) on Line 3 and 18.1 mm (standard deviation 2.3 mm) on Line 5 (Figure 8). The growth recorded from July 7 to October 20 was significantly lower than in other seasons (ANOVA, P < 0.05), although the initial size of mussels did not play a major role in determining their growth (ANCOVA, P > 0.05). The averaged growth rates of newly settled mussels between the sampling periods from March 19 to May 21, May 21 to July 9, July 9 to October 20, October 20 to December 19 2008 were 0.08, 0.08, 0.03, and 0.07 mm/day, respectively. The maximum shell length of mussels on Line 3 and Line 5 was 21.8 mm and 22.4 mm, respectively (Table 1). On March 19, 2008, the maximum shell length of individuals was 6.6 mm on Line 3 and 5.8 mm on Line 5 (Table 1). This shows that mussels still had significant growth in wintertime. The maximum individual shell length was always larger in Line 3 than in Line 5 for the five inspections (Table 1), however, a T-test did not reveal any significant difference between these two lines (P > 0.05).

Discussion

The higher settlement rate observed in this study during late autumn 2008 corresponded to a time when there was a higher percentage of competent pediveligers, in terms of the ability to settle (Gerstenberger et al. 2011). The settlement rates between the two experimental lines at two depths (7.7 m vs. 13.4 m) in Las Vegas Boat Harbor were not significantly different (Figure 5A). In the open water of the Boulder Basin of Lake Mead, the bi-monthly settlement rates of mussels on all substrates (ABS plastic, high density polyethylene plastic, concrete underlayment board, aluminum, stainless steel and fiberglass were cut into plates, each with an area of 10.2 cm^2) were monitored at different depths from
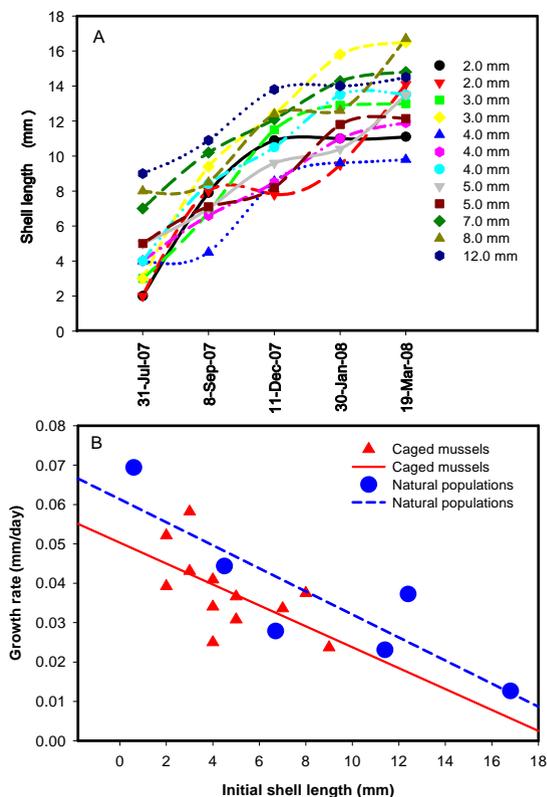
Figure 6. Growth rates of caged quagga mussels in Las Vegas Boat Harbor (A/B) and natural populations in Sentinel Island and Indian Canyon (B: Growth rate = 0.050 – 0.003 * Initial Shell Length, N = 12, R = 0.63, P < 0.01, for caged mussels; Growth rate = 0.061 – 0.003 * Initial Shell Length, N = 6, R = 0.87, P < 0.01).
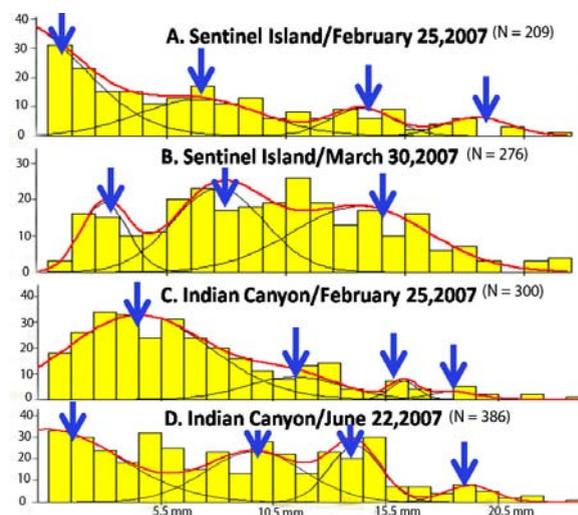
Figure 7. Size distribution of quagga mussels collected from Sentinel Island and Indian Canyon. X-Axis is the shell length and Y-Axis is the numbers of mussels. The arrows show the cohorts identified by FiSAT II.

Table 1. Maximum and minimum shell length of individual mussels from ABS pipes attaching to the two lines.

Line	Date	Maximum (mm)	Minimum (mm)	Mean (mm)	Standard deviation	N
Line 3	19/3/2008	6.6	0.6	1.5	1.4	700
	21/5/2008	14.9	0.6	1.4	2.3	700
	9/7/2008	17.3	0.6	1.6	3.1	700
	20/10/2008	17.6	0.3	7.2	3.8	601
	19/12/2008	21.8	0.3	6.4	4.5	594
Line 5	19/3/2008	5.8	0.3	1.1	1.0	800
	21/5/2008	10.9	0.6	1.6	2.5	800
	9/7/2008	14.4	0.6	1.00	1.8	800
	20/10/2008	15.3	0.3	5.9	3.7	549
	19/12/2008	18.2	0.4	5.5	4.4	443
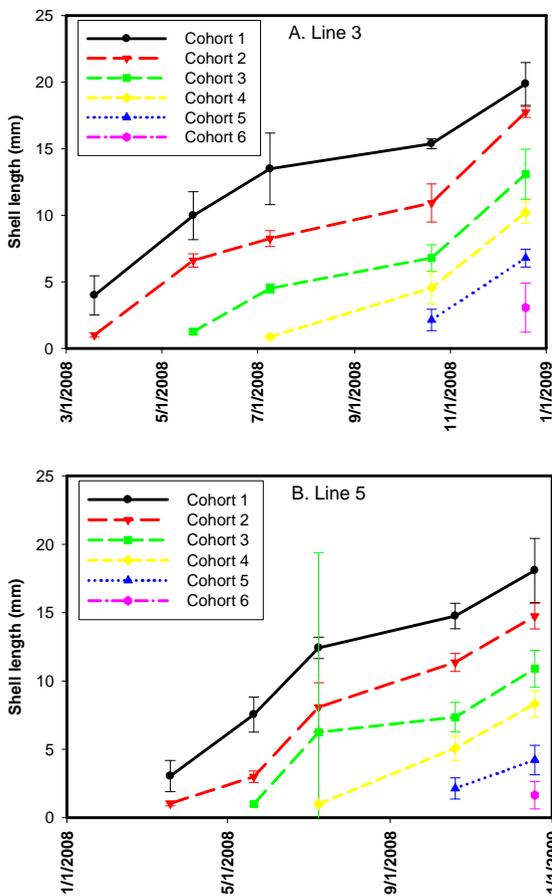
Figure 8. Shell length of each cohort for the mussels collected from ABS pipes attaching to the two lines.

March 27, 2008 to March 10, 2009 by Mueting et al. 2010. At depths from 6 to 28 m, the settlement rates did not differ, but they were significantly higher than those from 32 to 54 m (Mueting et al. 2010). In the study from Mueting et al. (2010), it was found that the settlement rate on ABS plate in the open water in depths between 10 and 20 m was only 19,079 (mussels/m^2/month), which is much lower than the observed settlement rate from the present study (680,590 mussels/m^2/month) with ABS pipes. This is probably due to the higher density of adult mussels colonizing on the facilities (i.e., docking slips and marina substructure) of Las Vegas Boat Harbor as well as the greater surface areas that are provided by the facilities but absent in the open lake in our previous study. Another possible reason is that ABS pipes with holes provide more edge surfaces that competent pediveligers prefer to settle. Finally, ABS pipes with higher abundance of juvenile and adult mussels also provide more rough surfaces from colonized quagga mussel shells for veligers to settle down. The lower abundance observed in October 2008 is mainly due to the lower recruitment between July and October (Figure 5A). Another potential factor is due to mortality. Significant summer morality of adult mussels has been observed in mussels attached to these ABS pipes in Las Vegas Boat Harbor (Wen Baldwin and Wai Hing Wong, personal observations) and natural populations in Lake Mead (Melissa Cheung, personal communication) in 2008. In late summer and early autumn, the water temperature in the epilimnion

15

was the highest ranging between 24 and 28°C (Figure 1), and surface water temperature could reach 30°C (Robert F. McMahon, personal communication). In the Lower Mississippi River, significant adult mortality of zebra mussels was recorded during summer months when the temperature was the highest (29 to 30°C) (Allen et al. 1999). Quagga/zebra mussels are very sensitive to heat (McMahon and Ussery 1995; McMahon 1996) and hot water (60°C or higher) is recommended as a tool to remove colonized mussels from a boat's hull (Morse 2009; Comeau et al. 2011). Adult mussels, especially those after spawning, cannot survive long at such high temperatures (around 30°C) and die. Slower growth of mussels from late summer and early fall in the ABS pipes is also likely a result of the higher water temperature during this time of the year. In the Lower Mississippi River, where the water temperature is 29–30°C for about 3 months in summertime, zebra mussels had depressed shell growth (Allen et al. 1999). The higher settlement rate from late October to early December resulted in higher abundance of mussels (Figure 5). It is interesting that no significant difference was found either in settlement rate or growth rate for mussels between the two experimental lines. There was a 41 day gap between the dates the two lines were placed in the water. The settlement of veligers is very active in Las Vegas Boat Harbor. Usually new settlers can be visualized from a hard substrate two weeks after it is placed in the water, even in wintertime (Wen Baldwin and Wai Hing Wong, personal observation). The water flow velocity in Las Vegas Boat Harbor is very low, which is one potential reason that can result in more settlement on substrates. Chen et al. 2011 found that flow velocity is a key factor affecting settlement of veligers, with higher settlement rates at low velocities (< 3 cm/s). If the new settlers had occupied the ABS pipe space in Line 3, veligers may have preferred to settle on unoccupied spaces and therefore the settlement rates may have slowed down. Future study is needed to address this question.

The caged mussel study shows that there is a negative linear relationship between the initial size of mussels and the growth rate (Figure 6). It is a common pattern in caged dreissenid mussels. In their review on the growth of zebra mussels, Karatayev et al. (2006) found that mussels living in lakes or reservoirs both showed the same trend, i.e., smaller individuals grow faster than large ones. They also found that zebra mussels

grow faster in reservoirs than in lakes. Although this experiment was conducted in Lake Mead, the largest reservoir by volume in its full capacity in the United States (LaBounty and Burns 2005; Holdren and Turner 2010), the growth rates are similar to those data generated in lakes (Figure 6B), instead of reservoirs (Karatayev et al. 2006). Caged studies have disadvantages, such as preventing water flow and being overgrown by periphyton (Karatayev et al. 2006), but also have advantages, such as mussels escaping predation (Bitterman et al. 1994; Karatayev et al. 2006).

Quagga mussel veligers are present year around (Figure 1), have high settlement rates, and they can colonize almost any substrate in Lake Mead, which is certainly the case with our caged study. The cage mesh size was 1.6 mm to provide flow and food for the experimental mussels. However, this also allowed competent veligers (around 0.22 mm) to settle inside of the cage. During the experimental course, new recruitment of quagga mussels occurred both outside and inside of the cage (Figure 4B). Therefore, apart from the physical barriers from the experimental cage mentioned above, the competition for space and food between the experimental mussels and others colonized inside and outside of the cage can be great. Given the fact that quagga mussel veligers are present year round and settlement activities are active in Lake Mead, it may not be a good method to address growth of mussels in this lake without additional work such as frequent cleaning of the inside and outside of the cage. The growth pattern of caged zebra mussels in Svisloch River is similar to lake mussels while the growth pattern of uncaged mussels was closer to those in reservoirs (Karatayev et al. 2006). The settlement and growth differences may possibly be due to Lake Mead's riverine characteristics, as Lake Mead, formed in 1935 following construction of Hoover Dam, is still part of Colorado River. Other factors such as species-specific differences and food quantity and quality can also potentially play significant roles.

In the temperate environments, such as the Great Lakes and Europe, the growing season for dreissenid mussels is from late spring to summer but there is no growth from autumn to early spring (Walz 1978; Smit et al. 1992; Sprung 1992; Dermott et al. 1993; Neumann et al. 1993; Garton and Johnson 2000) as temperature is a key factor in determining growth of dreissnid mussels (MacIsaac 1994; Jantz and Neumann

1998). In the Lower Mississippi River, where water temperature was high (29–30°C) in summertime and low (about 5°C) in wintertime, the growth of zebra mussels was not significant (Allen et al. 1999). In Lake Mead, quagga mussels gained significant growth even in wintertime in the present study. The annual growth from the size frequency study on mussels in Las Vegas Boat Harbor is higher than that in the Lower Mississippi River. These two large cohorts for Lines 3 and 5 had an annual (365 days/year) growth of 18.2 mm and 18.8 mm, respectively, while it was only about 11.5 mm in the Lower Mississippi River. For the natural populations in Lake Mead (Figure 6B), newly settled mussels can reach 16 mm within a year (without considering seasonal pattern and other physico-chemical factors). This is comparable to dreissenid mussels in temperate river systems with an annual shell length between 15–17 mm and higher than temperate lakes (< 15 mm) (Sprung 1992; Dermott et al. 1993; Dorgelo 1993; Neumann et al. 1993). It is clear that quagga mussels settle actively and grow well in this large subtropical reservoir.

Although the growth rates of the two natural populations from Sentinel Island and Indian Canyon were comparable to the caged mussels (Figure 6B), growth patterns at different seasons for these two natural populations can be a potential factor that makes the comparison difficult to interpret (with the caged study conducted from summer 2007 to the early spring of 2008 while the natural populations were only collected in early spring to early summer of 2007). A key factor affecting growth of quagga mussels in open waters of Lake Mead is the primary production. In the open water of Lake Mead, phytoplankton production is considered as a potential factor that can limit the survival of quagga mussels (Cross et al. 2011). Other environmental variables, such as calcium concentration, temperature, salinity/conductivity, pH, oxygen saturation and turbidity in Lake Mead (LaBounty and Burns 2005; Whittier et al. 2008), can all meet the requirement of survival and growth of quagga mussels (Spidle et al. 1995; McMahon 1996; Mills et al. 1996; Jones and Ricciardi 2005). The chlorophyll concentration in the open waters of Boulder Basin is only around 1 mg/m^3 (Wong et al. 2010). As mussels are herbivores with phytoplankton as their primary diet (Baker et al. 1998; Wong and Levinton 2004), the low

productivity of phytoplankton is probably an important reason for why natural populations grow slowly, while mussels in ABS pipes from Las Vegas Boat Harbor may have better nutritional input as the water in the marina area is partially affected by nutrient-rich flow from Las Vegas Bay. At the same time, based on the suspended ABS pipe study, the growth was only slowed down from late summer to early autumn when the water temperature in the epilimnion was high (Figure 1). It is also possible that growth in other seasons than late summer and early autumn may not differ significantly under natural conditions. Based on the growth rate of mussels under natural conditions (Figure 6B), the first detectable settlement of quagga mussels in Sentinel Island and Indian Canyon was estimated to be in late summer to early autumn and late autumn to early winter of 2005, respectively. Therefore, invasive quagga mussels could have been introduced to Lake Mead much earlier, which gave them enough time to produce this first detectable cohort in Sentinel Island (Figure 7A). This is in agreement with a study conducted by McMahon (2011) that estimated quagga mussels were first introduced to the Boulder Basin prior to 2005. Based on size distribution of quagga mussels collected from Las Vegas Boat Harbor, Callville Bay Marina, and Lake Mead Marina in the Boulder Basin of Lake Mead within two months of initial discovery of quagga mussels in Lake Mead on January 6, 2007, it is hypothesized that a reproducing quagga mussel population must have been established somewhere in the Boulder Basin by 2003 or 2004 in order to generate enough veligers to settle (McMahon 2011).

Not only are quagga mussel veligers present all year in Lake Mead (Holdren 2008; Mueting et al. 2010; Gerstenberger et al. 2011), settlement and growth also occur year round in this large reservoir (Mueting et al. 2010 and present study). The information on settlement and growth collected from the present study can help lake managers understand the biology of this new invasive species in the western United States and can shed light on how these invasive pests might impact the reservoir's biotic resources (e.g., fisheries, benthos, and planktonic community) and cultural (e.g., water quality and water-delivery facilities) and recreational values (e.g., cost associated with boat decontamination, unfavorable odors from decaying quagga mussels, etc.).

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